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Effects of Flow Reductions on Aquatic Biota of the Colorado River below Glen Canyon Dam, Arizona

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Abstract.—We examined influences of 3 d of reduced flows on biotic assemblages in the Colorado River below Glen Canyon Dam, Arizona. Exposure in the varial zone reduced standing crops of periphyton, pondweed *Potamogeton pectinatus,* and benthic macroinvertebrates, and losses following the drawdown were not explained by expected seasonal trends. Losses in macroinvertebrate densities and mass and in periphyton mass and chlorophyll *a* suggest that effects of a sudden reduction in dam discharge of moderate duration and magnitude are comparable with losses associated with the varial zone of fluctuating daily flows. Compared with expected seasonal changes, abundance of rainbow trout *Oncorhynchus mykiss* increased during and following reduced flows. Proportional composition of fish less than 152 mm total length (TL) was greater after the drawdown, whereas the percentage of trout 406–558 mm declined. Relative condition factor before, during, and after the drawdown did not differ significantly for all fish combined, following a long-term pattern. However, among length-classes, condition of fish 305–405 mm TL declined following reduced flows. Feeding and composition of dietary items generally followed expected patterns of seasonal change and failed to correspond with changes in periphyton, macrophyte, and macroinvertebrate benthic densities after the drawdown. However, fewer rainbow trout ate *Cladophora glomerata,* and they ate less of this alga. In comparison, fish ate more gastropods following the drawdown than accounted for by long-term patterns, but frequency of occurrence was unchanged. Sudden reduction in flows of moderate duration and magnitude, although significantly reducing benthic assemblages, had little apparent negative short-term consequence for rainbow trout.

Daily fluctuations in hydroelectric power releases create a varial zone in shallow fluvial habitat between high and low flow elevations. Daily exposure in the varial zone delimits colonization by epilithon, epiphyton, and macroinvertebrates (Hardwick et al. 1992; Angradi and Kubly 1993; Blinn et al. 1995; Shaver et al. 1997). Impacts of sudden, moderate duration (on the order of days) flow reductions on biota in large rivers are poorly understood (Peterson 1986), but previous studies suggest negative influences on benthic assemblages (Usher and Blinn 1990; Blinn et al. 1995; Stevens et al. 1997) and fish (Blinn et al. 1995). Recovery of the benthic community in the varial zone may be less complete under daily than under infrequent fluctuations (Perry and Perry 1986; Blinn et al. 1995), and recovery of benthic macroinvertebrates generally corresponds with that of epilithon (Blinn et al. 1995; Shaver et al. 1997).

Rainbow trout *Oncorhynchus mykiss*, benthic macroinvertebrates, a green alga, *Cladophora glomerata,* and diatom epiphytes of the alga are closely linked in the Colorado River below Glen Canyon Dam (Angradi 1994; Shannon et al. 1994; Blinn et al. 1995), and sudden flow reductions of moderate duration and magnitude may negatively influence benthic assemblages and rainbow trout. Since about 1993, sudden (within 24 h) 3-d reduced flow events (stable 227 m^3/s) have been periodically incorporated during regimens of higher releases (about 568–596 m^3/s from Glen Canyon Dam (GCD) for areal photodocumentation of river channel morphometry. We investigated periphyton, submerged macrophytes, benthic macroinvertebrates, and rainbow trout prior to and during or after a sudden, 3-d reduced flow event in 1997. Our objective was to determine effects of the flow reduction on these biota.

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Study Site

Glen Canyon Dam impounds the Colorado River near the Arizona–Utah border and forms Lake Powell, a 653-km^2 meromictic, oligotrophic reservoir. Hypolimnetic releases from the reservoir are clear and cold (Stanford and Ward 1991; Stevens et al. 1997). The Lee's Ferry reach, which extends between the dam at river kilometer (RK) 25.5 and Lee's Ferry at RK 0, is confined within a narrow, deeply incised canyon and has no perennially flowing tributaries.

