Lotic Community Responses in the Lees Ferry Reach

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Responses of periphyton, aquatic macrophytes, benthic macroinvertebrates, and rainbow trout to the 1996 controlled flood were investigated in the Lees Ferry tailwater reach below Glen Canyon Dam on the Colorado River. Lotic biota differed spatially and temporally in abundance and distribution following recession of flood waters, and there was no evidence that the flood benefitted trout or lower trophic levels. The flood was associated with short-term changes in lower trophic levels, but benthic vegetation and macrofauna with low resistance were resilient. Adverse impacts of the flood on lower trophic levels were greater and more prolonged in depositional areas than on cobble bar habitat, but recovery occurred in both habitat types 4-8 months after the flood. The flood likely resulted in some downstream displacement of smaller fish but had no effects on catch rate or condition indices of trout. Percentage of young-of-the-year trout 8 months after the event indicates that the flood did not prevent successful spawning. The flood had little direct influence on diets of trout, but relative gut volume increased in the week after the event, remained high in summer, and composition changed seasonally. Amphipods (*Gammarus lacustris*), chironomids, and snails were predominant food items, and *Gammarus* generally were eaten more often and comprised greater relative volume in the diet than other macroinvertebrate taxa.

1. INTRODUCTION

Floods are a common type of disturbance in unregulated streams and may dramatically influence the structure and dynamics of lotic communities [*Minshall*, 1988; *Steinman and McIntire*, 1990; *Wallace*, 1990; *Yount and Niemi*, 1990]. The response of lotic communities to floods differs widely, depending on frequency, severity and timing, but floods and spates generally reduce standing stocks of primary and secondary producers. Recovery of biotic assemblages following floods may require a few weeks to several years [*Wallace*, 1990; *Yount and Niemi*, 1990; *Pearsons et al.*, 1992], and frequency and timing of events influence recovery and resistance [*Tett et al.*, 1978; *Peterson*, 1996; *Peterson and Stevenson*, 1992; *Barrat-Segretain and Amoros*, 1995]. The best indices of ecosystem recovery remain uncertain, and no theoretical model is available to predict recovery by lotic communities following floods [*Yount and Niemi*, 1990].

Fish communities tend to be persistent in unregulated streams exposed to frequent flooding [*Matthews*, 1986; *Meffe and Minckley*, 1987; *Meffe and Berra*, 1988]. Floods

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can alter assemblage structure and abundance of fishes [*Pearsons et al.*, 1992] and may impact smaller fish more than adults [*Seegrist and Gard*, 1972; *Hanson and Waters*, 1974; *Harvey*, 1987]. Few investigation have addressed effects of floods on lotic biota in large regulated rivers [*Niemi et al.*, 1990; *Steinman and McIntire*, 1990; *Yount and Niemi*, 1990]. Natural floods are inherently unpredictable in duration, magnitude and timing, but floods incorporating discharge manipulations from hydroelectric power facilities allow timely comparison of the same sites prior to and following disturbance. Lack of pre-disturbance data commonly hinders flood-related investigations [*Lamberti et al.*, 1991].

Controlled floods are an element common to potential operating regimes for Glen Canyon Dam on the Colorado River, Arizona [*U.S. Department of Interior*, 1995]. The first controlled flood was implemented March 22 to April 7, 1996, to test effects of high discharges on sediment and lotic biota below the dam. This paper describes effects of this controlled flood on lotic communities in the Lees Ferry reach. The Lees Ferry reach extends between Glen Canyon Dam (-15.8 Mile) and Lees Ferry (0 Mile), and differs from the downstream system in that hypolimnetic releases from Lake Powell result in cold stenothermic, clear, and physicochemically stable tailwaters [*Stanford and Ward*, 1991; *Stevens et al.*, 1997]. We tested null hypotheses that the 1996 flood had no effects on periphyton, aquatic macrophytes, epiphytic diatoms, benthic macrofauna, and rainbow trout (*Oncorhychus mykiss*) in the Lees Ferry Reach.

2. METHODS

2.1. Periphyton and Aquatic Macrophytes

We collected samples of benthic vegetation prior to (March 22; pre-flood steady 227 m^3/s discharge) and following the controlled flood (April 4; post-flood steady 227 m^3/s discharge), July 28 and November 24. We collected cobbles (10-20 cm diameter) in a random manner along transects (-4.1 and -14.0 Mile) parallel to river flow (142 m^3/s flow stage). One to three 4.15 cm^2 areas (n = 15-16/site) of periphyton within a template were scraped from the upper surface of each cobble [*Angradi and Kubly*, 1993]. Pheophytin-corrected chlorophyll *a* content of periphyton (n = 6 March and April; n = 5, July and November) was determined spectrophotometrically [*Tett et al.*, 1975], and mass (ash free dry weight, AFDW) was determined by loss on ignition (550^0 C, 2 hrs).

We collected submerged macrophytes from depositional substrate (-3.5 Mile) using a Hess sampler (0.087 m^2, 0.25 mm mesh) at randomly-located points along a transect parallel to river flow (142 m^3/s flow stage). Subsamples (20 g wet weight) of macrophytes were added to 200 ml of deionized water and homogenized for 2 min in a blender. Aliquots (10 ml) of the homogenate were filtered onto a glass-fiber filter and analyzed for chlorophyll *a* [*Tett et al.*, 1975]. AFDW was determined for the unhomogenized portion of the sample by loss on ignition (550^0 C, 2 h). Chlorophyll *a* content and mass were expressed in units of mg/m^2.

