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Consequences of fluctuating discharge for lotic communities

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Abstract. We used five in situ experiments to test the influence of fluctuations in river discharge on the structure and function of the tailwaters benthos associated with cobble substrata in the Colorado River downstream from Glen Canyon Dam, Arizona, USA. Periods of daily desiccation and freezing during river fluctuation significantly limited community biomass and energy. The permanently submerged channel supported 4-fold higher macroinvertebrate mass than the varial zone. Daily harvests of benthos showed a 50% reduction in mass of *Cladophora glomerata* after 2 d of repeated 12-h summer exposure. Five days of repeated exposure resulted in >70% reduction in *C. glomerata* and >50% reduction in epiphyton mass. We observed a ≥85% reduction in benthic macroinvertebrate mass after only one 12-h summer exposure. One night time exposure to subzero winter air temperatures resulted in ≥50% loss of chlorophyll *a* and mass of *C. glomerata* and ≥90% loss in macroinvertebrate mass. Gastropod densities on resubmerged cobbles that were subjected to long-term desiccation (~6 mo) equalled submerged control cobbles within 1 wk, whereas recolonization by *C. glomerata, Gammarus lacustris,* and chironomid larvae was significantly slower; i.e., ≤30% of controls after 4 mo. Hence, our data showed that two 12-h exposure periods may require >4 mo for recovery to achieve the mass of permanently submerged benthos. Incremental increases in benthic energy (joules/m^2) over increased base discharge from 142 to 793 m^3/s may result in an increase in trout mass of approximately 42.5 kg/ha in the tailwaters at Lees Ferry.

Key words: river fluctuation, disturbance, recolonization, energy, *Cladophora,* epiphyton, *Gammarus,* chironomids, macroinvertebrates.

Large dams impose novel regimes of discharge, sedimentology, temperature, and/or water chemistry on downstream rivers, thereby affecting benthos, fisheries and even riparian community composition and production (Ward and Stanford 1979, 1983, Armitage 1984, Petts 1984, Gore and Petts 1989, Gregory et al. 1991, Allan and Flecker 1994). Generally, modifications of physico-chemical variables in tailwaters increase primary and secondary producer mass, but reduce biodiversity (Baxter 1977, Lowe 1979, Ward and Stanford 1979, King and Tyler 1982, Zimmerman and Ward 1984, Dufford et al. 1987, Rader and Ward 1988, Blinn and Cole 1991). Shallow fluvial habitats may contribute substantially to local and reach-wide biodiversity and productivity (Thorp and Delong 1994); but varial-zone habitats may be subject to regular exposure to ultraviolet light, desiccation or freezing in rivers with regulated fluctuations in discharge (e.g., peak power hydroelectric dams and some irrigation dams). Thus, the potential for increased productivity in dam tailwaters may be counteracted by exposure under fluctuating discharge (Stanford and Hauer 1992). However, little is known about incremental discharge effects and temporal changes in food webs as the tailwaters varial zone enlarges and contracts. Effects of discharge regulation may diminish downstream, causing lower reaches to resemble the pre-impoundment condition (Ward and Stanford 1983, Voelz and Ward 1989), depending on mainstream discharge characteristics, channel geomorphology, climate, and the location and flow patterns of significant tributaries (Storey et al. 1991).

The green alga *Cladophora glomerata* is common in tailwaters of hydroelectric dams (Lowe 1979, Blinn and Cole 1991). The thick cell walls, strong attachment matrix, and highly branched filaments that overlap and retain water during low flows are morphological attributes that make *C. glomerata* competitive in varial zones below dams and within marine intertidal zones (Usher and Blinn 1990, Lobban et al. 1985). The highly branched filaments of *C. glomerata* provide abundant surface area for the attachment of associated biota, but filaments have limited direct

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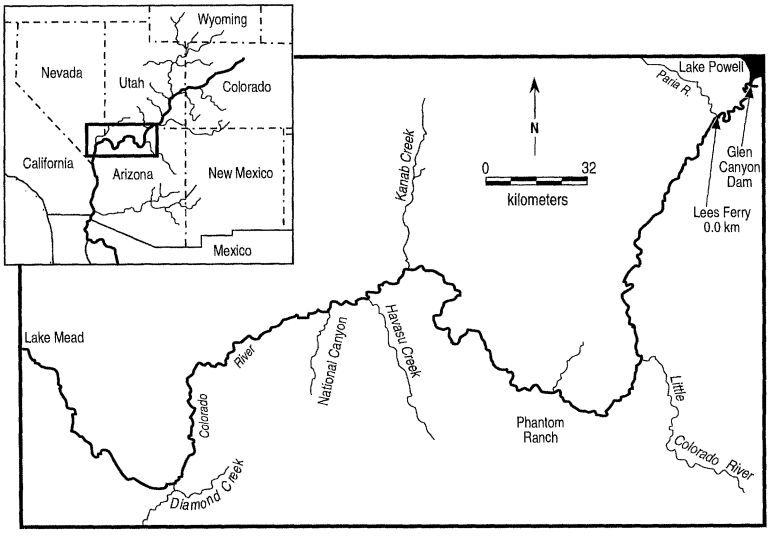

FIG. 1. Map of the Colorado River through Grand Canyon National Park, Arizona. Note that river distance through the Canyon starts at Lees Ferry (0.0 km).

food value in the Colorado River food web (Leibfried 1988, Pinney 1991, Shannon et al. 1994).

