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AQUATIC FOOD BASE RESPONSE TO THE 1996 TEST FLOOD BELOW GLEN CANYON DAM, COLORADO RIVER, ARIZONA

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Abstract. We examined the impact of the 1996 test flood released from Glen Canyon Dam (GCD) on the aquatic food base in the Colorado River through Grand Canyon National Park, Arizona, USA. Benthic scour and entrainment of both primary and secondary producers occurred at all study sites along the 385-km river corridor. The majority of the organic drift occurred within the first 48 h of the test flood with the arrival of the hydrostatic wave. Recent macrophyte colonizers (*Chara, Potamogeton,* and *Elodea*) of fine sediment in the tailwaters were scoured from the channel bottom, with recovery to pre-flood estimates within 1–7 months depending on taxa. Macroinvertebrates and filamentous algae recovered within three months depending on taxa. The test flood removed suspended particles from the water column and increased water clarity, which enhanced benthic recovery. The test-flood hydrograph was designed primarily as an experiment in sand transport and occurred during a period of sustained high releases from GCD starting in June 1995 due to above-average inflow into Lake Powell. We discuss the implications of the hydrograph shape, pre- and post-riverine conditions, and the slow response time of biological resources for design of aquatic ecosystem experiments.

Key words: adaptive management; aquatic food base; Cladophora; *Colorado River; desert biome; discharge; disturbance; flood; Glen Canyon Dam; macroinvertebrates; organic drift; river regulation.*

Introduction

Variability in river discharge can affect the structure and function of benthic communities by altering the stability and availability of substrata (Power et al. 1988, Cobb et al. 1992), water velocity (Peterson and Stevenson 1992), aerial exposure (Blinn et al. 1995), light quantity (Duncan and Blinn 1989), and water quality (Scullion and Sinton 1983). Regulated rivers eliminate seasonal hydrographic changes and remove important life history cues for some aquatic insects, thereby reducing biodiversity (Power et al. 1988). Alterations in hydrologic patterns also modify community interactions that have developed over evolutionary time (Resh et al. 1988).

Statzner and Higler (1986) contend that changes in stream hydraulics are the major determinants of benthic invertebrate distribution, based on the intermediate disturbance hypothesis as outlined for lotic systems by Ward and Stanford (1983) and Reice and co-workers (1990). Under extreme discharge conditions (i.e., spring run-off), species numbers are relatively low, whereas during highly inconsistent conditions (i.e., zones of hydraulic transition) species richness is relatively high due to an overlap of species inhabiting the fringes of their niche requirements. These same hydraulic criteria may operate in the regulated Colorado River if flooding frequency is increased. Conversely, the exotic post-dam aquatic communities may not respond similarly to natural streamflow conditions because they now flourish under very unnatural flow regimes.

Studies in smaller lotic ecosystems in the Southwest have revealed the importance of floods in nutrient availability, particularly nitrogen (Grimm and Fisher 1986). Spates increase nutrient concentrations through hyporheic upwelling and run-off (Peterson and Grimm 1992). Particulate organic matter can also be released into the water column from the floodplain, transported downstream, accumulated in depositional zones, and mineralized for assimilation following high flows (Elwood et al. 1983). The flood pulse concept (Junk et al. 1989) describes the role of periodic floods in floodplain rivers and the subsequent organic enrichment and increase in habitat variability as the floodplain slowly drains following the flood. However, the Colorado River through Grand Canyon is a deeply incised channel with a minimal floodplain and does not allow for retention of floodwater.

The structure of the benthic community in the Colorado River through Grand Canyon has been altered by the construction of Glen Canyon Dam (GCD)

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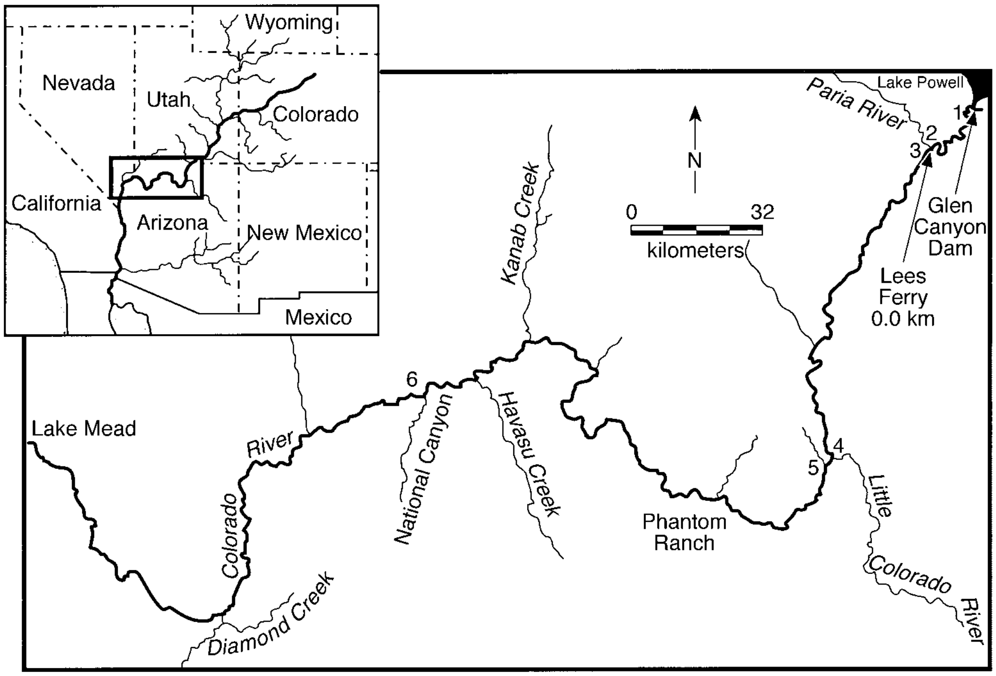

FIG. 1. Map of the Colorado River study area between Glen Canyon Dam and Lake Mead. General locations of collection sites are numerically listed along the river corridor. In numerical order these sites are named: 1, Glen Canyon Gage (River kilometer [Rkm] − 23.2); 2, Lees Ferry (Rkm 0.8); 3, Two-Mile Wash (Rkm 3.1); 4, Little Colorado River Island (Rkm 109.6); 5, Carbon Creek (Rkm 109.6); and 6, Lava Falls (Rkm 292.8).

through changes in river discharge, organic budget, suspended sediments, and water temperature (Blinn and Cole 1991, Stevens et al. 1997*b*). At present only discharge can be directly managed. Higher baseflows, reduced peak flow, and hourly fluctuation rates are the essential components of the selected discharge criteria from GCD as defined by the environmental impact statement process (U.S. Bureau of Reclamation 1995, Benenati et al. 2000). A similar reduction in flow regime implemented on the Patuxent River, Maryland, caused a doubling in benthic macroinvertebrate density and improved community condition (Morgan et al. 1991).

Construction and operation of Glen Canyon Dam (GCD) has created a food base alien to the desert Southwest. The food base community changes in composition and biomass with distance from the dam due to tributary release of suspended sediments (Blinn and Cole 1991, Stevens et al. 1997*b*). Discharge from GCD is stenothermic, averaging 10°C year-round, and is virtually free of suspended material, with water clarity routinely exceeding Secchi depths of 7 m in the tailwaters (Shannon et al. 1996*a*). Increases in water temperature are minimal through the 385-km study site, with the greatest increase in western Grand Canyon (≤17°C in early summer). Stevens et al. (1997*b*) estimated that an additional 520 km would be required to obtain the pre-dam annual high of 28°C. This protracted effect of hypolimnetic water released from GCD is due to the relatively large flow volume, confined channel, and reduced surface-area-to-volume ratio as the river traverses this seasonally hot, arid region of northern Arizona.