We collected additional periphyton and macrophyte samples (142 m^3/s flow stage) for analyses of diatom epiphytes. We collected cobbles along the transects described above and pooled (N=1/site) 4.15 cm^2 quadrats of periphyton scraped from the surface of each cobble. We collected samples of (N=1/site) of *Chara contraria* from three locations along the transect at -3.5 Mile. We clipped stalks (N = 2-3 at each location) of the macroalga between the second and fifth nodes below the growing tip. We pooled within-site samples of periphyton and *Chara* and preserved them in Transeau's Solution.

Diatom epiphytes were identified initially at 1000x magnification under oil immersion. Subsequent identification and enumeration were done at 20x magnification using 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 1500 algal units. Diatom densities on cobbles were calculated on the basis of cells per square millimeter of the area sampled on the stones; densities on *C. contraria* were calculated on the basis of number of cells per milligram AFDW.

We surveyed submerged macrophytes along each shoreline between Lees Ferry and GCD in March 16-17, April 15-16, July 15-16, and November 13-14, 1996. Distribution and relative abundance were estimated visually, plotted on topographic maps and ranked ordinally: 1 = low vertical growth, patchy and sparse distribution; 2 = moderate vertical growth, moderate and occasionally patchy distribution; and 3 = higher vertical growth, extensive, generally continuous distribution.

2.2. Macroinvertebrates

We collected benthos samples (Hess sampler, 0.087 m^2, 0.25-mm mesh) during pre- and post-flood steady flows (N=5/site) and during July and November (N=3/site) at the same transects, flow stage, and on the same dates as for the periphyton and macrophyte samples. Samples were preserved in 10% formalin, sieved (0.25-mm mesh), and macroinvertebrates were identified and sorted.

TABLE 1. Mean±1 standard error of mass (AFDW, g/m^2) and chlorophyll *a* for periphyton at -14.0 and -4.1 Mile and macrophytes at -3.5 Mile before (March) and following (April to November) the 1996 controlled flood

	PERIPHYTON -14.0 Mile		PERIPHYTON -4.1 Mile		MACROPHYTES -3.5 Mile	
Month	AFDW (g/m^2)	Chlorophyll *a* (mg/m^2)	AFDW (g/m^2)	Chlorophyll *a* (mg/m^2)	AFDW (g/m^2)	Chlorophyll *a* (mg/m^2)
March	143.5±19.9	1787.6±182.1	135.8±15.2	1104.0±284.5	96.8±15.5	352.7±30.7
April	160.7±18.0	1106.2±144.1	99.6±19.0	669.1±53.1	n.d.	n.d.
July	161.7±17.4	1846.1±336.3	139.7±27.2	1322.1±438.3	n.d.	n.d.
November	97.2±18.0	858.8±126.6	108.4±19.3	672.9±172.2	44.4±10.1	244.8±41.6

n.d., no data.

2.3. Rainbow trout

We electrofished 14-15 transects (ca. 33 min/transect) between dusk and dawn and between -15.0 Mile and -3.0 Mile during pre- (March 23-25) and post-flood (April 5-7) steady discharges, then again during August 28-30 (discharge ca. 425 m^3/s) and November 18-20 (discharge ca. 227 m^3/s). Rainbow trout were measured as total length (TL), weighed, and released unless collected for analysis of diet. Stomachs N = 30-60/trip) were preserved in 10% formalin, and contents were identified to the lowest possible taxonomic category and measured (±0.1 ml) using volumetric displacement.

2.4. Data Analysis

Analysis of variance (ANOVA) was performed on means for macroinvertebrates and periphyton standing stock (AFDW, chlorophyll *a*), total lengths, weights, condition factors ($K = \text{weight} \times 10^5/TL^3$), and relative gut volumes (RGV = volume of stomach contents in milliliters/fish length in meters; *Filbert and Hawkins*, 1995) and proportional composition of ingested items. Planned comparisons were conducted on data from the pre- and post-flood steady discharges. *Post hoc* analyses (Duncan's Multiple Range test) were used to explore patterns of differences between pairs of months. Analyses were performed on transformed data for benthic amphipods, oligochaetes and chironomid larvae (log[x+1]) and chironomid pupae and turbellarians (sqrt[x+1]+sqrt[x]).

Mean diatom densities and ordinal rankings of macrophyte abundance and distribution were compared between pre- and post-flood discharge periods using the Mann-Whitney U-test, and mean ordinal rankings were compared over all periods using the Kruskal-Wallis ANOVA. Chi-square tests were used to compare frequencies of occurrence of empty stomachs and of predominant taxonomic groups in the diet. Power of ANOVAs were computed for tests that failed to reject null hypotheses [*Peterman*, 1990; *Sokal and Rohlf*, 1995].

3. RESULTS

3.1. Periphyton and Aquatic Macrophytes

Mean mass of periphyton (predominantly *Cladophora glomerata*) did not differ between March and April or among sampling periods (Table 1), but power of the ANOVA was low (0.979). Mean chlorophyll *a* content differed among all sampling periods ($P<0.01$), declined from March to April ($P<0.01$), and was less ($P<0.05$) at one cobble bar (-14.0 Mile) in November than March (Table 1). Total diatom densities and densities of large/upright species declined in the reach ($P<0.05$), but densities categorized as small/adnate taxa were similar ($P>0.05$) between these months (Table 2).

Submerged macrophytes at -3.5 Mile were removed by the flood but colonized at the site by November (Table 1). Abundance and distribution of macrophytes throughout the reach (ordinal rankings based on river surveys) differed among sampling periods ($P<0.02$). Mean ±1 standard error of the ordinal rankings were: March, 1.5±0.2, N=19; April, 0.6±0.1, N=29; July, 2.1±0.1, N= 19; and November 1.7±0.1, N=34. *Chara contraria* was the most abundant macrophyte taxon in the tailwater prior to the flood. *Potamogeton pectinatus* occurred sparsely prior to the flood but colonized extensively and was dominant by July. Abundance and distribution of macrophytes declined between March and April ($P<0.02$) and increased in July. *Chara* and *Potamogeton* colonized extensively in November, when relative abundance and distribution of macrophytes did not differ significantly ($P>0.05$) from that

TABLE 2. Mean±1 standard error of densities of total and dominant small adnate and large upright diatoms on cobbles and *Chara contraria* before (March) and following (April to November) the 1996 controlled flood in the Lees Ferry reach. Densities for *C. contaria* in April and July reflect total loss of macrophytes from the sampling site.