Several studies have reported reduced algal and macroinvertebrate mass in varial zones downstream from hydroelectric dams (Fisher and Lavoy 1972, Lowe 1979, Irvine and Henriques 1984, Gislason 1985, Peterson 1986, 1987). Usher and Blinn (1990) found that repeated 12-h day exposures of *C. glomerata* for 3 d resulted in ≥40% losses in biomass and chlorophyll *a*, and Angradi and Kubly (1993) reported significant reductions in chlorophyll *a* in this alga after daytime exposures of <6 h. Also, Hardwick et al. (1992) reported that densities of epiphytic diatoms associated with *C. glomerata* decreased markedly in the varial zone compared with the continuously submerged channel of the Colorado River below Glen Canyon Dam.

We monitored cobble substrata in varial and submerged zones in the Colorado River below Glen Canyon Dam at biweekly intervals for one year and conducted five in situ experiments in this reach to test the influence of regulated discharges on the structure of aquatic communities associated with *C. glomerata*. Specifically, we asked: 1) Does fluctuation in discharge reduce the distribution of *C. glomerata* and its associated epiphyton and macroinvertebrates, and does this effect vary among day and night and summer and winter regimes? 2) What is the rate of loss in benthos mass and energy associated with daily fluctuations in discharge? 3) What is the rate of recolonization by *C. glomerata* and associated biota after short- and long-term drying induced by discharge fluctuations? 4) What are the consequences of incremental discharge fluctuations on trophic relations and energy? The influence of discharge regulation on community structure, energy flow, and rates of recovery in the tailwaters of the dam are also addressed.

Study Site

The Colorado River is 2253 km long and drains 631,687 km^2 in seven western states and Mexico (Fig. 1). Our study site was at Lees Ferry, Arizona (36°52′03″N, 111°35′40″W), 25.3 km downstream from Glen Canyon Dam, which is designated as 0.0 river kilometre (RKM). Lees Ferry is the only point accessible to road vehicles between Glen Canyon Dam and Diamond Creek (362 RKM). Glen Canyon Dam is a hypolimnial release hydroelectric structure which was completed in 1963 and has a maximum production discharge of 937 m^3/s (Stanford and Ward 1991). The impounded river upstream formed Lake Powell reservoir, which has a full-pool volume of 33.3 km^3 covering an area of 653 km^2. Studies were conducted to determine the effects of fluctuating discharge on beaches in Grand Canyon National Park, Arizona (Patten 1991, Kearsley

et al. 1994). Discharges ranged from 85 to 937 m^3/s, and water temperature ranged from 9 to 11°C in the tailwaters. The average (±1 SE) secchi depth at Lees Ferry was 6.8 m (±0.25), but decreased abruptly (<1.0 m) below the confluence of the Paria River (Fig. 1).

The reach between Glen Canyon Dam and the confluence of the Paria River (Fig. 1) is a vital source of organic matter for the Grand Canyon. The aquatic benthos at Lees Ferry is dominated by dense growths of *Cladophora glomerata* that nearly cover the entire channel and support associated epiphytes and macroinvertebrates (Usher and Blinn 1990, Hardwick et al. 1992, Shannon et al. 1994). Diatoms make up >95% of the epiphytic algal assemblage, and *Gammarus lacustris* and chironomid larvae (primarily *Cricotopus annulator*, *C. globistylus*, and *Orthocladius rivicola*) make up over 75% of macroinvertebrate biomass within the *C. glomerata* matrix (Blinn and Cole 1991, Shannon et al. 1994).

Methods

Biweekly monitoring of varial and submerged channel

Twelve random samples of macroinvertebrates were taken biweekly between September 1992 and September 1993 in both the varial (142–566 m^3/s) and permanently submerged channel (≤142 m^3/s) at Lees Ferry to monitor the impact of fluctuating discharge on macroinvertebrate mass. Samples were taken from the varial zone between 1500 and 1800 h when the zone was inundated, whereas samples were collected from the channel between 0600 and 0800 h during daily low discharges. Macroinvertebrates were removed and oven-dried to a constant weight at 60°C. River discharge ranged from 142 to 566 m^3/s, with a mean annual discharge of ~300 m^3/s during the monitoring period.