Tributary input of suspended sediments effectively alters the benthic community below the confluence of the Paria River, 28.1 km below GCD and 2.5 km below Lees Ferry, which is designated 0.0 km (Fig. 1). The Little Colorado River (98.6 km) also contributes seasonally high loads of suspended sediments. Average annual sediment input from these two tributaries is 8.25 $\times 10^6$ Mg, with the Paria River contributing one third of this amount. The Paria River has an average baseflow of only 0.77 m^3/s (Andrews 1991). This is an atypical example of a second order stream significantly altering the aquatic community of a fourth or fifth order river by reducing water clarity. Annual median discharge from GCD is 345 m^3/s (Stanford and Ward 1991); this can dilute the suspended sediments but not without negative consequences to the benthos. The high suspended loads of the Paria and Little Colorado rivers result from the erosion of soft sedimentary strata common on the arid Colorado Plateau (Beus and Morales 1990).

The Colorado River Management Plan in Grand Canyon National Park (NPS 1989) states that its resource management goals are "to preserve the natural resources and environmental processes of the Colorado River corridor and the associated riparian and river environments . . . (and) to protect and preserve the river corridor environment'' (NPS 1989:9). The Environmental Impact Statement (U.S. Bureau of Reclamation 1995) on the operation of GCD identified the aquatic food base as an ''indicator resource'' and important habitat for wildlife. Wildlife linked directly to the aquatic food base include native and nonnative fish, insectivorous birds and bats, reptiles, and waterfowl (Carothers and Brown 1991, Stevens et al. 1997*a*). Indirect links to the aquatic food base include endangered Peregrine Falcons feeding on waterfowl, insectivorous birds and bats, as well as Kingfishers, Great Blue Herons, Osprey, and Bald Eagles preying on fish. In response to the adaptive management guidelines from the GCD Environmental Impact Statement we investigated the impact and response of the aquatic food base from the 1996 test flood in the Colorado River below GCD by evaluating the following parameters: underwater light intensity, water quality, benthic standing mass of primary and secondary producers, and the biomass and composition of organic drift.

Materials and Methods

Study site

The cold and vacillating clear water habitat has selected for aquatic organisms normally found in nearctic regions such as various Chironomidae, *Simulium arcticum* complex, oligochaetes (including Lumbricidae, Lumbriculidae, Naididae, and Tubificidae), and an introduced amphipod *Gammarus lacustris* (Blinn and Cole 1991, Stevens et al. 1997*b*, Pomeroy et al. 2000). Recent colonizers since 1994, possibly as a result of reduced discharge variability, include Trichoptera (*Hydroptila arctia*, *Rhyacophila* spp., *Hydropsyche oslari*, and Limnephilidae), Diptera, (*Bibiocephala grandis*, *Wiedemannia* spp.), Ephemeroptera, (*Baetis* spp.), Coleoptera, (*Microcylloepus* spp.), Planariidae, and Hydracarina. Based on Merritt and Cummins (1984), these macroinvertebrates represent three functional feeding guilds: detritivores, filter feeders, and grazers.

Grazing macroinvertebrates consume epiphytic diatoms that colonize *Cladophora glomerata*, other filamentous algae, and aquatic macrophytes (Blinn and Cole 1991, Shannon et al. 1994). Recently *Cladophora* has been replaced seasonally in the tailwaters of GCD by other algal taxa including: Chlorophyta, (*Mougeotia* spp., *Oedogonium* spp., *Spirogyra* spp., *Stigeoclonium* spp.), Rhodophyta, (*Batrachospermum* spp., *Rhodochorton* spp.), a diatom mucilage matrix and the cyanobacterium, *Tolypothrix* spp. (Benenati et al. 1997). Benenati et al. (1997) suggested that changes in phytobenthos have resulted from an interaction between high inflow into upper Lake Powell which provided consistently high flows from GCD, lowered the specific conductance of lake water, and reduced nutrient concentrations. Soft bottom habitats in the tailwaters have been colonized by macroalgae and aquatic macrophytes (*Chara contraria*, *Potamogeton pectinatus,* and *Elodea* sp.) since modified flows have been released from GCD (Patten et al. 2001).

Discharge during the collection period ranged from 142 to 708 m^3/s, except for the test-flood peak of 1275 m^3/s. Discharges from GCD averaged $\leq$450 m^3/s, with minimal daily or monthly fluctuations from June 1995 to September 1996 as a result of above average inflow into Lake Powell, returning to fall fluctuating flows (227–424 m^3/s) in October.

Water quality

Water quality measurements of temperature (°C), specific conductance (mS), dissolved oxygen (mg/L), and pH were taken with a Hydrolab Scout 2 (Hydrolab, Austin, Texas) at the time of each sampling at Lees Ferry during the test flood and at all other collections. Water transparency was measured with a Secchi disk. We monitored light intensity at Lees Ferry and Carbon Creek during the test flood with submersible Onset data loggers (Onset HOBO, Pocasset, Massachusetts). These instruments were placed at a depth of 50 cm throughout the flood to measure light intensity at a uniform depth.

Benthic collections

Sampling was conducted in October 1995 and during March, June, and October of 1996 at four sites (0.8, 3.1, 109.6, and 326.4 km) in both pool and cobble habitats (Fig. 1). Sites were selected in conjunction with fish collection areas and also bracketed the two main tributaries with an additional site in western Grand Canyon. Test-flood collections were taken during pre- and post-flood steady 227 m^3/s flows and 2 and 6 mo after the Spike Flow (SF). In addition, 1 wk and 1 mo post-flood benthic collections were made at Lees Ferry Cobble (Rkm 0.8) and Two-Mile Wash (Rkm 3.1). Yount and Niemi (1990) reviewed 50 disturbance/recovery investigations and found that ~3 mo were required for complete recovery in lotic systems from spates. We based our collection intervals on this assumption.

Peterson or Petite Ponar dredges (Petite Ponar, Saginaw, Michigan) were used in pool habitats and Hess substrate samplers were employed on cobble bars. Six cobble and 12 pool samples were taken for abundance and mass determinations from transects established in 1990 (Stevens et al. 1997*b*). All samples were placed on ice and processed within 24 h. At the time of collection we recorded: depth, current velocity, relative distance to shore, time of day, and the discharge both estimated on site from local landmarks and verified from USGS gaging station data.

Biotic samples were sorted into the following 11 categories: *Cladophora glomerata,* cyanobacteria algal crust (*Oscillatoria* spp.), miscellaneous algae, detritus, chironomids, simuliids, *Gammarus lacustris,* gastropods, lumbriculids and tubificids (Oligochaeta), and miscellaneous macroinvertebrates. Each category was oven-dried at 60°C to a constant mass. Ash-free dry mass (AFDM) conversions were estimated from dry mass to AFDM regression equations. We calculated an error of ±0.04 g AFDM per 100 samples composed primarily of very fine particulate organic matter (detritus). Quality control calculations based on 1208 samples determined an overall error rate of 1.1% for AFDM estimates.

Sediment (~500 g) was collected at pools sites with either a Peterson or Petite Ponar dredge to compare test-flood effects on sediment clast size. Samples were oven-dried at 60°C and mechanically sieved for percentage clast size using the Wentworth scale: gravel, coarse sand, sand, and silt/clay (Welch 1948). These data were collected in order to indicate scour and/or deposition caused by the test flood.

Upper tailwater (GCD to the Paria River) fine sediment habitats were evaluated for macrophyte composition and cover at 14 sites at the following intervals: March, April, July, and November 1996. Ordinal values (OV) were assigned for relative abundance: OV1 = low vertical growth, patchy, and sparse; OV2 = moderate vertical growth, occasionally patchy; and OV3 = higher vertical growth, extensive, and generally no patchiness.