	Diatoms	March	April	July	November
Cobbles	Total	32,310.5±6107.4	10,501.0±80.0	19,984.0±235.0	2725.0±863.1
(number/mm^2)	Small adnate	6106.5±565.5	3407.0±297.0	8281.0±250.3	775.5±171.8
	Large upright	21,330.0±7857	5432.5±1161.8	9402.0±1279.9	1479.0±1031.0
C. contaria	Total	68,328	0	0	377,722
(number/mg AFDW)	Small adnate	25,696	0	0	173,978
	Large upright	26,280	0	0	163,744

prior to the flood, and *Chara* hosted abundant epiphytic diatoms (Table 2). *Egeria densa* (Brazilian elodea) was observed infrequently prior to November, when abundance and distribution became extensive. Exposed sand substrata (no observable macrophytes) were virtually absent in March, but occurred extensively in April.

3.2. Macroinvertebrates

Macroinvertebrate densities (Table 3) differed among sampling periods ($P<0.001$), but interaction between transect locations and sampling periods was significant ($P<0.02$). Total benthic macroinvertebrate densities did not differ at any site between March and April ($P>0.05$). Densities of individual taxa (Table 3) except oligochaetes (Power=0.586) differed among sampling periods ($P<0.01$), and interaction was significant ($P<0.01$) between transects and sampling periods for all taxa except *Gammarus lacustris*. Densities of the amphipod declined ($P<0.01$) from March to April in depositional and cobble areas (-3.5 and -14.0 Mile), but were similar between months ($P>0.05$) at -4.1 Mile. Amphipod densities at all sites in July and November exceeded ($P<0.01$; -14.0 Mile) or were similar ($P>0.05$) from the pre-flood concentrations.

Although densities of chironomid larvae (Table 3) differed ($P<0.001$) among sampling periods, densities were similar ($P>0.05$) between March and April (Power=0.787). Densities in July exceeded ($P<0.01$) those in March at -4.1 Mile and -3.5 Mile, but were lower ($P<0.001$) at -14.0 Mile. However, densities of larvae in November were less than ($P<0.001$) pre-flood concentrations at -14.0 Mile and -3.5 Mile. Densities of chironomid pupae (Table 3) differed among sampling periods ($P<0.001$), but were not significantly different ($P>0.05$) between March and April at -14.0 Mile and -3.5 Mile (Power=0.787).

Gastropod densities differed among sampling periods ($P<0.001$) and declined ($P<0.05$) between March and April at -4.1 Mile (Table 3). Densities in November exceeded ($P<0.05$) those in March on cobble bars (-4.1 and -14.0 Mile). Turbellarian densities in July and November exceeded ($P<0.001$) those in March at -14.0 Mile and -4.1 Mile, but were similar to pre-flood concentrations at -3.5 Mile.

3.3. Seasonal Patterns of Change

Comparisons of seasonal patterns of change between present data (Tables 1-3) and 1991-97 (Table 4) suggest that trends in standing stocks of periphyton, macrophytes, *Gammarus*, chironomids, gastropods, and oligochaetes (no seasonal pattern of change for oligochaetes) following the controlled flood exhibit seasonal trends comparable to those prior to the event. However, densities of diatoms (on cobbles: July 1994 = 45,300 /mm^2, November 1993 = 95,500 /mm^2; on *Chara:* November 1993 = 23,175 /mg; T. McKinney, unpublished data, 1997), gastropods, and macrophytes were lower than seasonal maxima during 1991-1997 (Tables 2, 3, and 4). All samples collected before March 1996 conformed with current procedures.

3.4. Rainbow trout

Catch per unit effort (CPUE, Table 4) of trout did not differ between March and April but was lower in August and November. The proportional catch of trout <152 mm TL [assumed to be mainly young-of-the-year; Arizona Game and Fish Department, unpublished data] increased more than 33% in November, compared to previous months (Table 5), consistent with a normal pattern of seasonal change. Prior to the controlled flood, trout <152 mm TL in late fall to early winter typically comprise 30-55% of fish captured by electrofishing (proportion of trout <152 mm TL in electrofishing samples: October 1993, 55%; December

TABLE 3. Mean±1 standard error of densities of benthic macroinvertebrates on cobble (-14.0 and -4.1 Mile) and depositional (-3.5 Mile) habitats in March (pre-flood) and April to November (post-flood) of 1996