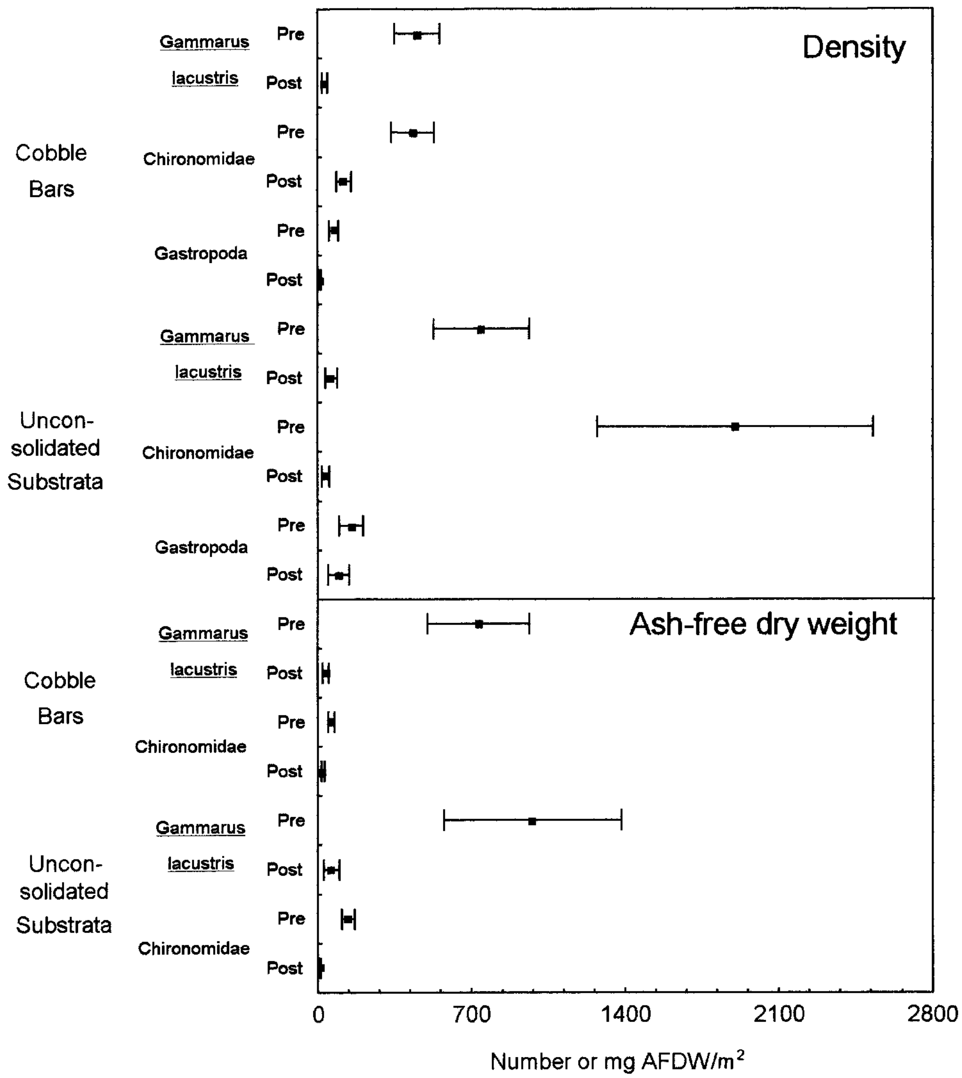

FIGURE 1.—Mean (±SE) densities (numbers/m^2) and ash-free dry weight (AFDW; mg/m^2) of benthic macroinvertebrate samples ($N = 9$) collected at the flow elevation of 511 m^3/s, Lee's Ferry reach, before (pre; 17 August) and after (post; 17 September) 1997 flow reductions.

Methods

Releases from GCD were reduced from 596 m^3/s to 227 m^3/s on 29–30 August 1997 (downramp at hourly decrements of 28 m^3/s) and maintained at that level until upramped (hourly increments of 85 m^3/s) on 2 September 1997 to 596 m^3/s. We estimate from data reported by Blinn et al. (1995) that more than 200,000 m^2 of cobble areas were exposed during the drawdown, or about 30% of estimated wetted area at releases of 596 m^3/s.