Estimates of cobble bar area at Lees Ferry

Channel area was measured for selected reaches at Lees Ferry from aerial videotapes taken during periods of constant discharge at 142, 227, 425, and 793 m^3/s (Fig. 2), which was the highest discharge during the study. Reaches with cobble bars were measured because they support ≥75% of the benthic mass in the mainstem of the Colorado River (Usher and Blinn 1990, Blinn and Cole 1991, Shannon et al. 1994). Aerial videotapes at each of these discharges were taken with a Panasonic 3/4″ format video camera attached to a helicopter with a Tyler mount. The helicopter maintained an elevation of ~610 m above the river during videotaping. Map and Image Processing System (MIPS) software by Microimages, Inc. was used to calculate the area of each cobble bar. Each image was calibrated by measuring the distance between two or more fixed points in the field that were visible in the video frame.

In situ experiments

We conducted two experiments in the Colorado River between 12 June and 16 July 1991 (Experiments I and II) and a third experiment (III) on 11 February 1992 to test diel effects of fluctuating discharges on *Cladophora glomerata* and associated epiphyton and invertebrate communities during summer and winter. Two additional experiments (IV and V) were conducted to determine rates of short- and long-term algal and macroinvertebrate recolonization onto exposed substrata. Experiments I and II were conducted on separate dates using an open-frame floating raft (2.7 × 4.3 m) anchored in the Colorado River approximately 20 m from shore. The raft consisted of a rectangular wooden frame (2.7 × 4.3 m) with five cross beams, 82 cm apart. Thirty-six plastic baskets (17 × 20 × 11 cm) which were open on the top and solid on the bottom, with 5 cm^2 openings along the sides, were suspended from the beams. This de-

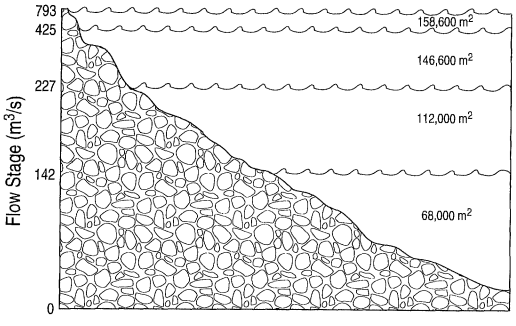

FIG. 2. Diagram showing the areas of a cobble bar in the river channel that are inundated at each stage under selected discharges in the Colorado River at Lees Ferry, Arizona.

sign allowed for continuous water flow with subsequent drifting and recruitment of macroinvertebrates. Experiments III, IV and V were conducted in the river channel during discharge ranging from 142 to 793 m^3/s. In all experiments involving sampling of cobbles, control and treatment substrata were handled in a similar manner to reduce differences between controls and treatments.

Experiment I: five night and day exposures

We experimentally simulated the effects of fluctuating discharges associated with Glen Canyon Dam on benthic algae and macroinvertebrates between 12 and 16 June 1991. We collected 108 cobbles (10 cm diameter) colonized by *C. glomerata* and associated epiphyton and macroinvertebrates from the river channel at Lees Ferry by snorkeling. Three randomly selected cobbles were placed in each basket. The experimental baskets (n = 12/treatment) were partitioned among three treatments: (1) control; colonized cobbles continuously submerged for the entire experiment, (2) daytime emersions with colonized cobbles exposed to air for 12 h (0600–1800 h) during the day, and (3) nighttime emersions with colonized cobbles exposed to air for 12 h (1800–0600 h) during the night. All baskets were submerged to a depth of 75 cm and treatment baskets were slowly raised 20 cm above the water during each 12-h day or night exposure and resubmerged after each exposure for five consecutive days. Air temperature and relative humidity readings (measured with a sling psychrometer 30 cm above the water surface) were taken three times each day (0600 h, 1200 h, 1800 h) during each experiment. One 2 × 2 cm quadrat of *C. glomerata* and associated biota was scraped with a razor blade from the upper surface of each of the three cobbles in each basket, at the start (initials) and at the end (after 5 d) of the experiment. Samples were sorted into *C. glomerata*, epiphyton, chironomids, oligochaetes, and *Gammarus lacustris*. Samples in each biotic category, except epiphyton, were oven-dried (60°C) to a constant mass. Epiphyton was removed from *C. glomerata* by vigorous agitation for 1 min in a bag filled with 50 mL of filtered (0.45 μm pore size) Colorado River water. This procedure removed at least 80% of the epiphyton from *C. glomerata*, based on microscopic examination, and was the most effective technique for separating intact epiphytic diatoms from *C. glomerata* filaments. *Cladophora* filaments were removed and the epiphyton suspension was filtered onto a pre-weighed glass fiber filter (0.45 μm pore size). Ash-free dry mass (AFDM) of epiphyton was determined by differential mass after ignition at 500°C for 1 h. Diatom cell densities were estimated from subsamples taken from these glass fiber filters for initial and final day-exposed treatment samples (n = 12 for each treatment). Ashed glass fiber filters were placed in 15 mL of distilled water and shaken vigorously for 15 s. The filter was then soaked for 2 min and vigorously shaken for an additional 15 s. Permanent Hyrax® (Auburn, California) slide mounts were prepared for each sample. A minimum of 300 diatom frustules were counted for each slide.

