Arizona Game and Fish Department
Research Branch

A Final Report

The Effects of an Experimental Flood on the Aquatic Biota and Their Habitats in the Colorado River, Grand Canyon, Arizona

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INTRODUCTION

Prior to closure of Glen Canyon Dam in 1963, the Colorado River in southern Utah and north central Arizona was free flowing and seasonally warm and muddy. Large, periodic spring flooding, which was seasonally predictable, transported large amounts of sediment downstream creating and maintaining a system of backwaters (Rubin et al. 1990; Schmidt 1990). Pre-dam mean annual maximum discharge was 2439 m^3/s (86,167 cfs; Steven 1983) and reached approximately 8,490 m^3/s (300,000 cfs; Carothers and Dolan 1982). Summer and winter river discharges were low, dropping to as low as 21 m^3/s (750 cfs; Valdez and Ryel 1995). Conversely, post-dam discharges have rarely exceeded the powerplant capacity of 890 m^3/s (31,500 cfs) and, since Interim Operations began, rarely drop below 142 m^3/s (5000 cfs; Valdez and Ryel 1995). Only the occasional large tributary flood, primarily from the Little Colorado River (LCR), has given the Colorado River in Grand Canyon a more natural hydrograph.

The use of a controlled flood discharge from Glen Canyon Dam to improve conditions for native fishes was addressed by Clarkson et al. (1994) who discussed recommendations for operating Glen Canyon Dam to benefit native fishes. Beach/habitat-building flows became an element of the preferred alternative of the Glen Canyon Dam Environmental Impact Statement, "designed to rebuild high elevation sandbars, deposit nutrients, restore backwater channels, and provide some of the dynamics of a natural system" (U.S. Department of the Interior 1995). In 1996, the Bureau of Reclamation conducted a beach/habitat building test flow (Experimental Flood) of 45,000 cfs (1274 m^3/s) for seven days (27 March - 2 April 1996) from Glen Canyon Dam (U. S. Department of the Interior 1996). The entire experiment lasted from 22 March through 7 April 1996 (23 March - 8 April near the LCR) and included four days of steady 226m^3/s (8,000 cfs) flows both before and after the flood (Fig. 1). Upramping was fast (113 $m^3/s/hr$; 4,000 cfs/hr) with a slower downramp of 14 - 42 $m^3/s/hr$ (500 - 1,500 cfs/hr). As a result of this experiment it was expected that backwater habitats for juvenile native fishes would be reformed and populations of some non-native fish species would be temporarily reduced. (U.S. Department of the Interior 1996).

Backwaters are quiet pockets of water connected to the mainchannel with little or no flow, and are usually formed in eddies where

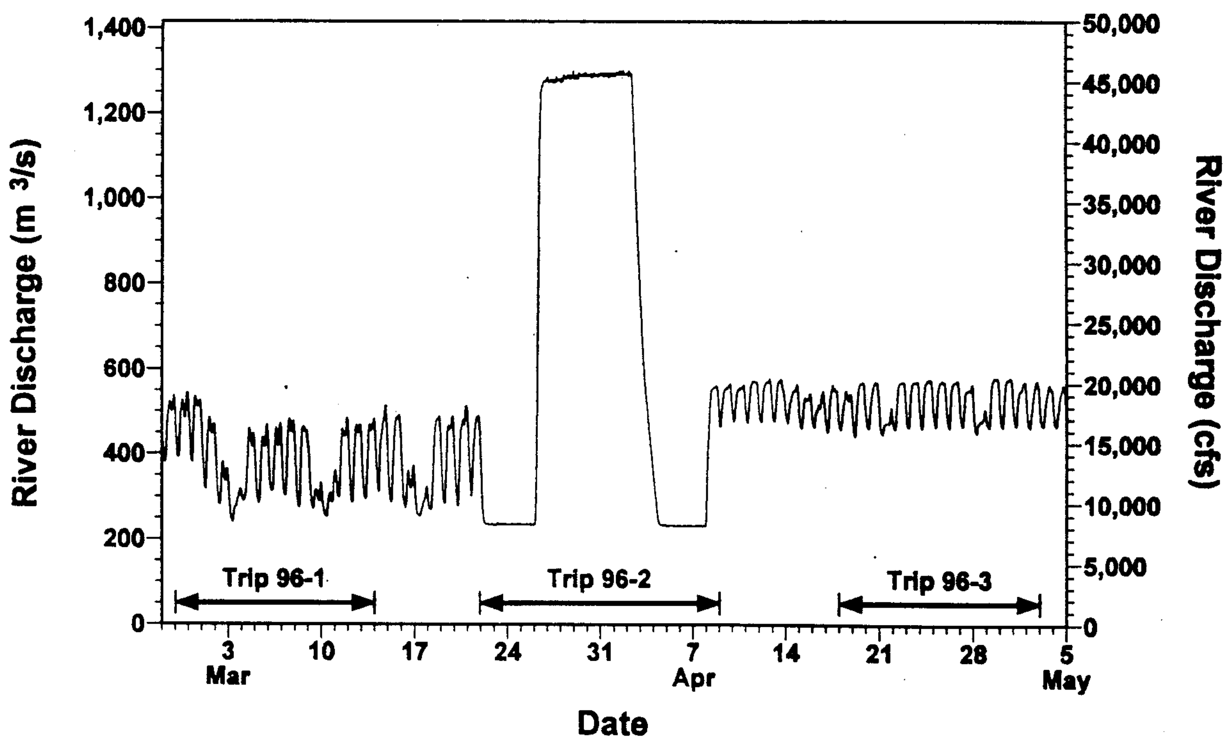

Figure 1. Colorado River discharge at Lee's Ferry, February 27 - May 5, 1996.

scouring and aggradation occur during high flows (Schmidt and Graf 1990). As water levels drop, a reattachment sand bar is exposed, partially isolating the eddy return-current channel, and forming a backwater (Rubin et al. 1990; Schmidt 1990; Schmidt and Graf 1990). However, over time the number of backwaters decreases as they fill in with sand and silt, and ultimately become marshes (Stevens and Ayers 1993), or the reattachment bar fails and the backwater becomes part of the eddy. Floods increase the number of backwaters by scouring return-current channels, removing marsh vegetation, and reforming reattachment bars (U. S. Department of the Interior 1995).

Backwaters have lower velocities than the mainstem and finer, more stable substrates with greater organic matter than mainchannel beachfaces (AGFD 1996). Backwaters also can be as much as 5°C warmer than the Colorado River mainstem during May and June (AGFD 1996). These characteristics permit accumulation of fine sediments and detritus and higher densities of benthic invertebrates, important food items for native fishes (Angradi et al. 1992; AGFD 1996). As fish grow, they become less dependent upon backwaters and juveniles begin to use other nearshore habitats such as debris fans, talus, and vegetated shorelines (Valdez and Ryel 1995).

Backwaters have become increasingly important as rearing areas for larval and juvenile native fishes in the Colorado River system, including Grand Canyon, due to changes in mainstem habitat; primarily decreased water temperature caused by hypolimnial discharge from dams (Holden 1978; Valdez and Clemmer 1982; Carter et al. 1985; Maddux et al. 1987; Minckley 1991; Angradi et al. 1992; AGFD 1996). Holden (1978) reported that 52% of juvenile humpback chub caught in the Green River, Utah, were found in backwaters. Maddux et al. (1987) and AGFD (1996) found mean densities of humpback chub juveniles to be 45/100 m^2 and 23/100 m^2, respectively, in backwaters of the Colorado River, Grand Canyon, immediately below the Little Colorado River (LCR). After one year of age, native fish continue to use backwaters, probably as feeding areas, particularly at night and when turbidity is high (AGFD 1996).

Four of the original eight native species remain in the Colorado River in Grand Canyon: bluehead sucker (*Catostomus discobolus*), flannelmouth sucker (*Catostomus latipinnis*), humpback chub (*Gila cypha*), and speckled dace (*Rhinichthys osculus*). An additional 25 exotic fish species have been reported from this reach of the Colorado River (Valdez and Ryel 1995). Table 1 lists the common and scientific names of all fish species handled in this study. The effect of flooding on native and exotic fishes and their habitats in the Colorado River, Grand Canyon, is unknown and is the focus of this report. Herein we address three general objectives, each with individual work tasks with specific hypotheses to be tested.

Objective 1: Determine distribution, dispersal, and habitat use of native and non-native fishes in the Lee's Ferry reach, near the mouth of the Little Colorado River, and below Lava Falls (RM 180-85) before and after the controlled flood.

Work Task 1.1: Determine juvenile fish distribution and dispersal.

Participants: Arizona Game and Fish Department, Bio/West, Hualapai Department of Natural Resources, U. S. Fish and Wildlife Service, Glen Canyon National Recreation Area

Hypotheses:

H_{o1a}: Distribution of juvenile fishes, including humpback chub, after the flood will not differ from that before the flood.

H_{o1b}: Displacement of juvenile humpback chub will not differ from displacement of fathead minnow.

Work Task 1.2: Determine habitat use by juvenile fishes during low and high steady flows.

Participants: Arizona Game and Fish Department, Hualapai Department of Natural Resources, Bio/West, U. S. Fish and Wildlife Service

Hypothesis:

H_{o2}: Habitat selection by juvenile fishes does not differ between flow regimes.

Work Task 1.3: Determine movement and habitat use of adult humpback chub during the flood.

Participants: Bio/West and Arizona Game and Fish Department

Hypotheses:

H_{o3a}: Movements by adult humpback chub during the flood will not differ from that before the flood.

Table 1. Common and scientific names of all species of fish handled in this study.

	Common Name	Scientific Name	Family
Native Species	Bluehead sucker	*Catostomus discobolus*	Catostomidae
	Flannelmouth sucker	*Catostomus latipinnis*	Catostomidae
	Humpback chub	*Gila cypha*	Cyprinidae
	Speckled dace	*Rhinichthys osculus*	Cyprinidae
Exotic Species	Common carp	*Cyprinis carpio*	Cyprinidae
	Fathead minnow	*Pimephales promelas*	Cyprinidae
	Redside shiner	*Richardsonius balteatus*	Cyprinidae
	Plains killfish	*Fundulus zebrinus*	Cyprinodontidae
	Rainbow trout	*Oncorhynchus mykiss*	Salmonidae
	Brown trout	*Salmo trutta*	Salmonidae

H_{o3b}: Habitat use by adult humpback chub during the flood will not differ from that before the flood.

Objective 2: Determine effects of the controlled flood on backwater habitats used by young-of-the-year and juvenile fishes.

Work Task 2.1: Determine changes in sediment characteristics of backwaters before and after the flood.

Participant: Arizona Game and Fish Department

Hypothesis:
H_{o4}: Sediment particle size in backwaters does not change over time.

Work Task 2.2 Determine short-term physical changes in backwaters caused by the flood.

Participant: Arizona Game and Fish Department

Hypothesis:
H_{o5}: Physical characteristics of backwaters do not change over time.

Work Task 2.3 Determine the change in number of backwaters caused by the flood.

Participants: Arizona Game and Fish Department and Glen Canyon Environmental Studies

Hypothesis:
H_{o7}: The number of backwaters pre-flood will not differ from the post-flood number.

Objective 3: Determine effects of the controlled flood experiment on lower trophic levels and food habits of humpback chub.

Work Task 3.1 Determine backwater use and re-colonization rates by benthic invertebrates and zooplankton.

Participant: Arizona Game and Fish Department

Hypotheses:
H_{o6a}: Benthic invertebrate and zooplankton density does not change over time.
H_{o6b}: Benthic invertebrate and zooplankton densities are not related to environmental or physical parameters of the backwater.
H_{o6c}: Benthic invertebrate density and species composition do not change with changes in sediment particle size.

Work Task 3.2 Determine food habits of adult and sub-adult humpback chub before and during high flows.

Participants: Bio/West and Arizona Game and Fish Department

Hypothesis:
H_{o8}: There will be no difference in the stomach contents of adult and sub-adult humpback chub before or during the high river discharge.

Study Area

The overall area of study is the Colorado River in Grand Canyon, Arizona, from Lee's Ferry (RK 0) to Diamond Creek (RK 363.16; Fig. 2). (Note: river locations are denoted as distance (river kilometer; RK) below Lee's Ferry. Specific sites are also given the notation of 'L' (left) or 'R' (right), the side of the river when facing downstream.). This section of river has been divided into eight sampling reaches of varying length, based on known fish populations and the availability of backwater habitat and spawning tributaries (Table 2). These reaches were used during pre- and post-flood sampling trips which covered the entire study area. In addition, sampling was conducted during the Experimental Flood. A reach ranging from Awatubi Canyon (RK 93.71) to Lava Chuar Rapid (RK 105.40) was the only area sampled during this period. This reach includes the confluence of the Little Colorado and Colorado Rivers (RK 98.95) and is an important rearing area, since all species of native fishes remaining in the Grand Canyon spawn in the Little Colorado River (Valdez and Ryel 1995; AGFD 1996).

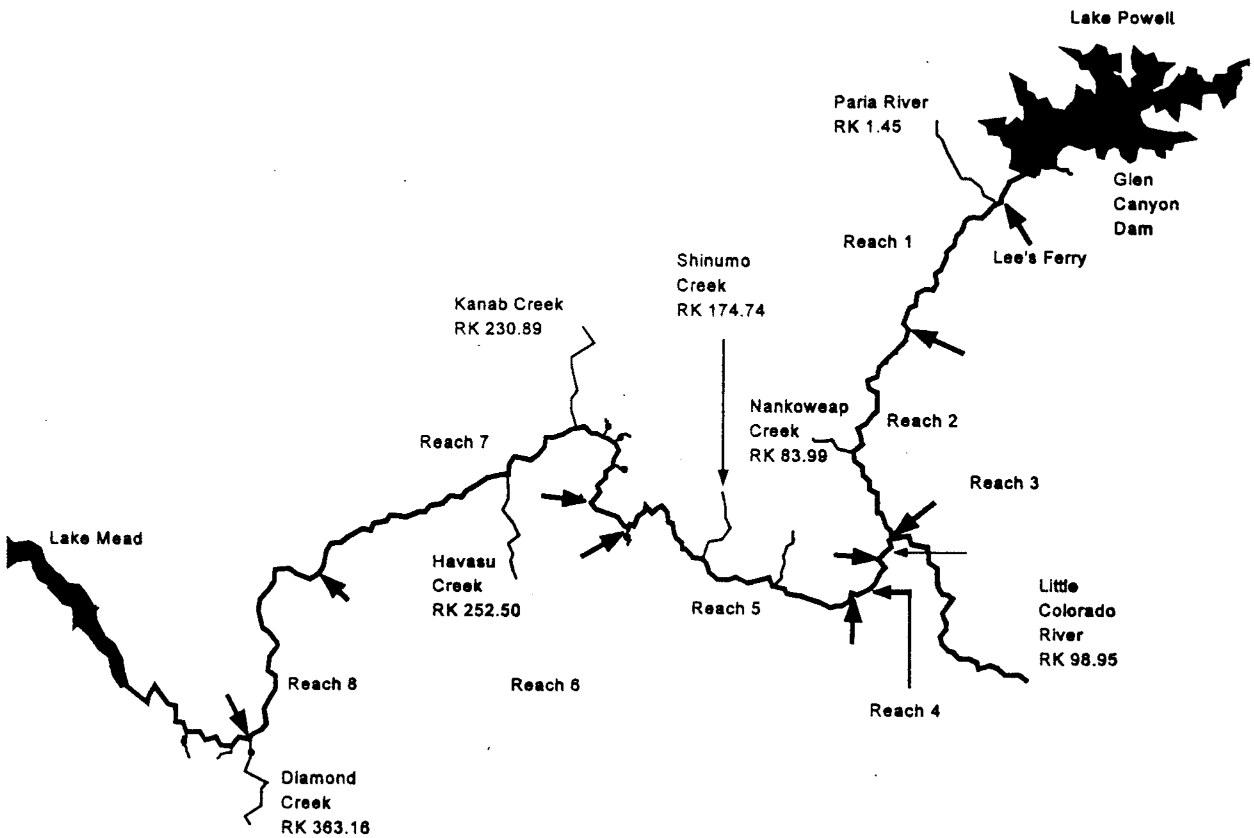

Figure 2. The Colorado River and major tributries between Lakes Powell and Mead. Large arrows indicate reach boundaries, as described in Table 2. Tributary locations are given as river kilometer (RK) below Lee's Ferry.

Table 2. Boundaries of sampling reaches used by AGFD during the 1996 Experimental Flood in the Colorado River, Grand Canyon, Arizona.

	Beginning of Reach			End of Reach		
Reach	Location	River Kilometer	River Mile	Location	River Kilometer	River Mile
CR1	Lee's Ferry	0.0	0.0	Shinumo Wash	47.1	29.3
CR2	Shinumo Wash	47.1	29.3	Little Colorado River	99.0	61.5
CR3	Little Colorado River	99.0	61.5	Lava Chuar Rapid	105.4	65.5
CR4	Lava Chuar Rapid	105.4	65.5	Hance Rapid	123.4	76.7
CR5	Hance Rapid	123.4	76.7	Elves Chasm	187.5	116.5
CR6	Elves Chasm	187.5	116.5	Forster Rapid	197.6	122.8
CR7	Forster Rapid	197.6	122.8	Hell's Hollow	293.6	182.5
CR8	Hell's Hollow	293.6	182.5	Diamond Creek	363.0	225.6

Methods

A number of different protocols and gear types were used during these studies, depending on the objectives of each study. Fish were captured using seines, trammel nets, minnow traps, and electrofishing. Some backwaters were sampled only for fish, while others were sampled intensively, for fish, benthic invertebrates, zooplankton, sediments, and backwater morphology. Backwaters were counted and their surface area measured by aerial videography and the Map and Image Processing System (MIPS) computer software. Specific methodologies are given in each chapter, but some methods common to many chapters are presented below.

Most backwaters were sampled quickly to provide an estimate of size and general habitat conditions in the backwater. A single seine haul through the site provided an index of the relative abundance of fishes (catch-per-unit-effort, CPUE) which was used to compare fish abundance with other backwaters. Habitat variables measured included: temperature (°C), dissolved oxygen (mg/L and percent saturation), specific conductance (μS/cm), pH, redox potential (mV), turbidity (NTU), mean depth (cm), maximum depth (cm), velocity (cm/s), and primary and secondary substrate types.

Twelve backwaters were selected on the pre-flood trip (Trip 96-1) for intensive sampling (Table 3). These sites were selected based on the presence of historical sampling data for these sites and the probability that they would remain as backwaters after the flood. However, only half of the sites remained as backwaters during Trip 96-3 after the flood (Table 3): three backwaters in Reach 2 (RK 71.23 L, RK 94.42 L, and RK 97.91 L) and one backwater each in Reach 3 (RK 100.16 L), Reach 6 (RK 188.90 R), and Reach 8 (RK 296.83 L). These remaining six backwaters were used to compare backwater morphology, sediments, and benthic invertebrate and zooplankton density and biomass before and after the Experimental Flood.

At each intensively sampled site, the backwater was first blocked off to prevent escape of fishes. Habitat measurements (as noted above), benthic invertebrate, zooplankton, and sediment samples were collected in at least three sites in each backwater (mouth, center, and foot). A "total station survey" was also made of the site to provide a detailed map of the site containing information on the morphology of the backwater, its sediments, vegetation, and areas of cover. Lastly, a minimum of three seine hauls were made through the backwater to provide population estimate by depletion (Bagenal 1978).

Electrofishing, minnow traps, and trammel nets were used to capture fishes in the mainchannel of the Colorado River. Trammel nets were used specifically for adult fishes (approximately >200 mm) and were set in areas of relatively low velocity, usually in large eddies. Electrofishing and minnow traps were used in vegetated, debris fan, and talus slope shoreline areas of the mainchannel. Minnow traps are selective for small fish (<100 mm) while electrofishing will capture all size ranges of fishes.

Table 3. Location of backwater sites intensively sampled before and after the 1996 Experimental Flood, Colorado River, Grand Canyon, Arizona. River kilometer and river mile are distance downstream from Lee's Ferry (RK 0.0) and side of the river is determined when facing downstream.

Site Location				Sampling Date	
River Kilometer	River Mile	Side of River	Reach	Pre-flood	Post-flood
71.23	44.27	Left	2	29 FEB 96	19 APR 96
94.42	58.68	Left	2	2 MAR 96	20 APR 96
97.91	60.85	Left	2	1 MAR 96	20 APR 96
100.16	62.25	Left	3	3 MAR 96	21 APR 96
119.16	74.06	Right	4	4 MAR 96	
119.81	74.46	Right	4	4 MAR 96	
188.90	117.40	Right	6	6 MAR 96	25 APR 96
265.49	165.00	Left	7	9 MAR 96	
296.83	184.48	Left	8	11 MAR 96	30 APR 96
309.60	192.42	Right	8	11 MAR 96	
312.07	193.95	Right	8	12 MAR 96	
323.51	201.06	Right	8	12 MAR 96	

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DISTRIBUTION AND DISPERSAL OF FISH

Work Task 1.1
Prepared by T. L. Hoffnagle

Floods were an integral part of the ecology of the Colorado River in Grand Canyon prior to the closure of Glen Canyon Dam (Minckley 1991; Valdez and Ryel 1995). These floods modified habitat (U. S. Department of the Interior 1996) and were probably spawning cues for native fishes (John 1963; Valdez and Ryel 1995). There is an abundance of literature on the affects of high flows on fish and fish communities in natural and regulated rivers (Seegrist and Gard 1972; Hoopes 1975; Harrell 1978; Ross and Baker 1983; Matthews 1986). Fishes native to the southwestern United States appear to be particularly resistant to flooding while fishes introduced to this area are vulnerable (Meffe and Minckley 1987; Minckley and Meffe 1987). The effect of a clear, cold water flood on present Colorado River fishes is unknown.

This chapter addresses a portion of Work Task 1.1: Determine distribution, dispersal, and habitat use of native and non-native fishes in 1) the Lee's Ferry Reach, 2) near the mouth of the Little Colorado River, and 3) below Lava Falls (RK 290 - 298) before and after the controlled flood. Herein we examine the changes in distribution and dispersal of fishes both near the confluence of the Colorado and Little Colorado Rivers and throughout the Grand Canyon. Specifically, we test the hypothesis that distribution of native and non-native fishes throughout the Colorado River, Grand Canyon, did not differ in response to the Experimental Flood. We had planned to examine dispersal of small fishes by marking (fin clip) juvenile humpback chubs *(Gila cypha)* and fathead minnows (*Pimephales promelas*) before the flood and recapturing them afterwards. However, no fish were marked since we did not catch enough of these fish that we were likely to recapture a sufficient number of them. Therefore, all inferences concerning dispersal of fishes were made solely on the basis of changes in distribution, as indicated by changes in catch-per-unit-effort in each reach during pre- and post-flood river trips.

Methods

Fish were collected using a variety of sampling gears. Seining was conducted in backwater habitats frequented by larval and juvenile fishes. Electrofishing and minnow trapping were conducted along talus, debris fan, and vegetated mainchannel shorelines. Trammel nets were used in deeper areas of the mainchannel, particularly in eddies.

Comparisons of collections of fish (catch-per-unit-effort; CPUE) were made on two separate time scales using different, but overlapping, reaches of the river. First, river trips (Lee's Ferry to Diamond Creek) were conducted before (28 February - 14 March 1996) and after (18 April - 3 May 1996) the Experimental Flood under fluctuating (operating) flow conditions. Backwaters were seined throughout this entire stretch of the river, but electrofishing, minnow trapping, and trammel netting was conducted by AGFD only from Lee's Ferry to National Canyon (RK 267.90), where the Hualapai Department of Natural Resources took over these tasks at this point, as part of joint monitoring/research. Secondly, sampling was conducted during the steady low (226 m^3/s; 8,000 cfs) flows immediately preceding (23 - 27 March 1996) and following (4 - 7 April 1996) the flood flows. All backwaters between RK 93.71 (Awatubi Canyon) and RK 105.40 (Lava Chuar Rapid) were seined. Sampling by electrofishing and minnow trapping was conducted between RK 98.95 (mouth of the Little Colorado River) and RK 105.40. Trammel netting was conducted between RK 96.54 - 105.40.

Minnow trapping, trammel netting, and electrofishing were conducted in the same areas before as after the flood under both time scales. However, backwater locations and availability changed dramatically after the flood and with changes in river discharge. New backwaters were created immediately after the flood, but variation in discharge and the resulting changes in flow pattern, between the flood and subsequent operating flows, destroyed many of these sites (see Backwater Number and Size chapter, this report). Nearly all available backwaters were sampled both before and after the flood, and sites were sampled on pre- and post-flood trips whenever possible.

Upon capture, all fish were identified to species, measured for total length (TL; mm) for all species (both total and standard length for humpback chub), weighed (g), and all data recorded. Additionally, humpback chub, flannelmouth suckers (*Catostomus latipinnis*), and bluehead suckers (*Catostomus discobolus*) >150 mm TL were checked for the presence of a PIT tag. If a PIT tag was present, the number was recorded. If the fish was not PIT tagged, a PIT tag was inserted and the number recorded. Fish were then released alive at the site of capture.

Electrofishing was conducted for 2-3 hours after dark. Electrofishing CPUE was calculated as the number of fish captured / 10 minutes of shocking time. Minnow traps were set overnight in groups of five traps. Minnow trap CPUE was calculated as the number of fish caught / 24 hour set / group of five traps. Trammel nets were deployed at dusk and checked every two hours for a total of four to six hours. Trammel net CPUE was calculated as the number of fish caught / 23 m (75 ft.) of net / 100 hours of netting. Seining was conducted only in backwaters and CPUE was calculated as the number of fish captured / 100 m^2 seined.

CPUE data could not be normalized due to the high frequency of zero captures. Therefore, the data were statistically analyzed using non-parametric tests (Sokal and Rohlf 1981). Comparisons of CPUE before and after the Experimental Flood were analyzed using the Mann-Whitney U test. Minnow traps and electrofishing were used to compare CPUE among debris fan, talus, and vegetated shorelines. Comparisons of CPUE among shoreline types were analyzed with the Kruskal-Wallis test. Comparisons of CPUE among reaches were analyzed with the Kruskal-Wallis test. Multiple Mann-Whitney U tests were used to discern differences among means for significant Kruskal-Wallis tests. Significance for all statistical tests was set at $\alpha = 0.05$.

Results

Ten species of fish were captured during the study: all four remaining native species plus common carp (*Cyprinus carpio*), fathead minnow, plains killifish (*Fundulus zebrinus*), redside shiner (*Richardsonius balteatus*), rainbow trout (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta*). All four native species were relatively common. Fathead minnow and rainbow trout were the only commonly captured exotics.

The collection of a redside shiner is noteworthy. This fish was caught in a minnow trap set at RK 102.49 during the post-flood steady 226 m^3/s flow. This fish was 53 mm TL and weighed 1.1 g.

226 m^3/s Flows Immediately Before and After the Experimental Flood

Few significant differences were seen in mean CPUE between sampling periods. No differences were seen in mean CPUE for any species by electrofishing ($P \geq 0.1656$). Mean CPUE for plains killifish decreased in backwater seining. Mean CPUE for speckled dace (*Rhinichthys osculus*) increased in minnow traps and for rainbow trout in trammel nets and backwater seining (Fig. 3; Table 4).

Speckled dace mean CPUE was significantly higher ($P = 0.0123$) in minnow traps after the flood than before the flood, increasing from 1.4 to 2.7 fish / 24 hour set. This increase in dace CPUE was due to an increase in the number of fish caught along talus shorelines ($P = 0.0018$) where mean CPUE increased from 0.3 to 1.8 fish / 24 hour set.

Mean CPUE of plains killifish in backwaters decreased significantly ($P = 0.0367$) from 0.12 to 0 fish / 100 m^2 seined. However, only 3 plains killifish were captured prior to the flood.

Mean CPUE for rainbow trout captured by trammel netting ($P = 0.0104$) and backwater seining ($P = 0.0371$) increased significantly. Mean CPUE of rainbow trout in trammel nets increased from 2.8 fish / 100 hours before the flood to 34.3 fish / 100 hours afterwards. Mean seine CPUE of trout in backwaters before the flood was 0.2 fish / 100 m^2 seined and increased to 0.9 fish / 100 m^2 seined.

Pre-flood vs. Post-flood River Trips

Few differences in catch rates were seen between river trips, with little evidence of native fishes being affected by the flood. Exotic fishes, however, appear to have been more affected by the flood, as represented by changes in CPUE in three species (Fig. 4; Table 5). Shoreline type type did not affect electrofishing catch rate ($P \geq 0.0811$) nor minnow trapping catch rate ($P \geq 0.1246$) for any species durint pre- and post-flood river trips..

Bluehead sucker mean CPUE in backwater seining decreased significantly ($P = 0.0443$) from 0.5 fish / 100 m^2 seined before the flood to 0.05 fish / 100 m^2 afterwards. Mean CPUE of all other native species in all other gear types did not vary between sampling periods ($P \geq 0.0937$).

Catches-per-unit-effort of fathead minnow, plains killifish, and rainbow trout all varied between sampling periods, indicating that they were affected by the Experimental Flood. Mean CPUE of plains killifish in backwater seining decreased significantly ($P = 0.0065$) from 1.1 fish / 100 m^2 seined prior to the flood to 0 fish / 100 m^2 afterwards. Conversely, mean backwater seining CPUE of rainbow trout increased significantly ($P = 0.0146$) from 0.04 fish / m^2 before the flood to 0.3 fish / 100 m^2 afterwards. Fathead minnows showed the most change with significant decreases in mean CPUE, from pre- to post-flood trips, in two gear types. In minnow traps, fathead minnow mean CPUE decreased ($P = 0.0001$) from

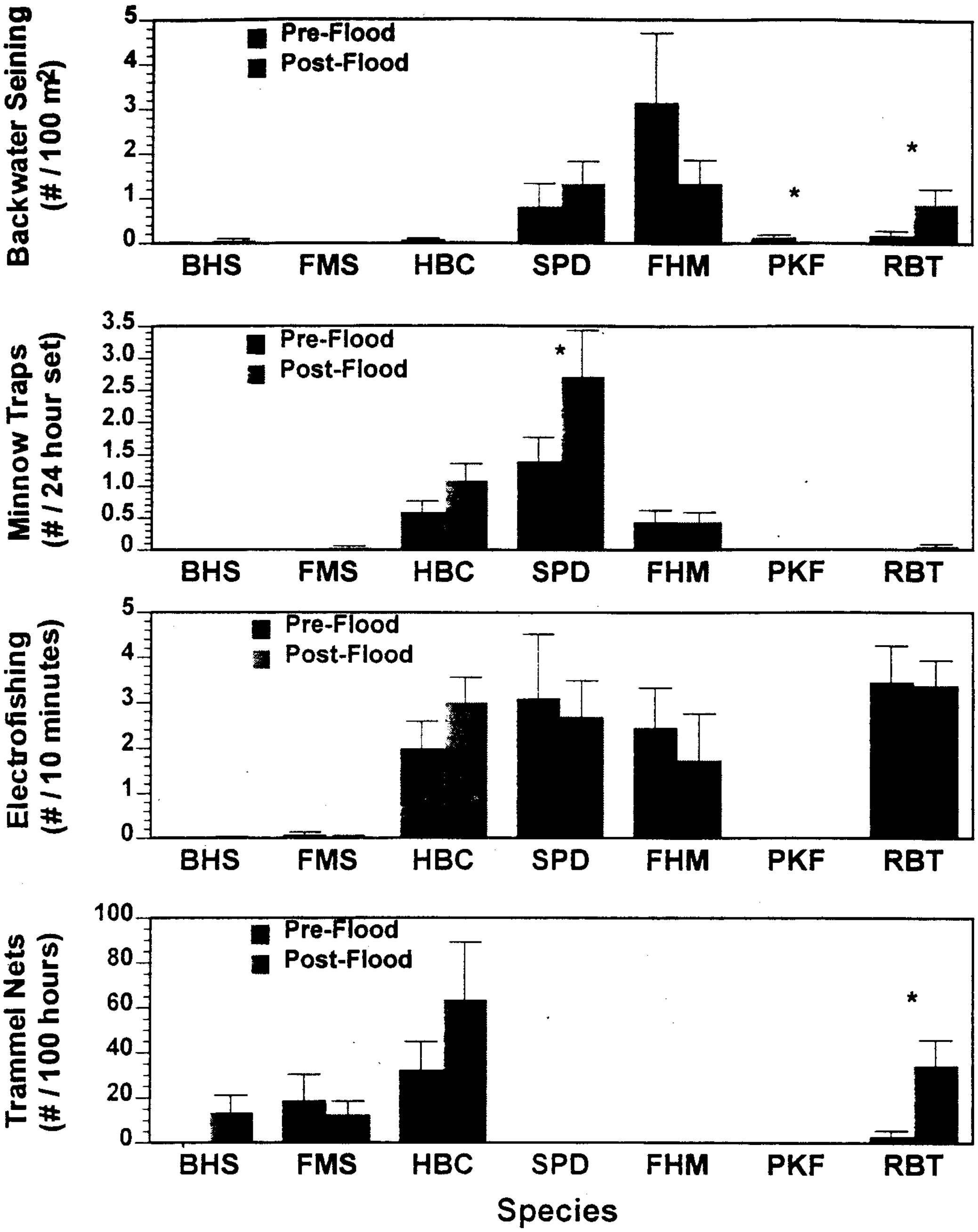

Figure 3. Mean (± standard deviation) of catch-per-unit-effort of fishes using various gear types in the vicinity of the confluence of the Colorado and Little Colorado Rivers during steady 227 m^3/s (8,000 cfs) flows immediately before and after the Experimental Flood in the Colorado River, Grand Canyon, Arizona, 1996. Species codes: BHS - bluehead sucker, FMS - flannelmouth sucker, HBC - humpback chub, SPD - speckled dace, FHM - fathead minnow, PKF - plains killifish, RBT - rainbow trout. * indicates significant difference at $\alpha = 0.05$.