Periphyton, macrophytes and macroinvertebrates.—Benthic macroinvertebrates and the pondweed *Potamogeton pectinatus* were sampled using a WILDCO Hess sampler (0.09 m^2; 0.25 mm mesh), and periphyton was sampled using a 0.415-cm^2 template (Angradi and Kubly 1993). Sample transects were stratified by substrate type, and samples were collected randomly at each cobble and fine-sediment site at the flow elevation of 511 m^3/s before (17 August) and after (17 September) the drawdown. At each transect, 3 samples were collected for benthic macroinvertebrates and 10 samples each for periphyton and macrophytes. Benthic assemblages were sampled within or as close as possible to electrofishing transects described below. Macroinvertebrates were sorted to the lowest practical taxonomic level and enumerated. Standing crops of *Gammarus lacustris*, chironomids, *P. pectinatus* and periphyton were estimated by ash-free dry weight, and chlorophyll *a* was determined spectrophotometrically (Tett et al. 1975).

Rainbow trout.—Rainbow trout were captured between dusk and dawn by single-pass electrofishing at nine standardized transects (about 33 min/transect) before (19–21 April), during (31 August–1 September), and after (5–7 December) flow reduction. We used a complex pattern of pulsed DC, applying 215 V and maintaining a 15-A output to a stainless steel ring (30 cm diameter) anode system (Sharber et al. 1994). Fish were measured in total length (TL; mm) and weight (g) and released, unless collected for analysis of stomach contents. Stomachs were removed in the field and preserved in 10% formalin. Stomach contents were identified in the laboratory to the lowest practical taxonomic category, and we measured dietary composition of each category using volumetric displacement (mL). We calculated relative condition factor (K_n; Murphy and Willis 1992) and a length-related measurement of total volume of ingested matter (RGV = total volume of stomach contents/TL [m]; Filbert and Hawkins 1995).

Statistical analyses.—Macroinvertebrate densities and masses and periphyton masses and chlorophyll-*a* values were heteroscedastic and distributed nonnormally and were compared before (17 August) and after (17 September) the drawdown using the Mann–Whitney *U*-test. Catch per unit effort (CPUE; fish/min) and K_n before (19–21 April), during (31 August–1 September), and after (5–7 December) the flow reduction were compared using a one-way parametric analysis of variance (ANOVA). Relative stomach volume and dietary composition were analyzed among sampling trips using a Kruskal–Wallis *H*-test. Fish length-class frequencies, percent empty stomachs, and frequencies of occurrence and proportional composition (percent composition by volume) of dietary items were compared for the same periods using chi-square analysis. Long-term seasonal patterns were calculated for samples collected monthly or quarterly during 1991–1997 (Arizona Game and Fish Department, unpublished data) from the same locations and following the same methods and procedures used in the present study (e.g., Ayers et al., in press; McKinney et al. 1999b) and compared qualitatively with present results.

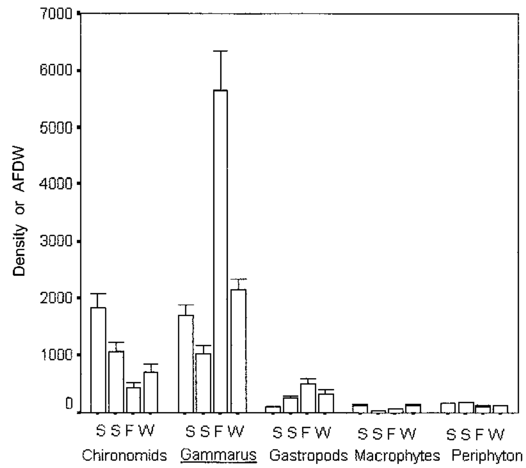

FIGURE 2.—Mean (+SE) seasonal (S = spring, S = summer, F = fall, W = winter) densities (numbers/m^2) of benthic macroinvertebrates and ash-free dry weight (AFDW; mg/m^2) of macrophytes and periphyton, Lee's Ferry reach, 1991–1997.