		DENSITIES OF BENTHIC MACROINVERTEBRATES (number/m^2)					
Month	Site (Mile)	*Gammarus lacustris*	Oligochaetes	Gastropods	Chironomid Larvae	Chironomid Pupae	Turbellarians
March	-14.0	404.6±147.0	41.4±13.4	27.6±3.9	3931.0±717.9	480.5±92.4	0
	-4.1	1331.0±276.8	1354.0±27.2	154.0±(20.8)	114.9±34.1	0	1802.3±273.1
	-3.5	1448.3±389.1	4223.0±2460.8	59.8±(9.9)	310.3±88.4	39.1±16.9	1285.1±249.1
April	-14.0	121.8±51.3	48.3±8.5	32.2±(7.6)	2763.2±841.0	703.4±174.4	0
	-4.1	820.7±245.2	3634.5±2045.6	48.3±(15.2)	416.1±146.7	62.1±39.8	579.3±122.3
	-3.5	512.6±390.4	1519.5±699.3	87.4±22.0	223.0±53.8	80.5±31.1	669.0±256.7
July	-14.0	2046.0±278.1	931.0±496.0	95.8±23.3	160.9±74.8	57.5±57.4	888.9±534.4
	-4.1	1379.3±40.4	977.0±309.1	137.9±40.4	2444.4±1049.8	636.0±257.0	1578.5±400.2
	-3.5	444.4±93.9	30.7±20.3	7.7±7.7	2796.9±855.7	398.5±63.7	0
Nov	-14.0	5153.3±953.6	92.0±23.9	118.8±20.3	95.8±61.7	0	15.3±7.7
	-4.1	7835.3±2005.2	241.4±28.9	245.2±20.3	30.7±7.7	0	3632.2±344.9
	-3.5	2532.6±981.7	494.3±154.3	88.1±16.7	19.2±13.8	0	1103.5±481.2

1994, 30%; December 1995, 55%; and November 1996, 49%; T. McKinney, unpublished data, 1997).

We captured trout 46-593 mm TL, and mean lengths and weights differed ($P<0.05$) among sampling periods (Table 5). Trout caught in April were longer ($P<0.001$) and heavier ($P<0.05$) than those captured in March. Mean length was less in November than in March ($P<0.05$), but mean weights (Power=2.551) and condition factors (Power=0.819) were similar ($P>0.05$) between months (Table 5). Condition indices in all months and CPUE in August and November were similar to those observed in the tailwater during 1994-1995 [T. McKinney, unpublished data, 1997: condition factor, April 1994=0.97, December 1994=0.98, May 1995=0.93, December 1995=0.95; CPUE: July 1994=2.62, December 1994=1.90, May 1995=2.75, December 1995=2.87].

Stomachs were collected from trout 121-538 mm TL. Proportional composition of trout diets differed significantly among sampling periods ($P<0.001$), and individual components differed in patterns of change (Table 6). *Cladophora* tended to be the predominant ingested item except in November. Amphipods, chironomids and snails dominated macroinvertebrates in the diet, and other taxa (Diptera, oligochaetes, terrestrial invertebrates) each generally comprised less than 2% of stomach content volume. Proportional composition of individual taxa in the diet did not differ ($P>0.05$) between pre- and post-flood steady flows, but composition of *G. lacustris* ($P<0.001$) and snails ($P<0.02$) increased above pre-flood levels in November, while proportional composition of chironomids and *Cladophora* declined ($P<0.001$).

Relative gut volume also differed ($P<0.001$) among sampling periods (Table 6). The RGV increased between pre- and post-flood steady discharges ($P<0.01$) and remained greater than prior to the flood in August ($P<0.01$), but declined from pre-flood levels in November ($P<0.002$). Frequency of occurrence of empty stomachs did not differ ($P>0.05$) among sampling periods (Table 6). Overall, more trout ate *Gammarus* than chironomids or snails ($P<0.001$), and more fish consumed amphipods and snails ($P<0.05$), but fewer ate chironomids and *Cladophora* ($P<0.001$) in November than prior to the flood.

4. DISCUSSION

Our results indicate that a controlled flood of brief duration and moderate magnitude in the spring influenced dynamics of the lotic system and produced short-term changes primarily in lower trophic levels. Some benthic vegetation and macrofauna were reduced by the event, but most were resistent, except that lower trophic levels were affected more on depositional than on cobble bar habitats. The flood also had little measurable impact on rainbow trout in the tailwater reach. No clear benefits of floods were apparent for lower trophic levels or trout. Conclusions for this study must be viewed with some caution due to limita-

TABLE 4. Mean±1 standard error of seasonal densities of macrophytes, periphyton collected in the Lees Ferry reach, 1991-97. Sample sizes: macroinvertebrates–spring = 132, summer = 132, fall = 58, winter =87; periphyton–spring = 175, summer = 257, fall = 249, winter = 175; macrophytes–spring = 15, summer = 34, fall = 40, winter = 15

	SEASONAL DENSITIES OF MACROPHYTES (g/m^2 AFDW) AND BENTHIC MACROFAUNA (number/m^2)			
Biota	Spring	Summer	Fall	Winter
Gammarus	1707.0±177.4	2030.1±139.3	5661.7±703.5	2175.5±161.2
Chironomids	1826.3±252.0	1070.3±150.5	434.3±76.3	709.1±141.0
Gastropods	111.1±11.2	244.2±34.7	497.7±93.5	326.7±58.6
Oligochaetes	928.1±256.3	822.6±137.2	729.1±108.6	952.4±173.4
Periphyton	153.9±6.4	171.8±7.7	114.0±5.5	123.4±5.6
Macrophytes	121.8±23.3	30.4±7.0	68.6±10.9	126.0±21.9

tions of data, including lack of true replicates and temporal control and generally low statistical power.

We found that changes in abundance and distribution of biota in the Lees Ferry reach differed spatially and temporally following the controlled flood, as evidenced by many interactions between month and site. The flood reduced diatom densities and standing stock of aquatic macrophytes and *G. lacustris*, but recovery occurred in 8 months or less. Other biota generally were resistant to the flood. All species examined followed expected seasonal patterns of change following the flood. Although it was not possible to establish an experimental control (not exposed to flooding) system, changes in benthic flora and macrofauna suggest that flooding can initiate a complex series of adjustments in regulated riverine environments [*Petts*, 1984].