Organic drift collections CPOM

Nearshore surface drift samples (0–0.5 m deep) were taken at each pool site and at Glen Canyon Gage (Fig. 1), during each trip for coarse particulate organic matter (CPOM). Collections were made with a circular tow net (48 cm diameter opening, 0.5 mm mesh) held in place behind a moored pontoon raft or secured to the riverbank. Sampling times were staggered across the test-flood hydrograph so that a particular parcel of water would be sampled at all sites ($n = 336$). CPOM collecting during the test flood occurred on the first and last days of the pre-and post-steady flows, as the hydrostatic wave arrived at each site, the initial pulse of water from Lake Powell and three times during the high steady flow period. Samples were placed on ice and processed live within 48 h and sorted into seven categories including: *G. lacustris*, chironomid larvae, simuliid larvae, miscellaneous invertebrates, *C. glomerata*, miscellaneous algae/macrophytes, and detritus. Miscellaneous invertebrates included lumbriculids, tubificids, physids, trichopterans, terrestrial insects, and unidentifiable animals. Detritus was composed of both autochthonous (algal/bryophyte/macrophyte fragments) and allochthonous (tributary upland and riparian vegetation) flotsam. Invertebrates were enumerated, oven-dried at 60°C, weighed, ashed (500°C, 1 h), and reweighed.

Current velocity was measured for volumetric calculations (mass·m^{-3}·s^{-1}) using a Marsh-McBirney electronic flow meter (model 201D, Marsh-McBirney, Gaithersburg, Maryland). The duration of all drift collections ($n = 411$) averaged 1.4 min (SE ± 0.06) with an average of 9.2 ± 0.5 m^3 of water sampled through nets. The seemingly low duration and volume of water filtered was due to the enormous amount of organic material drifting during the test flood. Had the sets not been limited to a few seconds in duration, the nets would have lost their effectiveness in collecting drift and samples would have been too large to process in a timely manner. The standard sampling error was within ±10% of the estimated mean total drifting mass (0.218 ± 0.024 g·m^{-3}·s^{-1}; Culp et al. 1994); therefore, collections were assumed to be consistent and representative of the study site.

We tested the hypothesis that organic drift was uniformly distributed across the river channel at Lees Ferry with simultaneous collections at two locations at the surface and at a depth of 3 m on 20 November 1995. Using the same drift nets as described above, two crews simultaneously made 25 collections at each location and depth ($n = 100$). Estimates of total drifting organic material were made by drying the entire sample at 60°C, combusting for 1 h at 500°C, and calculating ash-free dry mass (AFDM). Current velocity and duration of each set were recorded for volumetric calculations with the units reported as mg AFDM·m^{-3}·s^{-1}. Independent-samples t test indicated no significant differences in organic drift between sites at either the surface (4 ± 5 SD vs. 7 ± 5 mg·m^{-3}·s^{-1}; $P = 0.07$) or at a 3 m deep (7 ± 6 vs. 7 ± 5 mg·m^{-3}·s^{-1}; $P = 0.9$). Nor was there a significant difference at either depth between sites ($P = 0.1$). From this analysis we accept the hypothesis that single location collections are representative of the entire channel. This is probably the result of a restricted channel, which is common in the Colorado River below GCD. Surface collections had the most variability, possibly due to wind and erratic surface currents.

Drift samples were analyzed for size fractions after dry mass was obtained. Material from each collection interval and site was dry sieved into <1 mm, 1–10 mm, and ≥10 mm size fractions. Each sample was gently shaken by hand for 30 s, which allowed for the separation of size fractions without particulate degradation (Shannon et al. 1996*b*). This method was examined for accuracy by sieving known samples for 15, 30, and 45 s ($n = 12$). The 30-s sample had <3% error in mass. Precision was defined by sieving the same sample three times and we found <5% error in mass ($n = 4$). The errors were randomly distributed across the size fractions.

Organic drift collections FPOM

Fine particulate organic matter (FPOM) was collected during the test flood at the same time as CPOM. Surface drift collections (0–0.5 m deep) were made with a circular tow net (30 cm diameter opening, 153 μm mesh) held in place behind a moored pontoon raft or secured to the riverbank. Samples were preserved in 70% ETOH and sorted in the laboratory with a dissecting microscope into the following categories for biomass: (1) zooplankton; Copepoda, (Calanoida, Cyclopoida, Harpacticoida), Cladocera, Ostracoda and (2) miscellaneous zooplankton; small Chironomidae, Oligochaeta, *G. lacustris*, Tardigrada, etc. Samples were filtered through a 1-mm sieve to remove coarse particulate organic matter (CPOM). Depending on zooplankton density, samples were sorted in their entirety or were split into 2-, 5-, or 10-mL subsamples from a 100-mL dilution. Three subsamples were taken from split samples and these values were averaged and extrapolated for the entire sample.

Zooplankton was sorted into vials for dry mass estimates, then converted to ash-free dry mass (AFDM) using a regression equation. Densities for all zooplankton categories were also recorded. The remaining organic material was filtered onto glass microfiber filters (Whatman GF/A, Whatman, Clifton, New Jersey) with a Millipore Swinex system. These filters were then oven-dried at 60°C and combusted for 1 h at 500°C to obtain an AFDM for all detritus. The condition, reproductive state, and presence of nauplii were documented. Volumetric calculations, mass·m^{-3}·s^{-1}, were determined in the same fashion as CPOM drift.

Large flotsam

Our CPOM sampling did not include large flotsam (>0.1 m) that was common during the up-ramping and during the first couple of days of 1274 m^3/s test flood. Understanding the role of large flotsam is important in the overall context of the flood which is attempting to return some aspects of the pre-impoundment condition. Large woody flotsam is a primary source of carbon above Lake Powell today (Haden et al. 1999) and was probably an important pre-dam organic source. In an effort to quantify this portion of the organic budget we examined interval photographs from the Grand Canyon beach survey program taken during the test flood for large CPOM (M. Manone, *personal communication*). Cameras that showed the complete river channel with a clear view not obstructed by rapids or canyon shadows were selected at about every 35 km, including km 12.8, 88.0, 166.4, 195.7, 232.8, 275.5, and 323.2. While viewing each frame on CD-ROM, which was enlarged to the best resolution possible, every noticeable particle of flotsam was scored. The location and time of the picture taken was compared to the test-flood hydrograph so the scores could be placed in relation to other drift collections.

Statistical analyses

Multivariate analyses of variance (MANOVA) were used to analyze categorical predictor variables (physical parameters) against multiple response variables (mass estimates of biotic categories) for significant temporal and spatial trends for both benthic and organic drift patterns ([ln + 1]-transformed data). Influence of the test flood, including pre- and post-collections, on benthic and organic drift estimates within collection sites were analyzed with the Kruskal-Wallis test. Ordinal ranks for macrophyte cover were analyzed with Kruskal-Wallis among sampling periods, while 227 m^3/s flows were compared with the Mann-Whitney *U* test. All calculations were performed with SYSTAT Version 5.2 computer software (SYSTAT 1992).