Results

Macroinvertebrates

Gammarus lacustris and chironomid densities declined more than 90% and 72%, respectively, between 17 August and 17 September on cobble bars and fine-sediment substrata ($U \leq 13.5$, $P < 0.0001$, df = 1) and were lower after flow reduction than those associated with long-term patterns (Figures 1, 2). Gastropod densities declined on cobble bars after flow reduction ($U = 7.5$, $P = 0.0033$, df = 1) but did not differ significantly from levels prior to reduced flows on fine-sediment substrata. Densities on both substrate types were lower than those associated with long-term patterns. Reductions in mass of *Gammarus* and chironomids ($U \leq 13.5$, $P \leq 0.0142$, df = 1) following exposure and re-inundation reflected trends comparable to those for densities ($U \leq 14.5$, $P \leq 0.0208$, df = 1). *Gammarus* mass declined about 93% on cobble bars and fine-sediment sites following the discharge drawdown, whereas chironomid mass declined more than 95% on cobble bars and more than 60% on fine-sediment sites (Figure 1). Gastropod mass also declined 84% on cobble bars ($U = 10.0$, $P = 0.0056$, df = 1) following the drawdown but was not significantly different from predrawdown levels on fine sediments.

Periphyton and Macrophytes

Mass and chlorophyll-*a* concentrations of periphyton declined about 75% and 64%, respec-