4.1. Periphyton and Aquatic Macrophytes

Contrary to what has been reported for unregulated systems [*Whitton*, 1970; *Fisher et al.*, 1982; *Biggs and Close*, 1989; *Scrimgeour and Winterbourn*, 1989; *Steinman and McIntire*, 1990; *Lamberti et al.*, 1991; *Dodds and Gudder*, 1992], the controlled flood failed to reduce periphyton mass in the Lees Ferry reach. Lack of an effect likely was related to low magnitude of the flood and low entrainment of sediment particles that act to dislodge algae [*Steinman and McIntire*, 1990; *Stanford and Ward*, 1991; *Peterson*, 1996] and possibly reduce light penetration during the flood [*Fisher and Grimm*, 1988; *Shannon et al.*, in review]. Lower chlorophyll-*a* content of periphyton following the flood likely reflected loss of diatom epiphytes [*Haines et al.*, 1987; *Dodds*, 1991] due to water shear [*Biggs*, 1995]. *Tett et al.* [1978] also reported that phytopigment decreased abruptly after floods. Periphyton mass exhibited seasonal trends in July and November, consistent with the natural seasonal cycle in streams [*Steinman and McIntire*, 1990].

Densities of total epiphytic diatoms and of large upright taxa were reduced by the flood, and densities in July and November were lower on cobbles, but higher in November on *Chara*, than in previous years. Diatom epiphytes often are reduced by floods [*Grimm and Fisher*, 1989; *Peterson et al.*, 1994], and large upright taxa are impacted more than are small adnate species [*Robinson and Rushforth*, 1987]. Small adnate taxa typically dominate diatom epiphyte assemblages following severe scour events, but colonization by both physiognomic groups may be rapid [*Power and Stewart*, 1987; *Peterson and Stevenson*, 1992; *Peterson*, 1996]. Diatoms also may have colonized denuded substrata [*Grimm and Fisher*, 1989; *Peterson et al.*, 1994], providing food base for benthic macrofauna. Diatoms with small adnate physiognomies are less available than large upright taxa to benthic grazers [*Gregory*, 1983; *Steinman*, 1996]. Thus, the food base for benthic macroinvertebrates that consume diatoms — for example, amphipods [*Blinn et al.*, 1992, 1994, 1995; *Angradi*, 1994; *Stevens et al.*, 1997] — likely was reduced in the Lees Ferry reach by the flood.

The flood reduced distribution and abundance of aquatic macrophytes in the tailwater reach and *Chara* did not recolonize until the fall. Colonization of flood-denuded areas by *Chara* spp. also required several months in an Oklahoma stream [*Power and Stewart*, 1987]. *Potamogeton* colonized extensively in the Lees Ferry tailwater soon after the flood, likely increasing habitat and food base above those associated with exposed sand substrate [*Menon*, 1969; *Krull*, 1970; *Pip and Stewart*, 1976; *Pip*, 1978; *Sand-Jensen et al.*, 1989; *Newman*, 1991; *Angradi*, 1994; *Wollheim and Lovvorn*, 1996]. Macrophyte communities often are decimated by floods, influencing trophic webs [*Bilby*, 1977; *Power and Stewart*, 1987; *Barrat-Segretain and Amoros*,

TABLE 5. Total catch, mean±1 standard error of total length, weight, and condition factor, and catch per unit effort (CPUE) and percentage of catch <152 mm for rainbow trout caught by electrofishing prior to (March) and following (April to November) the 1996 controlled flood in the Lees Ferry reach

Month	Total Catch (number)	Total Length (mm)	Weight (g)	Condition Factor (K)	CPUE (number/ min)	Percent of Catch <152 mm
March	1513	230.8±2.8	198.5±5.7	0.961±0.006	3.52	35.9%
April	1685	239.9±2.6	211.2±5.1	0.954±0.005	3.58	28.3%
August	1306	228.4±3.2	232.0±6.7	0.979±0.010	2.61	36.5%
November	1335	214.7±3.2	208.2±6.5	0.986±0.010	2.58	49.1

1995]. Loss of macrophytes can reduce habitat and the food base for fish and macroinvertebrates [*Menon*, 1969; *Pip and Stewart*, 1976; *Pip*, 1978; *Sand-Jensen et al.*, 1989; *Hanson*, 1990; *Newman*, 1991; *Blinn et al.*, 1992; *Angradi*, 1994; *Stevens et al.*, 1997].

4.2. Macroinvertebrates

Macroinvertebrate populations often are negatively impacted by flooding [*Meffe and Minckley*, 1987; *Scrimgeour and Winterbourn*, 1989; *Giller et al.*, 1991; *Lamberti et al.*, 1991; *Cobb et al.*, 1992; *Palmer et al.*, 1996], but we found only moderate evidence of this following the 1996 controlled flood. Resistance and recovery of benthic fauna differed spatially and temporally in the Lees Ferry reach following the flood. *Gammarus*, more than other taxa, lacked resistance to the flood, but the amphipod was resilient, and all taxa examined generally exhibited seasonal patterns of change in densities comparable to non-flood conditions. Recovery by *Gammarus* occurred more slowly in depositional than on cobble habitat and was coincident in the soft-sediment area with colonization by *Chara*, suggesting that an algal resource is important in colonization dynamics of macroinvertebrates [*Robinson et al.*, 1990]. Macroinvertebrate populations reduced by floods often recover rapidly [*Fisher et al.*, 1982; *Meffe and Minckley*, 1987; *McElravy et al.*, 1989; *Lamberti et al.*, 1991; *Mackay*, 1992].

4.3. Rainbow trout

The controlled flood had no direct influence on CPUE or condition indices of rainbow trout in the Lees Ferry reach. Condition indices in all months and CPUE in August and November were similar to those observed in the tailwater during 1994-95. However, mean size of trout captured increased, and the proportion of fish <152 mm TL declined in the week after the flood, suggesting some downstream displacement of smaller-sized trout [Seegrist and Gard, 1972; Harvey, 1987; Lamberti et al., 1991].