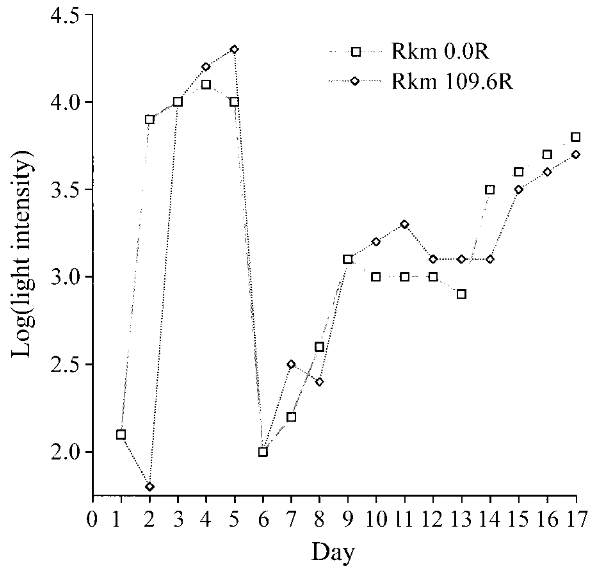

FIG. 2. Log of light intensity (measured in lumens per square meter) in the Colorado River at Lees Ferry (Rkm 0.0R [R following number refers to river right looking downstream]) and below the Little Colorado River (Rkm 109.6R) at 0.5 m depth prior to, during, and one week after the test flood (TF) below Glen Canyon Dam, Arizona. Day sequence on *x*-axis begins on 21 March and ends on 6 April 1996. Discharge at Lees Ferry for each day was as follows: day 2, five pre-227 m^3/s; day 6, 12 1274 m^3/s; day 13, 16 post-227 m^3/s. Values for the lower station were moved one day to the left because of lag time for the hydrostatic wave.

RESULTS

Water quality

Water clarity was the only water quality parameter monitored during the flood that varied outside of typical patterns (Shannon et al. 1996*a*, Stevens et al. 1997*b*). Light intensity measured at Lees Ferry and below the Little Colorado River revealed a similar pattern of diminishing light intensity as the test-flood hydrograph reached peak flow and then increased as the peak flow persisted (Fig. 2). The similarities in light intensities between sites, even though they are almost 110 km apart, is a reflection of how this river responded to the test flood. The reduction in light intensity 2 d

TABLE 1. Results of multiple analysis of covariance comparing pre- and post-flood benthic mass in the Colorado River through Grand Canyon in pool and riffle habitats for March (1995 and 1996) and June (1994 and 1996) collections.

Source	Wilks' lambda	Approximate *F* statistic	df	*P*	Response variable
Riffle habitats (March)					
Trip	0.6	6.8	11, 125	<0.0001	A,O,B,I
Site	0.6	7.2	11, 125	<0.0001	C,A,M,G,S,L,I
Pool habitats (March)					
Trip	0.9	2.2	11, 263	0.0162	D
Site	0.9	2.5	11, 263	0.0063	C,A,S,T
Riffle habitats (June)					
Trip	0.7	6.2	11, 125	<0.0001	A,D,M,B,L,T,I
Site	0.6	8.4	11, 125	<0.0001	C,A,M,G,S,B,T
Pool habitats (June)					
Trip	0.9	1.68	11, 263	0.07	M
Site	0.8	5.6	11, 263	<0.0001	D,M,I

Notes: Predictor variables of collection trip date covaried by collection site and were analyzed against response variables of biotic categories. Taxonomic categories include: *Cladophora* (C), *Oscillatoria* (O), miscellaneous algae/macrophytes (A), detritus (D), chironomids (M), *Gammarus* (G), gastropods (S), simuliids (B), lumbriculids (L), tubificids (T), and miscellaneous macroinvertebrates (I). Only significant univariate response variables are listed ($P < 0.04$). Overall Wilks' lambda, trip and site, was significant ($P < 0.0001$).

prior to the flood resulted from a spate that influenced the entire river corridor (Fig. 2). During the post-flood at a 227 m^3/s discharge, light intensity was increasing over time at both sites. Secchi depths, recorded at Lees Ferry, followed the same inverse relationship to discharge with a return to pre-flood depths by the end of the 1275 m^3/s release.

Water temperature released from GCD measured ~1 km downriver at Glen Canyon gage ranged from 9.1° to 9.5°C and pH ranged from 7.3 to 7.8. Dissolved oxygen (DO) concentrations at Glen Canyon gage during the pre-227 m^3/s were 8.8 mg/L at 86% saturation. As water was released through the four bypass tubes (~400 m^3/s) aeration increased the DO concentration to 13.8 mg/L, exceeding saturation at 122%. Conductivity increased from 0.71 mS in February at Glen Canyon gage to 0.87 mS during the test flood and returned to 0.72 mS by October.

Influence of test flood on sediment clast size in channel

A comparison of sediment clast composition during pre-flood (March) and post-flood (June) from five pool sites revealed that the flood removed silt from all sites and sand (very fine, fine, and medium) from Lees Ferry, exposing gravel. Coarse sand, including very coarse, decreased at all sites below Lees Ferry; it is unknown if it was buried with sand or scoured. This pattern explains the increase in tubificids in drift samples and the decrease in chironomid mass in pools, as we have found a significant positive relationship between silt/clay and macroinvertebrate biomass in pools (Blinn et al. 1994).

Sediment clast composition in pools collected in October 1996 showed that post-flood changes were site specific. At Lees Ferry the percentage of very coarse sand and sand both increased, while silt and gravel decreased. Sediment composition at Nankoweap and Tanner remained unchanged and were 100% sand. The Kanab Creek pool site (Rkm 203.4L [L refers to river left looking downstream]) was 100% gravel due to a flash flood from an adjacent drainage. The Spring Canyon (Rkm 326.5R [R refers to river right looking downstream]) pool site had more than regained the silt fraction lost to the test flood.

Benthic patterns: pre-flood

Discharges from Glen Canyon Dam (GCD) from June 1995 through the test flood were at the upper limits of allowable discharge. A comparison of the benthic community between March 1995 and March 1996 indicated an overall significant difference between these two periods for both riffle and pool habitats (Table 1). Evaluating the differences between these two periods is important in understanding the impacts of the test flood because the March 1996 trip established our system-wide baseline. We determined an overall significant difference between those two periods and for riffle habitats, but pools only varied significantly between sites and not between trips (Table 1).

Biomass in pools and riffles during March 1995 and March 1996 revealed a system-wide impact of a wetter than normal winter of 1995 (Table 1). Detrital loads in pools decreased by ~90% from March 1995 to March 1996 (Table 2). We observed evidence of spates or debris flows from every perennial tributary from Nankoweap Creek to Diamond Creek during our March 1995 monitoring trip (Shannon et al. 1996*a*). An influx of woody debris from these events, coupled with high discharges the following year, accounted for the removal of material by March 1996. In riffle habitats, *Oscillatoria* spp., miscellaneous algae/macrophytes/bryophytes (MAMB), and miscellaneous macroinver-

TABLE 2. Average system-wide benthic mass for pre-flood estimates from March 1996 and post-flood estimates from June 1996 in the Colorado River through Grand Canyon, for pool and riffle habitats.

Habitat	Taxonomic category	Non-flood Date	Non-flood AFDM†	Flood Date	Flood AFDM†
Pool	detritus	Mar 95	55.0 (32.6)	Mar 96	4.5 (1.7)
Riffle	*Oscillatoria*	Mar 95	0.244 (0.060)	Mar 96	3.123 (1.003)
	MAMB	Mar 95	0.215 (0.002)	Mar 96	8.994 (3.194)
	simuliids	Mar 95	0.022 (0.012)	Mar 96	0.006 (0.004)
	MM	Mar 95	0.005 (0.097)	Mar 96	0.025 (0.009)
Pool	chironomids	Jun 94	0.106 (0.012)	Jun 96	0.0001 (0.0001)
Riffle	MAMB	Jun 94	1.5 (1.4)	Jun 96	8.33 (3.46)
	detritus	Jun 94	1.22 (0.39)	Jun 96	8.45 (2.85)
	lumbriculids	Jun 94	0.146 (0.065)	Jun 96	0.037 (0.19)
	chironomids	Jun 94	0.093 (0.051)	Jun 96	0.08 (0.03)
	simuliids	Jun 94	0.005 (0.002)	Jun 96	0.014 (0.002)
	tubificids	Jun 94	0.012 (0.006)	Jun 96	0.045 (0.014)
	MM	Jun 94	0.024 (0.008)	Jun 96	0.113 (0.050)

Notes: June 1994 and March 1995 represent non-test-food patterns for comparison. All biotic categories listed are significantly different between trips ($P < 0.04$). MAMB = miscellaneous algae/macrophytes/bryophytes, and MM = miscellaneous maroinvertebrates.