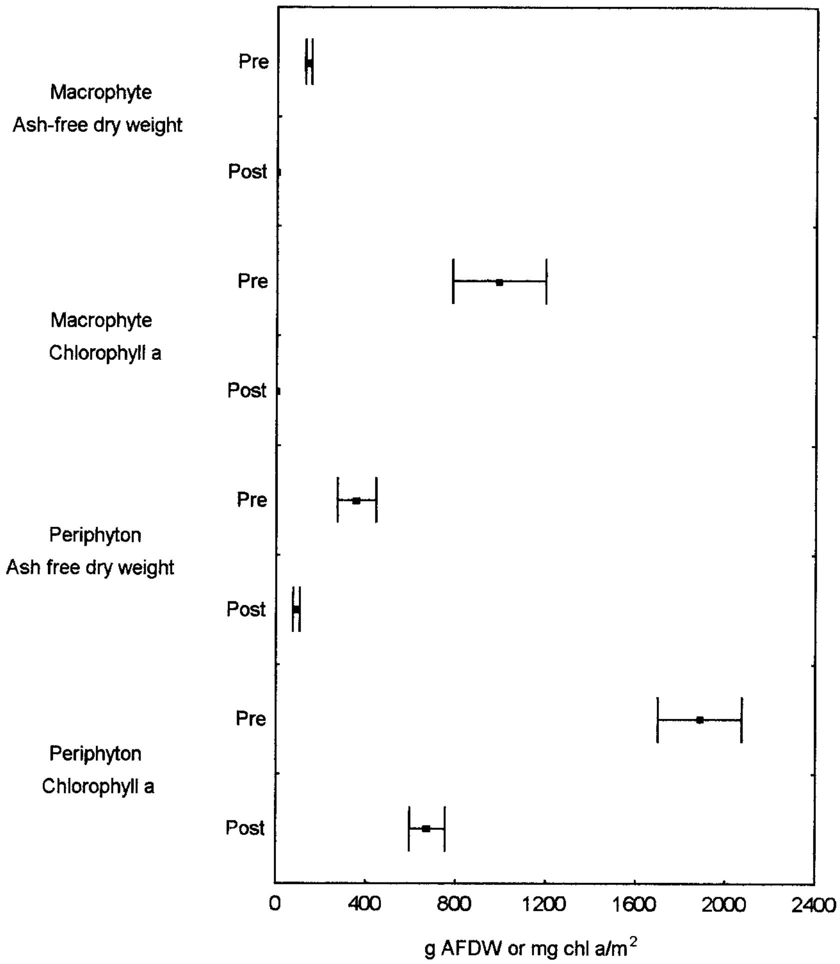

FIGURE 3.—Mean (±SE) ash free dry weight (AFDW; g/m^2) and chlorophyll *a* (chl *a*; mg/m^2) for periphyton and macrophyte samples collected at the flow elevation of 511 m^3/s, Lee's Ferry reach, before (pre; 17 August) and after (post; 17 September) 1997 flow reductions.

tively, following exposure and re-inundation of the varial zone ($U \leq 65.0$, $P \leq 0.0495$, df = 1; Figure 3). Densities of periphyton and macrophytes after the drawdown were lower than those associated with long-term patterns (Figure 2). Colonization by *P. pectinatus* on transects was variable, and means for standing stocks before and following reduced flows were not compared statistically. During 17 August, *P. pectinatus* was found at only two sites and was absent from all transects in September (Figure 3).

Rainbow Trout

Catch per minute for all trout differed among sampling periods ($F = 15.0$, $P < 0.0001$, df = 2), and CPUE during and following flow reduction tended to follow but exceed a long-term trend (Table 1). Relative condition of all fish did not differ significantly among sampling periods, following a long-term pattern (Table 1). Among length-classes, however, condition of fish 305–405 mm TL was significantly lower ($F = 6.29$, $P = 0.0064$, df = 2) following reduced flows (mean $K_n \pm$ SE for April = 79.5 ± 1.1, for August–September = 80.4 ± 0.9, for December = 75.6 ± 0.9). Distribution of length-classes also differed seasonally ($\chi^2 = 86.8$, $P = 0.001$, df = 6): fish less than 152 mm TL increased, whereas those 406–558 mm TL decreased, compared to long-term trends (Table 1).

Relative stomach volume and dietary composition of *Gammarus*, chironomids, *Cladophora* differed among sampling periods ($H \leq 8.8$, $P \leq 0.0177$, df = 2; Table 2). Fish consumed less and ate less *Cladophora* following the drawdown, but

TABLE 1.—Mean (SE) catch per unit effort (CPUE = number of fish caught/min), relative condition factor (K_n = [weight/total length^3] $\times$ 10^5), and proportional composition of total catch by length-group (number caught in square brackets) for rainbow trout captured by electrofishing in April, August–September (flow, 227 m/s), and December 1997 and by season (1991–1997), at Lee's Ferry reach. Flows during April and December were about 625 m/s.

Month or season	N	Mean (SE)		Percent (number) caught by length-group (mm)			
		CPUE	K_n	<152	152–303	304–405	406–558
Apr	726	2.4 (0.3)	79.4 (0.05)	29.6 [215]	24.3 [177]	36.8 [267]	9.2 [67]
Aug–Sep	1,836	7.1 (0.6)	80.3 (0.04)	45.3 [832]	20.1 [369]	30.1 [553]	4.5 [82]
Dec	1,429	5.3 (0.8)	77.2 (0.04)	48.9 [699]	18.1 [258]	28.8 [412]	4.2 [60]
Spring	5,993	2.2 (0.1)	81.4 (0.2)	36.5	26.7	24.7	12.2
Summer	5,965	2.9 (0.3)	84.0 (0.2)	43.7	28.6	21.3	6.4
Fall	7,588	2.5 (0.2)	81.5 (0.2)	43.9	23.0	23.0	10.1
Winter	3,295	1.4 (0.2)	79.5 (0.2)	26.7	20.6	26.2	26.6

they ate more chironomids and gastropods. Changes in RGV and percent composition by volume for predominant ingested items in the diet generally differed little from expected seasonal trends, except that consumption of gastropods was greater and *Cladophora* was less than expected from seasonal changes (Table 2; Figure 4). Feeding (i.e., percent empty stomachs) by trout did not differ significantly among sampling periods and was similar to an expected seasonal pattern (Table 2; Figure 4). Fewer trout ate *Gammarus* (χ^2 = 7.3, P = 0.0260, df = 2) and *Cladophora* (χ^2 = 14.3, P = 0.0010, df = 2) following reduced flows but more ate chironomids (χ^2 = 5.7, P = 0.0570, df = 2; Table 2).