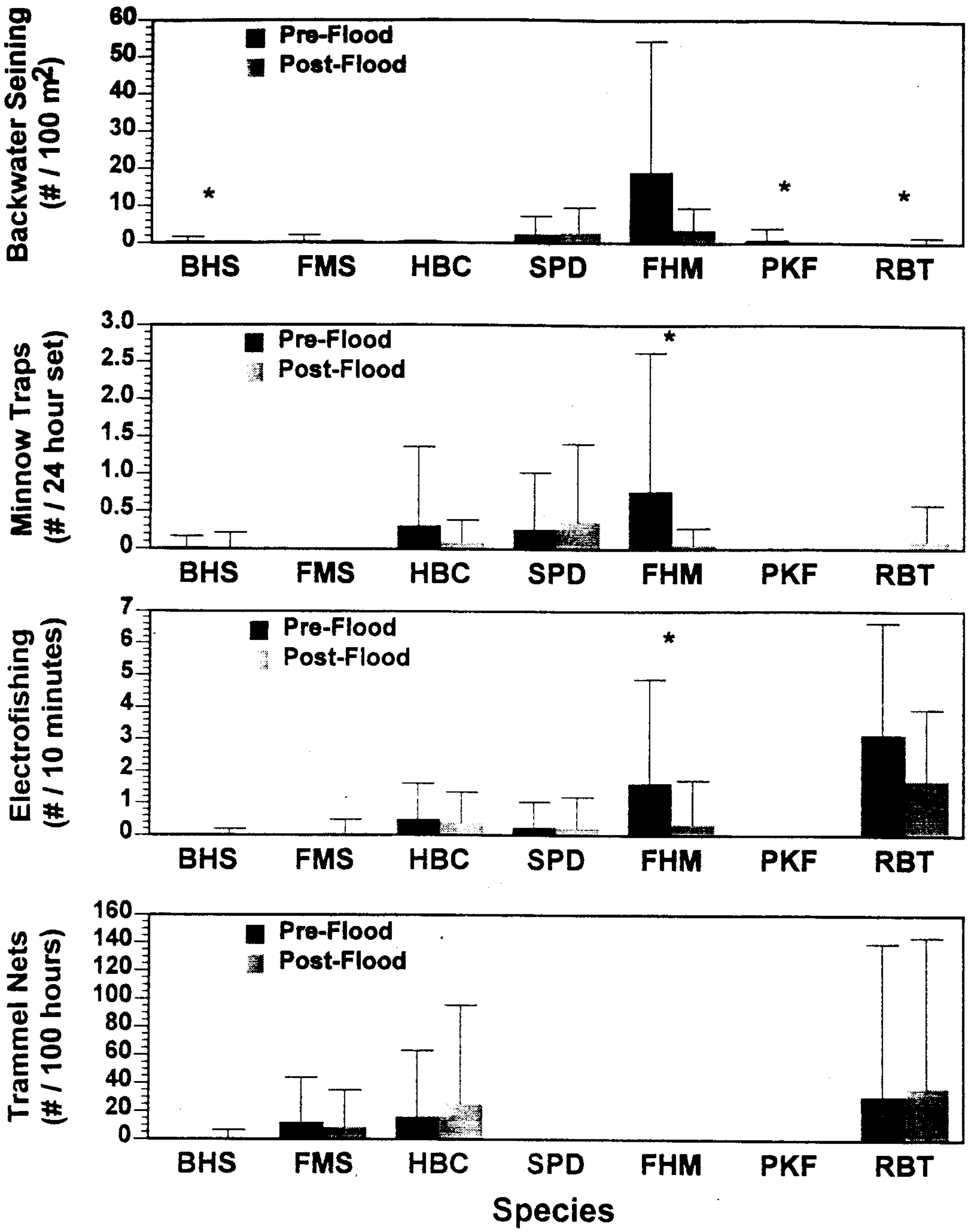

Figure 4. Mean (± standard deviation) of catch-per-unit-effort of fishes using various gear types during AGFD sampling trips before (28 February - 14 March 1996) and after (18 April - 3 May 1996) the Experimental Flood in the Colorado River, Grand Canyon, Arizona, 1996. Species codes: BHS - bluehead sucker, FMS - flannelmouth sucker, HBC - humpback chub, SPD - speckled dace, FHM - fathead minnow, PKF - plains killifish, RBT - rainbow trout. * indicates significant difference at $\alpha = 0.05$.

Table 4. Mean and standard deviation of catch-per-unit-effort (CPUE), mean total CPUE (total catch / total effort), and total catch of fishes using various gear types in the vicinity of the confluence of the Colorado and Little Colorado Rivers during steady 227 m³/s (8,000 cfs) flows immediately before and after the Experimental Flood in the Colorado River, Grand Canyon, Arizona.

	Pre-Flood				Post-Flood			
	CPUE				CPUE			
Gear Type/Species	Mean	Std Dev.	Mean Total	Total Catch	Mean	Std Dev.	Mean Total	Total Catch
Backwater Seining	Total Effort = 3192 m² seined				Total Effort = 5531 m² seined			
Bluehead sucker	0.00	0.000	0.00	0	0.06	0.044	0.09	5
Flannelmouth sucker	0.00	0.000	0.00	0	0.01	0.006	0.02	1
Humpback chub	0.07	0.045	0.13	4	0.01	0.014	0.02	1
Speckled dace	0.81	0.529	0.75	24	1.32	0.509	2.24	124
Fathead minnow	3.14	1.557	3.42	109	1.33	0.537	1.57	87
Plains killifish	0.12	0.065	0.09	3	0.00	0.000	0.00	0
Rainbow trout	0.17	0.110	0.19	6	0.87	0.343	0.99	55
Minnow Traps	Total Effort = 872.20 hours				Total Effort = 865.30 hours			
Flannelmouth sucker	0.00	0.000	0.00	0	0.03	0.031	0.03	1
Humpback chub	0.59	0.178	0.58	21	1.09	0.268	1.11	40
Speckled dace	1.39	0.383	1.35	49	2.71	0.721	2.77	100
Fathead minnow	0.43	0.192	0.41	15	0.43	0.158	0.44	16
Rainbow trout	0.00	0.000	0.00	0	0.05	0.037	0.06	2
Redside shiner	0.00	0.000	0.00	0	0.03	0.031	0.03	1
Electrofishing	Total Effort = 11889 seconds				Total Effort = 19702 seconds			
Bluehead sucker	0.00	0.000	0.00	0	0.02	0.019	0.03	1
Flannelmouth sucker	0.07	0.071	0.05	1	0.03	0.028	0.03	1
Humpback chub	1.99	0.597	2.62	52	3.00	0.562	3.11	102
Speckled dace	3.09	1.433	2.12	42	2.69	0.798	2.04	67
Fathead minnow	2.44	0.890	2.27	45	1.72	1.039	1.55	51
Rainbow trout	3.44	0.817	2.78	55	3.37	0.562	2.86	94
Trammel Netting	Total Effort = 50.38 hours				Total Effort = 45.29 hours			
Bluehead sucker	0.00	0.000	0.00	0	13.39	7.684	11.04	5
Flannelmouth sucker	18.86	11.648	11.91	6	12.42	6.219	11.04	5
Humpback chub	32.22	12.708	198.49	10	63.52	25.676	50.78	23
Rainbow trout	2.78	2.775	1.99	1	34.27	11.529	28.70	13

Table 5. Mean and standard deviation of catch-per-unit-effort (CPUE), mean total CPUE (total catch / total effort), and total catch of fishes using various gear types during AGFD sampling trips before (28 February - 14 March 1996) and after (18 April - 3 May 1996) the Experimental Flood in the Colorado River, Grand Canyon, Arizona.

	Pre-Flood				Post-Flood			
	CPUE				CPUE			
Gear Type/Species	Mean	Std. Dev.	Mean Total	Total Catch	Mean	Std. Dev.	Mean Total	Total Catch
Backwater Seining	Total Effort = 4342 m^2 seined				Total Effort = 6133 m^2 seined			
Bluehead sucker	0.46	1.079	0.51	22	0.05	0.188	0.07	4
Flannelmouth sucker	0.47	1.602	0.83	36	0.11	0.361	0.10	6
Humpback chub	0.56	2.632	1.01	44	0.00	0.000	0.00	0
Speckled dace	2.29	4.883	1.98	86	2.85	6.634	1.60	98
Fathead minnow	19.00	35.200	17.73	770	3.56	5.826	1.76	108
Plains killifish	0.86	3.032	0.99	43	0.00	0.000	0.00	0
Rainbow trout	0.04	0.161	0.07	3	0.32	1.227	0.11	7
Common carp	0.41	1.914	0.16	7	0.11	0.438	0.07	4
Minnow Traps	Total Effort = 870.15 hours				Total Effort = 1216.82 hours			
Bluehead sucker	0.02	0.145	0.03	1	0.02	0.192	0.02	1
Humpback chub	0.31	1.060	0.30	11	0.09	0.296	0.10	5
Speckled dace	0.26	0.765	0.30	11	0.36	1.048	0.39	20
Fathead minnow	0.77	1.856	0.72	26	0.05	0.223	0.06	3
Rainbow trout	0.00	0.000	0.00	0	0.10	0.482	0.08	4
Electrofishing	Total Effort = 10088 seconds				Total Effort = 16738 seconds			
Bluehead sucker	0.00	0.000	0.00	0	0.03	0.166	0.04	1
Flannelmouth sucker	0.00	0.000	0.00	0	0.09	0.396	0.07	2
Humpback chub	0.49	1.118	0.54	9	0.39	0.949	0.43	12
Speckled dace	0.24	0.797	0.18	3	0.23	0.961	0.22	6
Fathead minnow	1.62	3.251	1.55	26	0.34	1.369	0.14	4
Rainbow trout	3.15	3.486	3.09	52	1.71	2.221	1.51	42
Common carp	0.14	0.571	0.12	2	0.28	1.233	0.18	5
Trammel Netting	Total Effort = 109.32 hours				Total Effort = 113.40 hours			
Bluehead sucker	0.00	0.000	0.00	0	0.76	5.759	0.88	1
Flannelmouth sucker	12.05	31.952	9.15	10	8.68	26.129	8.82	10
Humpback chub	16.18	47.047	15.55	17	25.47	70.154	25.57	29
Rainbow trout	31.14	108.504	24.70	27	37.28	106.856	37.04	42
Common carp	1.02	8.038	0.91	1	0.72	5.517	0.88	1

0.8 fish / 24 hour set to 0.05 fish / 24 hour set. Mean electrofishing CPUE of fathead minnows also decreased (P=0.0185) from 1.6 fish / 10 minutes of electrofishing before the flood to 0.3 fish / 10 minutes after the flood.

Changes in Habitat Use

Electrofishing catch rates during the pre- and post-flood steady 226 m^3/s flows were affected by shoreline type for humpback chub, speckled dace, and rainbow trout (P ≤0.0104), but not for fathead minnows (P=0.0790). In minnow traps, shoreline type affected CPUE of speckled dace and fathead minnow (P ≤0.0108) but not humpback chub or rainbow trout (P ≥0.1316). Mean CPUE between pre- and post-flood trips among different shoreline types did not vary for electrofishing (P ≥0.0811) nor minnow trapping (P ≥0.1246) for any species.

Humpback chub CPUE by electrofishing was significantly higher (4.6 fish / 10 minutes) along talus shorelines than either debris fans (1.7 fish / 10 minutes) or vegetation (1.2 fish / 10 minutes; P=0.0008). This was the case during both pre-flood (4.076 fish / 10 minutes; P=0.0171) and post-flood (5.094 fish / 10 minutes; P=0.0357) sampling periods.

Speckled dace mean CPUE was higher in debris fans than in talus or vegetation in both minnow traps and by electrofishing (P=0.0001). There was no difference between talus and vegetation catch rates for either gear type. Speckled dace mean CPUE along debris fans was 6.6 fish / 10 minutes by electrofishing and 4.3 fish / 24 hours in minnow traps. Along the other shoreline types, speckled dace mean CPUE was ≤1.2 fish / 10 minutes by electrofishing and ≤1.0 fish / 24 hours in minnow traps. Speckled dace habitat use was similar between pre- and post-flood trips to that seen overall. In minnow traps, mean CPUE was higher in debris fans than both vegetation and talus during the pre-flood steady low flow (P=0.0001). Mean CPUE in debris fans was higher during post-flood sampling than in vegetation, but not higher than talus, which was also similar to vegetation (P=0.0161). Mean electrofishing CPUE before the flood was higher in debris fans than in talus, with vegetation not being different than the other two shoreline types (P=0.0426). After the flood, electrofishing CPUE was higher in debris fans than both talus or vegetation (P=0.0011).

Fathead minnow mean CPUE in minnow traps varied significantly by shoreline type (P=0.0108), but not by electrofishing (P=0.0790). Minnow trap CPUE was higher in vegetation (1.0 fish / 24 hour set) than in debris fans (0.2 fish / 24 hour set), which, in turn, was higher than talus (0.1 fish / 24 hour set). Before the flood, minnow trap CPUE did not vary among shoreline types (P=0.4868). However, after the flood, minnow traps caught more fathead minnows in vegetation than in talus, while debris fan catch did not vary between habitats (P=0.0124).

Rainbow trout CPUE did not vary between sampling periods in minnow traps (P=0.1316) but did by electrofishing (P=0.0104). Electrofishing CPUE for rainbow trout was significantly higher along debris fans (4.8 fish / 10 minutes) than talus (1.7 fish / 10 minutes). Catch-per-unit-effort in vegetation (3.6 fish / 10 minutes) was not significantly different from the other shoreline types. Pre-flood sampling showed no significant difference in CPUE among shoreline types (P=0.1085). However, CPUE during the post-flood steady low flows was significantly higher along debris fans than either vegetation or talus, which were not different from each other (P=0.0261).

Changes in Distribution

Few differences in fish distribution were seen between pre- and post-flood trips, and those differences were only in exotic species. Mean minnow trap CPUE of fathead minnow decreased between pre-flood and post-flood trips in the two reaches immediately below the LCR (Reaches 3 and 4). Mean CPUE in Reach 3 decreased from 0.1 fish / 24 hour set prior to the flood to 0.01 fish / 24 hour set afterwards. In Reach 4, fathead minnow mean CPUE decreased from 0.3 to 0.02 fish / 24 hour set.

Rainbow trout mean electrofishing CPUE in Reach 4 decreased significantly (P=0.0104). Prior to the flood, rainbow trout mean CPUE in Reach 4 was 4.1 fish / 10 minutes of electrofishing and decreased to 1.0 fish / 10 minutes following the flood.

Discussion

The results demonstrated that native Colorado River fishes were largely unaffected by this Experimental Flood while exotic species were affected. Plains killifish, as expected, were greatly affected by the flood: no fish were collected afterwards. However, there was an increase in the catch rates of rainbow trout during the period immediately following the flood, probably due to displacement from upstream areas or changes in habitat use. Although fathead minnows were not completely removed by the flood, significant decreases in their catch rates were noted. Bluehead sucker capture rates in backwaters decreased following the flood, while speckled dace captures in minnow traps increased.

The decrease in bluehead sucker CPUE is of interest since this is a native species well adapted to fast water (Minckley 1991) that should be able to withstand a relatively minor flood, such as this. However, ontogenetic behavioral changes may explain this decrease in CPUE in backwater seining. Bluehead suckers spend approximately the first year of their life schooling, commonly with similar sized flannelmouth suckers, in slow water areas, such as backwaters, feeding primarily on benthic invertebrates (AGFD 1996). However, as bluehead suckers reach approximately 50 mm (approximately one year of age), their cartilaginous scraper has developed and they move out of backwaters to feed by scraping algae and diatoms from rocks in riffles and other rocky areas (Minckley 1991). This trend was observed in bluehead suckers in the Colorado River, Grand Canyon, from 1991-1994 (AGFD 1996).

The overall increase in catch of speckled dace in minnow traps immediately after the flood was due to a sixfold increase in catches along talus slopes. This increase may not be due to an increase in number of fish in the system, but may be due to a change in habitat caused by the Experimental Flood. The flood moved sand from the channel bed and deposited it along the channel margins, often filling in the interstitial spaces between boulders of talus shorelines. This had the effect of making many talus shorelines similar to the sand and boulder structure of debris fans. Since speckled dace appear to prefer debris fan habitat (Valdez and Cowdell 1996; Work Task 1.2, this report) it appears that the newly deposited sand along talus shorelines may have been an improvement in conditions for speckled dace. Speckled dace commonly inhabit swift water in streams and rivers (Minckley 1973), including the Paria River where it survives floods of high discharge and turbidity (Rinne and Minckley 1991). Rinne (1992) found speckled dace in shallow areas (mean depth of 15.6 cm) of Aravaipa Creek, AZ, with a mean velocity of 38.5 cm/s and reaching 75 cm/s. Currents along debris fans in the Colorado River, Grand Canyon, are often fast, but not likely to displace speckled dace. Velocities along sandbars in the mainchannel Colorado River reached as high as 52 cm/s and speckled dace were the most common species captured in these habitats (AGFD 1996).

Although they were not commonly captured during pre-flood sampling, plains killifish populations in the mainstem Colorado River have been increasing in recent years. However, plains killifish populations were decimated by the Experimental Flood. Plains killifish were only caught by seining in backwaters. During the pre-flood trip, 43 killifish were captured, but none were captured during the post-flood trip. Cross (1967 *in* Minckley and Klaassen 1969) found plains killifish only in shallow water (<15 cm). Although I could find no information concerning the swimming ability of this species, it is unlikely that they could withstand current velocities found in the mainchannel of the Colorado River during a flood, particularly at the cold temperatures present.

Rainbow trout captures varied by gear and habitat type, but suggest that they were affected by the Experimental Flood. Catches increased during the steady 226 m^3/s flows immediately after the flood in both trammel nets (adults) and in backwaters (mostly fry, but some juveniles and adults). Rainbow trout catch also increased in backwater seining during the post-flood trip under operating flows. Conversely, trout electrofishing CPUE decreased in Reach 4 (RK 105.4 - 123.4), on the post-flood trip. Increases in rainbow trout catch are likely due to displacement downstream of fish from upstream. McKinney et al. (1996; Lee's Ferry chapter, this report) reported a decrease in the catch of rainbow trout <15 cm after the Experimental Flood in the Lee's Ferry Reach. These small fish, presumably, were flushed downstream and some of them ended up in backwaters. However, we also observed an increase in the catch of adults. Seegrist and Gard (1972) found flooding to greatly affect small rainbow trout but that large fish could also be affected by large floods. The decrease in rainbow trout capture by electrofishing in Reach 4 (a fourfold decrease) is puzzling, particularly considering that the river (as a whole) saw an increase in trout catch, including the reach immediately upstream during sampling immediately after the flood. It may be that sand deposition along the shorelines and changes in current patterns affected habitat for these fish.

Fathead minnow was the species that many had hoped would be removed from the system. These fish are suspected to be competitors, and possibly predators of larval native fishes. Indeed, chironomids, cladocerans, simuliids, and terrestrial insects are common components of the diets of both fathead minnows and juvenile humpback chubs (AGFD 1996). Fathead minnow catch rates did decrease in both minnow traps (tenfold) and by electrofishing (fivefold) during the post-flood trip, and their catches decreased tenfold in Reaches 3 and 4, the uppermost portion of their range in the Grand Canyon. However, it is unlikely that these decreases in abundance will severely affect the populations of these exotic fish. Their reproductive capacity is great: they breed throughout the summer and as many as 2622 eggs have been counted in a single female (Carlander 1969 and references therein). Also, since it is found as far north as Great Slave Lake (Scott and Crossman 1979) it is unlikely that cold temperatures are debilitating to this species.

The collection of a redside shiner in the mainchannel Colorado River is a rarity. Kaeding and Zimmerman (1983) collected ten fish from the mainstem Colorado River near the mouth of the LCR during May 1981 (unpublished data). AGFD also collected a single fish (85 mm TL) near Lees Ferry during electrofishing surveys in December 1995.

Both plains killifish and fathead minnows are potential competitors of larval and juvenile native fishes, particularly humpback chub. Both species show a considerable amount of diet overlap with the native cyprinids - humpback chub and speckled dace. Chironomids, ceratopogonids, cladocerans, simuliids, and terrestrial insects were commonly found in the gastrointestinal tract of each species collected in 1994 throughout the Colorado River in Grand Canyon (AGFD 1996).

The common small fishes caught in this study, humpback chub, speckled dace, and fathead minnow, appear to be segregated by habitat. Humpback chub were most likely to be caught among talus and speckled dace were clearly more common along debris fans. Fathead minnow appeared to be more of a generalist, but were most commonly caught in vegetation. These species show a fair amount of diet overlap, as explained above, but they appear to be consuming their prey in different areas, thus potentially reducing the amount of competition between them. Whether these same habitat preferences would be displayed by humpback chub or speckled dace without the presence of the exotic fathead minnow (or other exotics) should be studied. Interestingly, speckled dace became more common in talus after the flood. This may be due to the sand deposited among the talus boulders by the flood, which made talus more similar to debris fans.

The Experimental Flood did not appear to have hurt native fish populations and did succeed in slightly diminishing populations of exotic species, although this is probably only temporary. Meffe and Minckley (1987) and Minckley and Meffe (1987) have shown that native southwest fishes are unaffected by flooding. Indeed, they may require predictable flooding as part of their life history. John (1963) found that photoperiod and temperature changes prepare speckled dace for spawning and that flooding cues them to commence. It is likely that a similar set of cues are used by the other native fishes. It remains to be seen whether this type of flood can provide backwater rearing habitats for native fishes in the late spring and early summer when larvae are drifting downstream (see Backwater Number Chapter, this report). However, floods of a different magnitude and/or duration will be required to significantly diminish exotic fish populations.

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FISH HABITAT USE

Work Task 1.2.
Prepared by D.W. Speas and T. L. Hoffnagle

Prior to the closure of Glen Canyon Dam in 1963, flooding was an important part of the ecology of the Colorado River in Grand Canyon (Minckley 1991). Spring floods generally occurred in May - June, averaged approximately 2434 m^3/s (86,000 cfs), and have been recorded as high as 5660 m^3/s (220,000 cfs) (Stevens 1983; Valdez and Ryel 1995). Recession of such floods are important to native fishes as spawning cues (John 1963; Harvey 1987) and for their role in the creation of backwater habitats, which are important for larval and juvenile fishes dispersing from spawning areas (Valdez and Wick 1983; U.S. Department of the Interior 1995, 1996). After the closure of Glen Canyon Dam, flows rarely exceeded the power plant capacity of 31,500 cfs (892 m^3/s) and the seasonal high flows have been shifted from spring (May) to later in the year (Valdez and Ryel 1995). Occasional, large tributary floods are one of the few hydrological components of the Colorado River in Grand Canyon which have not been radically altered by mankind.

Modifying discharge from Glen Canyon Dam to include spring high flows for the benefit of native fishes in the Colorado River, Grand Canyon was addressed by Clarkson et al. (1994). Spring high flows were intended to stimulate gonadal maturation, create rearing habitats for young native fish at tributary mouths and other nearshore areas, and to reduce exotic fish populations. The Beach/Habitat-Building Test Flow (Experimental Flood) became an element of the preferred alternative of the Glen Canyon Dam Environmental Impact Statement (U.S. Department of the Interior 1995) and one of its stated purposes is "reforming backwater habitats for native fish" (U.S. Department of the Interior 1996). The timing of this 1274 m^3/s (45,000 cfs) flood was set in late-March and early-April, 1996 to avoid detrimentally affecting young-of-the-year (YOY) native fishes. However, during the Experimental Flood, age 1 fish may be affected by changing habitat. While many studies have documented the results of a flood on fish communities (see Work Task 1.1, this report), very little information is available concerning habitat use by small fishes during a flooding event. Minckley (1991) speculated that fish moved to the surface along channel margins to avoid high current velocities and the abrasive action of transported sediment.

It is rare that the timing of a flood is known sufficiently in advance to plan to conduct studies while it is occurring. This portion of the study addresses Work Task 1.2: Determine habitat use by juvenile fishes during low and high steady flows. We are testing the null hypothesis that habitat selection by juvenile fishes does not differ between flow regimes. The rising water levels of the flood inundated some quiet-water habitats (e.g., backwaters and vegetated cut banks) used by small native and exotic fishes at lower flows. However, new quiet-water habitats were created in flooded terrestrial vegetation and other areas. This chapter examines whether fish were able to find areas of refuge or were dispersed downstream.

Study Area

Samples were collected from the Colorado River, Grand Canyon, between the confluence of the Colorado and Little Colorado Rivers (RK 98.95) and Lava Chuar Rapid (RK 105.39). This reach of river is an important rearing area for larval and juvenile native fishes spawned in the Little Colorado River (Valdez and Ryel 1995; AGFD 1996). It is inhabited by four native species (humpback chub, bluehead sucker, flannelmouth sucker, and speckled dace) as well as common exotic species (fathead minnow, rainbow trout, plains killifish, and common carp).

The areas sampled for this portion of the study were delineated into three shoreline types: debris fan, talus, and vegetation. Debris fans are shallow areas with a substrate of sand around rocks ranging in size from cobble to boulders. Talus shorelines are usually found in deep, fairly fast-moving water, where large, angular boulders provide shelter from the current. Overhanging and submerged vegetation is found along shallow to deep cut-banks. The dominant substrate here is usually sand or hard-packed silt.

Methods

Fish were collected by electrofishing and minnow trapping along talus, debris fan, and vegetated mainchannel shorelines. These collections were made during four days of steady low flows (226 m^3/s = 8,000 cfs) immediately before and after the steady high flow (Experimental Flood; 1274 m^3/s = 45,000 cfs). Low steady flows in the study area occurred during 23-26 March and 5-8 April, and the high flows occurred from 28 March-5 April 1996.

Electrofishing was conducted for 2-3 hours after dark. Electrofishing catch-per-unit-effort

(CPUE) was calculated as the number of fish captured/10 minutes of shocking time. Minnow traps were set in groups of five traps and were checked every 24 hours. Minnow trap CPUE was calculated as the number of fish caught/24 hour set/group of five traps.

Upon capture all fish were identified to species, and their lengths [total length (TL; mm) for all species and both total and standard length for humpback chub] and weights (g) were recorded. Fish were then released at the site of capture.

Catch-per-unit-effort data could not be normalized due to the high frequency of zero captures. Therefore, the data were statistically analyzed using non-parametric tests (Sokal and Rohlf 1981). Comparisons of CPUE between low and high flows were analyzed using the Mann-Whitney U test. Comparisons of CPUE among shoreline types were analyzed with the Kruskal-Wallis test. Multiple Mann-Whitney U tests were used to discern differences among means for significant Kruskal-Wallis tests. Significance for all tests was set at $\alpha = 0.05$.

Results

The only small fish captured in sufficient numbers for statistical analysis were humpback chub, speckled dace, fathead minnow, and rainbow trout. Differences in CPUE were seen for humpback chub, fathead minnow, and rainbow trout under differing flow regimes (Table 6, Fig. 5) and shoreline types (Tables 7 and 8, Figs. 6 and 7). Capture rates for speckled dace did not vary between flow regimes, but did vary among shoreline types.

A single flannelmouth sucker x razorback sucker (*Xyrauchen texanus*) hybrid was captured by electrofishing in the LCR side channel (RK 99.0) during the high flow period. The fish was 612 mm TL and weighed 2135 g.

Humpback Chub. Humpback chub catch rates by electrofishing was greatest during low flows ($P = 0.0004$; 2.5 fish/10 min.; Table 6, Fig. 5) and varied by shoreline type ($P = 0.0235$). Catch rates in debris fans and vegetation did not vary between flow regimes ($P \geq 0.0764$), but they were significantly greater ($P = 0.0003$) along talus shorelines at low flows (4.6 fish/10 min.) than high flows (0.5 fish/10 min.; Table 8, Fig. 7). At low flows, catch rates were significantly higher ($P = 0.0008$) along talus shorelines than in debris fans (0.5 fish/10 min.) or vegetation (1.2 fish/10 min.). Electrofishing catch rates among shoreline types did not vary significantly during high flow ($P = 0.5501$).

Catch rates of humpback chub in minnow traps did not vary between flow regimes ($P = 0.1905$), but varied among shoreline types ($P = 0.0004$). During high flows, capture of humpback chubs was significantly greater ($P = 0.0001$) in talus shorelines (1.5 fish/24 hr minnow trap set) than debris fans and vegetation (0.2 and 0.1 fish/24 hr minnow trap set, respectively; Table 8, Fig. 6). At low flows, humpback chub capture in minnow traps did not vary significantly among shoreline types ($P = 0.4037$).

Speckled Dace. Speckled dace was the most common species captured in this study. Their capture did not vary between flow regimes for either gear type ($P \geq 0.0527$; Table 6, Fig. 5), but varied among shoreline types ($P = 0.0001$ for both gear types). Speckled dace capture in both gear types was greatest along debris fans ($P \leq 0.0004$; Table 8, Figs. 6 and 7) than along talus or vegetated shorelines, and capture in minnow traps was subsequently greater along talus shorelines than in vegetation ($P = 0.0183$). Speckled dace were captured at a rate of 7.2 fish/10 min. along debris fans. In both talus and vegetation, they were captured at a rate of only 1.1 fish/10 min. In minnow traps, 3.1 dace were captured/24 hr set along debris fans, while only 1.2 and 0.6 dace were captured/24 hr set along talus and vegetation, respectively.

Fathead Minnow. Fathead minnow catch rates were significantly greater ($P \leq 0.0340$) during low flows (2.1 fish/10 min., 0.4 fish/24 hr minnow trap set; Table 6, Fig. 5) than at high flows in both gear types. Electrofishing catch rates did not vary among shoreline types ($P = 0.1876$), but catch rates in minnow traps varied by shoreline type ($P = 0.0391$). During low flows, capture rates in minnow traps were significantly greater ($P = 0.0108$) along vegetated shorelines than along debris fans or talus shorelines. During both flow regimes, fathead minnow capture rates in minnow traps was greater in vegetation than in debris fans ($P = 0.0289$).

Rainbow Trout. Rainbow trout catch by electrofishing was significantly greater ($P = 0.0002$) under low flows (3.40 fish/10 min.; Table 6, Fig. 5) than at high flows, and their capture varied among shoreline types ($P = 0.0009$). During low flows, electrofishing catch rates were greater ($P = 0.0104$) along debris fans (4.83 fish/10 min.) than talus shores (Table 8, Fig. 7). Electrofishing

catch rates along talus slopes were greater (P=0.0424) during low flows (1.74 fish/10 min.) than at high flows. Rainbow trout catch rates in minnow traps did not vary between flow regimes (P=0.1647) or among shoreline types (P=0.1391).

Table 6. Mean and standard deviation of catch-per-unit-effort (CPUE) and total catch of humpback chub, speckled dace, fathead minnow and rainbow trout by electrofishing and in minnow traps deployed between the confluence of the Colorado and Little Colorado Rivers (RK 98.95) and Lava Chuar Rapid (RK 105.44) during steady high (1274 m^3/s; 45,000 cfs) and low (226 m^3/s; 8,000 cfs) discharges of the Experimental Flood in the Colorado River, Grand Canyon, Arizona, 1996.