Experiment II: daily loss rates under varial flows

We used a similar protocol to that employed in Experiment I during 29 June and 3 July 1991 to measure the daily loss of *C. glomerata* and macroinvertebrate mass from naturally colonized cobbles (~15 cm diameter) in experimental baskets. These baskets were subjected to fluctuating discharges over a 5-d period: 142 m^3/s during the first 3 d and 85–765 m^3/s the last 2 d. The design entailed harvesting *C. glomerata* and associated biota at daily intervals from night- and day-exposed treatments (12 h each). *Cladophora glomerata* and associated epiphyton and macroinvertebrate mass were estimated daily.

Experiment III: in situ responses to nightly exposure

To determine in situ resistance of the benthos to, and recovery from, repeated nightly exposures, we conducted a 16-d experiment in the river channel between 30 June and 16 July 1991 during fluctuating discharges (85–765 m^3/s). Thirty-six cobbles of similar size (~25 cm diameter) colonized by *C. glomerata* and associated biota were collected from below the 85 m^3/s stage in the river channel and placed on shore at the 425 m^3/s stage. These experimental cobbles were exposed to the air for 10–12 h each night for 11 d as a result of fluctuating discharges. Three quadrats (4 cm^2) of *C. glomerata* and associated biota were harvested from the

surface of each cobble at the time of initial translocation and after 5 d and 11 d. Thirty-six cobbles were randomly selected from below the 85 m^3/s stage and likewise harvested at the same intervals and used as controls. After 11 d, experimental cobbles were returned to the channel below the 85 m^3/s stage to determine recovery of *C. glomerata* and macroinvertebrates. Three quadrats (20 cm^2) of *C. glomerata* and associated macroinvertebrates were harvested from the surface of each experimental cobble and from 36 control cobbles for comparison after 5 d of submergence. Experimental cobbles were placed in the channel near shore while randomly selected controls were collected at least 10 m from shore to avoid disturbance and sampling error. *Cladophora* and macroinvertebrates were separated from each sample and oven-dried at 60°C to a constant mass.

Experiment IV: night exposure and freezing

The effects of night desiccation and freezing on *C. glomerata* biomass, chlorophyll *a*, and macroinvertebrate density were examined on 10–11 February 1993. Thirty submerged cobbles, ~25 cm diameter, were taken from below the 142 m^3/s stage and submerged in 15 cm of water at the 280 m^3/s stage at 1500 h on 10 February. Cobbles were placed in the shade of large boulders to reduce potential damage of ultraviolet light to *C. glomerata*. A Peabody Ryan thermistor (Model J) was placed in the middle of treatment cobbles to compare water and ambient air temperatures during periods of submergence and drying. Thermistor readings revealed that treatment cobbles were exposed ~8 h, of which 3 h were at freezing temperatures (−2°C). Average river water temperatures were ~11.0°C. Relative humidity was 60% at 0730 h at the end of the exposure period. Discharge ranged from a maximum of 400 m^3/s at 2100 h on 10 February, to a minimum of 255 m^3/s on 11 February. On 11 February at 0800 h, prior to contact with direct sunlight, treatment cobbles were resubmerged in the river channel to a depth of 15 cm until 1600 h. Paired samples (each 20 cm^2) were scraped from the surface of each cobble at 1600 h, one for *C. glomerata* mass and the second for abundance of macroinvertebrates. The second paired sample, which was protected from direct sunlight and placed on dry ice, was also used for chlorophyll *a* analysis. Control samples (20 cm^2) were collected randomly from 30 previously undisturbed channel cobbles from the continuously submerged zone (<142 m^3/s stage) at 1660 h on both 10 and 11 February. Samples were sorted into *C. glomerata*, *G. lacustris*, oligochaetes, and gastropods. Ash-free dry weights were determined for *C. glomerata* and dry weights for macroinvertebrates. Chlorophyll *a* was extracted with methanol and calculated according to Tett et al. (1977).