Discussion

Our results demonstrate that exposure during sudden flow reduction of moderate duration and magnitude within a regimen of steady higher discharges from a large dam can reduce standing crops of periphyton, macrophytes and macroinvertebrate taxa. Reductions of benthic assemblages were similar to those resulting from daily dewatering of nearshore cobble bars during dam operations (Usher and Blinn 1990; Angradi and Kubly 1993; Blinn et al. 1995).

Our results support the hypothesis that pulse disturbances of moderate duration and magnitude associated with releases from GCD, although significantly reducing macroinvertebrate habitat and densities in nearshore areas, have insignificant short-term consequences for rainbow trout (McKinney et al. 1999b). In comparison, daily fluctuations in flows may have negative long-term consequences for rainbow trout production (Blinn et al. 1995). Although there were significant exposure-related reductions in benthic assemblages, CPUE and K_n of rainbow trout did not change significantly following reduced flows. However, reduced condition of fish 305–405 mm TL following reduced flows suggests potential

TABLE 2.—Frequencies of occurrence (%), percent empty stomachs (EPT), and means (SE) of total relative gut volume (RGV) and of percent composition by volume (C) for predominant items in stomachs of rainbow trout captured by electrofishing in April, August–September (227 m/s steady flows), and December 1997, Lee's Ferry reach.

Month	N	EPT	RGV	*Gammarus lacustris*		Chronomids		Gastropods		*Cladophora glomerata*	
				Frequency	C	Frequency	C	Frequency	C	Frequency	C
Apr	51	13.7	9.5 (2.1)	45.5	26.4 (6.1)	61.4	29.7 (6.4)	6.8	0.5 (0.4)	56.8	42.4 (6.6)
Aug–Sep	79	15.9	13.7 (2.8)	78.4	57.2 (7.7)	37.8	0.7 (0.5)	27.0	4.2 (2.1)	54.1	37.9 (7.6)
Dec	45	17.8	3.6 (0.7)	72.9	56.0 (7.6)	43.2	12.8 (4.2)	29.7	11.9 (4.9)	18.9	17.2 (6.0)