† Values for ash-free dry mass (AFDM) estimates are expressed as grams per square meter with one standard error in parentheses.

tebrate (MM) AFDM estimates were all significantly higher in 1996 than 1995 collections (Table 2). However, estimates of simuliid larvae/pupae mass were significantly lower (~80%) during March of 1996 (Table 2). The biomass of the cyanobacterium, *Oscillatoria* spp. was more than 12-fold higher in 1996 over 1995, probably because we were sampling higher in the channel due to high flows. It is in the lower varial zone that *Oscillatoria* thrives with its ability to withstand periodic desiccation by storing moisture in its silt/clay matrix (Shaver et al. 1998).

Biotic categories also differed significantly by site between March 1995 and 1996, with pools being more resistant to annual change than riffles (Table 1, Fig. 3). The shift in dominance from the filamentous green alga *Cladophora glomerata* to miscellaneous algae and MAMB at Lees Ferry is noteworthy when comparing sites between years. MAMB also increased below the Little Colorado River confluence. Chironomid mass increased at many lower Grand Canyon sites and was less variable in collections during March 1996 than in March 1995. *Gammarus lacustris* mass showed an overall decrease in 1996 compared to March 1995 AFDM estimates except at Two-Mile Wash (km 3.1) and Little Colorado River Island (km 98.6).

Benthic patterns: during and post-flood

A comparison of benthic biomass in pool and riffle habitats between June 1994 and June 1996 showed more significant categorical differences within riffles than pools, with an overall increase in biomass in 1996 (Table 2). Some fine-sediment dwellers, such as chironomids and lumbriculids decreased in June 1996 collections, except for tubificids which increased by 80%. Faster turnover rates of tubificids in riffles as compared to chironomids or lumbriculids may be attributed to their use of detritus that collected from riffles in June 1996 but which was not available in June 1994.

Multivariate comparisons of benthic mass between June 1994 and June 1996 varied significantly by site, with riffles more susceptible to change than pools (Tables 1 and 2). June biomass estimates were higher overall at more sites in 1996 than in 1994 for *C. glomerata*, MAMB, chironomids, *G. lacustris*, tubificids, and gastropods; however, lumbriculid mass was lower.

Multivariate analysis of benthic biomass was conducted at five cobble sites (Lees Ferry, Two-Mile Wash, Little Colorado River Island, Tanner Cobble, and Lava Falls), with collection intervals designed to detect the impact and response of the benthos to the test flood. This analysis indicated significant change for both collection interval and site (Fig. 3, Table 3). Univariate analyses indicated that only MAMB, lumbriculids, and tubificids varied significantly for both collection interval and site. In order to assess the impact of the flood on the benthos, we compared Hess collections taken during both the pre- and post-flood steady 227 m^3/s discharges and determined that the biotic categories responded differently at each site.

Cladophora glomerata did not change significantly at Lees Ferry or Little Colorado River Island after the flood, but did at all other sites (Fig. 3, Table 4). The relative lack of suspended sediment at Lees Ferry probably did not scour *C. glomerata*, which was virtually eliminated at Two-Mile Wash, only 1 km downstream and below the Paria River confluence (Fig. 1). Recovery of *C. glomerata* was equaled or greater than that of the pre-flood estimates within 1 mo at Lees Ferry and within 2 mo at Two-Mile Wash and Tanner Cobble.

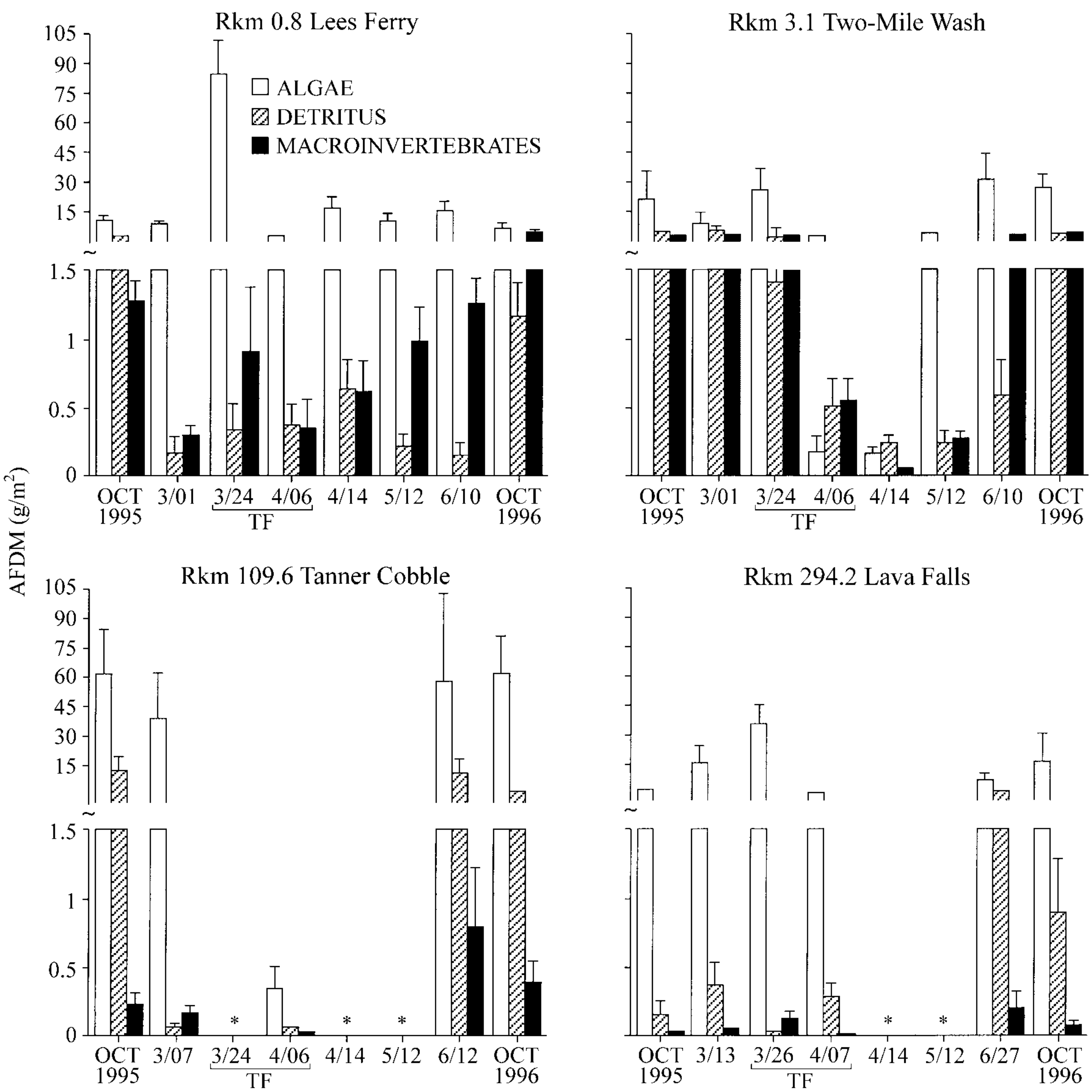

FIG. 3. Average standing mass (ash-free dry mass [AFDM] in grams per square meter; +1 SE) of aquatic benthos at selected sites along the Colorado River corridor for algae, macroinvertebrates, and detritus for selected periods prior to, during, and after the test flood (TF) below Glen Canyon Dam, Arizona, USA. Dates on *x*-axis are month/day; for example, 24 March is shown as 3/24.