Experiment V: long-term recolonization

To describe recolonization of firm substrata by the benthos after prolonged desiccation, 100 submerged cobbles (~25 cm diameter) were collected from the channel during December 1991 and placed above the high-water level along the shore. These cobbles were exposed for 6 mo, after which they were resubmerged in the channel (~60 cm in depth at 142 m^3/s) and used to measure temporal changes in structure of the benthic community. The 6-mo exposure period was used to simulate the maximum drying period experienced by the benthic community in the upper varial zone during seasonal low discharge (i.e., 425 m^3/s, Fig. 2). Treated cobbles were placed in a grid below the 142 m^3/s stage and one sample (20 cm^2) each was harvested from the surface of 20 randomly selected treatment cobbles after 1 wk of resubmergence, and thereafter at monthly intervals for 4 mo. Cobbles were replaced in the grid after sampling but not resampled, to maintain the velocity field on the experiment. Twenty control channel cobbles (~60 cm deep at 142 m^3/s) were also sampled at each interval. On each sampling date, AFDM of *Cladophora*, epiphyton, and macroinvertebrates (gastropods, *Gammarus lacustris*, chironomid larvae) were measured as described in Experiment I, and chlorophyll *a* as described in Experiment IV.

Energy measurements

We used results from our exposure experiments to evaluate drying effects on community energetics. Caloric content was determined for selected biota from the Colorado River with a Phillipson microbomb calorimeter (Phillipson 1964). Before calorimetry, the gut contents of numerically important macroinvertebrates (*G. lacustris*, oligochaetes, and chironomid larvae)

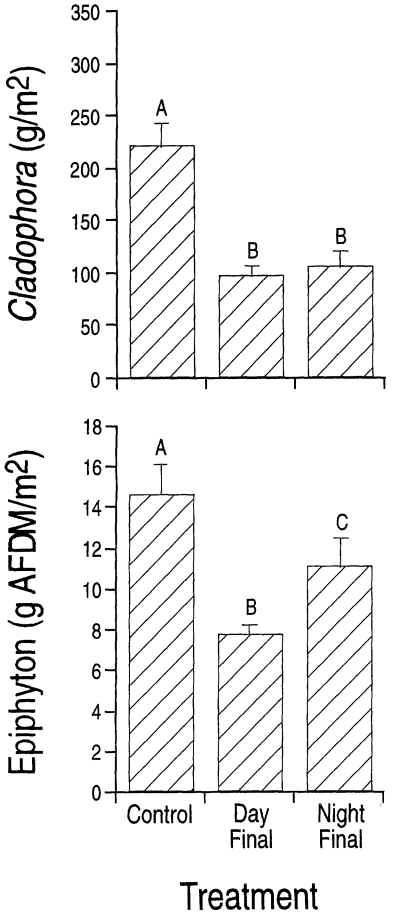

FIG. 3. Control and final mean (+1 SE) dry weight biomass for *Cladophora glomerata* and epiphytic diatoms after repeated day and night 12-h exposures for 5 d at Lees Ferry, Arizona, during 12–16 June 1991 (Experiment I). Bars with different letters are significantly different at $p < 0.01$ for univariate contrasts.

were cleared by starving animals for 20–24 h. Animals were then dried in a desiccator and prepared into pellets (13.5–14.5 mg). Epiphyton suspensions, epiphyton-free *C. glomerata* filaments, and macroinvertebrate taxa were dried in a desiccator and prepared into pellets (~14 mg) for microbomb calorimetry. Epiphyton pellets contained a 5% concentration of benzoic acid to insure complete burning. All samples were compared with standard benzoic acid ignitions. Energy values (joules/mg dry mass) for each biotic component were multiplied by respective losses in mass (mg/m^2) from our experimental exposure studies to obtain areal energy losses.

Biomass estimates from cobble bar areas

Potential algal and macroinvertebrate mass for several discharge regimes that occurred during this study were calculated from the product of the submerged channel area (m^2) below the 793 m^3/s stage at discharges of 425 m^3/s, 227 m^3/s, and 142 m^3/s (Fig. 2) and the mass (g/m^2) of benthic biota. Potential algal and animal energy were calculated from energy values of selected biota multiplied by the mass of each respective biotic component at each discharge.

We used energy per g AFDM for chironomid larvae and *G. lacustris* to estimate community energy per m^2 because these two macroinvertebrate taxa make up at least 75% of the macroinvertebrate mass at Lees Ferry and both are important constituents in fish diets at Lees Ferry (Shannon et al. 1994). This model assumes that the aquatic habitat below the 142 m^3/s stage is relatively uniform, an assumption corroborated by direct downstream observations and bathymetric measurements.

Statistical analyses for experiments

Analyses were conducted on ln-transformed data to reduce variance differences between treatment levels. Univariate and multivariate repeated measures analyses were performed on Experiments I, II, and III because control and/or treatment cobbles were sampled more than once (Zar 1984). Multivariate analyses (MANOVA) were performed on biweekly monitoring of the varial and submerged zones and Experiments IV–V. Post hoc univariate analyses were used to further explore patterns of changes with the taxonomic categories. Raft experiments (I and II) compared the impact of day and night atmospheric exposure on the benthos compared with submerged controls; all treatments were on the raft in baskets. Shore experiments (III, IV, V) compared desiccation and recovery of the benthos with benthos on control cobbles collected below the 142 m^3/s stage.