	High Flow			Low Flow		
	CPUE			CPUE		
Gear Type/Species	Mean	Std Dev	Total Catch	Mean	Std Dev	Total Catch
Electrofishing	Total Effort = 12507 seconds			Total Effort = 31591 seconds		
Humpback chub	0.36	0.613	5	2.53	2.763	154
Speckled dace	2.43	4.231	31	2.88	5.257	109
Fathead minnow	0.23	0.465	3	2.06	4.610	96
Rainbow trout	0.62	0.700	9	3.40	3.215	149
Minnow Traps	Total Effort = 1657.40 hours			Total Effort = 1737.50 hours		
Humpback chub	0.59	1.212	40	0.84	1.378	61
Speckled dace	1.22	1.890	84	2.05	3.505	149
Fathead minnow	0.06	0.237	4	0.43	1.047	31
Rainbow trout	0.00	0.000	0	0.03	0.159	2

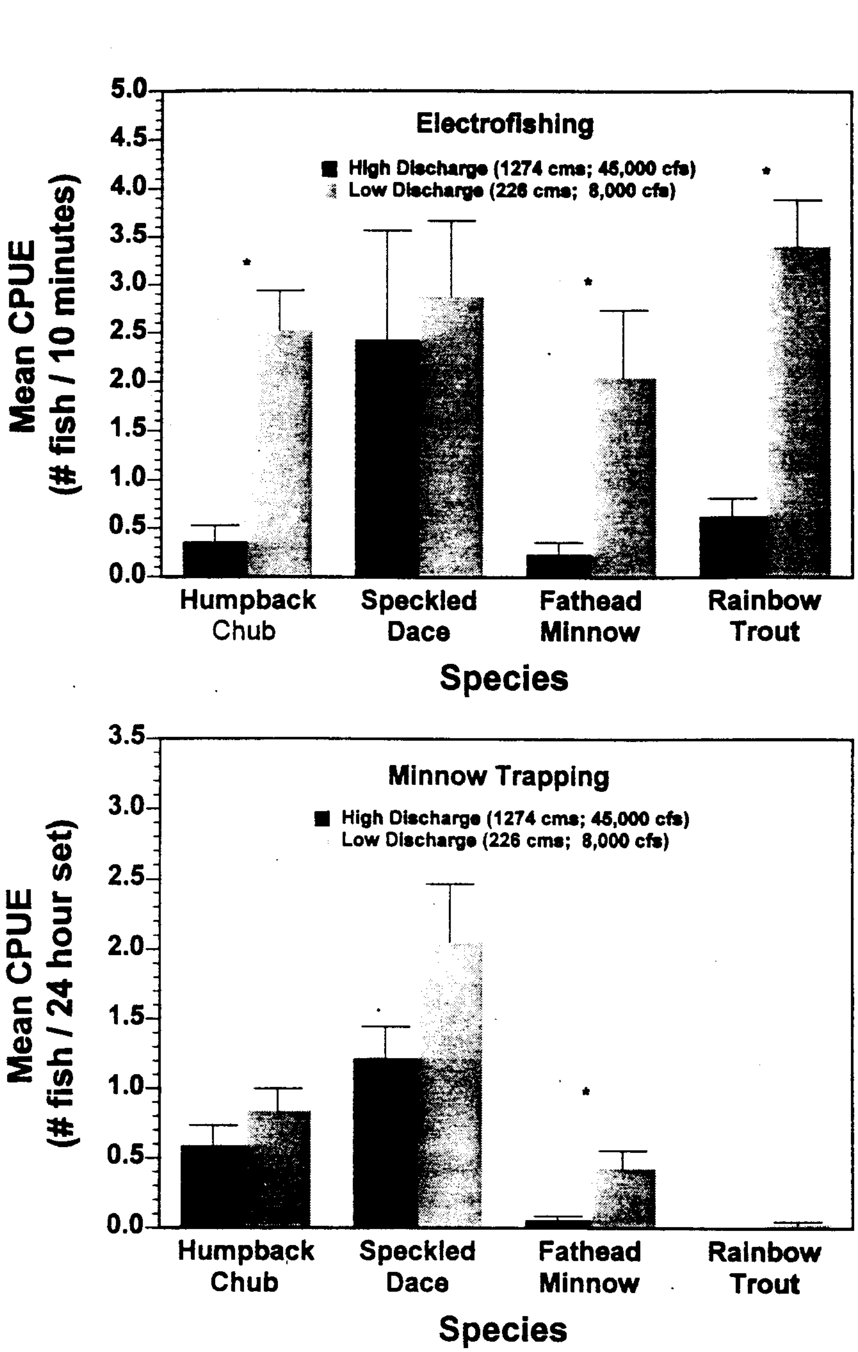

Figure 5. Mean (± 1 standard deviation) catch-per-unit-effort (CPUE) of humpback chub, speckled dace, fathead minnow and rainbow trout by electrofishing and minnow trapping during steady low (226 m^3/s, 8,000 cfs) and steady high (1274 m^3/s, 45,000 cfs) discharges in the Colorado River, Grand Canyon, 23 March - 8 April 1996. * indicates significant difference between means at high and low discharges (α=0.05).

Table 7. Mean and standard deviation of catch-per-unit-effort (CPUE) and total catch of humpback chub, speckled dace, fathead minnow and rainbow trout in debris fan, talus, and vegetated shorelines. Collections (electrofishing and minnow traps) were made between the confluence of the Colorado and Little Colorado Rivers (RK 98.95) and Lava Chuar Rapid (RK 105.44) during the Experimental Flood in the Colorado River, Grand Canyon, Arizona, 1996.

	Electrofishing			Minnow Traps		
	CPUE			CPUE		
Shoreline Type/Species	Mean	Std Dev	Total Catch	Mean	Std Dev	Total Catch
Debris Fans	Total effort = 9930 seconds			Total effort = 1162.80 hours		
Humpback chub	1.61	1.984	24	0.31	0.608	15
Speckled dace	7.17	7.915	92	3.06	4.050	150
Fathead minnow	0.62	0.915	8	0.12	0.442	6
Rainbow trout	4.59	3.047	69	0.00	0.000	0
Talus	Total effort = 19018 seconds			Total effort = 1147.18 hours		
Humpback chub	3.19	3.354	119	1.29	1.721	61
Speckled dace	1.14	1.462	29	1.20	1.773	57
Fathead minnow	0.67	1.155	25	0.10	0.305	5
Rainbow trout	1.28	1.392	40	0.04	0.194	2
Vegetation	Total effort = 14192 seconds			Total effort = 1084.92 hours		
Humpback chub	0.97	1.211	16	0.55	1.128	25
Speckled dace	1.13	1.455	19	0.57	1.048	26
Fathead minnow	3.52	6.578	66	0.54	1.237	24
Rainbow trout	2.95	3.678	49	0.00	0.000	0

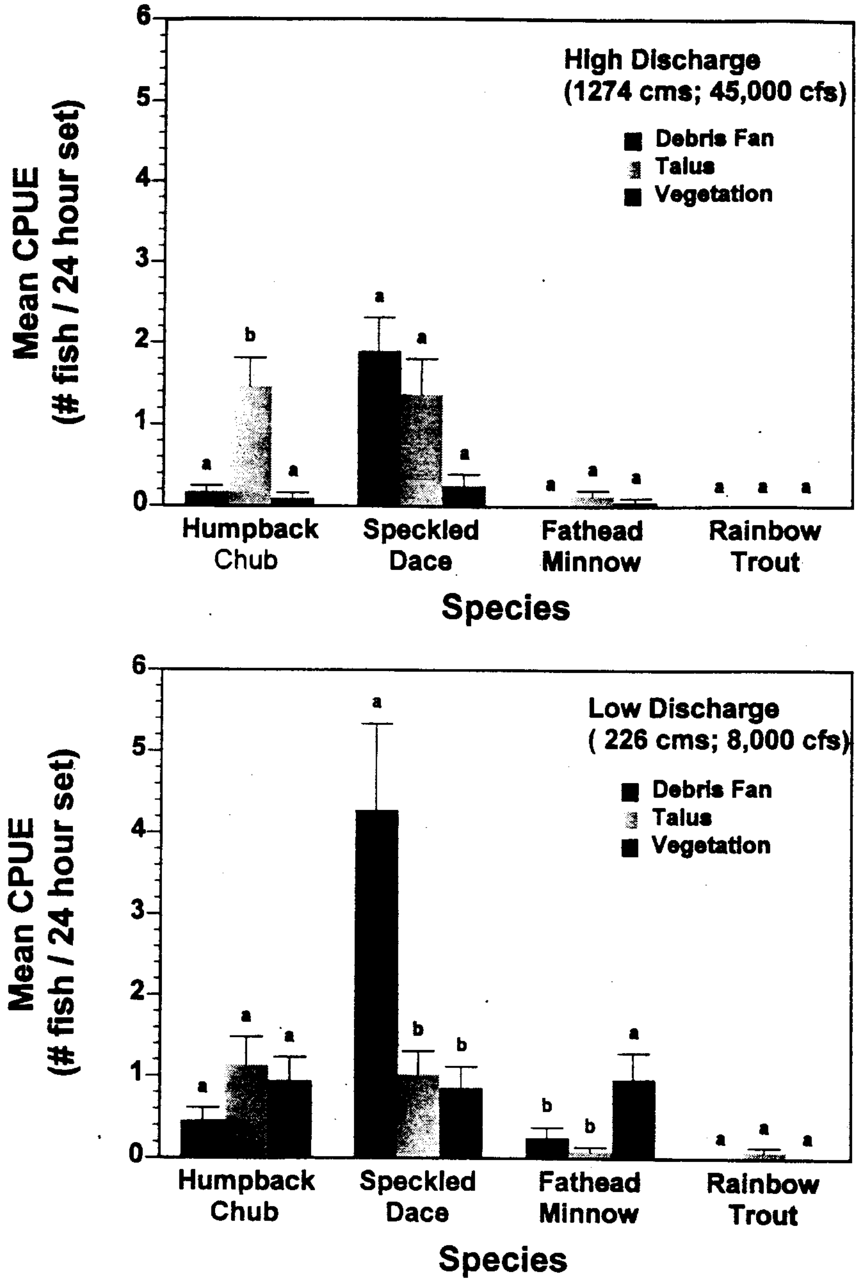

Figure 6. Mean (± 1 standard deviation) catch-per-unit-effort (CPUE) of humpback chub, speckled dace, fathead minnow, and rainbow trout by minnow trapping during steady low (226 m^3/s, 8,000 cfs) and steady high (1274 m^3/s, 45,000 cfs) discharges in the Colorado River, Grand Canyon, 23 March - 8 April 1996. Means with identical lettering are not significantly different (α=0.05).

Table 8. Mean and standard deviation of catch-per-unit-effort (CPUE) and total catch of humpback chub, speckled dace, fathead minnow and rainbow trout in debris fan, talus, and vegetated shorelines. Collections (electrofishing and minnow traps) were made between the confluence of the Colorado and Little Colorado Rivers (RK 98.95) and Lava Chuar Rapid (RK 105.44) during steady high (1274 m^3/s; 45,000 cfs) and low (227 m^3/s; 8,000 cfs) discharges of the Experimental Flood in the Colorado River, Grand Canyon, Arizona, 1996.

	High Flow			Low Flow		
	CPUE			CPUE		
Gear Type/Species	Mean	Std Dev	Total Catch	Mean	Std Dev	Total Catch
			Electrofishing			
Debris Fans	Total effort = 1465 seconds			Total effort = 8465 seconds		
Humpback chub	0.00	.	0	1.72	2.005	24
Speckled dace	15.31	.	15	6.63	7.878	77
Fathead minnow	1.02	.	1	0.59	0.941	7
Rainbow trout	1.02	.	1	4.83	2.996	68
Talus	Total effort = 5293 seconds			Total effort = 13725 seconds		
Humpback chub	0.52	0.732	4	4.62	3.339	115
Speckled dace	1.62	2.243	10	0.89	0.804	19
Fathead minnow	0.16	0.463	1	0.94	1.329	24
Rainbow trout	0.42	0.590	3	1.74	1.491	37
Vegetation	Total effort = 4791 seconds			Total effort = 9401 seconds		
Humpback chub	0.18	0.397	1	1.24	1.283	15
Speckled dace	1.17	2.149	6	1.12	1.246	13
Fathead minnow	0.18	0.397	1	4.64	7.305	65
Rainbow trout	0.87	0.884	5	3.64	4.011	44
			Minnow Traps			
Debris Fans	Total effort = 589.39 hours			Total effort = 573.41 hours		
Humpback chub	0.17	0.391	4	0.45	0.754	11
Speckled dace	1.89	2.079	47	4.28	5.167	103
Fathead minnow	0.00	0.000	0	0.25	0.613	6
Rainbow trout	0.00	0.000	0	0.00	0.000	0
Talus	Total effort = 567.00 hours			Total effort = 580.18 hours		
Humpback chub	1.46	1.722	34	1.13	1.741	27
Speckled dace	1.37	2.109	32	1.02	1.383	25
Fathead minnow	0.13	0.339	3	0.08	0.272	2
Rainbow trout	0.00	0.000	0	0.08	0.272	2
Vegetation	Total effort = 501.01 hours			Total effort = 583.91 hours		
Humpback chub	0.10	0.301	2	0.94	1.418	23
Speckled dace	0.25	0.656	5	0.86	1.244	21
Fathead minnow	0.05	0.226	1	0.96	1.573	23
Rainbow trout	0.00	0.000	0	0.00	0.000	0

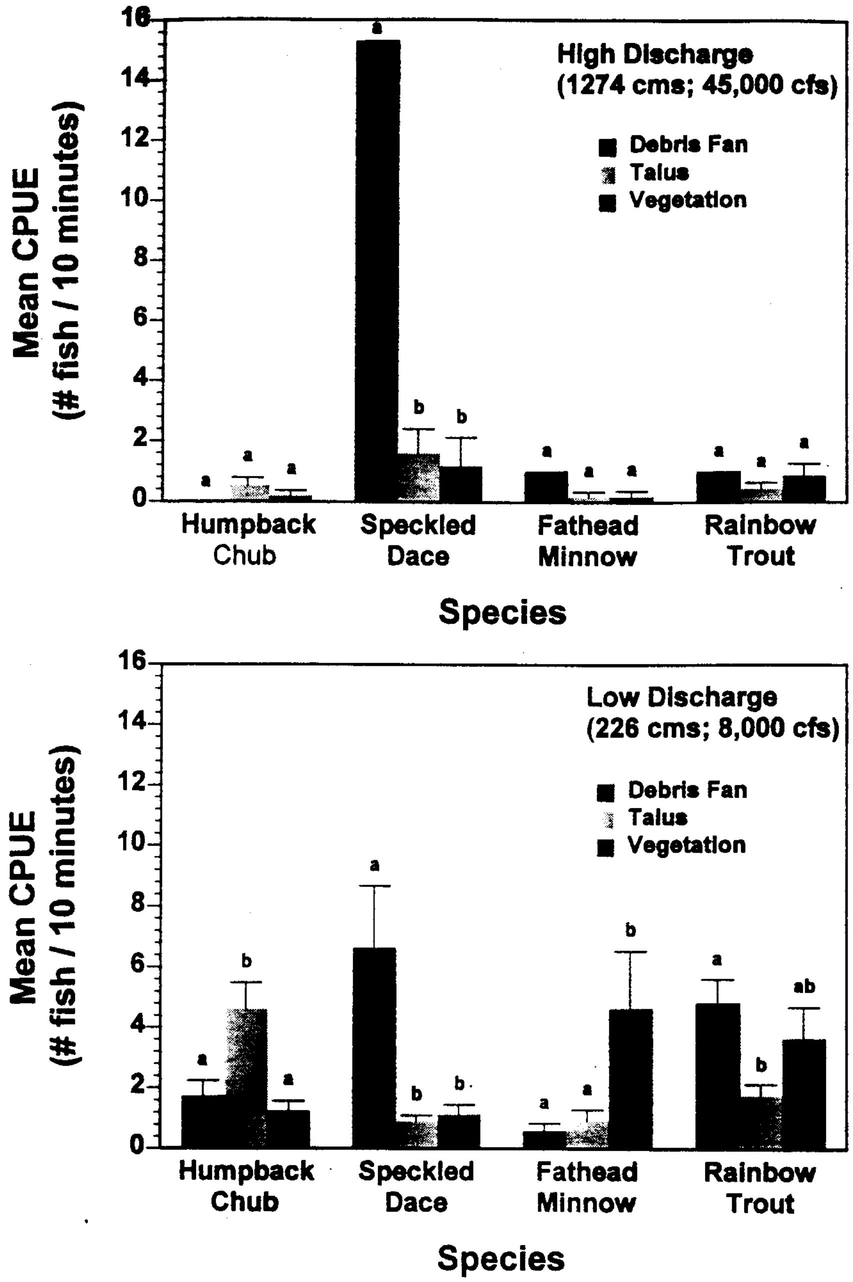

Figure 7. Mean (± 1 standard deviation) catch-per-unit-effort (CPUE) of humpback chub, speckled dace, fathead minnow, and rainbow trout by electrofishing during steady low (226 m^3/s, 8,000 cfs) and steady high (1274 m^3/s, 45,000 cfs) discharges in the Colorado River, Grand Canyon, 23 March - 8 April 1996. Means with identical lettering are not significantly different (α=0.05).

Discussion

The Experimental Flood provided an opportunity to test the hypothesis that native southwestern fishes respond to floods differently than introduced fishes. Minckley and Meffe (1987) hypothesize that morphological and/or behavioral attributes of fishes native to the southwest enable them to maintain their position in streams during floods, as movement to low velocity refugia is frequently impossible in canyon bound reaches. Moreover, displacement to such refugia or downstream reaches is disadvantageous because such habitats are often ephemeral at best and mortality by stranding is probable. Exotic fishes, particularly taxa which evolved in systems with extensive floodplain habitat, are more likely to seek refuge from floods by moving onto flood plains or drifting downstream to more quiet waters (Hynes 1970; Ross and Baker 1983).

In the present study, catch rates of speckled dace did not vary by flow regime or habitat type, which supports Minckley and Meffe's (1987) hypothesis. While their morphology varies from basin to basin, speckled dace are considered to be well adapted for holding their positions during floods (Minckley 1973; Rinne and Minckley, 1987). John (1963) identified floods as an important spawning cue for speckled dace. Their apparent preference for debris fans is best explained by the fact that cobbles and boulders in this habitat are typically embedded in a finer substrate, such as sand (Valdez and Ryel 1995), and speckled dace seem to prefer surfaces over interstices (Rinne 1992). Following the flood (Work Task 1.1, this report), speckled dace catch rates along talus shorelines were greater than they were prior to the flood. This apparent shift in habitat preference is probably an artifact of sand deposition in talus interstices, which caused talus habitats to be more similar to debris fans, the shoreline type where speckled dace were most commonly found under all flow regimes.

Catch rates of humpback chub by electrofishing decreased during the flood. As with all species collected in this study, turbidity probably impeded collection of humpback chub by electrofishing. Mean turbidity was significantly higher ($P = 0.0001$) during the flood ($= 58.2$ NTU) than before ($= 8.64$ NTU) or afterwards ($= 10.0$ NTU), which may have interfered with electrofishing efforts for all species in a variety of ways. The most important impact of turbidity on electrofishing effectiveness is decreased visibility for collectors. Whereas fish were usually seen and captured during electrofishing efforts at low flows, they were rarely seen at high flows due to turbidity. At high flows, most captures were made by blind sweeps and as a result catches were lower.

It is tempting to conclude from electrofishing data that humpback chub did not show a preference for shoreline type during the flood because riverine habitat types are frequently less heterogeneous during floods (Harrel 1978). Also, Valdez and Ryel (1995) hypothesizes that the perennially cold water temperatures of the mainstem Colorado River impairs swimming ability of young humpback chub and their displacement from shoreline habitats may result. However, catch rates of humpback chub in minnow traps discredit the conclusion that no habitat selection took place during the flood, as more fish were caught along talus slopes than other shorelines during the flood, the same pattern observed by electrofishing at low flows. Minnow trapping data suggest that young humpback chub were not stimulated by the flow increase to move from talus shorelines, which would make their capture more probable due to their temporal and spatial overlap with traps (Hubert 1983). Most of the decrease in CPUE by electrofishing, then, would be attributed to impaired fish visibility because of increased turbidity.

Humpback chub were commonly captured along talus shorelines in this experiment and in others (Maddux et al. 1987; Valdez and Ryel 1995). We expected to see a preference for talus shorelines by humpback chub at low flows by minnow trapping, but did not. It is possible that since more interstitial space in talus shorelines was available at low flows, the need for chub to seek cover was minimized and fish encountered gear less frequently.

At low flows, fathead minnow catch rates were highest in vegetation. Use of vegetated shorelines in Grand Canyon by fathead minnows has been documented previously by Maddux et al. (1987). Terrestrial vegetation inundated by the flood probably provided a great deal of cover and protection for fathead minnows, yet fewer were captured during the flood. The observed decrease in fathead minnow catch rates during the flood was probably due to displacement by flooding, as indicated by a net decrease in fathead minnow catch rates observed between pre-flood and post-flood trips (Work Task 1.1, this report). Also, electrofishing efficiency was especially ineffective in dense, flooded vegetation due to entanglement of dip nets in branches.

Electrofishing data indicate that rainbow trout commonly used debris fans at low flows, but no clear habitat preference was seen at high flows. Reduced electrofishing efficiency may have contributed to this change, but there is evidence (Work Task 1.1, this report) that displacement of rainbow trout from upstream reaches occurred during the flood. Assuming rainbow trout in the study area below the LCR were similarly affected, demonstration of habitat preference would be difficult if the majority of the fish were drifting during the sampling period. Immature trout usually select low velocity habitats and are more susceptible to displacement by high flows than adults (Seegrist and Gard, 1973; Maddux et al. 1987), especially at low temperatures (Heggenes and Saltveit 1990).

The capture of a flannelmouth x razorback sucker hybrid is of interest. This fish was captured during electrofishing in submerged terrestrial vegetation in the LCR side channel during steady high flows. It possessed a definite dorsal keel, but was reduced from that seen in true razorback suckers. Ten razorback suckers have been reported from the Grand Canyon from 1944 to 1990 (Valdez 1996). Hybrids between flannelmouth and razorback suckers have also been reported from the Colorado River in Grand Canyon, but such reports are exceedingly rare (Valdez 1996). The individual collected in this study had been previously PIT tagged (1F7B18715D), but we could not find it in the data base. Most likely, AGFD has not yet received the data file containing information concerning this fish.

In summary, electrofishing catch rates for humpback chub, fathead minnow and rainbow trout decreased during the flood, but minnow trap catch rates did not vary between flow regimes for humpback chub, speckled dace and rainbow trout. Contrasting catch rates by gear type suggests that high river discharge affected gear effectiveness, fish behavior, and perhaps habitat availability. Interactions between these components of the study may exist. Velocity, depth, sediment load, and turbidity increase with increased river discharge (Hynes 1970; Bain et al. 1988), and thus substrate and cover features of rivers are frequently altered during floods. These habitat alterations are side-effects of increased discharge, which in and of itself should elicit fish behavior patterns which vary with age (Schlosser 1985) and life history (Harvey 1987; Minckley and Meffe 1987) of individual fish taxa. Also, increases in turbidity interfered with electrofishing effectiveness, which contributed to low catch rates observed during the flood.

Despite these sources of variability, however, there is evidence in this study which supports Minckley and Meffe's (1987) hypotheses that native fish do not disperse downstream during floods. Speckled dace catch rates were unaffected by the flood and humpback chub maintained a preference for talus shorelines during the flood. Fathead minnows and rainbow trout, however, probably dispersed downstream in search of lower water velocity or were displaced.

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BACKWATER SEDIMENTS

Work Task 2.1
Prepared by M. J. Brouder

The fate of backwaters in the Colorado River, Grand Canyon, is largely dependent on sediment input and movement throughout the system (Rubin et al. 1990; Schmidt 1990; Schmidt and Graf 1990). The major sources of sediment input into the Colorado River in Grand Canyon are the Paria and Little Colorado Rivers (Andrews 1991). Backwaters located immediately downstream from the Little Colorado River (LCR) contained the highest percentage of fine sediments (< 65μm) and organic matter (AGFD 1996). Changes in discharge from Glen Canyon Dam and tributary floods can alter the sediment composition in backwaters (AGFD 1996). In 1993, there were significant differences in sediment composition of backwaters located downstream of the LCR after a large flood in the LCR in January and February of that year compared to other years without local flooding. These floods created backwaters comprised of mostly fine sediments.

Species abundance of benthic invertebrates is lowest in predominantly sandy substrates and higher in silt-sand substrates; while muddy substrates support greater biomass but not necessarily more species (Hynes 1970). Therefore, the type of sediment found within a backwater can affect the species composition and abundance of benthic invertebrates, an important food source for juvenile native fishes (AGFD 1996).

This chapter addresses Work Task 2.1: Determine changes in sediment characteristics of backwaters before and after the flood. We are testing the null hypothesis that sediment particle size in backwaters will not change after the flood. We anticipate that the scouring of backwaters by increased flows from Glen Canyon Dam will leave backwater habitats with a substrate largely comprised of clean sand. Over time, silt and organic detritus will be deposited in these backwaters, changing the substrate composition. These substrate changes will be important to the recolonization rates of benthic invertebrates and ultimately to the availability of food for juvenile native fishes.

Methods

Six backwaters were sampled both before and after the Experimental Flood. Sediment core samples were collected from these six backwaters before (28 February - 14 March 1996) and after (18 April - 3 May 1996) the Experimental Flood. Sediment samples were collected using a modified 60 mL syringe from each of three locations throughout the backwater: foot, center, and mouth. Each sediment sample consisted of a 50 mL core which was placed in a 125 mL Nalgene bottle and preserved in 40 % isopropyl alcohol.

In the laboratory, sediment samples were rinsed of preservative, mixed with 10 mL of sodium metaphosphate (Calgon) to prevent clumping of particles, and placed in a pre-weighed crucible. Each sample was mixed thoroughly and approximately half of the sample was placed into a pre-weighed tin, creating Samples A(crucible) and B (tin). Samples A and B were dried for 48 hours at 105°C, cooled, and crucible dry weight and tin dry weight were recorded. Contents of the crucible were wet sieved through a 65μm sieve. Coarse particles were returned to the crucible, dried for 24 hours at 105°C, cooled, and dry coarse particle weight was recorded. Both Sample A (crucible) and Sample B (tin) were placed in an ashing furnace for 2 hours at 500°C, cooled, and crucible ash weight and tin ash weight were recorded.

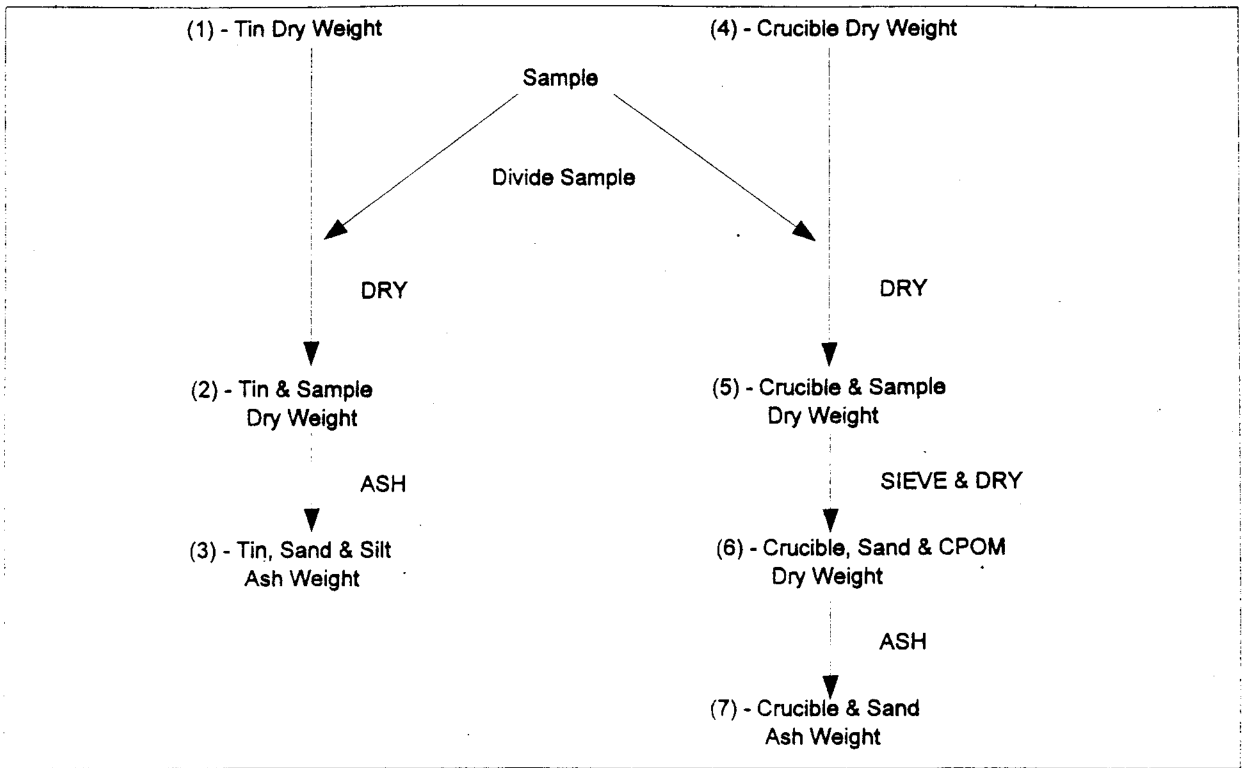
From these data, sediments were categorized as coarse (> 65μm) particulate organic matter (CPOM), fine (< 65μm) particulate organic matter (FPOM), coarse inorganic (sand), and fine inorganic (silt) components (Birklend 1984), and the percentages of each component were calculated for each sediment core sample. A detailed flow chart and calculations are presented in Figure 8. Significant differences in the percentages of sand, silt, CPOM, and FPOM before and after the flood were compared using a Mann-Whitney U-test with significance at $\alpha = 0.05$ (Sokal and Rohlf 1981). A sequential Bonferroni test was used to determine a critical α for all tests of significance.

Results

The sediment composition in each of the six backwaters changed after the Experimental Flood (Table 9). Overall, prior to the flood, sand and silt each comprised approximately 50% of the backwater sediments while CPOM and FPOM comprised < 2% combined (Fig. 9). After the flood, sand was the dominant sediment type in backwaters, and comprised a significantly higher percentage ($P = 0.0166$) of sediment in backwaters. Conversely, the flood significantly reduced the percentages of silt ($P = 0.0183$), CPOM ($P = 0.0016$), and FPOM ($P = 0.0244$) in the backwaters, by approximately 50% each.

Figure 8. Flow chart and calculations used to determine sediment composition in backwaters before and after the 1996 Experimental Research Flood.

Flow Chart
Calculations



A - Total Sample Weight = (2 - 1) + (5 - 4)
B - Weight of Sample in Crucible = 5 - 4
C - Weight of Coarse Particles = 6 - 4
D - Weight of Fine Particles = B - C
E - Weight of CPOM = 6 - 7
F - Weight of Sand = 7 - 4
G - Proportion of Sand = F / B;
H - Proportion of CPOM = E / B;
I - Proportion of Fine Particles = D / B;
J - Weight of Sample in Tin = 2 - 1
K - Weight of Inorganic Particles = 3 - 1
L - Proportion of Inorganic Particles = K / J
M - Total Weight of Sand = G * A
N - Percentage of Sand = (G / A) * 100
O - Total Weight of CPOM = H * A
P - Percentage of CPOM = (H / A) * 100
Q - Total Weight of Inorganic Particles = L * A
R - Total Weight of Silt = Q - M
S - Percentage of Silt = (R / A) * 100
T - Total Weight of FPOM = A - R - O - M
U - Percentage of FPOM = (T / A) * 100

Table 9. Mean percentages of sand, silt, CPOM, and FPOM in backwaters sampled both before and after the Experimental Flood in the Colorado River, Grand Canyon, 1996.

		Pre-Flood				Post-Flood			
Reach	RK	% Sand	% Silt	% CPOM	% FPOM	% Sand	% Silt	% CPOM	% FPOM
2	71.23 L	29.9	67.5	0.4	2.1	96.3	3.0	0.2	0.5
2	94.42 L	35.3	63.1	0.4	1.2	91.1	7.6	0.3	1.1
2	97.91 L	16.6	81.3	0.5	1.5	95.5	4.0	0.2	0.4
Reach 2 Mean		27.3	70.6	0.4	1.6	94.3	4.9	0.2	0.7
3	104.99 L	32.9	61.6	0.6	1.9	20.0	77.1	0.3	2.6
6	188.90 R	83.7	15.3	0.2	0.8	59.0	39.9	0.2	0.8
8	296.83 L	97.1	1.9	0.2	0.7	91.3	8.4	0.1	0.2
Overall Mean		52.2	46.1	0.4	1.4	81.4	17.7	0.2	0.8

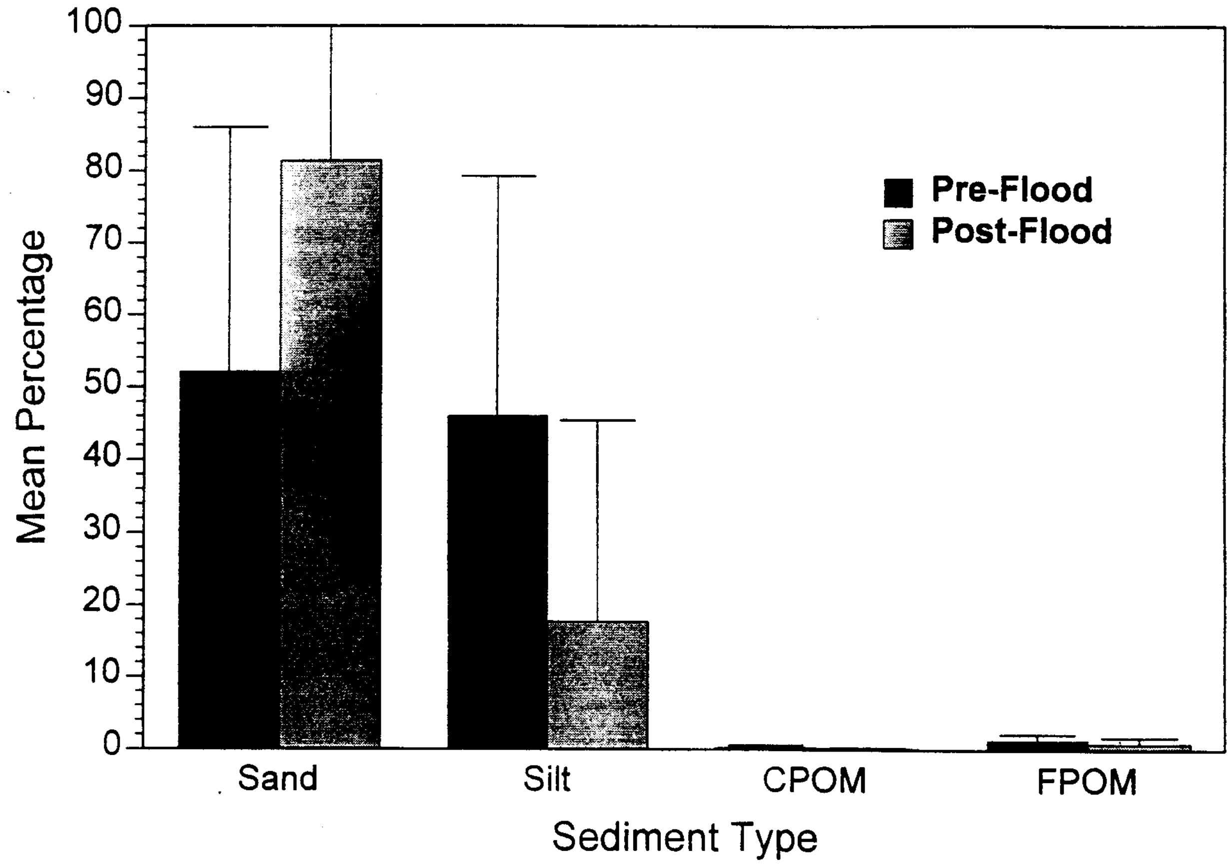


Figure 9. Mean percentage of sand, silt, CPOM, and FPOM in backwaters both before and after the Experimental Flood in the Colorado River, Grand Canyon, 1996.