A similar pattern of scour and recovery occurred for MAMB estimates.

There was little overall change in chironomid AFDM following the flood, but a steady increase in AFDM occurred over the 2-mo period for *G. lacustris.* We noted that many *G. lacustris* were stranded in pools as the water level dropped during the drawdown prior to the test flood, but egg masses and small size-class amphipods (<2 mm) were noted during 1-wk and 1-mo post collections. Whether this reproduction was a result of the flood or was normal for that time of year requires further investigation.

Macro-algae and aquatic macrophyte density was dramatically reduced following the test flood. Macrophyte ordinal values decreased from 1.5 (0.2) pre-flood to 0.6 (0.1) post-flood with full recovery by July, 2.1 (0.1) decreasing to 1.7 (0.1) by November. The November decrease can be attributed to a seasonal decrease in light availability and discharge through October and November (227–350 m^3/s). The macroalga, *Chara contraria,* was most vulnerable to the 1275 m^3/s experimental discharge and was co-dominant with *Potamogeton pectinatus* through the summer. *Elodea* was infrequently observed during surveys prior to No-

TABLE 3. Results of multiple analysis of variance comparing benthic biomass in the Colorado River through Grand Canyon from five cobble sites: Lees Ferry, Two-Mile Wash, Little Colorado River Island, Tanner Cobble, and Lava Falls.

Source	Wilks' lambda	Approximate F statistic	df	P	Response variable
Trip	0.3	2.4	55, 508	<0.0001	C,A,D,M,B,L,T,I
Site	0.7	4.1	11, 109	<0.001	O,A,G,L,T

Notes: Collection times were made to determine the influence of the spring test flood on benthic biomass, with all sites collected one month before the flood, during the steady 227 m^3/s flows both pre- and post-flood, and two months after the test flood. Lees Ferry and Two-Mile Wash were also sampled one week and one month after the test flood. Predictor variables of collection trip date covaried by collection site and were analyzed against response variables of biotic categories ([ln + 1]-transformed data, original units AFDM/m^2). Taxonomic categories include: *Cladophora* (C), *Oscillatoria* (O), miscellaneous algae/macrophytes (A), detritus (D), chironomids (M), *Gammarus* (G), gastropods (S), simuliids (B), lumbriculids (L), tubificids (T), and miscellaneous macroinvertebrates (I). Only significant univariate response variables are listed ($P < 0.04$). Overall Wilks' lambda, trip and site, was significant ($P < 0.0001$).

vember when it became dominant. These data indicate how variable and sensitive these soft bottom plants are to discharge.

Organic drift patterns: test flood

Multivariate analysis of coarse particulate organic matter (CPOM) in drift from five sites (Lees Ferry, Two-Mile Wash, LCR Island, Tanner Cobble, and Lava Falls) indicated a significant change for both collection interval and site (Fig 4, Table 5). All biotic drift categories varied significantly by collection interval, while only *G. lacustris* and miscellaneous macroinvertebrates varied significantly by site. Comparisons of CPOM in the hydrostatic wave vs. the actual flood discharge (1274 m^3/s) revealed a significant difference (Kruskal-Wallis; $P < 0.01$) with the hydrostatic wave carrying more organic material. These data indicated the greatest AFDM entrainment occurred during the up-ramp of the test flood and that duration was not a factor affecting either scour or entrainment.

TABLE 4. Results of Kruskal-Wallis tests comparing pre- and post-flood benthic biomass in the Colorado River through the Grand Canyon from five cobble sites: Lees Ferry, Two-Mile Wash, Little Colorado River Island, Tanner Cobble, and Lava Falls.

Site	Biotic category	Rank sum: Pre-flood	Rank sum: Post-flood	P
Lees Ferry (Rkm 0.8)	MAMB	57	21	0.004
	Oscillatoria	53	25	0.020
	MM	52	26	0.037
Two-Mile Wash (Rkm 3.1)	*Cladophora*	57	21	0.004
	MAMB	57	21	0.004
	Oscillatoria	54	24	0.005
	detritus	54	24	0.016
	chironomids	57	21	0.003
	tubificids	51	27	0.022
Little Colorado (Rkm 98.7)	simuliids	21	57	0.002
Tanner Cobble (Rkm 109.6)	*Cladophora*	53	25	0.025
	MAMB	54	24	0.016
	Oscillatoria	54	26	0.037
	MM	57	21	0.003
Lava Falls (Rkm 294.2)	*Cladophora*	25	53	0.004
	Oscillatoria	54	24	0.016
	detritus	25	53	0.020
	MM	54	24	0.007
	chironomids	57	21	0.004

Notes: Collections were made during the steady 227 m^3/s flows both pre- and post-flood from below the base discharge of 142 m^3/s. Except for the pre-flood, collections at Little Colorado River Island and Tanner Cobble were made on 6 and 7 March 1996, respectively. Only biotic categories that were significantly different between collections are listed ($P < 0.04$). For all categories, $n = 12$. Miscellaneous algae/macrophytes/bryophytes is abbreviated as MAMB and miscellaneous macroinvertebrates is abbreviated as MM.

Cladophora glomerata, MAMB, and detrital drift estimates all peaked during the hydrostatic wave and recovered or surpassed pre-flood drift mass at each site except for detritus which was probably swept through the river corridor to Lake Mead. Aquatic Diptera and miscellaneous macroinvertebrate drifting mass also peaked during the test-flood wave and recovered or surpassed that of pre-flood estimates after 1 mo at Lees Ferry and Two-Mile Wash. Miscellaneous macroinvertebrates were composed primarily of tubificid worms during the test flood which suggested disturbance and movement of the bedload. Terrestrial insects represented only 0.013% (36 out of 2600) of the miscellaneous macroinvertebrate category, which is low but two orders of magnitude higher than the values reported by Shannon et al. (1996*b*).

Percentage particle size of CPOM changed with site and collection interval with a decrease in the ≥10-mm size fraction during the steady 1274 m^3/s flows, whereas both 1–9 mm and the <1-mm size fraction increased. This pattern was consistent for all sites except for Lava Falls which may have resulted from the break-up of large flotsam as it moved through the rapids of middle and lower Grand Canyon. Lees Ferry and Two-Mile Wash sites regained the ≥10-mm size fraction within 1-wk after the flood, which coincided with the pattern for phytobenthos at these two sites.