Results

Bi-weekly benthic monitoring at Lees Ferry showed a significant ($p < 0.0001$) discharge-related difference in macroinvertebrate mass between the continuously submerged channel (<142 m^3/s) and the varial zone (142–566 m^3/

s). The channel supported an annual mean macroinvertebrate standing mass of 1.4 g/m^2 (SE ±0.2) compared with only 0.3 g/m^2 (±0.07) in the varial zone.

Experiment I: five night and day exposures

Biomass of *Cladophora glomerata*, epiphytic diatoms, and chironomid larvae were all significantly reduced by 5 d of repeated 12-h exposures ($p < 0.001$). Both day- and night-exposure treatments showed a significant reduction in dry mass of *C. glomerata*. Repeated day exposures had 65% less mass than control cobbles, whereas repeated night exposures had 55% less mass than controls (Fig. 3). Based on our estimates of *C. glomerata* energy (joules) content (Table 1), the removal of *C. glomerata* biomass during repeated 5-d exposures resulted in a loss of 2.4×10^6 j/m^2 and 1.5×10^6 j/m^2 from the benthic community for day and night exposures, respectively. There were no significant differences between day and night initial treatments ($p = 0.27$), or day and night final treatments ($p = 0.20$).

Epiphyton AFDM decreased by 50% after 5 periods of repeated day-time exposure ($p < 0.001$) and by ~20% after 5 periods of night-time exposures (Fig. 3). However, there were no significant reductions in dry mass ($p = 0.11$) or diatom cell densities ($p = 0.19$) for epiphyton assemblages after 5 periods of day and night exposures. Average dry mass (dm) of periphyton on initial substrates was 106.1 g/m^2 (SE = 26.3) compared with 75.1 g/m^2 (SE = 10.5) after 5 d of fluctuating flows. Average density of diatom frustules at the start of the experiment was 148×10^3 (SE = 18.9) frustules/cm^2 compared with 168×10^3 (SE = 29.2) frustules/cm^2 after 5 d of fluctuating flows. Also, there was no significant difference between control and initial treatment cobbles ($p = 0.74$). Based on our estimates of epiphyton energy content (Table 1), removal of epiphyton mass during repeated 5-d exposures resulted in a loss of 8.4×10^4 j/m^2 and 3.8×10^4 j/m^2 from the benthic community for day and night exposures, respectively.

Standing stocks of chironomid larvae were proportionately more strongly reduced by repeated day and night exposures than were algae. Dry mass of chironomid larvae was reduced by 80% following day exposures and by 85% following night exposures (Fig. 4). This translates to a loss in benthic community energy of 1.7×10^4 j/m^2 for repeated day exposures and 2.3×10^4 j/m^2 for repeated night exposures. Univariate analysis showed no significant reduction in dry mass for *Gammarus lacustris* after repeated exposures ($p = 0.717$), likely resulting from high variance among samples due to the mobility of *G. lacustris* and relatively small samples (4 cm^2 harvest). However, descriptive statistics indicated a substantial reduction in *G. lacustris* mass after exposure: a reduction of 78% after day exposures and 89% after night exposures after 5 d of repeated exposures (Fig. 4). Derived energy losses from the removal of *G. lacustris* mass [16.54 j/mg dw (SE = 0.61, n = 31)] during these discharge fluctuation schedules include 5.7×10^4 j/m^2 for day exposures and 1.8×10^4 j/m^2 for night exposures.

TABLE 1. Mean (±1 SE) energy values (n = 3) for *Cladophora glomerata*, diatom epiphyton, and various macroinvertebrates collected at Lees Ferry in the Colorado River, Arizona.

Biotic category	Energy (j/mg DW)
Cladophora glomerata	11.75 (±0.39)
Diatom epiphyton	14.43 (±0.42)
Lumbriculid assemblage	15.52 (±0.64)
Gammarus lacustris	16.54 (±0.37)
Tubificid assemblage	20.45 (±0.37
Chironomid assemblage	21.38 (±0.02)

Experiment II: daily loss rates under varial flows

Daily observations of aquatic communities subjected to 12-h experimental exposures at Lees Ferry showed a significant ($p = 0.03$) reduction in *C. glomerata* mass between initial measurements by day 2, and a significant ($p = 0.04$) reduction in macroinvertebrate mass by the end of day 1 in both day- and night-exposure treatments. After two 12-h day exposures, 48% of the *C. glomerata* was lost (Fig. 5), whereas 43% of the mass was removed after two 12-h night exposures. Macroinvertebrate mass was reduced by 90% after one 12-h day exposure (Fig. 6) and by 85% after one 12-h night exposure. In each case, no further reductions in biomass occurred after 1 d for macroinvertebrates and 2 d for algae. There were no significant differences between day versus night exposures for any treat-

ment ($p > 0.05$). Also, no significant differences occurred among control samples and between collection dates for *C. glomerata* ($p = 0.17$) or macroinvertebrates ($p = 0.07$) throughout the experiment. After 5 d of repeated daily exposures, 69% of the initial *C. glomerata* mass was removed and >98% of the initial macroinvertebrate mass was lost from cobbles (Figs. 5 and 6).