Discussion

Sediment analyses documented the expected changes in the sediment composition of backwaters after the 45,000 cfs (1,278 m^3/s) Experimental Flood. There was a significant shift in sediment type from approximately equal percentages of silt and sand prior to the flood to predominantly sand, and reduced percentages of silt, CPOM, and FPOM after the flood. The higher percentage of silt before the flood can be explained by findings of Stevens and Ayers (1993). They found that over time, backwaters fill in with silt and detritus and can ultimately become marshes. With the exception of an occasional tributary flood, flows in the Colorado River, Grand Canyon have averaged between 8,000 (227 $m^3\ s^{-1}$) and 19,000 cfs (568 $m^3\ s^{-1}$) (daily discharge) over the past 5 years of interim operations. A lack of scouring, high water velocities have allowed the accumulation of silt and organic particles in backwaters.

Immediately following the flood we observed significantly higher percentages of sand in backwaters than before the flood. The high water velocities created by the Experimental Flood and the process of backwater formation explain the shift in sediment type to predominantly sand after the flood. High water velocities scoured fine materials (silt, CPOM, and FPOM) out of backwaters. Sand from the river channel bottom was deposited in recirculation zones, creating a reattachment bar. When the water levels dropped, the reattachment bar was exposed forming an eddy return-current channel backwater.

Although new sand was deposited at most sites, there were exceptions. Silt remained the dominant particle size in the substrate of the backwater located at RK 104.99L (above Lava Chuar Rapid). Prior to the flood this backwater was comprised of hard, compact silt (81.3%) and sand (16.6%). After the flood there was still a higher percentage of silt (77.1%) than sand (20.1%) in this backwater. Apparently, a flood of 45,000 cfs (1,278 m^3/s) for seven days was not strong enough to completely scour out the compacted silt substrate of this backwater.

The specific effects of the 1996 Experimental Research Flood on benthic invertebrate diversity, density, and biomass are addressed elsewhere in this report (see Benthos Chapter, Work Task 3.1, this report). In this chapter we examined the short-term changes in sediment composition immediately after the 1996 Experimental Flood. Silt and organic matter will continue to be deposited in backwaters and will be monitored over time. These changes in sediment composition are important to benthic invertebrates; a major food source for juvenile native fishes.

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NUMBER AND AREA OF BACKWATERS

Work Task 2.3
Prepared by M.J. Brouder

Backwaters have become increasingly important as rearing areas for larval and juvenile native fishes in the Colorado River system due to changes in mainstem habitat; primarily decreased water temperature caused by hypolimnial discharge from dams, (Holden 1978; Valdez and Clemmer 1982; Carter et al. 1985; Maddux et al. 1987; AGFD 1996). Backwaters are quiet pockets of water connected to the mainchannel with no or greatly reduced flow, and are usually formed in eddies where scouring and aggradation occur during high flows (Schmidt and Graf 1990). In the absence of flooding, an 80% decline in the number of backwaters from 1985 - 1991 was documented by Weiss (1993). However, backwater numbers increased from 1992 - 1993 after LCR flooding in January and February 1993 (McGuinn-Robbins 1995)

This chapter addresses Work Task 2.3: Determine the change in the number of backwaters caused by the flood. We are testing the null hypothesis that the number of backwaters pre-flood will not differ from the number post-flood. We anticipate that the number of backwaters will increase after the flood. We also examined the change in surface area of backwaters after the flood. An objective of the Experimental Flood was to rejuvenate backwater habitats which are important to the survival of native fishes (U. S. Department of the Interior 1995).

Study Area

The study area extended 364 river kilometers (RK) from Lee's Ferry (RK 0.0), 25.4 km downstream from Glen Canyon Dam to Diamond Creek (RK 364.0).

Methods

Backwaters were documented by aerial videography during steady 8,000 cfs (226 m^3/s) flows immediately before and after the flood. Videotapes were analyzed using the Map and Image Processing System 3.30 (MIPS) software package (MicroImages, Inc.). Information obtained from the videos include number, surface area (m^2), and location of backwaters (recorded to the nearest hundredth river kilometer (RK) downstream from Lee's Ferry (Stevens 1983) and noted as left (L) or right (R) side of the river when facing downstream). All backwaters located between Lee's Ferry and Diamond Creek were included in the analyses.

Backwaters were also counted in the field between the Little Colorado River and RK 105.4 (Lava Chuar) during the 8,000 cfs flow before and after the Experimental Flood.

Flows of steady 8,000 cfs are not normal in the Grand Canyon. Therefore, in addition to backwaters counted by aerial survey, we also counted backwaters at operating flows as we traveled downstream from Lee's Ferry to Diamond Creek during AGFD Trips 96-1 (28 February - 14 March, 1996) and 96-3 (18 April - 3 May, 1996). This provided additional information concerning backwater prevalence under more common conditions.

The number of backwaters present before and after the flood was compared to determine the change in number caused by the flood throughout the study area and by reach. Significant differences in mean backwater surface area were tested using a Mann-Whitney U-test test (Sokal and Rohlf 1981). Significance was set at $\alpha = 0.05$.

Results

Based on aerial videography, the Experimental Flood resulted in the net formation of eight additional backwaters at 8,000 cfs throughout the study area (Table 10). Prior to the flood, no backwaters were counted in Reaches 3, 4, or 5. After the flood, four new backwaters were counted in Reach 3, one in Reach 4, and two in Reach 5 (Table 10).

Based on ground census, 68 backwaters were counted during AGFD pre-flood trip 96-1, and 42 were counted during AGFD post-flood trip 96-3. These counts were taken during daily mean Glen Canyon Dam discharges of 13,405 cfs (379 m^3/s) and 18,419 cfs (521 m^3/s), on the pre- and post-flood trips respectively. Based on ground census conducted between the Little Colorado River and RK 105.4 during the 8,000 cfs (227 m^3/s) before and after the flood, five backwaters were found before the flood and seven were found after the flood (Table 10).

Backwaters after the flood had a significantly greater ($P = 0.0002$) mean surface area (285.1 m^2) than backwaters before the flood (172.5 m^2). Of the seven backwaters that were present both before and after the flood, five of them showed an increase in surface area after the flood (Table 11).

Table 10. Number and mean surface area (m^2) of backwaters in each reach before and after the Experimental Beach/Habitat Building Flood in the Colorado River, Grand Canyon, Arizona, 1996.

	Pre- Flood			Post-Flood		
		Aerial Census 8,000 cfs			Aerial Census 8,000 cfs	
Reach	Ground Census (13,405 cfs)*	Number	Mean Surface Area (m^2)	Ground Census (18,419 cfs)*	Number	Mean Surface Area (m^2)
1	1	2	243.0	1	3	342.7
2	13	7	160.6	8	11	286.9
3	3	0	-	3	4	287.8
4	9	0	-	4	1	206.0
5	0	0	-	4	2	297.0
6	2	2	186.5	4	4	273.3
7	21	9	184.7	6	5	269.2
8	19	11	154.8	12	9	296.0
Total	68	31	172.5	42	39	285.1

* Mean daily discharge from Glen Canyon Dam

Table 11. Location (RK and side) and pre-flood and post-flood surface areas (m^2) of backwaters that were present both before and after the Experimental Beach/Building Flood in the Colorado River, Grand Canyon, Arizona, 1996.

Location	Pre-Flood Surface Area (m^2)	Post-Flood Surface Area (m^2)
35.64R	396	552
78.33R	240	159
97.90L	138	318
196.31R	190	240
285.48L	378	357
290.42R	106	539
293.64R	105	531

Discussion

An objective of the Experimental Flood was to rejuvenate backwater habitats which are important to the survival of native fishes (United States Department of the Interior 1995). The increase in number and size of backwaters immediately after the flood indicates a successful outcome based on an increase in potential rearing habitats for larval and juvenile native fishes. However, ground census conducted during late April at discharges greater than 18,000 cfs showed a decrease in the number of backwaters. The two methods used in this study to document changes in backwater numbers caused by the flood provided conflicting results. An increase in backwater numbers based on aerial videography was seen during the steady 8,000 cfs flows immediately before and after the flood. Conversely, backwater counts conducted during AGFD river trips documented a decrease in backwater number following the flood. The primary factor that explains this discrepancy is the difference in discharge between trips. Changes in river elevation may desiccate or inundate backwaters, particularly shallow sites or those with low reattachment bars. Backwater numbers based on aerial videography have been reported to be higher under lower discharges (Weiss 1993; McGuinn-Robbins 1995). Mean estimated river discharge increased from the AGFD pre-flood trip (13,405 cfs) to the post-flood trip (18,419 cfs) and continued to increase through the summer trip (estimated in the field at 19,000 cfs; 538 m^3/s). Also, the number of backwaters counted during ground census conducted between the LCR and RK 105.4 (Lava Chuar) during the 8,000 cfs before and after the flood conflicted with those taken using aerial videography. The difference in backwater numbers counted during the 8,000 cfs before and after the flood can be attributed to 1) difficulty in determining if reattachment bars were above water and 2) if backwaters existed in areas of the river where shadows from the canyon walls covered stretches of the river. Counts taken during the AGFD river trips may be a more accurate indicator of backwater numbers under more normal Colorado River flows. However, dam operations and the resulting differences in river discharge between trips make comparisons of backwater numbers between trips difficult using ground census techniques.

However, the difference in river discharge between the aerial and ground counts may not completely explain the differences in backwater numbers between counting methods. Time is also an important factor. Approximately two weeks elapsed between the post-flood 8,000 cfs count and the AGFD post-flood river trip. Although there was an increase in backwater numbers immediately following the flood, this increase may not have been long-lived, even if river discharge remained at a steady 8,000 cfs. Many of the reattachment bars created by the flood were rapidly eroding under 8,000 cfs due to differences in flow patterns between 45,000 and 8,000 cfs. Therefore, many of the newly created backwaters were likely to have been temporary, even under steady low flow conditions. It is possible that clear water floods with a lower magnitude and/or shorter duration may create backwaters that are more permanent than those that were seen following the Experimental Flood. With a smaller difference between flood discharge and operating discharge, the erosion of new reattachment bars may be lessened. Also, clear water floods of shorter duration may also create more backwaters. During the Experimental Flood, the rate of sand deposition in some large eddies (where new backwaters were expected to be created) was very high; creating large bars within 1 - 2 days. However, these bars failed 3 - 4 days later during the flood (T. Hoffnagle, AGFD, personal observation). A flood of shorter duration may keep newly created reattachment bars intact, possibly creating large backwaters.

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BENTHIC INVERTEBRATES

Work Task 3.1
Prepared by T.J. Dresser, Jr.

The benthic community is an important component in the food chain, productivity, nutrient cycling, and decomposition of an aquatic ecosystem (Reich and Wohlenberg 1993). Reich and Wohlenberg (1993) reported that contact with sediments and life histories that provide long-term exposures to ecosystem change causes benthic invertebrates to display greater sensitivity to environmental disturbances than other organisms.

Benthic invertebrates in backwaters were expected to be adversely impacted due to scouring of sediments. Minckley (1981) reported that chironomids and oligochaetes may be subject to decimation as substrates are mobilized and scoured. Fluctuations in water levels were also reported to limit invertebrate production in rivers (Kennedy 1979). Research by Fisher and LaVoy (1972), Trotzky and Gregory (1974), and Williams and Winget (1979) indicated that benthic organisms were reduced in diversity, density, and biomass as a result of fluctuating flows. These findings were supported by Resh et al. (1988), Niemi et al. (1990), and Giller et al. (1991), who reported that high discharge events can cause population losses and changes in community structure.

This study addresses the benthic invertebrate portion of Work Task 3.1: Determine backwater use and recolonization rates by benthic invertebrates and zooplankton. We compared benthic invertebrate density, diversity, and biomass in backwaters before and after the Experimental Flood. Specifically, we tested the null hypothesis that benthic invertebrate taxa density and species composition does not change overtime.

Methods

A petit Ponar dredge (0.0232 m^2) was used to collect three benthic samples at six backwaters prior to (28 February - 14 March 1996) and following (18 April - 3 May 1996) the Experimental Flood on the Colorado River. One sample was collected from the foot, center and mouth for a total of three samples per backwater.

Benthic samples were washed through a 12 L littoral bucket with 30-mesh (600 μm mesh) and remaining organisms and detritus preserved in 70% ethanol or isopropanol. Organisms were separated into major taxonomic groups (Pennak 1989, Merritt and Cummins 1984), enumerated, and placed into the following categories for analysis: Chironomidae, Oligochaeta, Nematoda, Mollusca (gastropods and bivalves), other Diptera (Simuliidae and Ceratopogonidae), and Arthropoda (Ostrocoda and *Gammarus lacustris*).

Individuals of each taxa were pooled for each trip and oven dried for 24 hours at 105°C to determine mean dry weights. Ash-free dry weights (AFDW) were then determined for each taxa (2 hrs at 500°C). Dry weights and ash-free dry weights were then used to estimate biomass (g/m^2) for each taxonomic category in each sample. The detritus component of each sample was dried and used to determine detrital biomass (AFDW).

Nonparametric procedures (Kruskal-Wallis test and Mann-Whitney U test) were used to evaluate the differences in invertebrate density, invertebrate biomass, detrital biomass, and total biomass between reaches and trips. Significance for all statistical tests was set at α=0.05.

Results

Benthic Invertebrate Density

Mean total invertebrate density was significantly higher (P=0.0380) before the flood (11,426.9 invertebrates/m^2) than after the flood (3,581.8 invertebrates/m^2; Table 12). Densities of individual benthic invertebrate taxonomic groups were also significantly higher before the flood than after the flood (P≤0.0480), with the exception of nematodes (P=0.8656; Table 12).

Mean total benthic macroinvertebrate density also differed significantly among reaches during the pre-flood trip (P=0.0039; Table 13). Mean total density ranged from 86 invertebrates/m^2 at RK 296.83 L (Reach 8) to 49,955.7 invertebrates/m^2 at RK 97.91 L (Reach 2). During the post-flood trip , mean total invertebrate density decreased at all backwater locations, with the exception of RK 94.42 L. Mean total density at this location increased from 5,332.7 invertebrates/m^2 to 13,463.7 invertebrates/m^2 (Table 13). Densities ranged from 0 invertebrates at RK 296.83 L (Reach 8) to 13,463.7 invertebrates/m^2 at RK 94.42 L (Reach 2) following the Experimental Flood (Table 13).

A significant difference in mean density of oligochaetes and nematodes was observed between Reaches prior to the flood (P=0.0050 and P=0.0320; respectively). Reach 2 had significantly higher mean densities of oligochaetes (10,879.3/m^2) and nematodes (5,584.4/m^2) than downstream reaches. No significant difference between reaches was observed for other benthic invertebrate taxa prior to the Experimental Flood (P≥0.0603). A significant difference in mean density between reaches following the experimental flood was found only for oligochaetes (P=0.0339). No benthic

Table 12. Mean density (#/m²) and standard errors of principle benthic invertebrates found in backwaters before and after the Experimental Flood in the Colorado River, Grand Canyon, Arizona, 1996. Arthropoda includes *Gammarus lacustris* and Ostrocoda. Other Diptera includes Simuliidae and Ceratopogonidae.

	Pre-Flood n=18		Post-Flood n=18		Kruskal-Wallis Prob > CHISQ
Taxa	Mean	SE	Mean	SE	
Arthropoda	1,082.1	518.2	36.2	33.7	P=0.0375
Other Diptera	105.9	66.3	2.4	2.4	P=0.0011
Chironomidae	398.4	199.5	31.2	12.5	P=0.0106
Mollusca	1,202.8	517.1	38.6	26.3	P=0.0184
Nematoda	2,794.6	1,508.2	166.6	63.7	P=0.8656
Oligochaeta	5,828.5	3,533.0	3,306.7	2,157.7	P=0.0487
Total Benthic Invertebrates	11,426.9	5,521.6	3,581.8	2,161.7	P=0.0380

Table 13. Mean density (#/m²) of principle benthic invertebrates found in backwaters before and after the Experimental Flood in the Colorado River, Grand Canyon, Arizona, 1996. Arthropoda includes *Gammarus lacustris* and Ostrocoda. Other Diptera includes Simuliidae and Ceratopogonidae.

		Benthic Invertebrate Taxonomic Groups						
Reach	River Kilometer	Arthropoda	Other Diptera	Chiron-omidae	Mollusca	Nematoda	Oligochaeta	Total Benthic Invertebrates
				Pre-Flood (28 February - 14 March 1996)				
2	71.23 L	2,202.7	28.7	130.3	4,101.3	116.0	3,637.7	10,216.7
2	94.42 L	0.0	434.3	1637.7	0.0	333.0	2,927.7	5,332.7
2	97.91 L	4,159.3	43.0	405.7	2970.7	16,304.3	26,072.7	49,955.7
Reach 2 Mean		2,120.7	168.7	724.6	2,357.3	5,584.4	10,879.3	21,835.0
3	104.99 L	101.3	72.3	43.3	232.0	0.0	2,043.7	2,492.7
6	188.90 R	29.0	43.0	130.3	0.0	14.3	2,606.7	477.3
8	296.83 L	0.0	14.4	43.0	0.0	0.0	28.7	86.3
				Post-Flood (18 April - 3 May 1996)				
2	71.23 L	202.7	0.0	0.0	145.0	101.3	4,971.0	5,420.0
2	94.42 L	0.0	0.0	0.0	0.0	304.0	13,159.3	13,463.7
2	97.91 L	14.3	0.0	101.0	0.0	231.7	188.3	535.3
Reach 2 Mean		72.3	0.0	31.2	48.3	212.4	6,106.2	6,473.0
3	104.99 L	0.0	0.0	14.3	86.7	290.0	1,478.3	1,869.7
6	188.90 R	0.0	14.3	72.0	0.0	72.3	43.3	202.0
8	296.83 L	0.0	0.0	0.0	0.0	0.0	0.0	0.0

invertebrates were collected from the backwater located at RK 296.83 L (Reach 8) during the post-flood sampling effort.

Oligochaetes (54.4%), nematodes (24.4%), and Mollusks (10.7%) comprised the highest percentage of benthic invertebrates found prior to the flood. The remaining invertebrate groups each comprised less than 10% of the mean total density. Arthropods comprised 9.4% (*Gammarus* and ostrocods) followed by chironomids (larvae and pupae) comprised 3.4%, and other dipterans (0.93%; ceratopogonids and simuliids). The benthic invertebrate community changed following the flood. Oligochaetes accounted for 92.3% of the mean total density, followed by nematodes (4.6%), and Mollusks (1.1%). Arthropods, chironomids, and other dipterans accounted for the remaining 2.0%.

Benthic Invertebrate Biomass

A significant difference in mean total invertebrate biomass (g/m^2) was observed between pre- and post-flood trips (P=0.0112; Table 14). Significant differences were observed in mean biomass of most benthic invertebrate taxa (P $\leq$0.0458), with the exception of Mollusca (P=0.6578) and Nematoda (P=0.8640; Table 14).

Mean total benthic invertebrate biomass differed significantly among reaches prior to the experimental flood (P=0.0073). Mean total invertebrate biomass ranged from 23.5 g/m^2 at RK 71.23 L (Reach 2) to 0.02 g/m^2 at RK 296.83 L (Reach 8; Table 15). Mean total invertebrate biomass was highest for all benthic invertebrate taxonomic groups in Reach 2 prior to and following the experimental flood (Table 15). Lowest mean total invertebrate biomass was observed at RK 296.83 L (Reach 8), which contained no invertebrates, followed by RK 188.90 R (Reach 6) following the experimental flood (Table 15).

Prior to the flood, Mollusks (gastropods and bivalves) comprised 69.5% of the mean total invertebrate biomass, followed by oligochaetes (17.4%), and arthropods (10.7%). The remaining invertebrate biomass (2.4%) was comprised of chironomids, other dipterans, and nematodes. In post-flood samples, oligochaetes comprised 71.0% of the total invertebrate biomass, mollusks comprised 24.7%, and arthropods comprised 2.9%. Chironomids and nematodes accounted for most of the remaining 1.4%. Mean biomass for other dipterans was <0.0000 1g/m^2.

Table 14. Mean biomass (#/g^2) and standard errors for of principle benthic invertebrates found in backwaters before and after the Experimental Flood in the Colorado River, Grand Canyon, Arizona, 1996. Arthropoda includes *Gammarus lacustris* and Ostrocoda. Other Diptera includes Simuliidae and Ceratopogonidae.

	Pre-Flood n=18		Post-Flood n=18		
Taxa	Mean	SE	Mean	SE	Kruskal-Wallis Prob>CHISQ
Arthropoda	0.8869	0.4786	0.0326	0.0302	P=0.0458
Other Diptera	0.0484	0.0299	0.0001	0.0001	P=0.0043
Chironomidae	0.0949	0.0638	0.0009	0.0004	P=0.0017
Mollusca	5.8	2.5	0.2701	0.1836	P=0.6578
Nematoda	0.0559	0.0304	0.0027	0.0011	P=0.8640
Oligochaeta	1.4427	0.8859	0.7839	0.5120	P=0.0390
Total Benthic Invertebrates	7.6	3.0	1.1	0.59	P=0.0112
Detritus	131.1	25.7	259.6	88.2	P=0.0184

Table 15. Mean biomass (g/m²) of principle benthic invertebrates found in backwaters before and after the Experimental Flood in the Colorado River, Grand Canyon, Arizona, 1996. Arthropoda includes *Gammarus lacustris* and Ostrocoda. Other Diptera includes Simuliidae and Ceratopogonidae.

		Benthic Invertebrate Taxonomic Groups							
Reach	River Km	Arthropoda	Other Diptera	Chironomidae	Mollusca	Nematoda	Oligochaeta	Total Benthic Invertebrates	Detritus
				Pre-Flood (28 February - 14 March 1996)					
2	71.23 L	3.026	0.002	0.0012	20.44	0.002	0.914	23.46	189.75
2	94.42 L	0.0	0.074	0.504	0.0	0.007	0.627	0.85	56.45
2	97.91 L	2.281	0.0	0.037	12.99	0.326	6.532	19.54	255.84
Reach 2 Mean		1.769	0.253	0.184	11.14	0.112	2.691	14.62	167.35
3	104.99 L	0.012	0.169	0.001	1.21	0.0	0.511	1.90	121.02
6	188.90 R	0.003	0.044	0.012	0.04	<0.001	0.065	0.12	28.22
8	296.83 L	0.0	0.002	0.004	0.0	0.0	0.007	0.02	135.18
				Post-Flood (18 April 3 May 1996)					
2	71.23 L	0.181	0.0	0.0	1.01	0.002	1.179	2.53	671.98
2	94.42 L	0.0	0.0	0.0	0.0	0.005	3.122	3.12	157.56
2	97.91 L	0.014	0.0	0.002	0.0	0.004	0.042	0.06	504.32
Reach 2 Mean		1.769	0.02	0.184	11.14	0.112	2.691	1.90	167.35
3	104.99 L	0.0	0.0	<0.001	0.61	0.005	0.349	1.12	78.80
6	188.90 R	0.0	<0.0	0.003	0.0	0.001	0.010	0.01	127.62
8	296.83 L	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17.13

Detrital Biomass

A significant difference (P=0.0184) in detrital biomass was found between pre- and post-flood sampling efforts. Mean detrital biomass increased from 131.1 g/m² during pre-flood sampling to 259.6 g/m² after the flood (Table 14). A difference in detrital biomass between reaches was also observed. In Reach 2, detrital biomass increased from 167.3 g/m² (pre-flood) to 444.6 g/m² (post-flood; Table 15). An increase in detrital biomass following the experimental flood was also observed in Reach 6. Detrital biomass increased from 28.2 g/m² (pre-flood) to 127.6 g/m² (post-flood).

Detritus was a major component of the biomass in the pre- and post-flood samples. Prior to the flood, detritus comprised 93.0% of the organic material in the samples with benthic macroinvertebrates comprising the remaining 7.0%. After the flood, detritus comprised 99.5% of the organic material in the samples. Detritus consisted of leaf litter, seeds, woody debris, and invertebrate body parts.

Discussion

During our study, overall mean density of benthic invertebrates in sampled backwaters was reduced by approximately 75%, while mean total invertebrate biomass was reduced by 86%. Decreases in mean density and biomass of benthic invertebrates can be attributed to high flows. Minckley (1981) reported that a single spate reduced the numbers of benthic invertebrates by as much as 99% in Aravaipa Creek, Arizona. Similar findings were reported by Gray (1981) and Gray and Fisher (1981) in Sycamore Creek, Arizona, where invertebrate numbers were reduced by 86% following a major flood event.

Removal of fine substrates, detritus, attached algae, and macrophytes from backwaters may have reduced food availability and habitat for benthic invertebrates in the Colorado River, Grand Canyon, during the Experimental Flood. Menon (1969) reported that *Potamogeton* sp. provides food and habitat for benthic macroinvertebrates. Prior to the Experimental Flood attached algae and macrophytes were observed growing in some backwaters. Following the flood, visual observations indicated that attached algae and macrophytes had been scoured from these backwaters indicating a loss of habitat and food. In addition, invertebrates were probably physically moved by high velocity flows. Poff and Ward (1991) reported that changes in streamflow can modify microhabitat characteristics, thus altering diel activity and drift patterns. Ward (1973) reported that certain benthic groups, such as amphipods are poorly adapted to resist current and may be restricted to areas with uniform currents or areas with flow refugia, such as backwater areas. Inundation of the backwaters by the flood would certainly remove these species.

During the flood, backwaters were inundated and scoured, thereby reducing flow refugia and physically removing even some of the flood-resistant taxa. Preliminary results from drift studies conducted by Northern Arizona University (NAU) prior to and during the Experimental Flood indicates that densities of simuliids, chironomids, and *Gammarus* in drift samples increased during the flood (J. Shannon NAU; personal communication); indicating a downstream transport and a possible loss of invertebrates from backwaters as well as other habitat types. McKinney et al. (see Lee's Ferry Chapter, this report) also reported decreases in *Gammarus* densities at sites downstream of Glen Canyon Dam (3.5, 4.1 and 14 miles upstream of Lee's Ferry).

Changes in substrate composition may have also contributed to the decrease in invertebrate density. Significant increases in the percentages of sand and decreases in silt in backwaters were observed between pre- and post-flood trips (see Work Task 2.1: Backwater Sediments, this report). The mean percentage of sand in backwaters increased approximately 35%, while the percentage of silt decreased approximately 30%. Decreases in the percentage of silt in backwaters probably contributed to the decreases in the mean biomass and mean density of taxa that utilize silt substrates (oligochaetes and nematodes).

Decreases in mean total biomass and mean total density of benthic invertebrates may also be the result of direct mortality. Immediately following the flood many *Gammarus* were observed stranded in isolated pools and were subjected to desiccation and predation as the water receded (personal observation). Minckley (1981) reported that chironomids and oligochaetes may be subjected to annihilation as substrates are mobilized and scoured. Studies by Resh et al. (1988), Niemi et al. (1990), and Giller et al. (1991) indicate that high discharge events can cause severe population losses and changes in benthic community structure. This supports the findings of Fisher and Lavoy (1972), Williams and Winget (1979), Trotzky and Gregory (1974), and Abbott and Morgan (1975) who reported that benthic organisms are reduced in diversity, density, and biomass as a result of rapidly varying flows.

Densities of benthic invertebrates collected in backwaters during this study decreased between pre- and post-flood sampling efforts, with the exception of oligochaetes. Increases in oligochaete density at two backwaters in Reach 2 (RK 71.23 L and RK 94.42 L) may indicate a rapid recolonization rate following a disturbance. Research conducted by McKinney et al. (see Lee's Ferry Chapter, this report) also indicated that densities of oligochaetes were higher at some locations following the Experimental Flood. Lancaster and Hildrew (1993) reported that the speed with which the benthic community recovers from spates is often rapid and much less than the generation time of the organisms. Research by Mackay (1992) indicated that the recolonization of areas which have been disturbed depends largely on the individual and its mobility, substrate texture, food supply, competition, and predation. Winterborn (1981) reported that although invertebrate densities are severely reduced after major spates, certain taxa are able to recover quickly. Such taxa includes some species of mayflies, filter-feeding hydropsychids, predatory hydrobiosid caddisflies, and chironomid larvae (Mackay 1992). McElravy et al. (1989) reported that Chironomidae are consistently recorded among the first colonizers after scouring spates and washouts. Similar results were reported by McKinney et al. (see Lee's Ferry Chapter, this report) who reported increased densities of chironomids (larvae and pupae) following the Experimental Flood at two locations below Glen Canyon Dam. Mackay (1992) suggested that the early arrival of browsers and gathers is consistent with their ability to exploit the earliest food materials on bare substrates. Meffe and Minckley (1986) suggested that long-term and short-term persistence of benthic invertebrates is high, unless frequent and intensive flooding occurs, then repeated local extinction and recolonization occur.

Hildrew et al. (1991) and Lancaster and Hildrew (1991) found that physical patches in or associated with stream channels may facilitate recovery by acting as refugia. Refugia appears to have been available in all backwaters, as benthic invertebrates were not totally eliminated, with the exception of the backwater RK 296.83 L (Reach 8). No benthic invertebrates were collected at this location following the flood. Invertebrates may have survived by burrowing into the substrate or may have been sheltered in debris or vegetation. Gray (1981) reported that even after catastrophic flood events, recolonization by survivors which were buried deeply can occur. Therefore, we would suspect that benthic invertebrates will recovery fairly rapidly in backwaters of the Colorado River. Studies of these colonization rates and the relationship between benthos and sediments are ongoing.

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ZOOPLANKTON

Work Task 3.1
Prepared by D.W. Speas

Zooplankton are an important food resource for larval and juvenile native fishes in the Colorado River system (Maddux et al. 1987; Marsh and Langhurst 1988; Muth and Snyder 1995; AGFD 1996). Detailed information on zooplankton in the Colorado River through Grand Canyon, Arizona, is sparse, however some generalities exist. Most or all zooplankton found in the Colorado River through Grand Canyon originates in Lake Powell, the mainstem reservoir formed by Glen Canyon Dam (Haury 1981; 1986). The zooplankton community in the Colorado River below Glen Canyon Dam is usually dominated by copepods (Haury 1986; Maddux et al. 1987; AGFD 1996), a condition also observed in Lake Powell (Stanford and Ward 1991; Ayers and McKinney 1996).

Zooplankton density has been shown to vary longitudinally along the Colorado River, but the pattern is not consistent among studies. Maddux et al. (1987) observed that total zooplankton density decreased with distance below Glen Canyon Dam. Downstream reductions in zooplankton abundance have been noted in recent years (AGFD 1996), but Haury (1986) documented no such trend over a five year period (1980-1985). He speculated that production of zooplankton was occurring in backeddies, backwaters, and tributary terminal pools, which compensated for zooplankton losses due to exposure to lotic conditions. This speculation is supported in part by other studies where zooplankton densities were observed to be higher in backwaters as opposed to mainchannel habitats (Grabowski and Hiebert 1989; Blinn and Cole 1990 and references therein; AGFD 1996).

From 22 March through 7 April 1996, the U. S. Bureau of Reclamation conducted an experimental flood release (Experimental Flood) from Glen Canyon Dam, designed in part to create sandbars and associated backwater fish habitats in the Colorado River, Grand Canyon. Discharge from Glen Canyon Dam attained a steady maximum release of 1,274 m^3/s for a period of six days (U. S. Department of the Interior 1996).

The scouring, redistribution of sediment, and inundation of backwaters that took place during the Experimental Flood may have affected the zooplankton communities in the Colorado River. The taxonomic composition of zooplankton in rivers is frequently altered by flooding events (Hynes 1970). As a result of scouring, benthic taxa are frequently observed in mainchannel plankton assemblages where they are subsequently washed downstream (Holden and Green 1960). Floodplain inundation results in the transfer of taxa from floodplain habitats or channel margins to mainchannel plankton assemblages (Mohgraby 1977; Saunders and Lewis 1988).