Particle size of CPOM drift in June 1996 was pri-

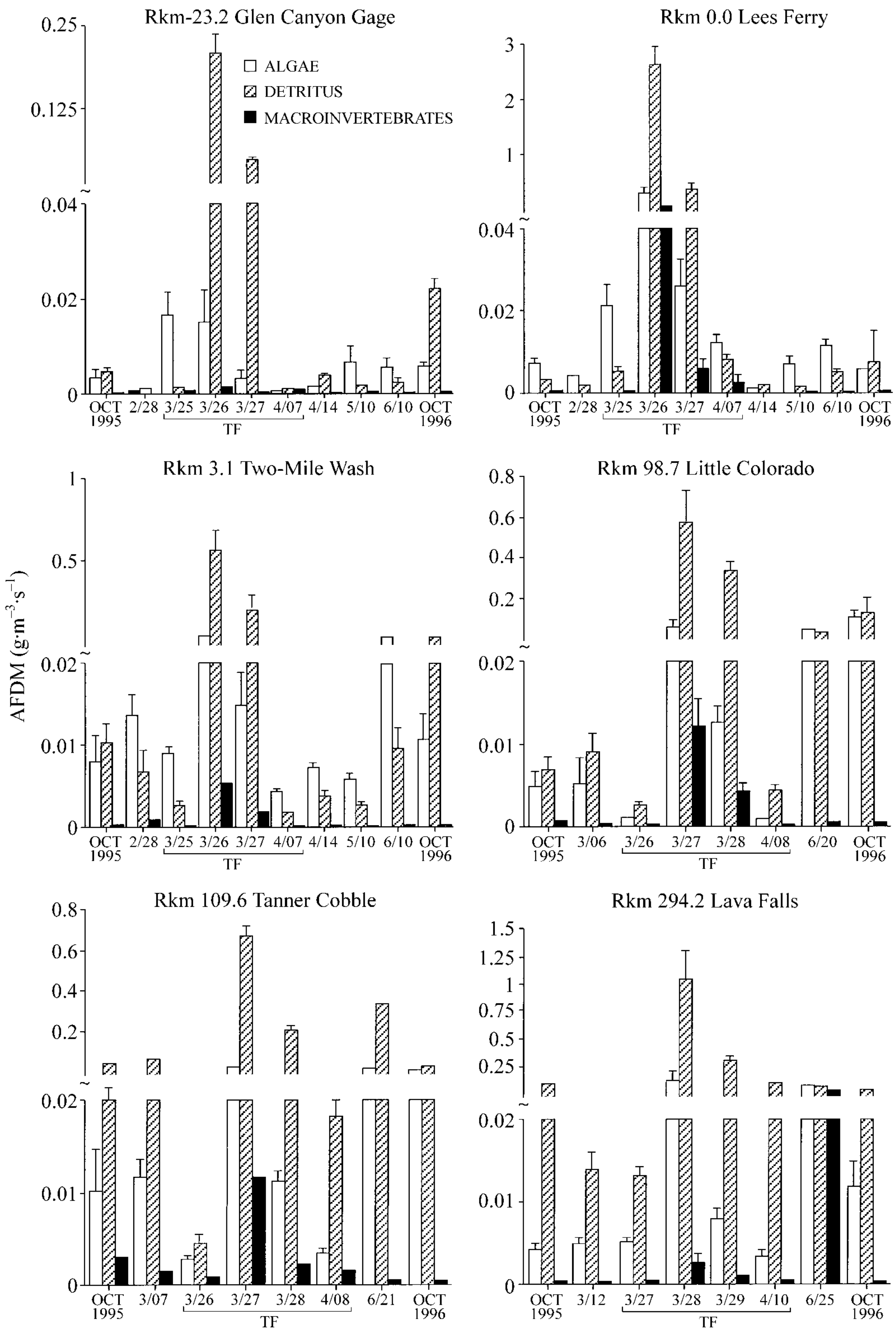

FIG. 4. Average standing mass (ash-free dry mass [AFDM] in grams per cubic meter per second; +1 SE) of organic drift at selected sites along the Colorado River corridor for algae, detritus, and macroinvertebrates for selected periods prior to, during, and after the test flood (TF) below Glen Canyon Dam, Arizona, USA. Dates on the *x*-axis are month/day; for example, 25 March is shown as 3/25.

TABLE 5. Results of multiple analysis of variance comparing coarse particulate organic matter (CPOM) in the Colorado River through Grand Canyon from five sites with collection times pre-, post-, and during the March 1996 test flood.

Source	Wilks' lambda	Approximate *F* statistic	df	*P*	Response variable
Trip	0.4	6.7	54, 2018	<0.0001	C,A,O,D,AD,G,I
Site	0.9	6.1	6, 395	<0.0001	G,I

Notes: Collection sites include Glen Canyon Gage, Lees Ferry, Two-Mile Wash, Little Colorado River Island, Carbon Creek, and Lava Falls. Collection times included one month prior to the test flood, during the pre-flood steady 227 m^3/s flow, during the hydrostatic wave from 1274 m^3/s test flow, actual water from the 1274 m^3/s test flow, during the post-flood steady flow from 227 m^3/s, one week and one month post-flood at only Glen Canyon Gage, Lees Ferry, and Two-Mile Wash, and two months post-flood at all sites. Predictor variables of collection date covaried by collection site and were analyzed against response variables of biotic categories. Taxonomic categories include: *Cladophora* (C), miscellaneous algae/macrophytes (A), detritus (D), aquatic diptera (AD), *Gammarus* (G), and miscellaneous macroinvertebrates (I) (n = 2060). Only significant univariate response variables are listed ($P < 0.04$). Overall Wilks' lambda, trip and site, was significant ($P < 0.0001$).

marily ≥10 mm and reflected the extensive growth of aquatic primary producers after the flood. Collections of CPOM in late October 1996 were highly variable, probably a result of monsoon spates and late fall storms. Both collection periods demonstrated a reach-based pattern for the distribution of organic matter drift. For example, in October, Nankoweap (Rkm [river km] 84.8) had no CPOM ≥10 mm in size, but the gage site above the Little Colorado River, only 14 km downriver, had 50% of the CPOM ≥10 mm in size.

Estimates for FPOM biomass varied significantly by collection date and site during the test flood. Zooplankton, miscellaneous zooplankton, detritus, and total FPOM exhibited similar patterns to CPOM; i.e., the highest FPOM concentrations occurred within the hydrostatic wave and decreased through the steady discharge. Lees Ferry collections carried the highest total FPOM (1.7 ± 18 $g \cdot m^3 \cdot s^{-1}$ AFDM) in the hydrostatic wave. The FPOM estimates at Lees Ferry increased by 92% while traveling the 24-km reach below Glen Canyon Dam, probably picking up riparian debris. At the post-227 m^3/s flow collections, FPOM estimates returned to pre-SF values at Glen Canyon (0.004 ± 0.0006 $g \cdot m^3 \cdot s^{-1}$ AFDM) and Lees Ferry (0.02 ± 0.003 $g \cdot m^3 \cdot s^{-1}$ AFDM). However, at Lava Falls FPOM estimates were 2.5 times higher at the post-flood collection than at the pre-SF collection. This may be a function of a higher discharge carrying more FPOM at Lava Falls during this collection interval because river discharge never dropped below 340 m^3/s, due to the draining of bank stored water. These areas generally have elevated FPOM concentrations in comparison to upriver sites (Shannon et al. 1996*a*).

Zooplankton biomass followed a similar pattern to that of FPOM during the flood with the hydrostatic wave carrying the most zooplankton, with a decrease downstream and through the test-flood hydrograph. Zooplankton composition was dominated by cyclopoid copepods at all sites and collection intervals except at Lees Ferry where the hydrostatic wave transported a high concentration of miscellaneous zooplankton (3073 animals/L ± 511 $m^3 \cdot s^{-1}$). This concentration of miscellaneous zooplankters corresponds with the relatively high biomass of secondary producers in the tailwaters.

Large flotsam

Examination of interval camera photographs during the flood showed an average of 1.4 large flotsam (>0.1 m) bundles photographed during the up-ramp, 2 bundles during the arrival of the water at 1274 m^3/s, 0.5 bundles during the steady 1274 m^3/s discharge, and 1.2 bundles during the post-flood. We made the assumption that each photograph represented a one-second time interval. No large CPOM bundles were sighted immediately prior to the test-flood steady flows. These data indicate entrainment of large flotsam, primarily tamarisk and some up-land vegetation, during the up-ramp that was stranded on beaches below the 1274 m^3/s stage.