Experiment III: in situ responses to nightly exposure

Channel experiments showed significant differences in macroinvertebrate and *C. glomerata* mass between control channel cobbles (continuously submerged) and shore cobbles (exposed 10–12 h nightly) after 5 and 11 d of fluctuating discharges between 142 and 793 m^3/s ($p < 0.001$). Fifty-five percent of the initial *C. glomerata* mass and 99% of the initial macroinvertebrate mass were lost from shore cobbles that were exposed nightly for 11 d (Figs. 7 and 8). There was no significant difference in either macroinvertebrate or *C. glomerata* mass between the initial (pre-treatment) cobbles and cobbles that were continuously submerged in the channel throughout the entire experiment ($p = 0.296$).

The recolonization (recovery) of macroinvertebrate mass on cobbles that were submerged for 5 d after nightly exposure for 11 d was more rapid than recolonization by *C. glomerata* (Figs. 7 and 8). Gastropods were the first to recolonize cobbles after the first day, followed by *G. lacustris* and chironomid larvae. No significant difference was found in macroinvertebrate mass on continuously submerged controls and cobbles that had been resubmerged for 5 d after nightly exposure for 11 d on shore ($p = 0.858$). However, *C. glomerata* mass on continuously submerged cobbles was ~1.5-fold higher ($p = 0.001$) than that on cobbles resubmerged after repeated exposure (Fig. 7).

Mean relative humidity ranged from 26 to 34% (SD = 3.1%) during Experiments I–III, while mean daily air temperature ranged from 21.1 to 23.6°C (SD = 1.2°C). Relative humidity and air temperature did not differ significantly among the three experiments.

Experiment IV: night exposure and freezing

Nighttime winter exposures (3 h of freezing during an 8-h exposure) resulted in significant losses in *C. glomerata* biomass ($p = 0.003$) and chlorophyll *a* ($p = 0.0009$). Frozen filaments of *C. glomerata* were soft and jelly-like, as though cell walls had ruptured. Mean AFDM of *C. glomerata* decreased from 80.1 g in controls to 44.5 g in exposed samples within 24 h, whereas chlorophyll *a* decreased from 8.71 to 3.62 mg/m^2.

Although multivariate analysis showed no significant effects of exposure/freezing on macroinvertebrate dry mass ($p = 0.24$), descriptive statistics suggested a reduction in biomass. Control cobbles had 400 lumbriculids/m^2, 325 gastropods/m^2, 175 *G. lacustris*/m^2, and 75 oligo-

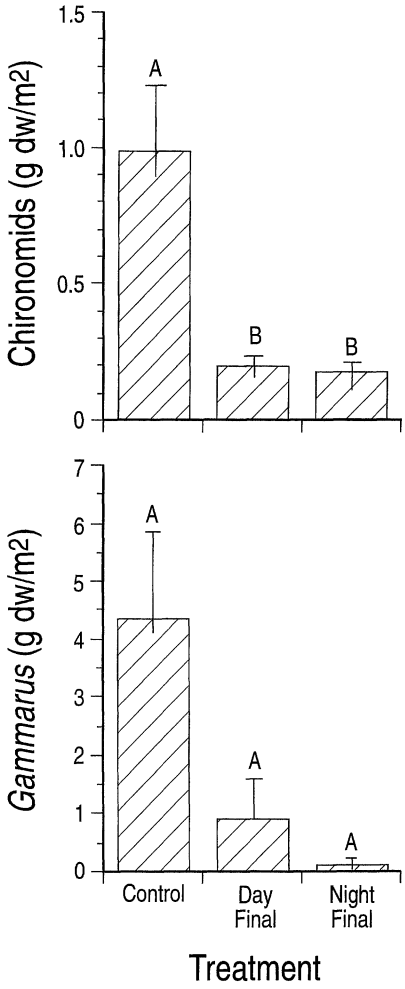

FIG. 4. Control and final mean (+1 SE) dry weight mass for *Gammarus lacustris* and chironomid larvae after repeated day and night 12-h exposures for 5 d at Lees Ferry, Arizona, during 12–16 June 1991 (Experiment I). Bars with different letters are significantly different at $p < 0.05$ for univariate contrasts.