This chapter addresses that portion of Work Task 3.1 pertaining to zooplankton: Determine backwater use and recolonization rates by benthic invertebrates and zooplankton. We address two hypotheses: 1) Zooplankton density does not change over time (this study) and 2) Zooplankton densities are not related to environmental or physical parameters of backwaters (forthcoming). Flushing and reformation of backwaters allows us to examine the response of zooplankton in backwaters to such flooding events in the Colorado River, Grand Canyon. Additionally, in this report we will examine differences in zooplankton density along the length of the river and between habitat types (backwater versus mainchannel). Longitudinal differences in zooplankton density, previously documented by AGFD (1996), will be reexamined in relation to the Experimental Flood.

Study Area

Zooplankton samples were collected from backwater sites in the Colorado River, Grand Canyon, at 12 locations from 29 February-12 March 1996 (pre-flood) and from nine locations during 19-30 April 1996 (post-flood). However, in the interest of maintaining a balanced experimental design, only locations sampled on both trips were included in the analysis. These sites were located from RK 71.23 to RK 296.83 (see Introduction, this report). All backwaters sampled were connected to the mainchannel, allowing water exchange between the two habitats.

Methods

Each sampling location consisted of a backwater site and a mainchannel site, and three replicate samples were collected from each site. One replicate was collected from each of the mouth, center, and foot portions of backwaters, and replicates from the mainchannel were collected along a transect running perpendicular to the shoreline. Water temperature was recorded (with a HydroLab H20) at each sampling site. Zooplankton samples were collected by filtering

50 L of water through a #40 Wisconsin "bucket" net (80 μm mesh). Samples were preserved in 50% ethanol or isopropanol and labeled with a study number and site code.

In the laboratory, each sample was resuspended in 50 mL of water, from which five 1 mL subsamples were withdrawn (with replacement) and enumerated in a Sedgwick-Rafter counting cell (Wetzel and Likens 1991). Mean abundance of zooplankton per subsample was used to estimate number per sample, from which density was calculated by using the formula:

Total density (#/m^3) = 1000 L/m^3 * (Mean #/mL)* (50 mL/50 L)

Zooplankton taxa were enumerated to the lowest practical level, usually genus, using keys by Pennak (1978), Stemberger (1979), and Thorp and Covich (1991). Copepod nauplii and copepodites were identified to family. Philodinid rotifers were identified to family level for lack of exposed key characteristics.

Statistical analyses ($\alpha = 0.05$ for all tests) were performed on total zooplankton density estimates and also zooplankton density by major taxonomic group (Copepoda, Branchiopoda, Rotifera). Also, Copepoda were analyzed as either nauplii or adults/subadults. Distribution of the data was tested using the Shapiro-Wilk test for normality (SAS 1990). Total zooplankton density was normally distributed following square-root transformation ($P = 0.3712$), and so a parametric analysis of variance was performed on total density. Density estimates of individual zooplankton taxa, however, were not normally distributed despite transformations, so a Mann-Whitney U-test was conducted on these data to detect differences in zooplankton density between trips and habitat types. A Kruskal-Wallis test was used to detect differences in zooplankton taxa density among reaches. If differences among reaches existed, multiple comparisons of means were made using either a Ryan-Einot-Gabriel-Welsch multiple F-test (after a parametric test; Day and Quinn 1989) or multiple Mann-Whitney U-tests (after a nonparametric test). The resulting P-values of the Mann-Whitney comparisons were further subjected to sequential Bonferroni tests (Rice 1989) to determine significance.

Analysis of covariance was conducted on total zooplankton density using sampling dates as a main effect and water temperature as a covariate. The purpose of this analysis was to detect differences in zooplankton density over time while correcting for the accompanying change in water temperature.

Results

Total zooplankton density differed significantly by sampling period ($P = 0.0011$) and by reach ($P = 0.0041$), but not by habitat ($P = 0.4810$) so mainchannel and backwater samples were pooled for further analyses. Interactions between main effects were also not significant ($P \geq 0.1268$). Total zooplankton density was greater after the flood (4422.2/m^3) than before (2916.7/m^3; Table 16, Fig. 10). Analysis of covariance indicated that mean water temperature was significantly correlated with sampling period ($P = 0.0054$) and total zooplankton density ($P = 0.0006$) and that sampling period was not a unique estimator of total zooplankton density. Mean water temperature in backwaters was significantly ($P = 0.0001$) greater during the post flood trip (12.0 °C) than during the pre-flood trip (9.9 °C).

Mean zooplankton density also differed significantly among reaches ($P = 0.0041$; Fig. 11). During the pre-flood trip, mean zooplankton density was greater in Reach 3 (4966.7/m^3) than in Reach 6 (1666.7/m^3), and mean density in Reach 6 was greater than in Reach 8 (400.0/m^3). During the post-flood trip zooplankton density was greater in Reach 6 (5466.7/m^3) than in Reach 8 (1566.7/m^3)

Densities of copepods ($P = 0.0006$) and copepod nauplii ($P = 0.0013$) were greater after the flood than before the flood (Table 16, Fig. 10). Conversely, branchiopods were significantly reduced in number ($P = 0.0420$) after the flood. Rotifer density after the flood was not different than before the flood ($P = 0.3307$). During the post-flood trip, copepod nauplii ($P = 0.0062$) and rotifers ($P = 0.0063$) were significantly more abundant in Reach 6 than in Reach 8 (Fig. 12). Zooplankton taxa density did not differ significantly ($P \geq 0.0841$) between habitats on either sampling trip.

Percentages of each zooplankton group were different before and after the flood ($P \leq 0.0318$). Rotifers comprised 50.8% of the zooplankton on the pre-flood trip, but their contribution to the plankton had fallen significantly ($P = 0.0158$) to 37.3% after the flood despite no significant ($P = 0.3307$) change in density. Copepod nauplii comprised 29.5% of the plankton prior to the flood but increased significantly to 46.6% after the flood. Percentages of copepodites and adult copepods increased significantly from 16.9% before the flood to 19.4% afterwards. Branchiopods comprised 2.7% of the plankton before the flood but fell significantly to 0.6% afterwards.

A total of 24 zooplankton genera were identified from samples, including five Copepoda, five Branchiopoda, and 14 Rotifera (Table 17). The rotifer *Lecane* sp. was also observed but was not included in the analysis because it occurred in a backwater which was sampled before but not after the flood. Eleven genera, mostly rotifers, were collected only during the pre-flood trip, and two genera were unique to the post-flood samples.

Table 16. Mean density and standard error of major zooplankton taxonomic groups at backwater study locations, Colorado River, Grand Canyon, during pre-flood (29 February-11 March 1996) and post-flood (19-30 April 1996) trips. Means are those of backwater and mainstem habitats. Location is in RK followed by channel side (L or R). Total effort (water volume filtered) at each location during each period was 0.3 m^3.

		Pre-flood		Post-flood	
Taxa	Location	Mean (#/m^3)	SE	Mean (#/m^3)	SE
Copepoda	71.23 L	633.3	189.2	1233.3	355.6
	94.42 L	266.7	84.3	733.3	229.0
	97.91 L	266.7	111.1	500.0	100.0
	104.99 L	2033.3	989.8	1133.3	240.4
	188.90 R	133.3	84.3	833.3	174.5
	296.83 L	100.0	68.31	433.3	182.0
Copepod nauplii	71.23 L	1566.7	332.3	3833.3	996.6
	94.42 L	966.7	344.2	1066.7	341.2
	97.91 L	1366.7	348.0	1300.0	295.2
	104.99 L	1166.7	270.4	2633.3	493.7
	188.90 R	300.0	85.6	2966.7	512.3
	296.83 L	66.7	42.2	566.7	255.2
Branchiopoda	71.23 L	366.7	149.8	133.3	84.3
	94.42 L	66.7	66.7	0.0	-
	97.91 L	0.0	-	66.7	66.7
	104.99 L	100.0	68.3	0.0	-
	188.90 R	100.0	68.3	0.0	-
	296.83 L	0.0	-	0.0	-
Rotifera	71.23 L	2133.3	530.8	1766.7	517.5
	94.42 L	1200.0	103.3	1800.0	247.7
	97.91 L	1633.3	221.6	1266.7	197.8
	104.99 L	1666.7	168.7	2033.32	270.4
	188.90 R	1133.3	245.9	1666.7	240.4
	296.83 L	233.3	130.8	566.7	158.5
Total	71.23 L	4700.0	848.1	6966.7	1822.4
	94.42 L	2500.0	472.6	3600.0	640.8
	97.91 L	3266.7	402.2	3133.3	349.0
	104.99 L	4966.7	1305.8	5800.0	801.7
	188.90 R	1666.7	295.2	5466.7	770.6
	296.83 L	400.0	115.5	1566.7	457.3

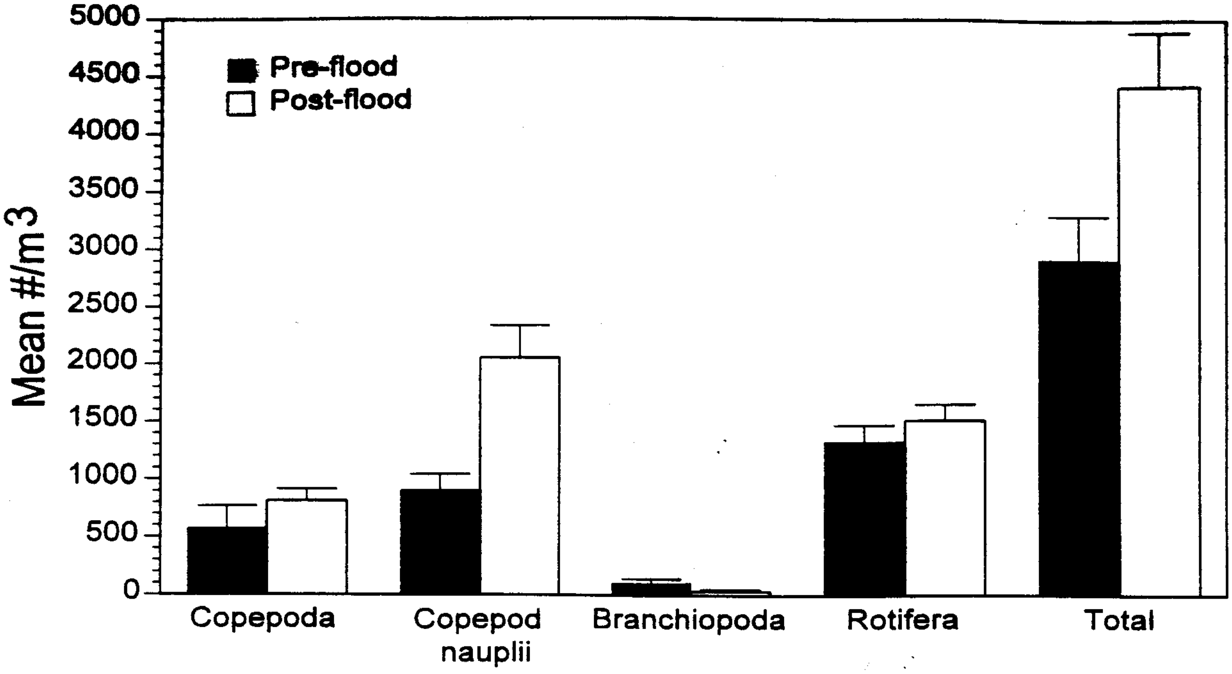

Figure 10. Mean zooplankton density (#/m³) before and after the 1996 Experimental Flood in the Colorado River, Grand Canyon, Arizona. Pre- versus post-flood changes were significant ($P \leq 0.0420$) for all classifications except Rotifera ($P=0.3307$). Bars indicate ± 1 standard error of the mean.

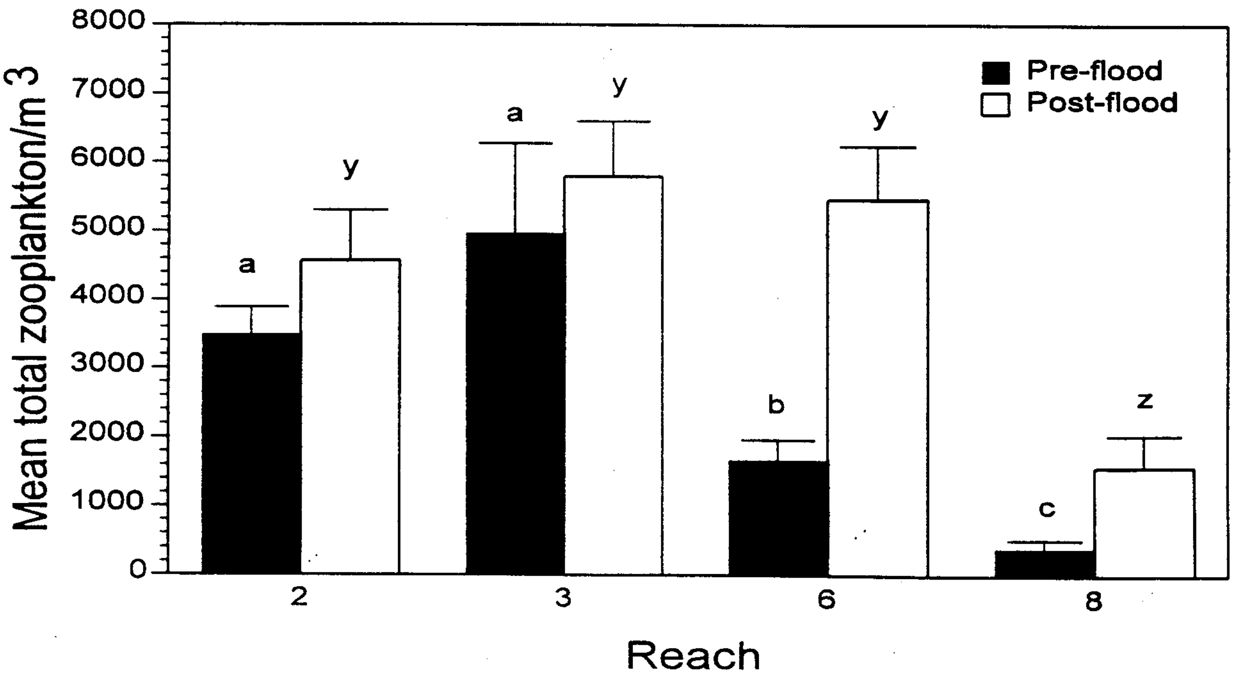

Figure 11. Mean total zooplankton densities among river reaches before and after the 1996 Experimental Flood in the Colorado River, Grand Canyon, Arizona. Means with identical lettering are not significantly different ($\alpha = 0.05$). Bars indicate ± 1 standard error of the mean.

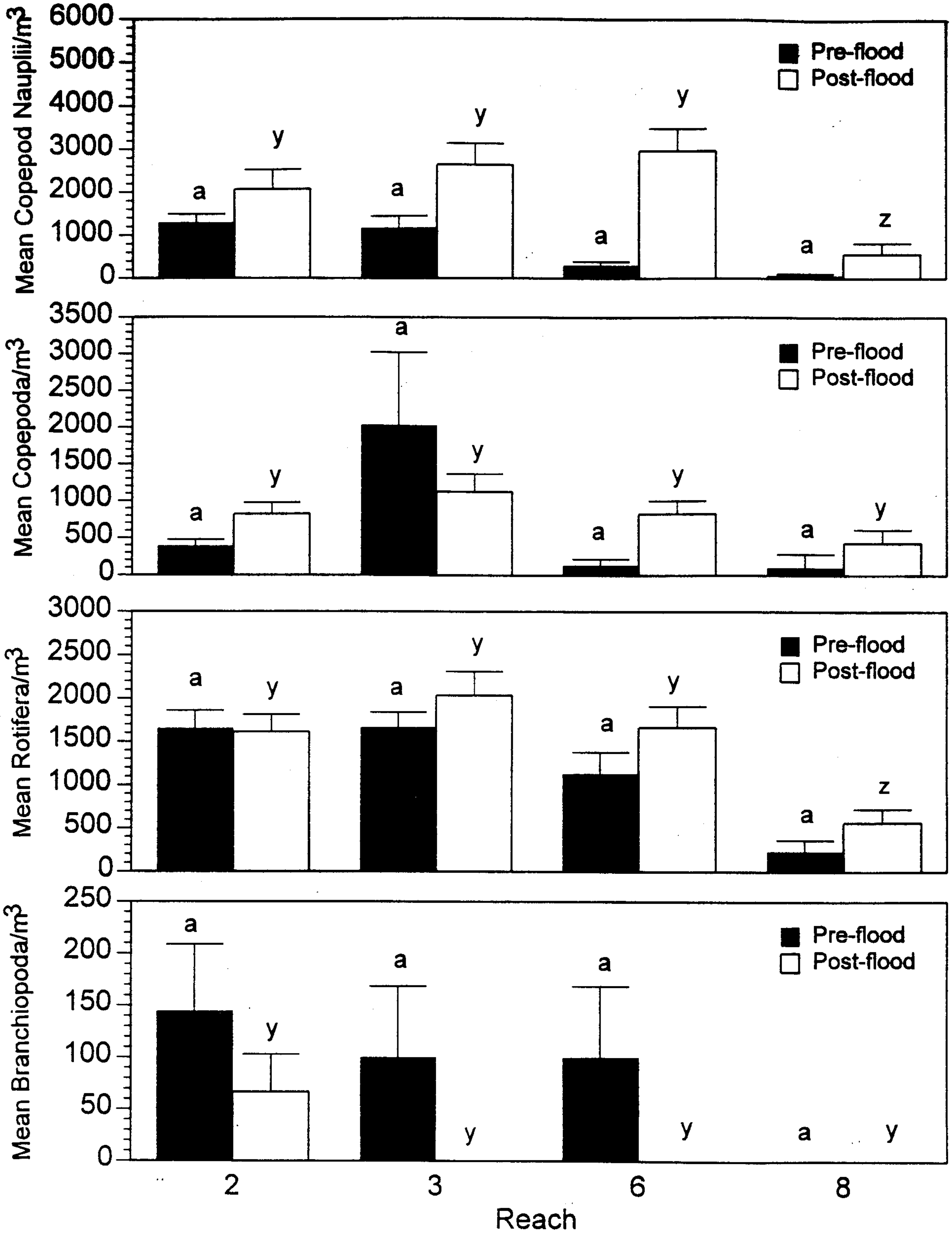

Figure 12. Mean zooplankton taxa density by river reach before and after the 1996 Experimental Flood Release, Colorado River, Grand Canyon, AZ. Means with identical lettering are not significantly different (α=0.05). Bars indicate ± 1 standard error of the mean.

Table 17. Mean density and standard error of zooplankton taxa (#/m^3) collected from the Colorado River, Grand Canyon, Arizona, during pre-flood (29 February-11 March 1996) and post-flood (19-30 April 1996) trips. Total effort (water volume filtered) for each period was 1.8 m^3.

	Pre-flood		Post-flood	
Taxa	Mean (#/m^3)	SE	Mean (#/m^3)	SE
Copepoda				
Calanoid nauplii	627.8	99.6	1033.3	162.3
Cyclopoid nauplii	277.8	59.2	1027.8	148.9
Calanoid copepodites	100.0	30.3	61.1	17.5
Cyclopoid copepodites	322.2	160.0	600.0	90.5
Diacyclops bicuspidatus thomasi	55.6	17.1	144.4	29.4
Paracyclops fimbriatus poppei	33.3	23.2	0.0	-
Mesocyclops sp.	0.0	-	5.6	5.6
Eucyclops sp.	22.2	22.2	0.0	-
Diaptomus sp.	38.9	15.6	0.0	-
Total Copepoda	1477.8	277.6	2872.2	357.8
Branchiopoda				
Alona sp.	44.4	29.3	0.0	-
Daphnia sp.	16.7	12.3	22.2	13.3
Chydorus sp.	22.2	13.3	0.0	-
Bosmina sp.	16.7	9.3	11.1	7.7
Macrothrix sp.	5.6	5.6	0.0	-
Total Branchiopoda	105.6	36.1	33.3	18.7
Rotifera				
Proales sp.	572.2	119.6	283.3	51.3
Philodinidae	133.3	34.7	44.4	14.1
Kellicotia longispina	438.9	63.7	644.4	90.2
Synchaeta sp.	33.3	12.6	494.4	75.8
Notholca accuminata	38.9	12.5	16.7	9.3
Notholca squamula	27.8	16.2	0.0	-
Notommata sp	11.1	7.7	0.0	-
Filinia longiseta	0.0	-	11.1	7.7
Polyarthra sp.	11.1	7.7	5.6	5.6
Tricotria sp.	5.6	5.6	0.0	-
Cephalodella sp.	16.7	9.3	0.0	-
Monostyla lunaris	5.6	5.6	0.0	-
Euchlanis sp.	5.6	5.6	0.0	-
Encentrum sp	5.6	5.6	5.6	5.6
Lindia sp.	5.6	5.6	0.0	-
Total Rotifera	1333.3	143.9	1516.7	138.3
Total Zooplankton	2916.7	378.8	4422.2	470.3

The most common rotifers collected were *Proales* sp. (572.2/m^3) before the flood and *Kellicotia longispina* (644.4/m^3) following the flood. *Synchaeta* sp. increased significantly (P=0.0001) from 33.3/m^3 before the flood to 494.4/m^3 after the flood. Cyclopoid nauplii increased (P=0.0001) in density from 277.8/m^3 before the flood to 1027.8/m^3 afterwards, but calanoid nauplii did not change significantly (P=0.1121). Advanced copepod instars collected on the post-flood trip were comprised mainly of cyclopoids (600.0/m^3) and adult calanoids were absent. *Diacyclops bicuspidatus thomasi* was the most common adult copepod both before (55.6/m^3) and after (144.4/m^3) the flood, and its density increased significantly (P=0.0177). *Alona* sp. was the most abundant branchiopod collected on the pre-flood trip (44.4/m^3) but was absent from the plankton after the flood. *Bosmina longirostris* and *Daphnia* sp. were the most commonly observed branchiopods after the flood, (16.7/m^3 for each), but their densities were unchanged from those before the flood (P=0.6645 and P=0.6547, respectively)

Discussion

Differences in Zooplankton Density Between Pre- and Post-Flood Trips.

The Experimental Flood of 1996 was expected to negatively impact the zooplankton community by flushing backwater zooplankton communities downstream as backwaters were inundated. Most studies conducted during floods hypothesize that in the absence of zooplankton transport from inundated floodplain habitats (i.e., isolated backwaters and side channels), the cumulative effect of increased discharge is a dilution of zooplankton densities and downstream displacement of resident backwater populations (Holden and Green 1960; Hynes 1970; Mohgraby 1977; Saunders and Lewis 1988; Ferrari et al. 1989; Thorp et al. 1994). Quantitative analyses in this study, however, demonstrated an increase in total zooplankton following the flood.

At least two explanations exist for the observed increase in zooplankton density following the Experimental Flood. First, it is probable that at least some of the observed increase in zooplankton density may be due to production resulting from increased water temperature. Second, increased inflow from Lake Powell may have imported unusually high numbers of zooplankton into the Colorado River. The resulting increase in zooplankton density, particularly in backwaters and other low velocity habitats, may have occurred when water volume decreased as the flood receded.

Mean water temperature in backwaters was greater during the post flood trip than during the pre-flood trip. The temperature change was correlated both with sampling dates and with increased zooplankton density. Ayers and McKinney (1996) also found correlations between temperature and zooplankton density in the Colorado River during 1993-1995. Intrinsic rates of increase of zooplankton populations are positively correlated with increased temperature (Allen 1976), and rotifer densities typically increase more rapidly than crustacean densities.

If the increase in zooplankton density was due to temperature, however, the response was not uniformly positive among Copepoda, Branchiopoda, and Rotifera. The increase in total density was the result of increases in both naupliar and more mature copepod instars. Rotifera was the only taxonomic group in which densities did not change after the flood, while branchiopod densities declined. Increased copepod abundance during April was also observed in the Colorado River by Ayers and McKinney (1996) at RK -24.62 to 0.00 (upstream from Lee's Ferry) from 1993-1995, and similar patterns have been reported from the Missouri River system (Armitage 1961; Cowell 1967; Repsys and Rogers 1982).

Differential response in densities of individual rotifer genera to flooding or seasonal effects probably prevented an increase in total rotifer density. Declining *Proales* sp. and philodinid populations were offset by increases in *Kellicotia longispina* and *Synchaeta* sp. after the flood. Such dynamics among zooplankton species are often indiscernible when densities of individual genera are pooled by phylum or class for analysis (Rossaro 1988), as was done in this study. Additionally, densities of both Rotifera and Branchiopoda after the flood may have been further affected by biotic interactions within the zooplankton community. Copepods, especially *Cyclops* spp. (McQueen 1989) and *Mesocyclops* spp. (Williamson and Gilbert 1980) can exert measurable predation pressure on zooplankton communities. The increase in Copepoda observed after the flood may have been accompanied by increased predation on rotifers and branchiopods, explaining their lack of change and decrease in density, respectively.

It is also possible that increases in zooplankton density may have occurred through the transport of unusually high numbers of zooplankton from Lake Powell to its tailwaters and the subsequent reduction in water volume in the Colorado River following the flood. Variations in discharge through Glen Canyon Dam influences the size and orientation of the withdrawal zone in Lake Powell, and thus the extent to which zooplankton are entrained (Johnson and Merritt 1979; Ayers and McKinney 1996). Haury (1986) concluded that periods of elevated discharge from Lake Powell would result in increased zooplankton abundance in the Colorado River because of greater export of epilimnial water. Other studies also indicated that zooplankton density below impoundments increased with elevated discharge (Cowell 1967; Hynes 1970; Matter et al. 1983).

Since most zooplankton in the Colorado River below Glen Canyon Dam originate in Lake Powell (Haury 1986; Ayers and McKinney 1996), the observed differences in zooplankton density in this study may result to a great extent from changes in zooplankton densities in the reservoir. No zooplankton data from early 1996 are currently available to support or refute this speculation (B. Vernieu, GCES, personal communication), but zooplankton density in the Lake Powell forebay is known to vary greatly by season (Ayers and McKinney 1996). However, while zooplankton density in the Colorado River may reflect seasonal zooplankton dynamics in Lake Powell, it is difficult to assume that high rates of water withdrawal (and presumably zooplankton entrainment) from the reservoir during the flood had little or no effect on zooplankton density below Glen Canyon Dam.

The subsidence of flooding events is often accompanied by a rise in zooplankton abundance. Saunders and Lewis (1988) found that post-flood zooplankton populations originate from those that were stranded in backwater areas as the floods subsided. Such an explanation for the observed increase in zooplankton in the Colorado River following the 1996 flood is plausible, particularly because the subsidence of the flood may have coincided with seasonal pulses in density of cold water groups such as copepods. No significant differences in zooplankton density were noted between habitat types, but mean zooplankton taxa densities in backwaters were higher than those in the mainchannel in most instances. If backwaters were in fact areas where recolonization by zooplankton took place, then water exchange rates due to fluctuating flows must have been sufficient to dilute backwater zooplankton populations to mainchannel levels.

Taxa richness declined between the two trips, suggesting that displacement of some zooplankton taxa occurred. Eight of the 11 taxa found before but not after the flood are considered by most authorities to be typical of littoral habitats and/or associated with vegetation or sediments (Edmondson, 1959; Stemberger, 1973; Ruttner-Kolisko, 1974; Pennak, 1978; Thorp and Covich, 1992). They included *Paracyclops fimbriatus poppei* (Copepoda), *Alona* sp. (Branchiopoda), and rotifers *Notommata* sp., *Trichotria* sp., *Cephalodella* sp., *Monostyla lunaris*, *Euchlanis* sp., and *Lindia* sp.

The copepod *Paracyclops fimbriatus poppei* commonly occurs in organic sediments (Pennak 1989). Although it occurred at moderately low densities (33.3/m^3), its absence from the post flood samples is probably a direct result of scouring. The littoral, phytophytic branchiopod *Alona* sp. was the most abundant branchiopod prior to the flood (44.4/m^3) and was collected only in backwaters. The inundation and scouring which took place during the flood may have displaced *Alona* sp. populations and also damaged or removed emergent vegetation, which would impede their recolonization.

Littoral rotifers collected prior to the flood were not extremely common and ranged from 5.6 to 16.7/m^3. However, only two taxa were unique to the post flood samples (*Mesocyclops* sp. [5.6/m^3] and *Filina* sp. [11.1/m^3]), and both are considered limnetic (Pennak 1978). The absence of the littoral rotifers from the post-flood samples is probably not a response to temperature because rotifers are essentially eurythermic (Berzins and Pejler 1989). A more likely explanation is that they were exported from backwaters when they were inundated during the flood, a process which has been observed elsewhere (Holden and Green 1960; Saunders and Lewis 1988).

Zooplankton taxa which increased or showed no change in density after the flood were generally limnetic in nature and probably originated in Lake Powell. *Diacyclops bicuspidatus thomasi* and *Diaptomus* sp. were the most common copepods in this study and are very common in Lake Powell (Sollberg et al. 1988; Ayers and McKinney 1996). The limnetic branchiopods *Bosmina longirostris* and *Daphnia* sp. are also common in Lake Powell, although some evidence suggests that some branchiopod production may occur from RK -24.62 to RK 0.00 (Ayers and McKinney 1996). The only rotifer genus which significantly increased in density after the flood was *Synchaeta* sp., which is also considered to be a limnetic organism. Sollberger et al. (1988) found *Synchaeta* sp. to occur at maximum densities in the lower regions of Lake Powell during April, so it is very likely that the increase in *Synchaeta* sp. in the

Colorado River is a result of population changes in the reservoir.

In terms of density and taxa richness, rotifers were the dominant zooplankton group in the Colorado River prior to the 1996 flood. As a group, rotifers are considered to be "r-selected", and thus one would expect disturbances such as floods to promote their diversity and density (Allen 1976). Ferrari et al. (1989) concluded that disturbances such as flooding events increased zooplankton taxa richness in rivers in agreement with the intermediate disturbance hypothesis (Huston 1979). The short term results of this study are in conflict with the above hypotheses, as rotifer density did not increase after the flood and their taxa richness decreased. The rotifer fauna of the Colorado River is numerically dominated by limnetic taxa (*Proales* sp., *Kellicotia longispina*, *Synchaeta* sp., *Notholca* sp.) originating in Lake Powell (Haury 1986; Sollberg et al. 1988; Ayers and McKinney 1996) with sporadic occurrences of littoral taxa which may originate in backwaters (*Notommata* sp., *Tricotria* sp., *Cephalodella* sp., *Euchlanis* sp., etc.). We hypothesize that the 1996 Experimental Flood replaced populations of littoral taxa in backwaters with limnetic taxa, which in turn suppressed recolonization of littoral taxa through predation (especially copepods on rotifers) and/or competition.

Differences in Zooplankton Density Among River Reaches.

Downstream reductions in zooplankton density were observed from Reach 3 through Reach 8 during the pre-flood trip. However, mean densities of nauplii, copepodites, adult copepods, rotifers, and total zooplankton during the post-flood trip did not decrease along the longitudinal axis of the river until below Reach 6. It is reasonable to assume that relatively high zooplankton densities commonly observed in Reaches 2 and 3 before the flood were displaced to Reach 6 during the flood. Flooding events are capable of transporting zooplankton without observable decreases in abundance because during high flows, organisms are less prone to entanglement in periphyton or other vegetation than at low flows (Chandler 1937; Hynes 1970; Walburg et al. 1981). This explanation was also proposed by Haury (1981) to explain the continued presence of zooplankton over 362 km of the Colorado River from Lee's Ferry to Diamond Creek. Also, the macroalga *Chara* sp. is an efficient filterer of zooplankton from running water (Hynes 1970; Petts 1984) The standing crop of *Chara* sp. was reduced by 60-70% in the Lee's Ferry reach during the Experimental Flood through scouring (see Work Task 1.1, Lee's Ferry section) and thus at least one source of zooplankton depletion was significantly reduced.

Zooplankton densities decreased from Reach 6 to Reach 8 at a rate of 0.70%/km during the pre-flood trip, and 0.74%/km during the post flood trip. Loss rates of zooplankton below impoundments tends to decrease with distance from dams (Repsys and Rogers 1982). The loss rates from this study from RK 189 to 297 are on the same order of magnitude as that reported by Williams (1971) at 145 km below Lewis and Clark Lake, Missouri River (0.20%/km). We would thus expect to see more dramatic zooplankton losses in Reaches 2 and 3, but none was observed. However, reductions in zooplankton density in the vicinity of Reaches 2 and 3 have been observed by AGFD (1996) in previous studies. It may be difficult to demonstrate differences in zooplankton over 29 RK (the distance over which sampling sites in Reaches 2 to 3 were located) in the Colorado River without pooling zooplankton densities over longer periods of time, as has been done in other studies for short distances (Ward 1975; Armitage and Capper 1976; Zurek and Dumnicka 1989; Jackson et al. 1991; Maslikov et al. 1991). Alternatively, Ayers and McKinney (1996) suggested that downstream losses of zooplankton in the Colorado River are probably at a minimum during winter and early spring because of depressed seasonal growth of the periphytic alga *Cladophora glomerata*, which is probably a more efficient zooplankton filter than *Chara* sp.

It is possible, but perhaps unlikely, that input of planktonic organisms from tributaries compensate for zooplankton losses in the mainstem Colorado River. Tributaries contribute less than 10% of the mean discharge of the regulated Colorado River in Grand Canyon (Kubly and Cole 1979), and the percentage was probably minimal during the Experimental Flood. Tributaries of the Colorado River in Grand Canyon are thought to be depauperate in zooplankton (Haury 1986). While quantitative contributions from tributaries to the mainstem zooplankton density may be small, their contribution to mainstem species richness may be notable because tributaries are frequently inhabited by invertebrate taxa not occurring in the mainstem (Cole and Kubly 1976).