Rainbow trout in the Lees Ferry reach spawn primarily during late fall and winter, and larvae may remain in the gravel for a week to a month after hatching before emerging as free-swimming fry [*Kondolf et al.*, 1989]. Flood impacts likely would be greatest when eggs are in the gravel and when fry are emerging [*Seegrist and Gard*, 1972; *Hanson and Waters*, 1974; *Pearsons et al.*, 1992]. Thus, it is likely that most trout fry had emerged prior to the controlled flood. The high proportion of wild-spawned (stocked trout were distinguished by presence of coded wire tags implanted at the hatchery) young-of-the-year fish in our electrofishing samples during fall and proportional similarity in previous years indicate that the flood did not prevent successful spawning.

We electrofished only at night and assume that diel changes in feeding behavior [*Bisson*, 1978; *Angradi and Griffith*, 1990] likely had little influence on trout diets in our study. Increased food intake in the week following the flood likely reflected opportunistic feeding associated with greater drift of macroinvertebrates [*Elliott*, 1973; *Scullion and Sinton*, 1983; *Bres*, 1986; *Filbert and Hawkins*, 1995]. Food intake failed to correspond with declines in benthic macroinvertebrate densities following the flood, suggesting that reductions in the benthos had little impact on food availability to fish. Composition of stomach contents changed seasonally during the study, and the pattern was similar to that previously observed in the tailwater [*Angradi et al.*, 1992], suggesting long-term temporal stability and continued low diversity of available food in the reach. Among predominant food items, *Gammarus* generally were eaten more than other macroinvertebrates, and chironomids were consumed more than snails. *Cladophora* also was consumed frequently and comprised a large percentage of stomach contents, but the alga likely provides little direct nutritional benefit [*Angradi*, 1994], although epiphytic diatoms provide high lipid content that apparently is utilized by rainbow trout [*Leibfried*, 1988].

TABLE 6. Percent frequencies of occurrence and mean±1 standard error of percent composition by volume and relative gut volume (RGV) of predominant items in stomachs of rainbow trout prior to (March) and following (April to November) the 1996 controlled flood

	March (n=36)		April (n=30)		August (n=60)		November (n=54)	
Ingested Item	Frequency (%)	Volume (RGV)	Frequency (%)	Volume (RGV)	Frequency (%)	Volume (RGV)	Frequency (%)	Volume (RGV)
Gammarus	62.5	25.2±6.1	74.1	38.1±6.7	75.9	31.6±5.1	82.4	71.6±5.2
Chironomids	71.5	23.8±6.7	54.6	8.0±3.6	59.6	14.3±3.5	15.8	8.3±3.6
Gastropods	9.7	2.1±1.3	7.8	0.1±0.1	24.8	9.1±2.9	35.1	6.0±2.2
Cladophora	58.5	46.2±7.8	62.4	50.1±9.1	58.3	43.0±5.6	12.3	7.1±3.1
RGV		4.8±1.0		11.8±2.6		11.7±1.4		3.9±0.7
Empty Stomachs	16.7	0	16.7	0	9.0	0	22.9	0

In conclusion, the controlled flood of moderate magnitude and short duration had limited impact on, and no apparent benefits to, lotic biota. Future research and management decisions should address questions of spatial, temporal, and species variability in resistance and resiliency and the potential effects of frequency, severity and seasonal timing if we hope to predict influences of controlled floods on biota in the Lees Ferry reach.

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REFERENCES

Angradi, T.R., Trophic linkages in the lower Colorado River: multiple stable isotope evidence, *J.N. Am. Benthol. Soc.*, 13, 479-495, 1994.

Angradi, T.R., and J.S. Griffith, Diel feeding chronology and diet selection of rainbow trout (*Oncorhynchus mykiss*) in the Henry's Fork of the Snake River, Idaho, *Can. J. Fish. Aquat. Sci.*, 47, 199-209, 1990.

Angradi, T.R., and D.M. Kubly, Effects of atmospheric exposure on chlorophyll *a*, biomass and productivity of the epilithon of a tailwater river, *Regul. Rivers*, 8, 345-358, 1993.

Angradi, T.R., R.W. Clarkson, D.A. Kinsolving, D.M. Kubly, and S.A. Morgensen, *Glen Canyon Dam and the Colorado River: responses of the aquatic biota to dam operations*, Research Rept., 155 pp., Ariz. Game Fish Dept., Phoenix, AZ, 1992.

Barrat-Segretain, M.H., and C. Amoros, Influence of flood timing on the recovery of macrophytes in a former river channel, *Hydrobiologia*, 316, 91-101, 1995.

Biggs, B.J.F., The contribution of flood disturbance, catchment geology and land use to the habitat template of periphyton in stream ecosystems, *Freshwater Biol.*, 33, 419-438, 1995.

Biggs, B.J.F., and M.E. Close, Periphyton dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biol.*, 22, 209-231, 1989.

Bilby, R., Effects of a spate on the macrophyte vegetation of a stream pool, *Hydrobiologia*, 56, 109-112, 1977.

Bisson, P.A., Diel food selection by two sizes of rainbow trout *(Salmo gairdneri)* in an experimental stream, *J. Fish. Res. Board Can.*, 35, 971-975, 1978.

Blinn, D.W., L.E. Stevens, and J.P. Shannon, *The effects of Glen Canyon Dam on the aquatic food base in the Colorado River corridor in Grand Canyon, Arizona*, Rept. CA-8009-8-0002, 98 pp., Glen Canyon Environ. Studies, Flagstaff, AZ, 1992.

Blinn, D.W., L.E. Stevens, and J.P. Shannon, *Interim flow effects from Glen Canyon Dam on the aquatic food base in the Colorado River in Grand Canyon National Park, Arizona*, Final Rept., 136 pp., Glen Canyon Environ. Studies, Flagstaff, AZ, 1994.