Large flotsam contributed a considerably smaller mass to drifting organic material during the flood in comparison to FPOM and CPOM. Organic drift during the flood, including both pre- and post steady flows averaged 0.24 $g \cdot m^3 \cdot s^{-1}$ of CPOM. This extrapolates to ~1.06×10^6 kg of CPOM after multiplying the mass of organic drift by the total estimate of water discharged during the test flood. FPOM organic drift for the flood averaged 0.22 $g \cdot m^3 \cdot s^{-1}$ or 0.97×10^6 kg for the entire test-flood period. In contrast, we estimated ~2.3×10^4 kg of flotsam was transported by the flood. These values were calculated from an average of ~22.2 bundles that passed a given point every hour, calculated from an average of 1.5 bundles per 250-m camera view at a water velocity of 3.7 km/h and each bundle at 4 kg AFDM (n = 10), and then for the 11-d test flood when bundles passed by the cameras. To demonstrate how little large flotsam contributed to the organic drift mass we need to increase the mass estimate by threefold or 400 kg AFDM for each bundle to reach the same order of magnitude of CPOM and FPOM ($\sim$2.3 $\times$ 10^6 kg).

Discussion

Test-flood effects

The test flood of March 1996 significantly altered the aquatic food base in the Colorado River throughout the river corridor of Grand Canyon National Park over the short term. Scour and entrainment of both primary and secondary producers occurred at all sites, but varied among biotic categories. Those biota associated with fine sediments in the river channel (e.g., aquatic macrophytes, tubificids, and lumbriculids) were more susceptible to disturbance compared to those associated with the surfaces and interstitial spaces of the more stable armored cobble (e.g., *Cladophora glomerata* and *Gammarus lacustris*). Phytobenthic fine sediment taxa were scoured and remained unstable as taxonomic shifts in dominance were documented eight months after the flood.

Our results indicated that >90% of the benthos was removed at the arrival of the hydrostatic wave or 24 h from the start of the test flood. Also, drift mass reached highest levels during the first 2 d of the flood and subsided after that period. Drift mass during the flood was also an order of magnitude higher than that reported by Shannon et al. (1996*b*) during normal dam operations. Angradi and Kubly (1995) reported on CPOM and FPOM mass in the Glen Canyon reach from September 1990 through December 1991, during the GCES Phase II Research Flows (Patten 1991). Both CPOM and FPOM values in their study were an order of magnitude lower than values during the test flood. These differences may be attributed to the highly fluctuating research flows, which may have flushed the study site of POM during high flows, and produced results similar to post-flood results. Also, Angradi and Kubly (1995) used an active collection system with diaphragm pumps and Miller Tubes from a moving boat which may have caused an under estimation of drift mass.

Test-flood recovery

Recovery of the phytobenthos on hard substrata to pre-flood conditions was complete after one month for some sites. This recovery was much faster than experimental results reported by Blinn et al. (1995) or Benenati et. al. (1998). Although the phytobenthos was scoured, cobbles were not completely barren of algal rhizoidal holdfasts, especially *C. glomerata.* This fact coupled with virtually no tributary input of suspended sediment, which resulted in optimum water clarity, allowed for relatively quick recruitment of the phytobenthic community. The test flood flushed the system of fine particles, also contributing to the relatively high transparency of the water column.

Macroinvertebrate biomass followed the same pattern as that of phytobenthos and recovered within two months at all sites. Furthermore, collections for primary consumers during the post-flood trip of June of 1996 included some of the highest biomass values and most diverse fauna ever recorded during a six-year monitoring program (Blinn et al. 1994, Shannon et al. 1996*a*, Stevens et al. 1997*b*). Other investigators have reported similar fast recruitment times for phytobenthos and invertebrates under optimum conditions following a major disturbance (Steinman and McIntire 1990, Yount and Niemi 1990, Peterson 1996).

However, it is not clear whether the rapid colonization of biota would have occurred without the high steady discharges and the extended period of high water clarity that followed the test flood. Our data indicate that steady flows, high or low, contribute to increases in the aquatic food base. Furthermore, discharges $\geq$450 m^3/s tend to mitigate the negative influence of suspended sediments, delivered by tributaries, on water clarity. The higher discharges also provide more wetted perimeter for colonization by benthos.

Estimates for drift mass during June 1996, after two months of near steady flows, reached levels reported by Leibfried and Blinn (1986) for fluctuating flows. These investigators suggested that a potential positive effect of fluctuating flows was the entrainment of drifting food for fish. Our data indicate that high phytobenthic production under near steady flows result in equal or higher drift mass for downstream fish, without the negative features of a widely fluctuating varial zone (Usher and Blinn 1990, Angradi and Kubly 1993, Blinn et al. 1995). Unfortunately, we were not able to document this pattern further because low steady flows (3 d at 142 m^3/s), conducted in August 1996 for post-flood aerial photo-documentation of river channel morphometry, resulted in desiccation of developing benthos in the varial zone.

Management implications

Was this test flood a worthwhile experiment in dam operations? Yes, in regards to what was learned and no in terms of lasting impact. This low magnitude flood (about half of the annual peak flow) did little to return pre-dam characteristics to the aquatic community. The fundamental aspects of the aquatic community structure prior to impoundment of the Colorado River included variable temperature regime, muddy water, allochthonous carbon sources, and consistent seasonal changes in discharge. An occasional test flood such as that released from GCD can not possibly return all the parts of the community structure that are now missing. River temperature did not change during the flood from normal operations at that time of the year. The water was muddy during the beginning of the test flood but cleared up toward the end of the flood. Allochthonous input did increase during the beginning of the test flood according to stable isotope analysis but was not sustained (Blinn et al. 1998). Scour of the benthos did occur and recovered quickly, possibly in response to the consistent flows following the flood. However, benthic biomass estimates were higher than ever reported probably aiding recovery rates. Had the tributaries been running and the flows fluctuating on a daily, weekly, and monthly basis as usual, then recovery may not have occurred as fast and the test flood would have been a detriment to the aquatic food base.

The fundamental reason for the test flood in Grand Canyon, i.e., to move sand from the channel to the riverbanks to create larger beaches for the river-running industry, was accomplished. Managers need to define the natural resources that will benefit from a test flood and whether the ecosystem in general will benefit. It is possible that managing discharge in order to replace some pre-dam components will create more of a disturbance and reduce any ecosystem vitality. The aquatic food base in the Colorado River through Grand Canyon is an alien assemblage that responds more favorably to reduced daily fluctuations and may not benefit from the occasional test flood.

Conclusions

The hypothesis that regulated rivers can be managed for the benefit or protection of natural resources with higher than normal discharges was tested in March 1996 with a 7-d discharge of 1274 m^3/s from GCD. This experiment was conducted in response to the environmental impact statement on the operations of GCD, and was a component of the selected operating alternative. Effects of this experiment varied among resources, as this symposium issue has defined. The overall influence of the test flood on the aquatic benthos is not clear due to post-flood conditions of high steady flows with relatively high water clarity. We believe that both the antecedent and subsequent hydrograph conditions were as much, if not more responsible, for the rapid recovery of the benthic community.

Negative attributes of the test-flood hydrograph were the low steady 227 m^3/s flows that desiccated the varial zone at the expense of the biota and the timing of the flood. March and April are historically wet periods in northern Arizona, which results in elevated suspended sediment input from tributaries that would typically slow benthic recovery. The positive attributes of the flood include delivery of organic food into the water column for downstream fish during the first two days of the flood and the removal of fine sediments from shorelines which ultimately enhanced water clarity and benthic recovery. Consideration of pre- and post-flows are important when constructing hydrographs for managed high flows, especially when considering response times of biotic resources that are much slower than abiotic resources such as sand. Future test floods should experiment with shorter durations, higher peak flows, and take place on consecutive years with similar dam releases so natural variability can be assessed against dam operations.

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