No significant differences in zooplankton density were found between mainchannel and backwater habitats in this study. Zooplankton production in backwaters was proposed by Haury (1981; 1986) as a means by which downstream losses of zooplankton losses are offset. He also found that in areas where water exchange rates between mainchannel and backwater habitats were high, zooplankton densities were the same in both habitats. Mean diel variation in discharge of the Colorado River was 162.6 m^3/s on the pre-flood trip and 108.4 m^3/s on the post-flood trip. It likely that zooplankton densities in mainchannel and backwater habitats were equalized due to continual exchange of water between the habitats, caused by daily fluctuations in river discharge. Water exchange was particularly observable when the river stage was changing. During the pre-flood trip, lower water temperatures may have also limited zooplankton production in backwaters.

The Serial Discontinuity Concept developed by Ward and Stanford (1983) provides theoretical foundations for the observed impacts of impoundments on riverine environments below them. Their model was based on observations from regulated systems 1) which were unpolluted and undisturbed except for impoundment, 2) in which the remaining lotic environments were undisturbed, and 3) which received hypolimnial releases from thermally stratified reservoirs. The Colorado River in Grand Canyon is thus an excellent system to test the Serial Discontinuity Concept, which predicts that downstream elimination of zooplankton should be accompanied by a transition from zooplanktivorous macroinvertebrates in upstream reaches to other functional feeding groups in downstream reaches. Tailwater food web linkages between zooplankton and filter-feeding taxa such as hydropsychid trichopterans and simuliid dipterans have been documented in many studies (Cushing, 1963; Walburg et al. 1981). Simuliid dipterans (black flies) are the only abundant filter-feeder in the Colorado River, Grand Canyon, and Blinn et al. (1992) found that simuliid biomass increases with distance from Glen Canyon Dam in riffle habitats. While this finding conflicts with the predictions of the Serial Discontinuity Concept, it does aid in explaining the pattern of zooplankton density reduction observed in the present study. Blinn et al. (1992) found that maximum simuliid biomass was found from RK 232 to 240, which lies between Reaches 6 and 8 where zooplankton density reductions were observed both before and after the flood. Simuliids are opportunistic feeders capable of filtering food items up to 350 µm (Anderson and Wallace 1984), which encompasses the size range of most plankton encountered in the present study (nauplii and rotifers). By contrast, Angradi (1994) found that zooplankton originating in Lake Powell were utilized directly by fishes in the Colorado River from RK -24.62 to 0.0. Invertebrate biomass in this region of high periphytic productivity is dominated by herbivorous taxa such as chironomids and *Gammarus* sp. (Blinn et al. 1992) to the exclusion of simuliids, which require algal-free surfaces for attachment.

In summary, zooplankton densities in the Colorado River, Grand Canyon, increased following the 1996 Experimental Flood due to increases in water temperature or introduction of greater quantities of zooplankton from Lake Powell, or some interaction of both factors. Zooplankton losses downstream were less pronounced during the post-flood trip due to downstream displacement of Copepoda and Rotifera. Eight uncommon littoral taxa (one copepod, six rotifers and one branchiopod) were absent from post flood samples, perhaps due to replacement by limnetic taxa introduced during the flood. No difference in zooplankton density was detected between backwater and mainchannel habitats due to high water exchange rates between the two habitats.

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DIET OF ADULT HUMPBACK CHUB

Work Task 3.2
Prepared by T.J. Dresser, Jr.

The impact of high flow releases on the feeding behavior of humpback chub is not known, because no information exists on the diet of this species under such conditions. Research by Kaeding and Zimmerman (1983) on the mainstem Colorado River indicated that the larvae of simuliids and chironomids were the most dominant stomach content of humpback chub. Jacobi and Jacobi (1982) reported that Ephemeroptera and Diptera were important food items for young-of-year humpback chub in the Green and upper Colorado Rivers. In another study, *Cladophora glomerata* was found to comprise 77% by volume of the total stomach contents with aquatic and terrestrial insects accounting for only 10% of the volume (Kubly 1990). Mormon crickets *(Anabrus simplex)* have also been consumed by humpback chub in the Green and Yampa Rivers (Tyus and Minckley 1988). The opportunistic feeding behavior of humpback chubs is further supported by the findings of Valdez and Ryel (1995), who showed that adult chubs (>250 mm) in the Grand Canyon consumed both aquatic and terrestrial invertebrates, seeds or pods, and human food. Simuliids were the most common food item by number in humpback chub stomachs with *Gammarus lacustris*, chironomids, formicids, and coleopterans also commonly found.

This study addresses Work Task 3.2: Determine food habits of adult humpback chub (>250 mm) before and during high flows. Samples were also collected during the post-flood steady 8,000 cfs (226 m^3/s) period in addition to the samples collected during the flood and pre-flood. The null hypothesis being tested is that there is no difference in the stomach contents of adult humpback chub before, during, or after the high river discharge. We anticipate that scouring caused by the flood will alter food availability, which will alter the diet of these opportunistic fish.

Study Area

A total of fourteen sites was sampled in the Colorado River during the 1996 Experimental Flood. Of these, six were above the confluence of the Colorado and Little Colorado Rivers between river kilometer (RK) 97.10 (distance downstream from Lee's Ferry; RK 0) and RK 98.95. The remaining eight sites were located downstream of the confluence of the Colorado and Little Colorado Rivers extending from RK 99.11 to RK 105.15, just above Lava Chuar Rapids (RK 105.23).

Methods

Fish Collection

Trammel nets were the primary gear type used to collect adult humpback chub (>250 mm TL) for stomach content analysis. Nets were generally set for a 4-hour period in the evening, which included approximately two hours of dusk and two hours of dark. Nets were checked approximately every two hours to minimize the risk of injury to entangled fishes. In addition to trammel netting; nighttime electrofishing was conducted to supplement captures. All captured humpback chub were measured for standard length (SL), total length (TL), weighed to the nearest tenth of a gram.

Food Habits

Stomach contents of captured adult humpback chub were collected using non-lethal gastric lavage techniques described by Wasowicz and Valdez (1994) and used on humpback chub by Valdez and Ryel (1995). Stomach contents were individually stored in whirl-packs and preserved in 70% ethanol.

In the laboratory, macroinvertebrates and identifiable material were separated into taxonomic groups (Pennak 1989) and enumerated. The following taxonomic categories were created for analyses: simuliids (larvae and pupae), chironomids (larvae and pupae), *Gammarus lacustris*, terrestrial invertebrates, and other aquatic invertebrates. Terrestrial invertebrates consisted of Coleoptera, Diptera (adults), Formicidae, Acarina, Orthoptera, and Lepidoptera. The aquatic invertebrate group consisted of Hydracarina, Culicidae, and larval Diptera. Ash-free dry weights (AFDW) for each taxonomic group were determined. Analysis of variance (ANOVA) and Ryan-Einot-Gabriel-Welsh multiple F test (Day and Quinn 1989) were used to compare differences among flood stages (pre-flood, flood and post-flood) for percent AFDW and number of invertebrates. Significance for all statistical tests was set at α=0.05.

Results

A total of 45 adult humpback chub (>250 mm) was collected during the Experimental Flood in the Colorado River, Grand Canyon. These fish ranged in size from 250 mm to 450 mm TL, weighing between 143 - 815 grams. Of these, two fish contained only human food remains and were not included in the analyses. Of the remaining fish (n=43), nine were collected during the pre-flood stage, 16 during the flood, and 18 from the post-flood stage.

Table 18. Aquatic and terrestrial invertebrates found in the stomach contents of 43 adult humpback chub (> 250 mm; TL) collected during the 1996 Experimental Flood on the Colorado River, Grand Canyon, Arizona.

Taxa		Aquatic Organisms	Terrestrial Organisms
Lepidoptera			X
Coleoptera			X
Orthoptera			X
Formicidae			X
Hymenoptera			X
Acarina			X
Diptera		X	X (Adults)
	Chironomidae	X	
	Simuliidae	X	
	Culicidae	X	
Hydracarina		X	
Amphipoda			
	Gammarus lacustris	X	

A total of seven aquatic and six terrestrial invertebrate groups were found in the stomach contents of adult humpback chub (Table 18). The food items found most frequently in the guts of humpback chub were simuliids (97.6% of stomachs sampled), followed by chironomids (93%), *Gammarus* (79.1%), coleopterans (72.1%), and adult dipterans (48.8%; Table 2).

Occurrence of simuliids and chironomids in the stomach contents during the experiment ranged from 93.7% during the flood to 100% during the pre- and post-flood phases. The occurrence of *Gammarus* was lowest during the pre-flood phase (44.4%), but increased during the flood and post-flood stage (93.7% and 88.9%; respectively). The occurrence of other terrestrial organisms and miscellaneous food items in the stomach contents of adult humpback chub during pre-, flood and post-flood phases was $<62.5\%$, except for coleopterans (100%; post-Flood; Table 19). *Cladophora glomerata* (green algae) occurred in 22.2% of the stomachs during the pre-flood phase and 11.1% during the post-flood stage. Human food remains were found in 14% of all fish sampled.

Overall, no significant difference ($P=0.1786$) was observed in the mean total number of invertebrates found in the stomach contents of adult humpback chub. No significant differences ($P=0 \geq 0.0615$) were found in invertebrate taxa among the three flood phases, except for chironomids ($P=0.0057$; Table 20). Although, a higher incidence of *Gammarus* was found in the gut contents during and after the flood; no significant differences in mean number were observed between the pre-flood, flood, or post-flood phases ($P=0.0852$). The incidence of coleopterans in the gut contents of chub increased from 56% during the pre-flood phase to 100% in the post-flood stage. No significant differences were found in the mean number of terrestrial invertebrates (mainly coleopterans) found in the stomach contents of chub during the three flow levels ($P=0.1818$).

No significant difference was observed in mean total biomass (AFDW) of invertebrates found in the stomach contents of chub among the flood stages ($P=0.6139$; Table 4). Biomass varied significantly for simuliids and *Gammarus* ($P= \leq 0424$). Biomass for all other invertebrate taxonomic groups was non-significant among the three flood phases ($P= \geq 0.0956$; Table 21). No significant difference in the biomass of *Cladophora* was observed among the three flood phases ($P=0.2174$).

Overall, no significant difference was observed in the percentage of total invertebrate biomass (AFDW) in the stomach contents of chub collected during the three flood phases ($P=0.3521$; Table 22). The percent biomass (AFDW) of simuliids in the stomach contents was significantly higher during the pre- and post-flood phases than the flood phase ($P=0.0119$). Percent biomass of chironomids was significantly higher during the pre-flood phase than the other phases (P=0.0447). The percent biomass (AFDW) of *Gammarus* and terrestrial invertebrates in the stomach contents of humpback chub was significantly higher (P=0.0056) during the experimental flood than the pre- and post-flood phases (Table 22).

Table 19. Frequency of occurrence of food categories (number and percentage of total) in the stomach contents of adult humpback chub (>250 mm, TL) from the Colorado River, Grand Canyon, Arizona, collected during the 1996 Experimental Flood.

	All Fish		Pre-Flood		Flood		Post-Flood	
Food Category	n	%	n	%	n	%	n	%
Aquatic Organisms								
Diptera (Larvae)	2	4.7	0	0.0	1	6.3	1	5.6
Simuliidae	42	97.6	9	100.0	15	93.7	18	100.0
Chironomidae	40	93.0	9	100.0	15	93.7	17	94.4
Hydracarina	2	4.7	1	11.1	0	0.0	1	5.6
Amphipoda *Gammarus lacustris*	34	79.1	4	44.4	15	93.7	16	88.9
Terrestrial Organisms								
Diptera (Adults)	21	48.8	3	33.3	10	62.5	3	16.6
Culicidae (Adults)	3	6.9	2	22.2	0	0.0	1	5.6
Lepidoptera	1	2.3	0	0.0	0	0.0	1	5.6
Orthoptera	1	2.3	4	44.4	0	0.0	0	0.0
Coleoptera	31	72.1	5	55.6	10	62.5	18	100.0
Formicidae	5	11.6	0	0.0	3	18.8	0	0.0
Acarina	1	2.3	0	0.0	0	0.0	1	5.6
Miscellaneous								
Cladophora glomerata	4	9.3	2	22.2	0	0.0	2	11.1
Human food remains	6	13.9	0	0.0	5	31.3	1	5.6
Seeds or pods	1	2.3	1	11.1	0	0.0	0	0.0
Lizards	2	4.7	0	0.0	1	6.3	1	5.6

Table 20. Mean number of principle food categories in the stomach contents of adult humpback chub (>250 mm; TL) collected during the three phases of the 1996 Experimental Flood on the Colorado River, Grand Canyon. Arizona. Superscripts indicate significant differences among flood phases for each taxa with a significant ANOVA. Identical letters indicate non-significance between means (Ryan-Einot-Gabriel-Welsch Multiple F test; P<0.05). The terrestrial invertebrate group consisted of Coleoptera, Diptera (adults), Formicidae, Acarina, Orthoptera, and Lepidoptera. The other aquatic invertebrate group consisted of Hydracarina, Culicidae, and larvae Dipterans.

	Pre-Flood 8,000 cfs n=9		Flood 45,000 cfs n=16		Post-Flood 8,000 cfs n=18		ANOVA
Taxa	Mean	SE	Mean	SE	Mean	SE	(df=2,40)
Simuliids	409.8	21.9	169.1	12.1	364.4	17.1	P=0.061
Chironomids	37.0^{a}	6.2	16.2^{b}	5.9	24.2^{a}	4.5	P=0.005
Gammarus lacustris	7.2	3.5	23.1	6.0	6.2	2.5	P=0.085
Terrestrial Invertebrates	10.1	3.6	12.6	3.9	3.3	1.8	P=0.181
Other Aquatic Invertebrates	0.1	0.6	0.2	0.6	0.1	0.5	P=0.505
Total Invertebrates	464.2	22.6	221.2	13.4	398.3	17.5	P=0.178

Table 21. Mean ash-free dry weight of principle food categories in the stomach contents of adult humpback chub (> 250 mm; TL) collected during the three phases of the 1996 Experimental Flood on the Colorado River, Grand Canyon, Arizona. Superscripts indicate significant differences among flood phases for each taxa with a significant ANOVA. Identical letters indicate non-significance between means (Ryan-Einot-Gabriel-Welsch Multiple F test; P<0.05). The terrestrial invertebrate group consisted of Coleoptera, Diptera (adults), Formicidae, Acarina, Orthoptera, and Lepidoptera. The other aquatic invertebrate group consisted of Hydracarina, Culicidae, and larvae Dipterans. Asterix indicates <0.0001.

	Pre-Flood 8,000 cfs n=9		Flood 45,000 cfs n=16		Post-Flood 8,000 cfs n=18		ANOVA
Taxa	Mean	SE	Mean	SE	Mean	SE	(df=2,40)
Simuliids	0.012^{a}	0.010	0.003^{b}	0.003	0.007^{ab}	0.007	P=0.0120
Chironomids	0.001	0.001	0.004	0.001	0.001	0.001	P=0.3837
Gammarus lacustris	0.0009^{a}	0.002	0.005^{b}	0.007	0.002^{ab}	0.002	P=0.0424
Terrestrial Invertebrates	0.0002	0.0002	0.002	0.003	0.001	0.001	P=0.0956
Other Aquatic Invertebrates	*	*	*	*	*	*	P=0.5056
Total Invertebrates	0.027	0.020	0.024	0.020	0.021	0.013	P=0.6139
Cladophora glomerata	0.005	0.016	0.0	0.0	0.001	0.003	P=0.2174

Table 22. Percent ash-free dry weight of principle food categories in the stomach contents of adult humpback chub (>250 mm; TL) collected during the three phases of the 1996 Experimental Flood in the Colorado River, Grand Canyon, Arizona. Superscripts indicate significant differences among flood phases for each taxa with a significant ANOVA. Identical letters indicate non-significance between means (Ryan-Einot-Gabriel-Welsch Multiple F test; P<0.05). The terrestrial invertebrate group consisted of Coleoptera, Diptera (adults), Formicidae, Acarina, Orthoptera, and Lepidoptera. The other aquatic invertebrate group consisted of Hydracarina, Culicidae, and larvae Dipterans.

	Pre-Flood 8,000 cfs n=9		Flood 45,000 cfs n=16		Post-Flood 8,000 cfs n=18		ANOVA
Taxa	Mean	SE	Mean	SE	Mean	SE	(df=2,40)
Simuliids	65.8[a]	6.0	37.2[b]	5.5	65.2[ab]	4.7	P=0.0119
Chironomids	18.8[a]	5.7	3.1[b]	2.0	5.9[b]	2.1	P=0.0447
Gammarus lacustris	4.8[a]	3.09	3.9[b]	5.5	19.0[ab]	4.5	P=0.0056
Terrestrial Invertebrates	0.9[a]	1.1	22.7[b]	5.8	6.3[ab]	2.2	P=0.0272
Other Aquatic Invertebrates	0.2	0.3	0.0002	0.03	0.0001	0.01	P=0.1551
Total Invertebrates	90.2	5.4	100.0	0.0	96.3	3.8	P=0.3521
Cladophora glomerata	9.7	5.3	0.0	0.0	3.7	3.8	P=0.3535

Discussion

Humpback chub in the Colorado River, Grand Canyon, consumed a variety of aquatic and terrestrial invertebrates during the study period. Simuliids were the most common aquatic invertebrates ingested by humpback chub during all phases of the experiment. Chironomids and *Gammarus lacustris* were next in occurrence. The bulk of terrestrial invertebrates found in the stomach contents of humpback chub were primarily Coleoptera. *Cladophora glomerata* was found in 9% of all the fish collected. Our findings were consistent with those of Valdez and Ryel (1995) who reported that simuliids were the most common food items by number. Kaeding and Zimmerman (1983) reported that simuliids and chironomids were numerically dominant in the stomach contents of adult humpback chub examined from the Little Colorado and Colorado Rivers in 1979-1981. During the pre-flood phase, simuliids and chironomids comprised the bulk of the diet by ash-free dry weight. In a study by Valdez and Ryel (1995), *Gammarus*, simuliids, chironomids, and terrestrial invertebrates composed the bulk of the diet by volume. They concluded that *Gammarus* was an important component of the diet, comprising 44.8% of the food volume for fish collected from the mainstem Colorado River. During our study, *Gammarus* was found in 79% of the stomachs examined, but averaged only 3.9-19.0% of the AFDW of stomach contents. Kaeding and Zimmerman (1983) reported that *Gammarus* were not used to a large extent and found that only 11% of the stomachs examined contained *Gammarus*, although *Gammarus* were abundant in the littoral areas of the mainstem Colorado River.

The observed increases in *Gammarus* in the stomach contents of humpback chub during the flood and post-flood phases and may be attributed to increased flow. High flows that scoured the backwaters and margins of the Colorado River transported *Gammarus* downstream making them more accessible to the chub. Leibfried and Blinn (1986) reported an increase of *Gammarus* in stream drift during the rising arm of discharges following low flow periods. They further reported that *Gammarus* were swept downstream during high flows and numbers ranged from 10.7 individuals/hr during steady flows to 42.3 individuals/hr for months with more fluctuating flows. Further evidence of this downstream transport of *Gammarus* was provided by McKinney et al. (see Lee's Ferry Chapter, this report), who observed decreases in *Gammarus* densities above Lee's Ferry after the flood. Increases of *Gammarus* in drift samples collected at RK 103.78 also indicate downstream transport (J. Shannon, NAU, personal communication). Visual observation of isolated pools at RK 103.94 immediate following the flood suggests that high numbers of *Gammarus* had been transported downstream.

Based on ash free dry weights (percentage), simuliids and chironomids in the stomach contents of humpback chub decreased significantly during the flood. This decrease in simuliids and chironomids biomass (percentage AFDW) may be attributed to increased turbidity, which may have made these organisms less visible to the chub. Decreases in simuliids and chironomids biomass may also be related to changes in benthic community structure because of high discharges. Research by Resh et al. (1988), Niemi et al. (1990), and Giller et al. (1991) indicated that high discharge events can cause severe population losses and changes in benthic community structure. Results from our benthic invertebrate study conducted before and following the flood indicates that overall mean density of benthic invertebrates in backwater areas was reduced by approximately 75% (see Benthos Chapter, Work Task 3.1; this report). We reported significant decreases in the number and biomass of chironomids, arthropods (*Gammarus lacustris* and ostrocods), oligochaetes and other dipterans (simuliids and ceratopogonids) in backwaters before and following the Experimental Flood.

Human food remains, seeds, pods, and reptiles (lizards) were also found in the stomach contents of eight humpback chub collected during this study. Thereby, providing further support that humpback chub are opportunistic in their feeding behavior. Valdez and Ryel (1995) reported the presence of seeds or pods and human food remains in the stomachs of chub. Tyus and Minckley (1988) observed humpback chub feeding on Mormon crickets in the Green and Yampa Rivers.

The presence of *Cladophora* in the stomach contents of chub further indicates that chub are opportunistic feeders; although it is unknown if this item is deliberately or incidentally ingested. Valdez and Ryel (1995) reported that *Cladophora* made up 20% of the stomach contents (by volume) of chub from the Colorado River. Kubly (1990) examined 17 chub from the Colorado River and found that *Cladophora* comprised 77% of the gut contents (by volume). The occurrence of *Cladophora* in the stomachs of chub collected during the Experimental Flood was highest during the pre-flood phase. The absence or decreased frequency of *Cladophora* in the stomach contents of chub during and after the flood is likely related to the increased flows. Pulverization and agitation of *Cladophora* during the flood may break *Cladophora* into smaller clumps, thereby affecting ingestion rates. Valdez and Ryel (1995) hypothesized that decreases in the use of *Cladophora* in the Middle Granite Gorge may be a result of the loss of epiphytic diatoms and associated organisms. Blinn et al. (1994) reported that diatoms and macroinvertebrates associated with drifting *Cladophora* decreased with distance downstream from Glen Canyon Dam.

Increases in the occurrence and percent (AFDW) of terrestrial invertebrates in the stomach contents of humpback chub were observed during this study. Increases in terrestrial invertebrates can be attributed to increased flows washing them into the river. During the flood water levels rose quickly (4,000 cfs/hr; 113 m^3/hr), inundating riparian vegetation and shoreline areas, flushing terrestrial invertebrates into the water column, and making them more accessible to humpback chub. Valdez and Ryel (1995) hypothesized that periodic increases in the availability of terrestrial and aquatic invertebrates from irregular spates may have been an important factor in the evolution of the feeding behavior of the humpback chub.

Based on the findings of this study, we conclude that humpback chub are very opportunistic in their feeding habitats and can use food sources as they become available. Our findings indicate no significant changes in mean total biomass or mean number of invertebrates in the stomach contents of chub. Therefore we conclude that the effects of the 1996 Experimental Flood on the feeding behavior of the adult humpback chub were minimal.

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CONCLUSIONS

The immediate impacts of the Experimental Flood on morphology, number, sediments, and the benthic macroinvertebrate community of backwaters, and the zooplankton and fish communities in the Colorado River, Grand Canyon, have been shown. Many of these were as expected, some were surprising.

The number and surface area of backwaters immediately after the flood increased from that immediately prior. However, the effect of flooding on long-term backwater number and size remains uncertain. It is apparent that changes in flow patterns from flood discharge to operating flows and the subsequent fluctuating flows of normal dam operations were detrimental to the longevity of backwaters created by the flood. Floods of a lower magnitude and/or a much slower downramp may alleviate some of these problems, making the new backwaters more permanent. Higher flows, without much slower downramps, are highly likely to produce the same kinds of negative effects on backwater numbers observed in this study. The loss of backwaters observed after the resumption of operating flows may detrimentally affect survival and growth of larval and juvenile native fishes.

The availability of nursery/rearing habitats to larval and juvenile native fishes in the reach below the LCR is important because all native species spawn in the LCR, particularly humpback chub. Robinson et al. (1996) found that near-shore, low-velocity habitats are important nursery areas for larval fishes in the LCR. Larval fishes transported out of the LCR into the mainstem continue to seek out near-shore, low-velocity habitats such as backwaters (Valdez and Ryel 1995; AGFD 1996). Larval fish migrating out of the LCR are faced with colder water temperatures (>8°C mean temperature change), which decreases swimming ability (Berry and Pimentel 1985; Lupher and Clarkson 1994; Childs and Clarkson *in press*) and probably causes larvae to have difficulty reaching backwaters. Although large numbers of larvae are transported out of the LCR into the mainstem Colorado River each year, few are believed to survive (Robinson et al. 1996). An increase in the number of backwaters immediately below the LCR will likely help increase the survival of larval native fishes spawned in the LCR.

How closely the environmental conditions within a backwater conform to those preferred by larval and juvenile native fishes (i.e., water temperature, depth, area, amount of cover, invertebrate density, etc.) is also of importance. **Holden (1977) reported that young-of-year humpback chub preferred backwaters with no current, a firm silt bottom, and 0.6 m maximum depth.** Maddux et al. (1987) found that flannelmouth sucker larvae and juveniles were more abundant in backwaters with vegetated cover than those without vegetated cover. Juvenile flannelmouth suckers, humpback chub, and speckled dace were all more common in backwaters with high turbidity, and flannelmouth suckers and speckled dace were more common in warmer sites (AGFD 1996). The preferred temperature was 21.0 - 24.4° C for juvenile humpback chub (Bulkley et al. 1982), 21.9 - 27.6° C for yearling Colorado squawfish (Black and Bulkley 1985), and it is likely that the other Colorado River native fishes have similar temperature preferenda. Pimentel and Bulkley (1983) found that humpback chub preferred conductivity levels of 1563 - 3906 μS/cm (1000 - 2500 mg/L total dissolved solids) and avoided levels as low as 7969 μS/cm (5100 mg/L total dissolved solids). Backwater temperature and conductivity immediately following the Experimental Flood were mostly sub-optimal for larval and juvenile native fishes. Indeed, specific conductance of water in the mainstem (mainchannel and backwaters) Colorado River in Grand Canyon usually ranges from 800 - 1200 μS/cm, below that preferred by humpback chub, and water temperature near the LCR, even in backwaters, rarely exceeds 20° C (AGFD 1996). The new backwaters created by the flood had larger surface areas and greater zooplankton densities, but had no vegetation, sediments made up of primarily clean sand, and decreased benthic invertebrate densities. However, over time fine sediments and detritus will accumulate in backwaters, and benthic invertebrates will recolonize. Then, these newly created backwaters may become better rearing habitats for native fishes. The time that it takes for this to occur is not known, but is currently under study.

In backwaters, fine and organic substrates were scoured and replaced by additional sand. This scouring also reduced benthic invertebrate densities and the changing sediments may affect benthic invertebrate recolonization. Many benthic invertebrate species are important prey items for juvenile native fishes (AGFD 1996) and their loss may detrimentally affect growth of these fish.

Zooplankton densities increased following the flood, but this was probably a result of seasonal increases in temperature. However, nearly half (11 of 24) of the zooplankton taxa found before the flood were not found afterwards. These were mostly littoral species, probably less capable of withstanding high current velocities. The effect that these changes will have on diet of larval and juvenile fishes is unknown.

Native fishes appear to have been unaffected by the flood. The timing of the flood largely prevented newly hatched fish from being affected. Small native fishes (speckled dace and young-of-year humpback chub) were able to maintain themselves in their sheltered, preferred habitats during the flood and showed no evidence of being displaced downstream. Diet of adult humpback chub varied, but they demonstrated their omnivory and adaptability to this type of perturbation. During the flood they consumed more terrestrial invertebrates and less aquatic invertebrates and *Cladophora*.

Although some exotic species were affected, it is unlikely that these are long-term effects. Plains killifish populations were decimated, but summer and fall sampling shows that they are recolonizing (T. Hoffnagle, personal observation). Fathead minnow populations were reduced in reaches immediately below the LCR, but the reproductive capacity of this species is great and they will likely recover. Rainbow trout catches increased, probably a result of displacement of individuals from upstream areas.

There are long-term questions concerning the effects of this flood on aquatic biota and their habitats to be answered. What is the longevity and successional pattern of backwaters? What is the recolonization rate of backwater benthic invertebrates and zooplankton? Did the flood affect spawning and recruitment of exotic fishes, particularly fathead minnow and plains killifish? Studies of the aquatic biota in the Colorado River, Grand Canyon, will continue through 1996 and should provide more information regarding these questions. The usefulness of such flooding as a tool to improve habitat for larval and juvenile native fish depends in part on flooding effects on invertebrate biota and their habitat, and the response of these communities to disturbance should become clearer in the context of a larger study.

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EFFECTS ON ALGAE, MACROPHYTES, MACROINVERTEBRATES, RAINBOW TROUT AND FLANNELMOUTH SUCKERS IN THE GLEN CANYON DAM TAILWATER

Ted McKinney, R. Scott Rogers, Andrew Ayers and William R. Persons

Abstract

1. Algae, macrophytes, macroinvertebrates, rainbow trout and flannelmouth suckers were investigated in the tailwater of Glen Canyon Dam, Arizona prior to and following or during experimental flooding. Lotic biota varied spatially and temporally following the flood.

2. Biomass (AFDW) densities of epilithon were unaffected within one week following the flood, but densities of chlorophyll *a* declined about 40%. Standing stock of submerged macrophytes was reduced throughout the tailwater by flooding. Colonization of exposed sand substrate by *Potamogeton* sp. began within about one month after the flood, but *Chara contraria* colonized extensively by about seven months after the spate.

3. Densities of diatom epiphytes on epilithon were reduced by about 66% within the week following the flood. Large/upright diatom taxa were more severely impacted than were small/adnate species.

4. Effects of the flood were similar at sites in cobble bar and depositional habitat. Densities of *Gammarus lacustris* were negatively affected in both habitats more than those of other macroinvertebrates within the week after flooding. *Gammarus* densities on sites in cobble bar and depositional habitat seven months after the flood were comparable to or exceeded pre-flood levels. Densities of chironomids, gastropods, oligochaetes and planarid flatworms in both habitats showed little immediate (one week) effect of flooding. Chironomid concentrations in both habitats were lower or similar to pre-flood levels seven months after the flood, while snail densities exceeded or were similar to, respectively, pre-flood levels on cobble bars and depositional habitat.

5. Relative abundance, condition factor, distribution within the reach and health of rainbow trout were affected little during about seven months following the flood. However, the severity index for health analysis during November appeared to be high, possibly reflecting spawning-related factors. The mesenteric fat index for trout was reduced five months following the flood but increased three months later, indicating seasonal change or effects of the flood. Catch per unit effort was lower five and seven months after the spate than during pre-flood steady flows, possibly due to discharge-related factors or changes in abundance and distribution of macrophytes. Length-frequency distributions and the numbers of ripe trout in electrofishing samples were altered immediately (one week) following the experimental flood, but distribution of size classes about five months later was similar to that prior to flooding. Strong recruitment of young-of-the-year trout into the population was apparent in November, seven months after the flood. Numbers of flannelmouth suckers in electrofishing samples were low, but no effect of flooding was apparent on relative abundance or distribution within the tailwater.

6. The frequency of empty stomachs of trout doubled, but total and relative volumes of ingested items were unchanged, in the week following flooding. Frequencies of occurrence for most food items were lower than prior to the flood. Five months following the flood, the frequency of occurrence of empty stomachs was below, and total volume of ingested items was above, values prior to the flood. Three months later during the fall, frequency of empty stomachs was higher, total stomach content was lower, and consumption of *Gammarus* and *Cladophora*, respectively, increased or decreased. Frequencies of occurrence of chironomids and *Gammarus* in trout stomachs were similar during all sampling periods except November, but proportions of amphipods in the diet were consistently greater than those for chironomids or snails.

INTRODUCTION

Flooding is a common source of disturbance in lotic systems and has long been recognized to influence the structure and dynamics of ecosystem communities (Minshall 1988, Steinman and McIntire 1990, Wallace 1990, Yount and Niemi 1990). Numerous investigations have shown that floods can alter the assemblage structure and abundance of fishes in streams (Pearsons et al. 1992). Flood events differ widely in frequency and severity but generally reduce standing stocks of primary and secondary producers. Recovery of the biotic community following floods may require from a few weeks to several years (Pearsons et al. 1992, Wallace 1990, Yount and Niemi 1990). Frequency and timing of the event influence the impact on the lotic community (Barrat-Segretain and Amoros 1995, Peterson 1996, Peterson and Stevenson 1992, Tett et al. 1978). However, the "best" indices of recovery remain uncertain, and no theoretical model is available to predict recovery by lotic communities following flooding (Yount and Niemi 1990). River impoundment may reduce resiliency of the downstream lotic system, and flooding may initiate a complex sequence of adjustments within the biotic community (Petts 1984).

Present studies examined short-term effects of experimental flooding on biota in the tailwater of Glen Canyon Dam. Specific objectives defined in the joint proposal for this project segment were:

Work Task 4.1–Determine distribution, density, diet and relative health of rainbow trout between Glen Canyon Dam and approximately River Mile 3.0. *Null hypothesis*: The distribution, density, diet and relative health/condition of fish before the experimental flow will not differ from that after the experimental flow.

Work Task 4.3–Determine benthic invertebrate density and distribution in the Lee's Ferry reach before and after the experimental flow. *Null hypothesis*: Benthic invertebrate density, amphipod biomass and invertebrate distribution will not be affected by the experimental flow.