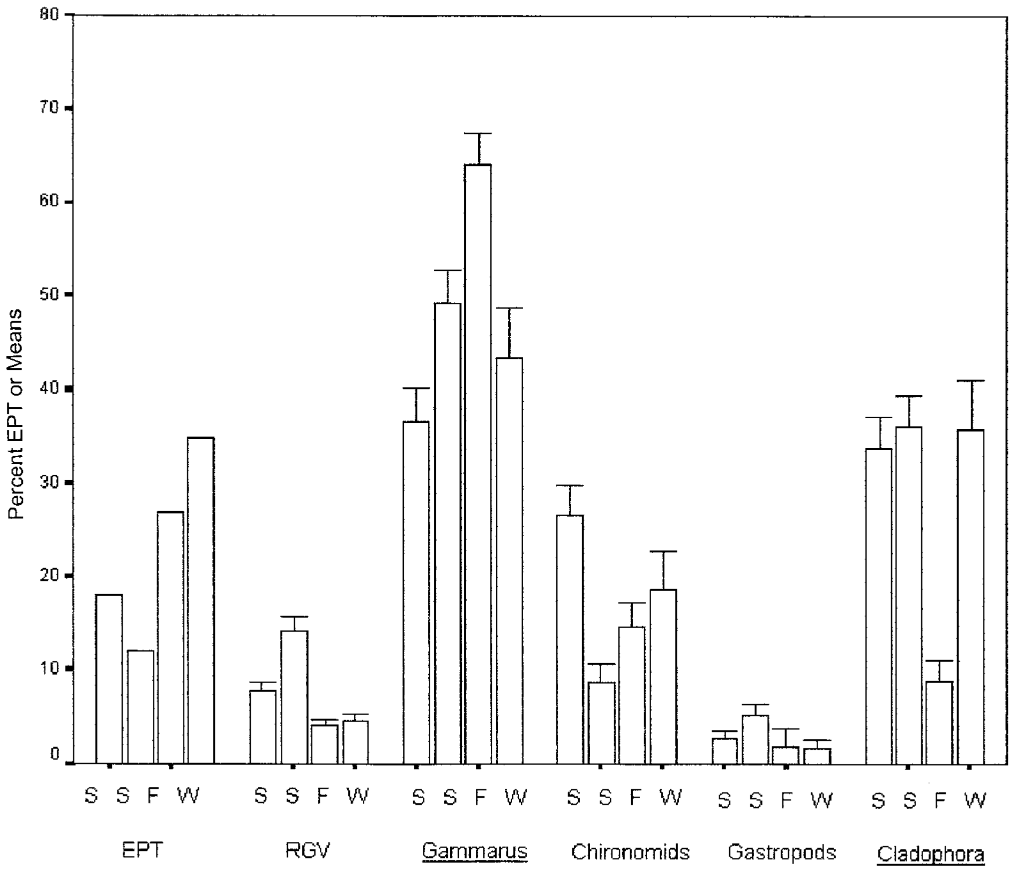

FIGURE 4.—Seasonal (S = spring, S = summer, F = fall, W = winter) percent empty stomachs (EPT) and means (+SE) of total ingested matter (RGV) and proportional diet composition (percent composition by volume) of rainbow trout, Lee's Ferry reach, 1991–1997.

food-limitation for the group. Several authors suggested that medium-sized rainbow trout were food-limited in dam tailwaters (Filbert and Hawkins 1995; Weiland and Hayward 1997) and unregulated streams (Cada et al. 1987). Consumption of total ingested matter and *Cladophora* were lower after the drawdown, whereas consumption of chironomids and gastropods were greater. Changes in RGV and consumption of *Gammarus* and chironomids corresponded with long-term trends, but rainbow trout consumed more gastropods and less *Cladophora* following flow reduction than expected, in comparison to long-term patterns. Trout did not eat *Gammarus,* chironomids or gastropods more in December than during discharge drawdown, but fewer trout consumed *Cladophora.*

Patterns of consumption by rainbow trout corresponded generally with seasonal changes in drift of *Gammarus, Cladophora,* and chironomids in the tailwater (Shannon et al. 1996; McKinney et al. 1999a). Food habits of rainbow trout often correspond with abundance and composition of the drift in unregulated streams (Elliott 1973; Cada et al. 1987; Angradi and Griffith 1990) but correspond poorly with abundance and composition of the benthos (Elliott 1973; Allan 1982). Recolonization of the varial zone by periphyton, macrophytes and macroinvertebrates may have occurred within a few months after exposure, but densities probably remained low (Blinn et al. 1995; Shaver et al. 1997). Our results agree generally with a lack of correspondence between benthic macroinvertebrate densities in nearshore areas and rainbow trout food habits following an experimental flood of moderate duration and magnitude (McKinney et al. 1999b). Findings support complexity of relationships between the benthic food base and diets of rainbow trout (Allan 1982; Angradi and Griffith 1990).

Potential effects of operating alternatives for hydroelectric power facilities on lotic biota merit consideration by resource managers (Blinn et al. 1995; Stevens et al. 1997). Fluctuating daily releases reduce standing crops of lower trophic levels in the varial zone (Blinn et al. 1995), and colonization of exposed cobble substrata by macroinvertebrates after re-wetting may require several months (Blinn et al. 1995). However, infrequent pulse disturbances of moderate duration and magnitude during spring (McKinney et al. 1999b) or late summer to early fall probably have insignificant short-term consequences for rainbow trout.

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