Blinn, D.W., J.P. Shannon, L.E. Stevens, and J.P. Carder, Consequences of fluctuating discharge for lotic communities, *J.N. Am. Benthol. Soc.*, 14, 233-248, 1995.

Bres, M., A new look at optimal foraging behaviour: rule of thumb in the rainbow trout, *J. Fish Biol.*, 29, 25-36, 1986.

Cobb, D.G., T.D. Galloway, and J.F. Flannagan, Effects of discharge and substrate stability on density and species composition of stream insects, *Can. J. Fish. Aquat. Sci.*, 49, 1788-1795, 1992.

Dodds, W.K., Micro-environmental characteristics of filamentous algal communities in flowing freshwaters, *Freshwater Biol.*, 25, 199-209, 1991.

Dodds, W.K., and D.A. Gudder, The ecology of *Cladophora*, *J. Phycol.*, 28, 415-427, 1992.

Elliott, J.M., The food of brown and rainbow trout *(Salmo trutta* and *S. gairdneri)* in relation to drifting invertebrates in a mountain stream, *Oecologia*, 12, 329-347, 1973.

Filbert, R.B., and C.P. Hawkins, Variation in condition of rainbow trout in relation to food, temperature, and individual length in the Green River, Utah, *Trans. Am. Fish. Soc.*, 124, 824-835, 1995.

Fisher, S.G., and N.B. Grimm, Disturbance as a determinant of structure in a Sonoran Desert stream ecosystem, *Verh. Internat. Verein. Limnol.*, 23, 1183-1189, 1988.

Fisher, S.G., L.J. Gray, N.B. Grimm, and D.E. Busch, Temporal succession in a desert stream ecosystem following flash flooding, *Ecol. Mono.*, 52, 93-110, 1982.

Giller, P.S., N. Sangpradub, and H. Twomey, Catastrophic flooding and macroinvertebrate community structure, *Verh. Internat. Verein. Limnol.*, 24, 1724-1729, 1991.

Gregory, S.V., Plant-herbivore interactions in stream ecosystems, in *Stream Ecology: Application and Testing of General Ecological Theory*, ed. J.R. Barnes and G.W. Minshall, pp. 17-190, Plenum Press, NY, 1983.

Grimm, N.B., and S.G. Fisher., Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream, *J.N. Am. Benthol. Soc.*, 8, 293-307, 1989.

Haines, D.W., K.H. Rogers, and F.E.J. Rogers, Loose and firmly attached epiphyton: their relative contributions to algal and bacterial carbon productivity in a *Phragmites* marsh, *Aquat. Bot.*, 29, 169-176, 1987.

Hanson, D.L., and T.F. Waters, Recovery of standing crop and production rate of a brook trout population in a flood-damaged stream, *Trans. Am. Fish. Soc.*, 103, 431-439, 1974.

Hanson, J.M., Macroinvertebrate size-distribution of two contrasting feshwater macrophyte communities, *Freshwater Biol.*, 24, 481-491, 1990.

Harvey, B.C., Susceptibility of young-of-the-year fishes to downstream displacement by flooding, *Trans. Am. Fish. Soc.* 116, 851-855, 1987.

Kondolf, G.M., S.S. Cook, H.R. Maddux, and W.R. Persons, Spawning gravels of rainbow trout in Glen and Grand Canyons, Arizona, *J. Arizona-Nevada Acad. Sci.*, 23, 19-28, 1989.

Krull, J.N., Aquatic plant-macroinvertebrate associations and waterfowl, *J. Wildl. Manage.*, 34, 707-718, 1970.

Lamberti, G.A., S.V. Gregory, L.R. Ashkenas, R.C. Wildman, and K.M.S. Moore, Stream ecosystem recovery following a catastrophic debris flow, *Can. J. Fish. Aquat. Sci.*, 48, 196-208, 1991.

Leibfried, W.C., *The utilization of* Cladophora glomerata *and epiphytic diatoms as a food resource by rainbow trout in the Colorado River below Glen Canyon Dam, Arizona*, M.S. thesis, N. Ariz, Univ., Flagstaff, AZ, 1988.

Mackay, R.J., Colonization by lotic macroinvertebrates: a review of processes and patterns, *Can. J. Fish. Aquat. Sci.*, 49, 617-628, 1992.

Matthews, W.J., Fish faunal structure in an Ozark stream: stability, persistence and a catastrophic flood, *Copeia*, 1986, 388-397, 1986.

McElravy, E.P., G.A. Lamberti, and V.H. Resh, Year-to-year variation in the aquatic macroinvertebrate fauna of a northern California stream, *J.N. Am. Benthol. Soc.*, 8, 51-63, 1989.

Meffe, G.K., and T.M. Berra, Temporal characteristics of fish assemblage structure in an Ohio stream, *Copeia*, 1988, 684-690, 1988.

Meffe, G.K., and W.L. Minckley, Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream, *Am. Midl. Natur.*, 117, 177-191, 1987.

Menon, P.S., Population ecology of *Gammarus lacustris* Sars in Big Island Lake. I. Habitat preference and relative abundance, *Hydrobiologia*, 33, 14-32, 1969.

Minshall, G.W., Stream ecosystem theory: a global perspective, *J.N. Am. Benthol. Soc.*, 7, 263-288, 1988.

Newman, R.M., Herbivory and detritivory on freshwater macrophytes by invertebrates: a review, *J.N. Am. Benthol. Soc.*, 10, 89-114, 1991.

Niemi, G.J., P. deVore, N. Detenbeck, D. Taylor, A. Lima, J. Pastor, J.D. Yount, and R.J. Naiman, Overview of case studies on recovery of aquatic systems from disturbance, *Environ. Manage.*, 14, 571-587, 1990.