Work Task 4.4–Determine biomass and chlorophyll *a* content before and after the experimental flow. *Null hypothesis*: Periphyton biomass and chlorophyll *a* content before the experimental flow will not differ from that after the experimental flow.

Work Task 4.5–Determine periphyton species composition and density before and after the experimental flow. *Null hypothesis*: Periphyton algal species composition and density before the experimental flow will not differ from that after the experimental flow.

Work Task 4.6–Determine *Chara/Potamogeton* bed distribution and density before and after the experimental flow. *Null hypothesis*: *Chara/Potamogeton* bed distribution and density before the flood will not differ from that after the experimental flood.

METHODS

Study Area

Glen Canyon Dam impounds the Colorado River near the Utah-Arizona border and forms Lake Powell, a 653 km^2 warm-monomictic reservoir. Hypolimnial releases from the reservoir are perennially clear and cold (7°-11° C) (Stanford and Ward 1991). What we refer to as Glen Canyon extends between the dam (-15.5 mi) and Lee's Ferry (0 mi), is narrow and has no major tributaries.

Prior to construction of Glen Canyon Dam, seasonal flow patterns of the Colorado River were unimodal and maximum during May and June (Persons et al. 1985). Following impoundment of the river by Glen Canyon Dam in 1963, flooding of the Glen Canyon tailwater has been rare and constrained by law but catastrophic when it occurred. The 1996 experimental flooding (releases from the dam) schedule was:

1) 227 m^3s^{-1} (8,000 cfs) steady discharge–March 22-26
2) upramp to 1,278 m^3s^{-1} (45,000 cfs) at 113 m^3/hr (4,000 cfs)–March 26
3) 1,278 m^3s^{-1} steady discharge–March 26-April 2
4) downramp to 227 m^3s^{-1}–April 2-4
5) 227 m^3s^{-1} steady discharge–April 4-7
6) return April 8 to regulated discharge under the interim flow regime (U.S. Department of Interior 1995); flows generally were in the range of about 426 m^3s^{-1} to 568 m^3s^{-1} during the post-flood study period (Bureau of Reclamation, unpublished data)

Periphyton

Samples were collected during the periods of 227 m^3s^{-1} steady flows prior to and following the 1,278 m^3s^{-1} discharge and during July and November 1996. Cobbles (10 cm-20 cm diameter) were collected haphazardly at the 142 m^3s^{-1} (5,000 cfs) flow elevation from fixed transects (50 m) parallel to river flow on bars at -14 mi and -4.1 mi. Subsamples (1-3 per cobble) of periphyton were taken by placing a 4.15 cm^2 cylinder haphazardly on the rock surface (Angradi and Kubly 1993). Material within the cylinder was removed by cutting, scraping and rinsing with river water. Cylinder contents and rinse water were stored in plastic vials on ice for transport and held frozen pending analysis.

The macroalga *Chara contraria* and the angiosperm *Potamogeton* sp. (probably *P. pectinatus*; Blinn et al. 1994) were sampled (n=5; Hess sampler, 0.087 m^2) simultaneously (due to complex intergowth) at haphazardly-located points (142 m^3s^{-1} flow elevation) within a transect (50 m) parallel to river flow on depositional substrate at -3.5 mi. Material within the Hess was removed by hand, stored in plastic bags for transport and held frozen pending analysis.

Pheophytin-corrected chlorophyll *a* (n=6 March, April; n=5 July, November) was analyzed spectrophotometrically (Tett et al. 1975), and ash free dry weight (AFDW; n=10) was determined by loss on ignition. Subsamples (20 g wet weight) of *Chara/Potamogeton* were homogenized (2 min) in a blender (200 ML deionized water). Aliquots (10 mL) of the homogenate from each sample were filtered (2.27 kg vacuum) onto a 4.7 cm glass fiber filter and analyzed for chlorophyll *a*. AFDW was determined for the unhomogenized portion of the sample. Chlorophyll *a* and AFDW densities were expressed in terms of the area sampled on cobbles and in terms of fixed area (Hess sampler) of river bed for macrophytes.

Additional cobbles (n=3) were collected at -14 mi and -4.1 mi as above from locations upstream from and contiguous with the other transects and were submersed in river water in open plastic bags on ice. Additional samples (n=3) of *Chara/Potamogeton* were collected as above from the transect at -3.5 mi and submersed in river water in open plastic bags on ice. Cobbles and macrophytes were held in this manner on ice pending analysis of epiphytic diatoms.

Epiphytic diatoms from epilithon and *C. contraria* (separated from *Potamogeton*) samples were identified initially using an Olympus compound microscope at 1000X magnification under oil immersion. Subsequent identification and enumeration incorporated a Wild inverted microscope at 20X magnification and a Sedgewick-Rafter counting cell. Two or more 0.09 mm^3 fields were observed from each of three counting cells to identify and count a minimum of 500 algal units per sample, although counts often exceeded 1,500 algal units. Samples collected from each transect were combined for analysis. Population densities for cobbles were calculated on the basis of cells per mm^2 of the area sampled on the stones; densities on *C. contraria* were calculated on the basis of cells per mg AFDW of the alga.

Surveys of submerged aquatic macrophytes were conducted between Lee's Ferry and Glen Canyon Dam on March 16-17, April 15-16, July 15-16 and November 13-14, 1996. The tailwater was traversed slowly along shoreline, and distribution and relative abundance of macrophytes were estimated visually, mapped on topographic sheets and coded for relative abundance: 0=absent; 1=low vertical growth, low horizontal distribution, patchy and sparse (presented as patchy, Figs. 13-18); 2=moderate vertical growth, generally continual horizontal distribution, occasionally patchy; 3=highest vertical growth, extensive horizontal distribution, slight or no patchiness (codes 2-3 presented as extensive, Figs. 13-18).

Underwater surveys of macrophyte beds at seven sites (-0.5 mi, -2.3 mi, -4.1 mi, -7.0 mi, -10.0 mi, -14.3 mi) were conducted during March 15-16 and again during April 12-13. Percent of substrate cover by macrophytes and vertical dimensions of beds were estimated using visual observation and photography.

Macroinvertebrates

Benthos was collected (n=5 during pre- and post-flood steady flows; n=3 during July, November; Hess sampler, 0.087 m^2) at the same times and flow elevation as the periphyton samples and from fixed transects (50 m) contiguous with those above (-14 mi, -4.1 mi, -3.5 mi) at a depth of <1m. Samples were preserved in the field (10% formaldehyde solution) and rinsed in the laboratory through a 250 μm sieve; invertebrates were sorted and counted.

Electrofishing

Electrofishing was conducted during 227 m^3s^{-1} pre- and post-flood steady flows, the 1,278 m^3s^{-1} (flood) discharge, August (flow ca. 568 m^3s^{-1}) and November (flow ca. 227 m^3s^{-1}). Fixed transects between Lee's Ferry and the dam (Arizona Game and Fish Department 1994) and three opportunistic sites (selected by M. Yard, GCES Flagstaff) between Lee's Ferry and the confluence of Cathedral Wash (3 mi) were electrofished (2,000 sec/site) during pre- and post-flood steady flows. During the 1,278 m^3s^{-1} discharge, seven opportunistic sites were electrofished between the dam and Lee's Ferry on March 26-27 and again on April 1-2 (599 sec to 865 sec each site). Fixed transects between the dam and Lee's Ferry were electrofished (2,000 sec/site) during August and November. Rainbow trout (RBT; *Oncorhynchus mykiss*) and flannelmouth suckers (FMS; *Catostomus latipinnis*) were weighed, measured and released alive unless collected (RBT) for analysis of health (trout > 350 mm; n=30-39/sampling period) (Goede 1993, Goede and Barton 1990) or food habits. Stomach samples were preserved in the field (10% formaldehyde solution), and ingested material was analyzed in the laboratory using volume displacement.

Data Analysis

Means for macroinvertebrates, periphyton standing stock and trout lengths, weights, condition factor (K) and volumes of ingested items were compared using ANOVA. Planned (*a priori*) comparisons between means were conducted on data from the pre- and post-flood 227 m^3s^{-1} steady flows. Duncan's Multiple Range test was used for unplanned (*a posteriori*) comparisons of means for epilithon standing stock and macroinvertebrate data obtained during March through November. Amphipod, oligochaete and chironomid larvae data were normalized for analysis using a $\log(x+1)$ transformation; chironomid pupae and planarid flatworm data were normalized using $\mathrm{sqrt}(x+1)+\mathrm{sqrt}(x)$ transformations. Composition and proportions of diatom epiphyte assemblages were compared using a similarity index (SIMI) (Tuchman and Blinn 1979). A maximum SIMI value of 1.0 indicates identical communities; values >0.75 indicate close similarity in species proportions and composition.

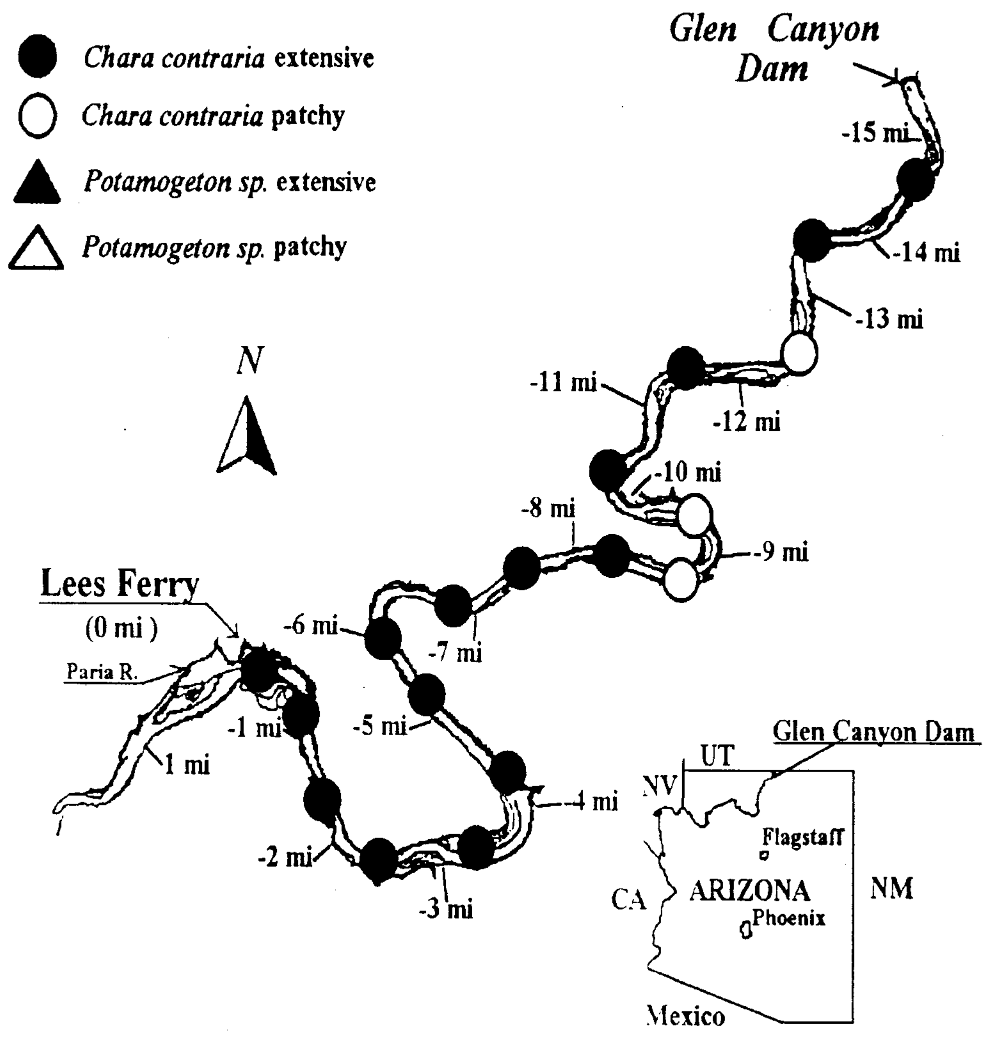

Figure 1. Distribution and relative abundance of *Chara contraria* and *Potamogeton* sp. in the Glen Canyon Dam tailwater to Lee's Ferry, March 16-17, 1996.

Figure 13. Distribution and relative abundance of *Chara contraria* and *Potamogeton* sp. in the Glen Canyon Dam tailwater to Lee's Ferry, March 16-17, 1996.

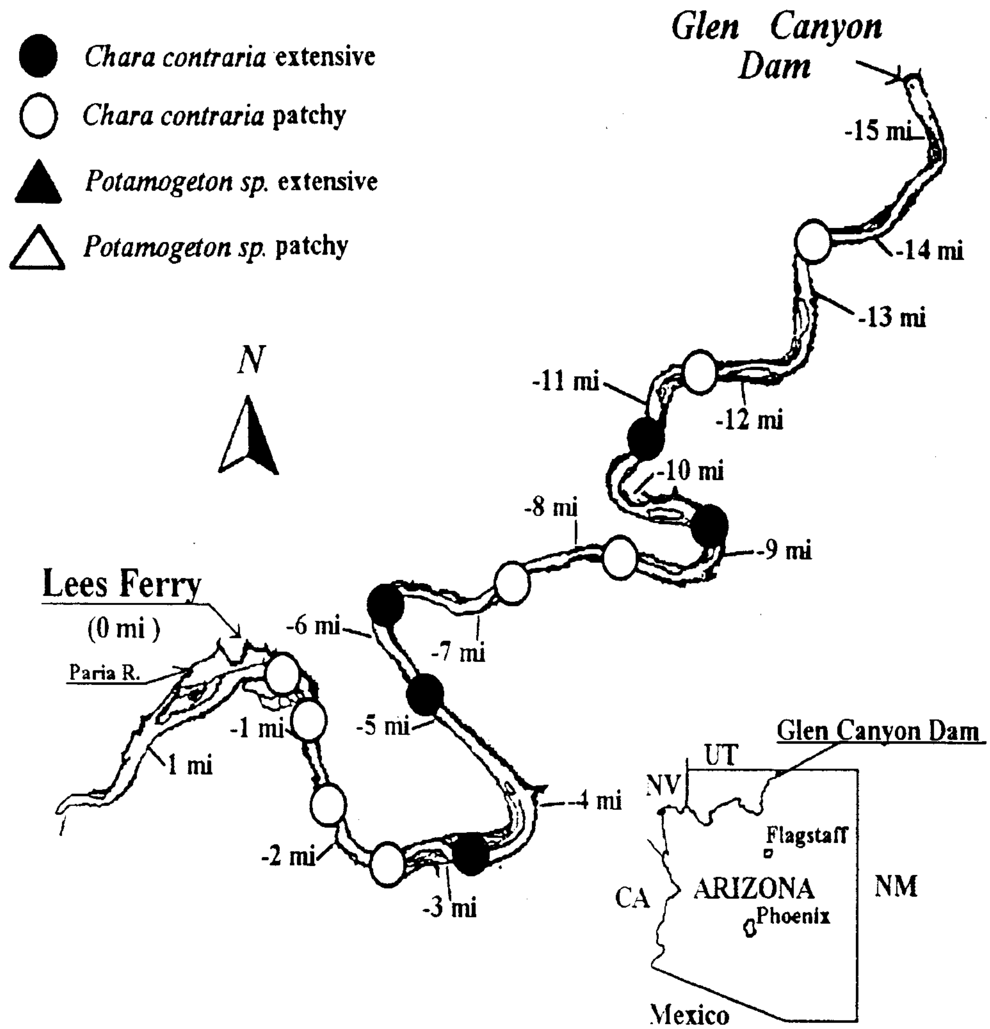

Figure 2. Distribution and relative abundance of *Chara contraria* and *Potamogeton* sp. in the Glen Canyon Dam tailwater to Lee's Ferry, April 15-16, 1996.

Figure 14. Distribution and relative abundance of *Chara contraria* and *Potamogeton* sp. in the Glen Canyon Dam tailwater to Lee's Ferry, April 15-16, 1996.

Figure 15. Distribution and relative abundance of *Chara contraria* and *Potamogeton* sp. in the Glen Canyon Dam tailwater to Lee's Ferry, July 15-16, 1996.

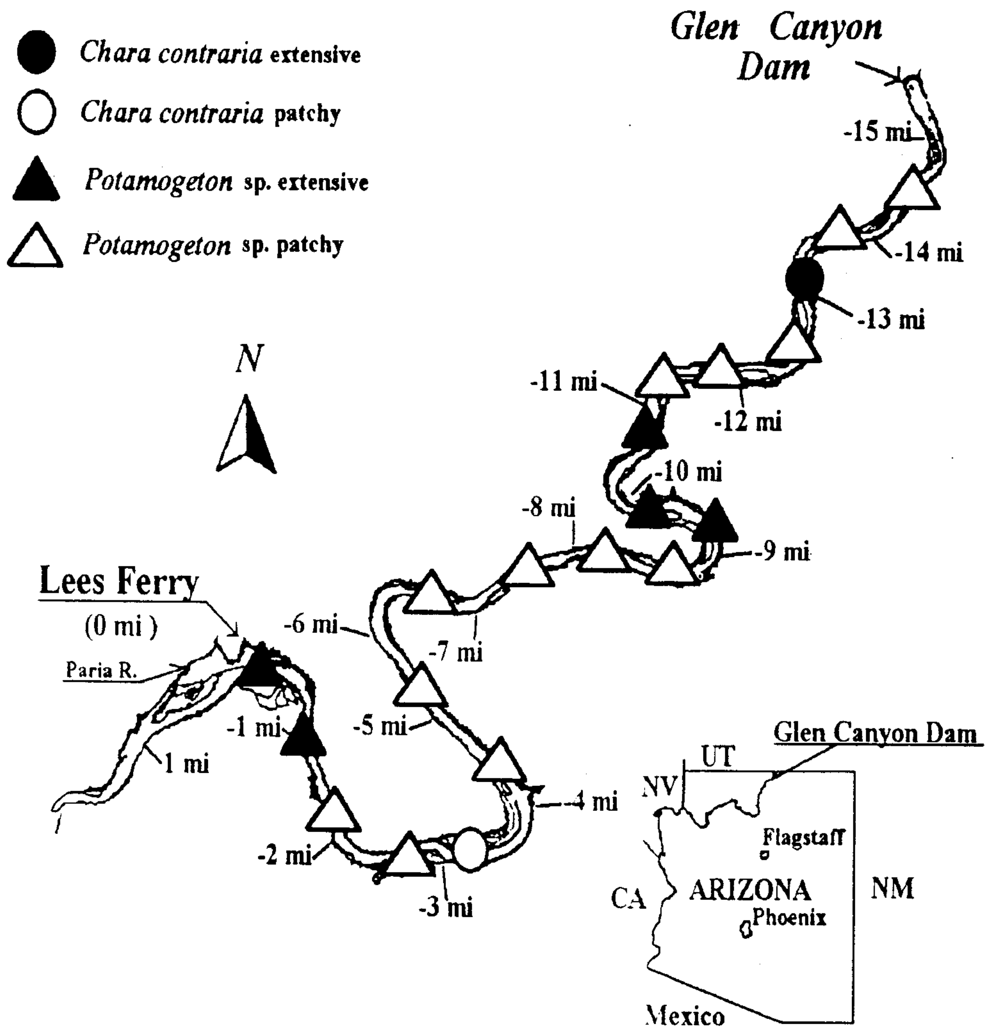

Figure 3. Distribution and relative abundance of *Chara contraria* and *Potamogeton* sp. in the Glen Canyon Dam tailwater to Lee's Ferry, July 15-16, 1996.

Figure 16. Distribution and relative abundance of *Potamogeton* sp. in the Lee's Ferry reach, November 13-14, 1996.

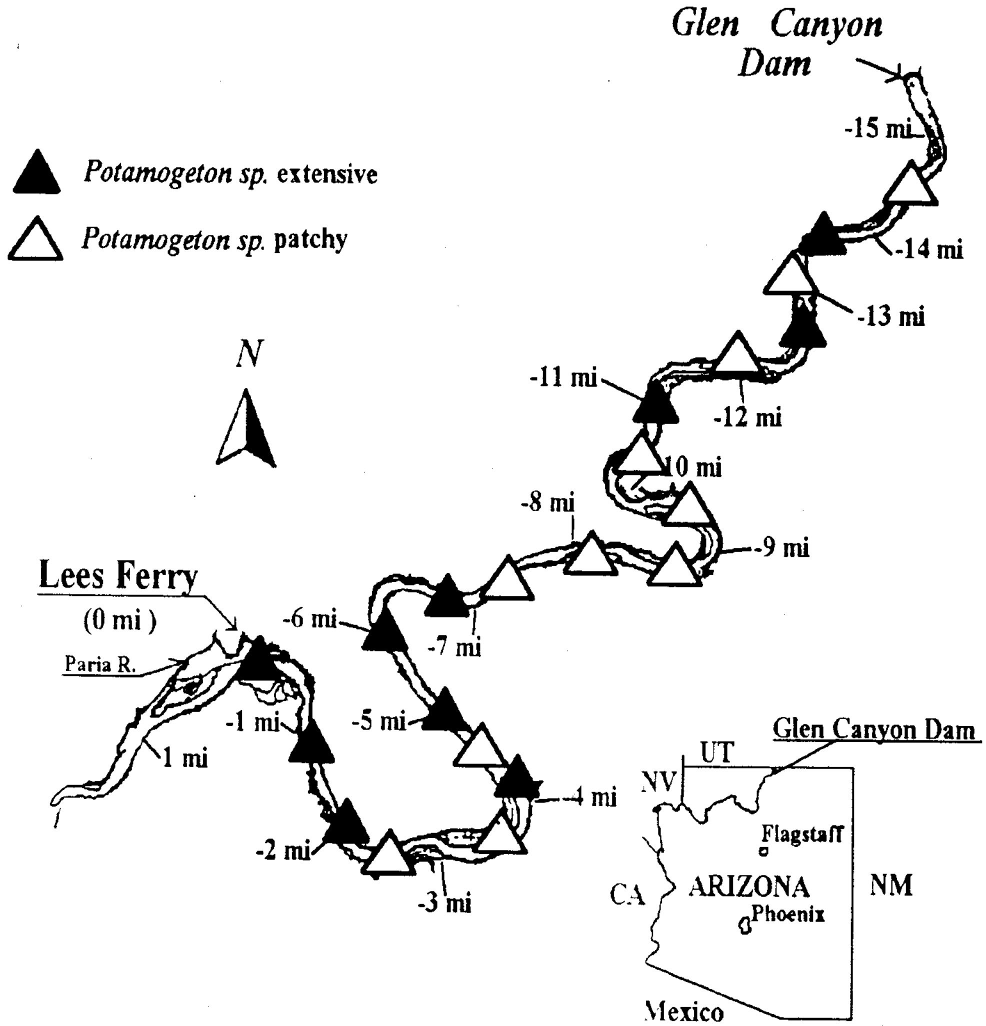

Figure 4. Distribution and relative abundance of *Potamogeton* sp. in the Lee's Ferry reach, November 13-14, 1996.

Figure 17. Distribution and abundance of *Chara contraria* in the Lee's Ferry reach, November 13-14, 1996.

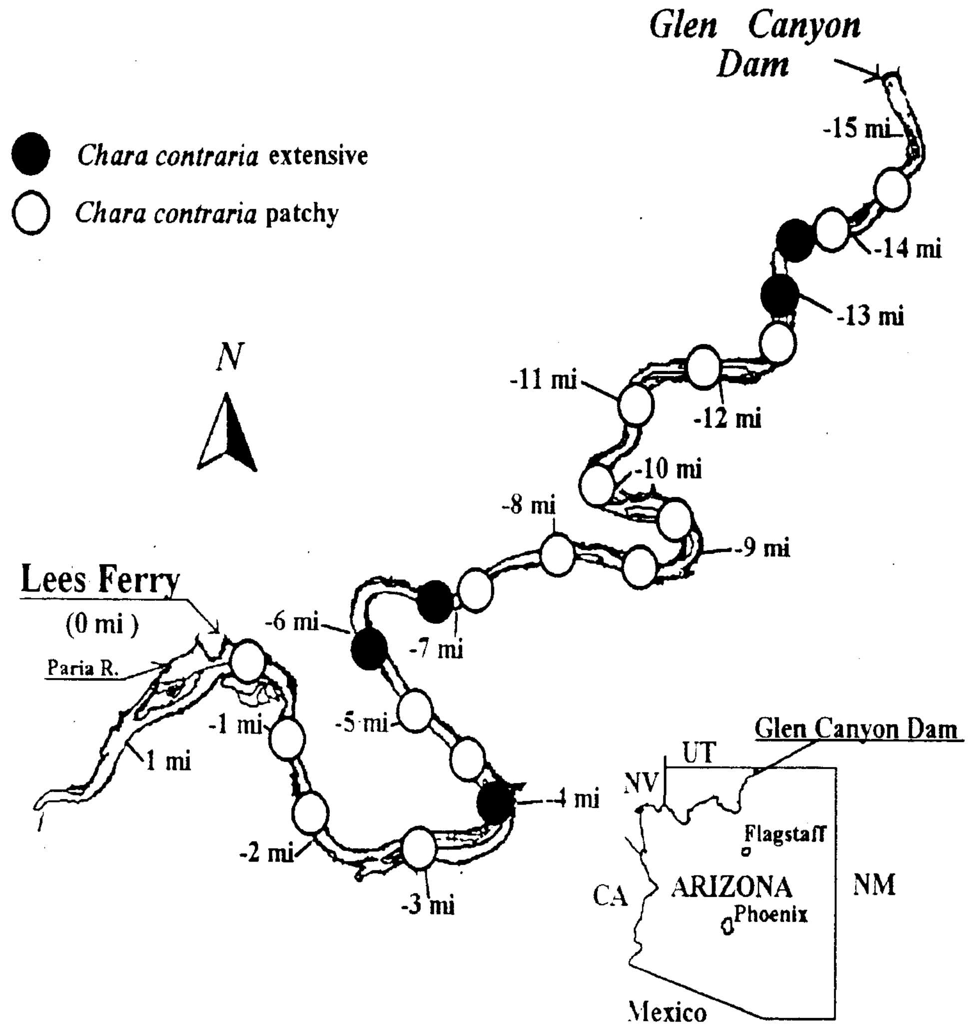

Figure 5. Distribution and abundance of *Chara contraria* in the Lee's Ferry reach, November 13-14, 1996.

Figure 18. Distribution and relative abundance of *Egeria densa* in the Lee's Ferry reach, November 13-14, 1996.

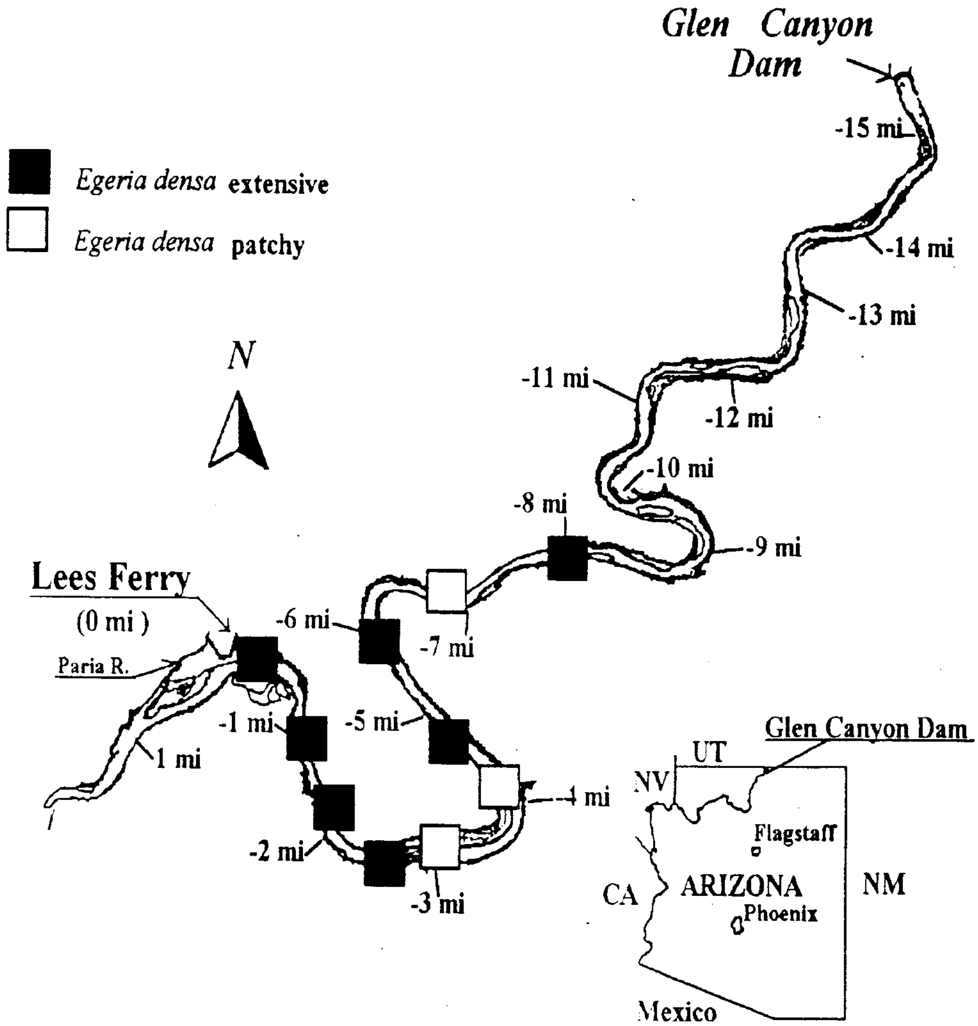

Figure 6. Distribution and relative abundance of *Egeria densa* in the Lee's Ferry reach, November 13-14, 1996.

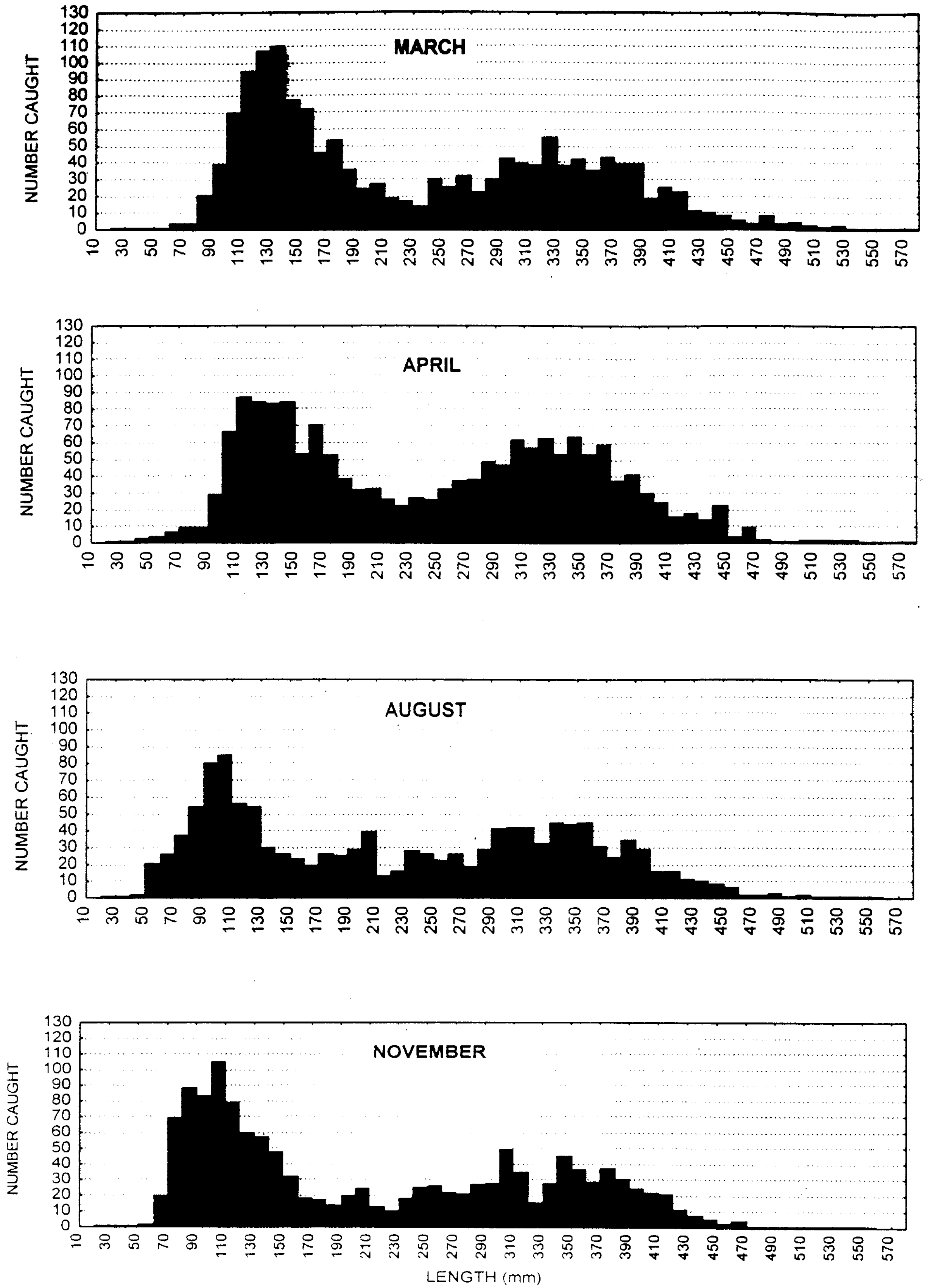

Figure 19. Length-frequency distributions of rainbow trout caught by electrofishing in the Glen Canyon Dam tailwater, March-November, 1996.

RESULTS

Algae and Macrophytes

Mean AFDW concentrations of epilithon did not differ ($P > 0.05$) among sampling periods or between the 227 m^3s^{-1} pre- and post-flood steady flows. However, mean densities of chlorophyll *a* differed ($P < 0.01$) among all sampling periods, declined ($P < 0.01$) during the post-flood steady flows, and were lower ($P < 0.05$) at-14 mi during November than March (Table 1). The submerged macrophytes at -3.5 mi were removed by flooding but re-colonized at the site by November (Table 23).

Epilithon and *Chara* hosted abundant communities of diatom epiphytes (Tables 24, 25). Densities of diatoms on epilithon reflect primarily epiphytes on *Cladophora glomerata* and were similar prior to the flood at -14 mi and -4.1 mi. However, mean diatom densities on epilithon were reduced 66% following the flood (both sampling sites combined), and dominant small/adnate and large/upright taxa, respectively, decreased 45% and 77% (Table 24). Proportional composition of the diatom assemblages was similar during the pre- and post-flood 227 m^3s^{-1} steady flows at -14 mi (SIMI=0.725) and at -4.1 mi (SIMI=0.795). However, similarity of the assemblages between -14 mi and -4.1 mi was high prior to the flood (SIMI=0.922) but low afterward (SIMI=0.595). Results indicate a relatively greater loss on epilithon of large/upright than small/adnate taxa due to the flood (Tables 24, 25).

During April (post-flood), macrophytes generally occurred in low abundance and were absent or reduced in many areas that previously (March, pre-flood) were colonized extensively (Figs. 13 and 14). Underwater surveys indicated that substrate area colonized by macrophytes and vertical dimensions of beds may have been reduced 50% to 60% by the flood. Prior to the flood, *Chara* was more abundant than *Potamogeton* in macrophyte beds, but the angiosperm was predominant at many locations during April (personal observation). Little exposed (no macrophytes) sand substrate occurred in the tailwater during March, but open sand areas were extensive during April. *Potamogeton* colonized the tailwater extensively by July; *Chara* occurred in only two locations (Fig. 15) and was absent in the *Potamogeton* beds, except for very sparse occurrence at -3.5 mi (personal observation). *Chara* colonized extensively in the tailwater by November and had become comparably or or more abundant than *Potamogeton* in many areas (Figs. 16, 17). *Egeria densa* was sparse in the tailwater prior to November (Arizona Game and Fish Department, unpublished data), when it occurred extensively (Fig. 18).

Macroinvertebrates

Mean total macroinvertebrate densities differed ($P < 0.001$) over all sampling periods. Interaction between transect location and sampling period was significant ($P < 0.02$). Total densities were similar ($P > 0.05$) during pre- and post-flood steady flows. Densities of individual taxa (Table 26) except oligochaetes differed ($P < 0.01$) over all sampling periods. Interaction between transect and sampling period occurred ($P < 0.01$) for all taxa except amphipods. Mean densities of *Gammarus lacustris* declined ($P < 0.01$) at -14 mi and -3.5 mi, but not at -4.1, mi during the 227 m^3s^{-1} flows following the flood. During July to November, mean amphipod densities at all sites were comparable to ($P > 0.05$) or exceeded ($P < 0.01$; -14 mi) pre-flood levels (Table 26).

Although mean densities of chironomid larvae differed ($P < 0.001$) among sampling periods, densities were similar ($P > 0.05$) during pre- and post-flood steady flows. Mean densities during July were greater ($P < 0.01$) than pre-flood levels at -4.1 mi and -3.5 mi but lower ($P < 0.001$) at -14 mi. During November, however, densities of larvae were below ($P < 0.001$) pre-flood concentrations at -14 mi and -3.5 mi (Table 26).

Mean densities of chironomid pupae differed ($P < 0.001$) among sampling periods but were similar ($P > 0.05$) during pre- and post-flood steady flows at -14 mi and -3.5 mi. Pupae were absent in pre-flood samples at -4.1 mi but occurred during April and July. During July to November, mean densities declined ($P < 0.001$) to or below pre-flood levels, and pupae were absent in samples from all locations during November (Table 26).

Mean snail densities differed ($P < 0.001$) among sampling periods but were comparable ($P > 0.05$) during pre- and post-flood steady flows at -14 mi and -3.5 mi and declined ($P < 0.05$) during post-flood steady discharge at -4.1 mi. During November, mean densities were greater ($P < 0.05$) than pre-flood levels at -4.1 mi and -14 mi and were similar ($P > 0.05$) to pre-flood levels at -3.5 mi (Table 26).

Densities of planarid flatworms differed ($P < 0.001$) among sampling periods and declined ($P < 0.01$) at -4.1 mi during post-flood steady flows. Flatworms were absent at -14 mi until July, and densities declined ($P < 0.001$) in July at -3.5 mi, compared to pre-flood steady flows. During July to November, mean flatworm densities were greater ($P < 0.001$) than pre-flood levels at -14 mi and -4.1 mi and similar ($P > 0.05$) to pre-flood concentrations at -3.5 mi (Table 26).

Table 23. **Mean (±SD) densities** of biomass (AFDW, mg/m²) and chlorophyll *a* (Chl *a*, mg/m²) for epilithon collected at -14 mi and -4.1 mi and for macrophytes collected at -3.5 mi at the 142 m^3s^{-1} flow elevation during 227 m^3s^{-1} steady flows in March (pre-flood) and April (post-flood) and during operational flows in July and November 1996, Glen Canyon tailwater.

	-14 mile		-4.1 mile		-3.5 mile	
	AFDW	Chl *a*	AFDW	Chl *a*	AFDW	Chl *a*
March	144 (63)	1,788 (446)	136 (48)	1,104 (697)	97 (35)	353(69)
April	161 (57)	1,106 (353)	100 (60)	669 (130)	0	0
July	162 (55)	1846 (752)	140 (86)	1322 (980)	0	0
November	97 (57)	858 (283)	108 (61)	673 (385)	52 (28)	287(49)

Table 24. Mean densities of dominant small/adnate and large/upright taxa and total diatom epiphytes from epilithon (number/mm²) collected at -14 mi and -4.1 mi and *Chara contraria* (number/mg AFDW) collected at -3.5 mi at the 142 m^3s^{-1} flow elevation during 227 m^3s^{-1} steady flows pre- (March 1996) and post-flood (April 1996), Glen Canyon tailwater. Post-flood densities for *C. contraria* reflect total loss of macrophytes from the sampling site.

		Densities	
	Diatoms	Pre-flood	Post-flood
Epilithon	Total	31,341	10,501
	Small/adnate	6,473	3,590
	Large/upright	20,808	4,767
C. contraria	Total	68,328	0
	Small/adnate	25,696	0
	Large/upright	26,280	0

Table 25. Relative frequencies (%) of dominant small/adnate and large/upright diatom epiphytes on periphyton collected at the 142 $m^3 s^1$ flow elevation from -14 mi, -4.1 mi (epilithon) and -3.5 mi (*Chara contraria*) during pre-and post-flood 227 $m^3 s^1$ steady flows, Glen Canyon tailwater. Post-flood samples at -3.5 mi reflect total loss of macrophytes from the site.

	Small/Adnate Forms			Large/Upright Forms		
Location	Species	Pre-Flood	Post-Flood	Species	Pre-Flood	Post-Flood
-14 mi	*Achnanthes minutissima*	9.8	19.6	*Diatoma vulgare*	45.2	17.8
	Cocconeis pediculus	3.1	7.6	*Synedra affinis*	8.6	1.3
	Achnanthes lanceolata	0	3.1	*Navicula tripunctata*	4.3	10.7
				Nitzschia frustulum	1.1	9.4
				Tabellaria fennestrata	1.9	4.9
				Rhoicosphenia curvata	0.6	4.5
Total for -14 mi		12.9	30.3		61.7	48.6
-4.1 mi	*Cocconeis pediculus*	14.1	26.0	*Diatoma vulgare*	34.3	21.5
	Achnanthes minutissima	6.7	0	*Tabellaria fennestrata*	5.9	0
				Navicula tripunctata	4.0	6.7
				Gomphonema olivaceum	3.7	0.2
				Rhoicosphenia curvata	2.5	16.2
Total for -4.1 mi		20.8	26.0		50.4	44.6
-3.5 mi	*Achnanthes minutissima*	22.0	0	*Synedra affinis*	15.2	0
	Cocconeis pediculus	6.8	0	*Tabellaria fennestrata*	5.3	0
				Nitzschia frustulum	4.5	0
Total for -3.5 mi		28.8	0		25.0	0

Table 26. Mean (±SD) densities (number/m^2) of benthic macroinvertebrates collected from the 142 m^3s^{-1} flow elevation at -14 mi, -4.1 mi and -3.5 mi, Glen Canyon tailwater, during March (pre-flood) and April (post flood) 227 m^3s^{-1} steady flows and during July and November 1996. G = *Gammarus lacustris*, O = oligochaetes, S = gastropods, CL = chironomid larvae, CP = chironomid pupae, T = planarid flatworms.

	G	O	S	CL	CP	T
-14mi						
Pre-flood	404.6 (±328.8)	41.4 (±30.0)	27.6 (±31.1)	3931.0 (±1605.3)	480.5 (±206.6)	0
Post-flood	121.8 (±114.65)	48.3 (±18.9)	32.2 (±17.0)	2763.2 (±1880.5)	703.4 (±389.9)	0
July	2046.0 (±481.7)	931.0 (±859.1)	95.8 (±40.4)	160.9 (±129.5)	57.5 (±99.5)	888.9 (±925.6)
November	5153.3 (1651.6)	92.0 (41.4)	118.8 (35.1)	95.8 (106.8)	0	15.3 (13.3)
-4.1mi						
Pre-flood	1331.0 (±619.6)	1354.0 (±604.8)	154.0 (±46.4)	114.9 (±76.2)	0	1802.3 (±610.6)
Post-flood	820.7 (±548.2)	3634.5 (±4574.2)	48.3 (±33.9)	416.1 (±328.1)	62.1 (±88.9)	579.3 (±273.5)
July	1379.3 (±69.9)	977.0 (±535.3)	137.9 (±69.9)	2444.4 (±1818.2)	636.0 (±445.2)	1578.5 (±693.1)
November	7835.3 (3473.1)	241.4 (50.1)	245.2 (35.1)	30.7 (13.3)	0	3632.2 (597.4)
-3.5 mi						
Pre-flood	1448.3 (±870.0)	4223.0 (±5502.6)	59.8 (±22.1)	310.3 (±197.6)	39.1 (±37.8)	1285.1 (±556.9)
Post-flood	512.6 (±872.9)	1519.5 (±1563.6)	87.4 (±49.2)	223.0 (±120.2)	80.5 (±69.5)	669.0 (±573.9)
July	444.4 (±162.7)	30.7 (±35.1)	7.7 (±13.3)	2796.9 (±1482.1)	398.5 (±110.4)	0
November	2532.6 (1700.3)	494.3 (267.3)	88.1 (28.9)	19.2 (23.9)	0	1103.5 (833.4)

Electrofishing

Mean lengths and weights of rainbow trout caught by electrofishing fixed transects differed ($P<0.05$) among sampling periods (Table 27). Trout caught during the post-flood 227 m^3s^{-1} steady flows had greater mean length ($P<0.001$) and mean weight ($P<0.05$) than those collected during pre-flood steady flows, but mean length and weight in August and November were similar to or higher than those in March (Table 27). During the post-flood steady flows, 10% fewer RBT were caught in the <152 mm size classes, and 10% and 20% more, respectively, were caught in the 152-305 mm and 305-406 mm size classes (Fig. 19). Total catches of ripe males during pre- and post-flood steady flows, respectively, were 88 and 17; 29 and 65 ripe females, respectively, were caught during the same periods. Length-frequency distributions in August were similar to those observed during pre-flood steady flows. During November, however, catch of RBT in the <152 mm size classes increased 30% and catch in the 152-305 mm size classes declined 24%, compared to pre-flood levels; catch of fish 305-406 mm decreased 4% (Fig. 19).

Catch per unit effort (CPUE) was about 25% lower during August and November than prior to the flood (Table 27). No consistent differences were apparent in CPUE of RBT among sampling transects, although CPUE declined during August and November at some sites (Table 28). No differences ($P>0.05$) were apparent during March to November for condition factor (weight x 10^5/length^3) (Table 27). Condition factors were similar to those observed in the tailwater prior to the experimental flows (AGFD, unpublished data). Sex ratio (female:male) during our study was generally about 1.2:1.

Flannelmouth suckers were caught intermittently and in low numbers during the 1,278 m^3s^{-1} flows (Table 29) and prior to and following the flood (Table 30). No effects of the flood were apparent on numbers caught or distribution within the reach. Catch per unit effort for RBT during the flood (Table 29) was lower than at other times (Table 27), but there was no indication of downstream displacement due to the flood (Tables 27, 28, 29).

Through August, normality indices of trout health and condition exceeded 90% and severity indices were below 0.05%, but normality and severity indices, respectively, were 87.4% and 1.43% during November. November indices were associated with increased frequencies of fatty livers (40.0%), frayed (5.7%) and clubbed (8.6%) gills and swollen pseudobranchs (37.1%). However, fish health data collected during November had an increased proportion of "snakey" trout ($K<0.7$) in the sample. During March to August, five "snakes" were analyzed for health (total fish analyzed = 94). During November, 18.0% (7/39) of trout examined for health were "snakes" (March = 3.4%, April = 8.6%, August = 3.3%). Proportion of "snakes" in all trout >350 mm collected by electrofishing during the study averaged about 12% (March = 12.7%; April = 13.6%; August = 10.2%; November = 11.5%). Mean condition factors of trout analyzed for health were: March 0.98, April 0.94, August 0.88, November 0.93.

The relative proportion of fish which probably had fed within a day or two (bile clear to straw-yellow) increased during each sampling period from March (73.3%) through August (93.3%) but declined slightly during November (85.7%). However, the percentage of RBT which likely had fed within the past 24 hr (gall bladder empty or partially full) declined from March (73.3%) to April (42.9%), August (33.0%) and November (25.7%). The percentages of RBT with 50%-100% coverage of pyloric caeca with fat increased from March (16.7%) to April (25.7%), declined in August (0%) and increased in November (14.3%) to near the pre-flood level. Mean total volume of ingested material differed ($P<0.01$) over all sampling periods but was unchanged ($P>0.05$) during the post-flood steady discharge (Table 31). Relative consumption of *Gammarus* ($P<0.001$), snails ($P<0.01$), chironomid pupae ($P<0.05$), *Cladophora* ($P<0.001$) and terrestrial insects ($P<0.001$) differed among sampling periods. No significant differences ($P>0.05$) occurred among sampling periods for relative volumes of other ingested items, and no significant differences ($P>0.05$) occurred in proportional consumption between pre- and post-flood steady flows. However, the proportional volume of ingested *Gammarus* increased during November, and relative volume of chironomid larvae and pupae were highest in March, lowest in November. Relative consumption of snails increased during August and November, and consumption of *Cladophora* declined about 85% during November, compared to other months. Terrestrial insects were consumed primarily during March and April. Fish eggs occurred in the diet during March and November, and terrestrial insects were consumed primarily during March (Table 31).

Gammarus, *Cladophora*, chironomid larvae and pupae and snails were frequently ingested over all months (Table 31). Frequencies of occurrence for snails and amphipods were lowest during April and highest during August and November. Fequencies of *Cladophora* and chironomid larvae and pupae were lowest during November. Occurrence of empty stomachs was more than twofold higher during April and November than during March and August.

Table 27 . Total catch (N), catch/min (CPUE) and mean lengths (mm), weights (g) and condition factors (K; ±SD) for rainbow trout caught by electrofishing in the Glen Canyon Dam tailwater, March-November 1996. Dam discharge during electrofishing: March, April = $227 m^3s^{-1}$; August = ca. $568 m^3s^{-1}$, November = ca. $227 m^3s^{-1}$.

Month	N	Length	Weight	CPUE	K
March	1,513	230	195	3.52	0.961 (0.217)
April	1,685	244	211	3.58	0.954 (0.209)
August	1,306	228	232	2.61	0.979 (0.311)
November	1,335	215	208	2.58	0.986 (0.335)

Table 28. Catch/min for rainbow trout caught by electrofishing in the Glen Canyon Dam tailwater to Lee's Ferry (fixed transects) and below the Paria River (opportunistic transects) March-November 1996. Dam discharge during electrofishing: March, April = $227 m^3s^{-1}$; August = ca. $568 m^3s^{-1}$, November = ca. $227 m^3s^{-1}$.

Transect	March	April	August	November
Fixed				
1	3.0	3.3	1.6	2.6
2	2.2	3.8	2.3	1.9
3	3.2	4.0	2.1	1.7
4	2.4	2.4	1.9	3.6
5	2.9	3.2	3.2	3.4
6	6.6	4.0	2.3	4.2
9	1.5	2.4	0.5	0.7
10	5.3	4.2	2.8	4.9
11	4.2	3.8	2.7	2.9
13	3.8	5.3	3.9	1.0
15	1.7	2.8	2.6	1.5
		Opportunistic		
PAR1	3.0	4.3	---	—
PAR2	2.6	3.5	---	—
PAR3	2.9	2.5	---	—

Table 29. Flannelmouth suckers (FMS) and rainbow trout (RBT) caught (N=total catch; CPUE=catch/min) by opportunistic electrofishing March 16-17 and April 1-2, Glen Canyon tailwater to Lee's Ferry, during 1,278 m^3s^{-1} discharge from the dam.

				Mean	
Month	Species	N	CPUE	Length (mm)	Weight (g)
March	RBT	90	1.5	328	319
	FMS	2	---	541	1856
April	RBT	118	1.3	285	321
	FMS	0	---	---	---

Table 30. Flannelmouth suckers caught (N=total catch) by electrofishing fixed transects, Glen Canyon tailwater to Lee's Ferry, March-November 1996. Dam discharge during electrofishing: March, April= 227 m^3s^{-1}; August=ca. 568 m^3s^{-1}, November =ca. 227 m^3s^{-1}.

Month	N	Mean Length (mm)	Mean Weight (g)
March	12	495	1,244
April	3	527	1517
August	3	482	1,128
November	8	480	1,260

Table 31. Frequencies of occurrence and mean proportional (±SD)and total (±SD) volumes (ml) of macroinvertebrates and other organic matter in stomachs of rainbow trout collected by electrofishing, Glen Canyon Dam tailwater, during 227 m^3s^{-1} steady flows prior to (March) and after (April) experimental flooding and during August (flows=ca. 568 m^3s^{-1}) and November (flows=ca. 227 m^3s^{-1}) 1996.

	March (n = 56)		April (n = 48)		August (n = 66)		November (n= 70)	
Food Item	% Frequency	% Volume	% Frequency	% Volume	% Frequency	% Volume	% Frequency	% Volume
Gammarus	57.1	22.3 (33.8)	47.9	27.3 (40.6)	72.3	28.7 (38.9)	67.2	55.2 (45.2)
Chironomid larvae	32.1	3.3 (13.7)	22.9	1.9 (8.1)	40.0	2.4 (6.1)	2.4	0.2 (1.5)
Chironomid pupae	44.6	12.3 (28.0)	35.4	6.1 (19.4)	29.2	7.4 (18.3)	7.1	2.1 (12.6)
Chironomid adult	3.5	0.6 (4.5)	0.0	0.0	4.6	3.2 (15.9)	4.3	4.1 (19.7)
Cladophora	48.2	34.9 (41.4)	35.4	28.2 (42.3)	54.0	39.1 (42.9)	10.0	5.5 (20.4)
Gastropods	12.5	1.2 (5.4)	4.1	0.1 (0.3)	23.1	8.4 (21.7)	28.6	4.6 (14.6)
Oligochaetes	3.5	0.0 (0.1)	6.2	1.7 (9.7)	1.5	0. (0.1)	0.0	0.0
Fish eggs	3.5	1.9 (13.4)	0.0	0.0	0.0	0.0	2.0	0.0 (12.6)
Fish remains	1.7	0.3 (2.2)	0.0	0.0	0.0	0.0	0.0	0.0
Terrestrial insects	21.4	8.5	10.4	1.4	1.5	0.2	1.4	0.0 (0.1)
Unidentified organic matter	12.5	2.0 (7.4)	6.2	4.0 (19.3)	4.6	1.6 (12.3)	25.7	3.5 (15.9)
Diptera (unknown; other than chironomid)	5.3	1.9 (13.4)	10.4	4.4 (16.8)	0.0	0.0	0.0	0.0
Empty stomach	10.7	---	25.0	---	9.0	---	22.9	---
Total Volume	3.0 (4.3)		3.0 (4.8)		4.3 (6.1)		1.5 (2.4)	

DISCUSSION

Lotic biota in the Glen Canyon tailwater varied spatially and temporally during the seven to eight month period following experimental flooding. Biomass (AFDW) densities of epilithon were unaffected following the flood, but chlorophyll *a* concentrations were reduced. In contrast, Biggs and Close (1989) reported that AFDW was more readily reduced than chlorophyll *a* by flooding. Impact of entrained sediment particles and shear stress imposed by elevated current velocities may dislodge attached algae (Peterson 1996, Steinman and McIntire 1990), but low sediment load in the tailwater (Stanford and Ward 1991) likely reduced negative impact of the flood on epilithon biomass. Epilithon standing stock is often reduced following flooding, but recovery may be rapid (Fisher et al. 1982, Lamberti et al. 1991, Scrimgeour and Winterbourn 1989, Steinman and McIntire 1990, Whitton 1970). Chlorophyll *a* densities in epilithon recovered to near or above pre-flood levels in July, and mean concentrations during March, July and November are consistent with seasonal trends previously observed in the tailwater (Ayers and McKinney 1996c).

Consistent with our results, other studies (Grimm and Fisher 1989, Peterson et al. 1994) reported a reduction in diatom epiphytes following flooding, and Robinson and Rushforth (1987) found that large/upright taxa were more adversely affected than small/adnate species. Small/adnate taxa typically dominate diatom epiphyte assemblages following severe scour events, and colonization by diatoms following flooding may occur rapidly (Peterson 1996, Peterson and Stevenson 1992, Power and Stewart 1987). Thus, the food base for macroinvertebrates (Angradi 1994, Blinn et al. 1992) in habitat colonized by *Cladophora* may be affected little by the changes in the diatom epiphyte community following flooding in the Glen Canyon tailwater.

Macrophytes provide habitat and food for macroinvertebrates (Hanson 1990, Menon 1969, Newman 1991, Pip 1978, Pip and Stewart 1976). Loss of macrophytes due to flooding in the tailwater reduced habitat and the food base for fish and macroinvertebrates. Bilby (1977), Power and Stewart (1987) and Barrat-Segretain and Amoros (1995) also reported macrophyte loss following flooding. Recolonization of the Glen Canyon tailwater by *Potamogeton* was extensive and began soon following flooding. Colonization by the angiosperm likely increased the habitat and food base for trout above that associated with exposed sand substrate (Angradi 1994, Persons et al. 1985, Sand-Jensen et al. 1989). *Potamogeton* hosts fewer diatom epiphytes than *Chara* in the tailwater (Blinn et al. 1994), but the angiosperm provides food and habitat for macroinvertebrates (Krull 1970, Menon 1969, Newman 1991, Pip 1978, Pip and Stewart 1976, Wollheim and Lovvorn 1996). *Chara* colonized extensively in the Glen Canyon tailwater within about seven months after the flood. Power and Stewart (1987) also reported that recolonization of denuded areas by *Chara* required several months in an Oklahoma stream

Effects of the flood on macroinvertebrate densities generally were similar in cobble and depositional habitat. Amphipod densities initially (pre- versus post-flood steady flows) were more negatively affected by the flood than those of other macroinvertebrates at both cobble and depositional sites. Densities of snails and flatworms declined during post-flood steady flows at only one cobble site and were unchanged in depositional habitat. Densities of these three taxa were equal to or greater than pre-flood levels in both habitat types by November, reflecting previously-reported (Ayers and McKinney 1996a, 1996b) seasonal patterns of change.

Concentrations of chironomid larvae and pupae were not reduced at any site during post-flood steady flows. However, Palmer et al. (1996) reported site-dependent changes in chironomid densities within 1-2 weeks after flooding. During July, larvae densities were below pre-flood concentrations at one cobble site but exceeded pre-flood levels on the other cobble site and in depositional habitat. By November, however, larvae were below pre-flood levels in both habitat types, and pupae were absent at all sites. In contrast to our results, Lamberti et al. (1991) reported that chironomids were particularly abundant within six months following floods during late winter.

Macroinvertebrate populations often are negatively impacted by flooding (Cobb et al. 1992, Giller et al. 1991, Lamberti et al. 1991, Meffe and Minckley 1987, Palmer et al. 1996, Scrimgeour and Winterbourn 1989) but recover rapidly (Fisher et al. 1982, Lamberti et al. 1991, Mackay 1992, McElravy et al. 1989, Meffe and Minckley 1987).

Effects of flooding on fish populations depend on frequency, timing and magnitude of the event (Harvey 1987, Seegrist and Gard 1972, Yount and Niemi 1990). Rainbow trout in the Glen Canyon tailwater spawn primarily during late fall and winter (Persons et al. 1985), and the young after hatching may remain in the gravel for a week to a month before emerging as free-swimming fry (cited in Kondolf et al. 1989). The greatest impact of flooding likely would occur when eggs still are in the gravel and when fry are emerging from the gravel (Seegrist and Gard 1972, Hanson and Waters 1974, Pearsons et al. 1992). Recovery of trout populations negatively affected by flooding may occur due to natural recruitment during the next year following spawning (Hanson and Waters 1974, Lamberti et al. 1991).

We observed little effect of flooding on relative abundance, condition factor or health of rainbow trout in the tailwater through the fall, and there was no clear evidence of downstream displacement of trout or flannelmouth suckers. Mean length and weight of RBT increased during post-flood steady flows but during August and November were similar to or greater than means prior to the flood. The severity index for health during November appeared to be high but may be related to spawning-related factors rather than departure from normal. The proportional catch by electrofishing of trout <152 mm declined, and that of size classes >152 mm increased, during post-flood steady flows. Catch of reproductively ripe trout also differed between the steady flow surveys, indicating a short-term effect of flooding on behavior or localized displacement of size classes and spawning fish. Smaller size classes may be more adversely impacted by flooding (Seegrist and Gard 1972, Harvey et al. 1987, Lamberti et al. 1991), but Gerking (1950) reported no effects of a severe flash flood in a small stream on length-frequency distributions of fish populations. Length-frequency distributions of trout in the Glen Canyon tailwater were similar to pre-flood levels during August, and size classes <152 mm increased during November, indicating strong fall recruitment of young-of-the-year fish into the population.

Discharge regime from Glen Canyon Dam may have influenced electrofishing success (Reynolds 1996). The lower CPUE during August possibly resulted from higher flows (ca. 568 m^3s^{-1}) during sampling and a brief but severe fluctuation in dam discharge (due to power failure) about 2 ½ weeks prior to electrofishing. Discharge on August 10 fell from 464 m^3s^{-1} to 66 m^3s^{-1} during 1800-1900 hr and was less than 142 m^3s^{-1} between 1900-2000 hr before rising rapidly to about 482 m^3s^{-1} (Bureau of Reclamation, unpublished data). Relative abundance of trout in deeper water during the August survey appeared to reduce effectiveness of electroshocking (personal observation). Flows during electrofishing in November were about 227 m^3s^{-1} but were preceeded by higher daily maxima and minima in discharge than was sampling during March pre-flood steady flows (Bureau of Reclamation, unpublished data).

Reduced distribution or abundance of submerged macrophytes in littoral zones of the reach also may have contributed to lower CPUE during August and November (Randall et al. 1996). However, CPUE during August and November were greater than or comparable to those during November 1991 to December 1995 in the tailwater (Arizona Game and Fish Department, unpublished data). Consistent with our results, long-term persistence of catostomids and other fishes was high in a small desert stream subject to frequent and intense flash flooding (Meffe and Minckley 1987).

The biological significance and cause of changes in the mesenteric fat and health severity indices during August or November are unknown, and additional data are needed to interpret the results. Although a lower mesenteric fat index indicates reduced feeding intensity and energy deposition, the index is somewhat subjective and can vary seasonally and between years (Goede and Barton 1990). Feeding frequencies, condition factors and food habits data in our study fail to correspond with change in the mesenteric fat index, and the high severity index during November may reflect spawning-related factors. Change in indices of fish condition and health can indicate departure from normal within a population, but comparisons need to be based on fish of the same age, strain, sex and season (Goede and Barton 1990).

Drift of macroinvertebrates typically increases during spates (Brittain and Eikeland 1988). *Gammarus* concentrations in the drift increased in the Glen Canyon tailwater during the post-flood steady flows (D.W. Blinn and J. P. Shannon, Northern Arizona University, unpublished data), and Scullion and Sinton (1983) reported increased chironomids in the drift following a flood. However, opportunistic feeding (Bres 1986) was not indicated by change in relative or total ingested items in our studies.

Numbers of RBT feeding within 1-2 days increased, but numbers feeding within 24 hr declined, from March to August and November. This likely indicates that trout were feeding at longer intervals, as well as consuming more total or larger (*Gammarus*, snails) food items, in August and November than during the spring months (Swenson and Smith 1973).

Prior to (April-July 1991) inception of the interim flow regime in 1993 (U.S. Department of Interior 1995), *Gammarus*, chironomids and snails comprised 90%-98% of the volume of animals eaten by trout in the tailwater (Angradi et al. 1992). We found that these taxa comprised 35% and 68%, respectively, of animals ingested during the pre- and post-flood steady flows, about 70% during August and 100% during November. Throughout the study, *Gammarus* comprised a greater proportion of trout stomach contents than did chironomids or snails, but frequencies of occurrence of amphipods and chironomids generally were similar, except during November. Consistent with previous studies in the tailwater (Angradi et al. 1992), *Gammarus*, chironomids and *Cladophora* comprised most (64%-91%) of the volume of ingested items during all months. *Cladophora* and epiphytic diatoms may provide nutritional benefit for trout (Leibfried 1988). The filamentous alga was prominent in trout stomachs during all months, but consumption was least during November, likely reflecting seasonally lower drift concentrations (Ayers and McKinney 1996c).

CONCLUSIONS AND MANAGEMENT CONSIDERATIONS

Work Task 4.1--We reject the null hypothesis. Condition factors and densities of rainbow trout were unaffected by the experimental flood through fall. Diet of trout was unaffected during the week following the flood, but diet and feeding indices varied among sampling periods. Compared to pre-flood levels, frequencies of occurrence and proportional volumes of *Gammarus* and snails were higher in trout stomachs during August-November, but those of chironomid pupae and terrestrial insects were lower. Differences in feeding indices and diet following the flood may reflect seasonal trends in trout behavior, drift and standing stock of lotic biota, but we are unable to discount possible effects of the flood. Differences in mesenteric fat and severity indices may indicate changes in trout health following the flood, but we are unable to determine whether changes are flood-related or of biological importance. Length-frequency distributions and sex ratios of ripe trout were altered during the week following the flood but returned to pre-flood parameters by August. Strong recruitment of young-of-the-year trout into the tailwater population occurred during November. Little or no downstream displacement of fish was apparent due to the experimental spate.

Work Task 4.3--We reject the null hypothesis. Densities and distributions of benthic macroinvertebrates were altered by the flood. Temporal, spatial and taxonomic differences occurred in effects of the flood and subsequent recovery of the zoobenthos through the fall.

Work Task 4.4--We reject the null hypothesis. Biomass (AFDW) of epilithon was unaffected by the flood, but densities of chlorophyll *a* were reduced. Standing stock of submerged aquatic macrophytes was severely impacted.

Work Task 4.5--We reject the null hypothesis. Densities of diatom epiphytes on epilithon were reduced, and composition of diatom assemblages was altered, favoring small/adnate taxa. Diatom epiphytes associated with macrophytes were lost, and composition and density of submerged aquatic macrophytes were altered, due to the flood

Work Task 4.6--We reject the null hypothesis. Relative abundance and distribution of submerged aquatic macrophytes were reduced and species composition was altered following the experimental flood. *Potamogeton* initially re-colonized extensively following the flood, but *Chara and Egeria* colonized throughout the reach by November.

Flooding may initiate a complex sequence of adjustments extending over prolonged periods within the lotic biotic community of impounded rivers. Moreover, timing, frequency and intensity of flooding potentially influence the impact of spates on lotic biota. Spatial, temporal and taxonomic variability of the lotic system are important considerations in developing paradigms of regulated flood releases. Impacts of flooding on the hyporheic zone of regulated rivers are unknown but likely influence the lotic ecosystem and recovery and resilience of biota (Hendricks 1993, Hendricks and White 1991, Stanford and Ward 1993, Stanley and Boulton 1993, White 1993) and merit consideration in designing investigations on effects of experimental flooding. Hyporheic zones are important to fish reproduction and as habitat for zoobenthos and likely affect nutrient cycling and system metabolism (Valett et al. 1990). Further research and long-term monitoring are needed to evaluate impacts of flooding on and the recovery and resilience of the lotic community in the Glen Canyon Dam tailwater.

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