Palmer, M.A., P. Arensburger, A.P. Martin, and D.W. Denman, Disturbance and patch-specific responses: the interactive effects of woody debris and floods on lotic invertebrates, *Oecologia*, 105, 247-257, 1996.

Pearsons, T.N., H.W. Li, and G.A. Lamberti, Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages, *Trans. Am. Fish. Soc.*, 121, 427-436, 1992.

Peterman, R.M., Statistical power analysis can improve fisheries research and management, *Can. J. Fish. Aquat. Sci.*, 47, 2-15, 1990.

Peterson, C.G., Response of benthic communities to natural physical disturbance, in *Algal Ecology, Freshwater Benthic Ecosystems*, ed. R.J. Stevenson, M.L. Bothwell, and R.L. Lowe, pp. 375-402, Academic Press, NY, 1996.

Peterson, C.G., and R.J. Stevenson, Resistance and resilience of lotic algal communities: importance of disturbance timing and current, *Ecol.*, 73, 1445-1461, 1992.

Peterson, C.G., A.C. Weibel, N.B. Grimm, and S.G. Fisher, Mechanisms of benthic algal recovery following spates: comparison of simulated and natural events, *Oecologia*, 98, 280-290, 1994.

Petts, G.E., *Impounded Rivers*, 326 pp., John Wiley Sons, NY, 1984.

Pip, E., A survey of the ecology and composition of submerged aquatic snail-plant communities, *Can. J. Zool.*, 56, 2263-2279, 1978.

Pip, E., and J.M. Stewart, The dynamics of two aquatic plant-snail associations, *Can. J. Zool.*, 54, 1192-1205, 1976.

Power, M.E., and A.J. Stewart, Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream, *Am. Midl. Natur.*, 117, 333-345, 1987.

Robinson, C.T., and S.R. Rushforth, Effects of physical disturbance and canopy cover on attached diatom community structure in an Idaho stream, *Hydrobiologia*, 154, 49-59, 1987.

Robinson, C.T., G.W. Minshall, and S.R. Rushforth, Seasonal colonization of macroinvertebrates in an Idaho stream, *J.N. Am. Benthol. Soc.*, 9, 240-248, 1990.

Sand-Jensen, K., E. Jeppesen, K. Nielsen, L. Van Der Bijl, L. Hjermind, L.W. Nielsen, and T.M. Iversen, Growth of macrophytes and ecosystem consequences in a lowland Danish stream, *Freshwater Biol.*, 22, 15-32, 1989.

Scrimgeour, G.J., and M.J. Winterbourn, Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river, *Hydrobiologia*, 171, 33-44, 1989.

Scullion, J., and A. Sinton, Effects of artificial freshets on substratum composition, benthic invertebrate fauna and invertebrate drift in two impounded rivers in mid-Wales, *Hydrobiologia*, 107, 261-269, 1983.

Seegrist, D.W., and R. Gard, Effects of floods on trout in Sagehen Creek, California, *Trans. Am. Fish. Soc.*, 101, 478-492, 1972.

Shannon, J.P., D.W. Blinn, T. McKinney, P.L. Benenati, K.P. Wilson, and C. O'Brien, Aquatic food base response to the 1996 test flood below Glen Canyon Dam: Colorado River, Arizona, *Ecological Applications*, In Review.

Sokal, R.R., and F.J. Rohlf, *Biometry*, third edition, 887 pp, W.H. Freeman Co., New York, 1995.

Stanford, J.A., and J.V. Ward, Limnology of Lake Powell and chemistry of the Colorado River, in *Colorado River Ecology and Dam Management*, ed. G.R. Marzolf, pp. 75-101, Natl. Acad. Press, Washington, D.C., 1991.

Steinman, A.D., Effects of grazers on freshwater benthic algae, in *Algal Ecology: Freshwater Benthic Ecosystems*, ed. R.J. Stevenson, M.L. Bothwell, and R.L. Lowe, pp. 341-373, Academic Press, New York, 1996.

Steinman, A.D., and C.D. McIntire, Recovery of lotic periphyton communities after disturbance, *Environ. Manage.*, 14, 589-604, 1990.

Stevens, L.E., J.P. Shannon, and D.W. Blinn, Colorado River benthic ecology in Grand Canyon, Arizona, USA: dam, tributary and geomorphological influences, *Regul. Rivers*, 13,129-149, 1997.

Tett, P., M.G. Kelly, and G.M. Hornberger, A method for the spectrophotometric measurement of chlorophyll *a* and pheophytin *a* in benthic microalgae, *Limnol. Oceanogr.*, 20, 887-896, 1975.

Tett, P., C. Gallegos, M.G. Kelly, G.M. Hornberger, and B.J. Cosby, Relationships among substrate, flow, and benthic microalgal pigment density in the Mechums River, Virginia, *Limnol. Oceanogr.*, 23, 785-797, 1978.

U.S. Department of Interior, *Operation of Glen Canyon Dam: Final Environmental Impact Statement*, 337 pp., Bur. Reclam., Salt Lake City, UT, 1995.

Wallace, J.B., Recovery of lotic macroinvertebrate communities from disturbance, *Environ. Manage.*, 14, 605-620, 1990.

Whitton, B.A., Biology of *Cladophora* in freshwaters, *Water Res.*, 4, 457-476, 1970.

Wollheim, W.M., and J.R. Lovvorn, Effects of macrophyte growth forms on invertebrate communities in saline lakes of the Wyoming high plains, *Hydrobiologia*, 323, 83-96, 1996.

Yount, J.D., and G.J. Niemi, Recovery of lotic communities and ecosystems from disturbance — a narrative review of case studies, *Environ. Manage.*, 14, 547-569, 1990.

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