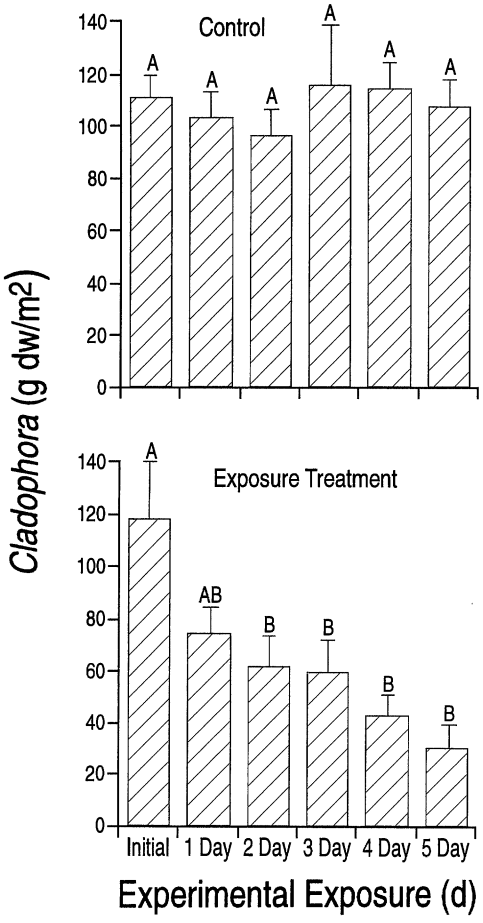

FIG. 5. Mean (+1 SE) daily biomass of *Cladophora glomerata* for submerged control and experimental daytime exposure treatments over a 5-d period at Lees Ferry, Arizona, 29 June–3 July 1991 (Experiment II). Bars with different letters are significantly different at $p < 0.05$ for univariate contrasts.

chaetes/m^2 compared with only 75 *G. lacustris*/m^2 in exposed treatments.

Experiment V: long-term recolonization

The benthic community on cobbles exposed for 6 mo differed significantly, after 4 mo of resubmergence, from control cobbles ($p < 0.0001$); however, different benthic components differed in recovery rates. The density of gastropods (*Physella* sp. and *Fossaria obrussa*) were equivalent on resubmerged treatment and control cobbles after 1 wk (univariate, $p = 0.119$), whereas chlorophyll *a* on treatment cobbles recovered to control levels after 1 mo ($p > 0.05$). In contrast, differences between exposed samples and controls for both epiphyton ($p < 0.0001$) and *C. glomerata* ($p = 0.008$) mass remained significant, and mass for *G. lacustris* and chironomids remained <30% of the controls throughout the 4 mo of resubmergence.

We derived potential energy for *G. lacustris* and chironomid larvae by extrapolating aerial estimates of river channel area and the normal maximum high stage (793 m^3/s) for selected discharges. Approximately 6.8 ha of river channel occurs below the 142 m^3/s stage at Lees Ferry, whereas 11.2 ha, 14.7 ha, and 15.9 ha occurs below discharges of 227 m^3/s, 425 m^3/s, and 793 m^3/s, respectively (Fig. 2).

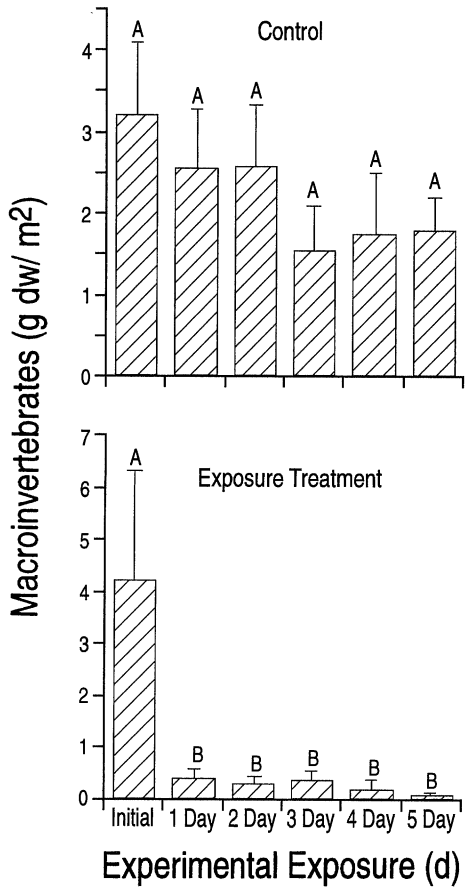

FIG. 6. Mean (+1 SE) daily biomass of macroinvertebrates for submerged control and experimental daytime exposure treatments over a 5-d period at Lees Ferry, Arizona, 29 June–3 July 1991 (Experiment II). Bars with different letters are significantly different at $p < 0.05$ for univariate contrasts.

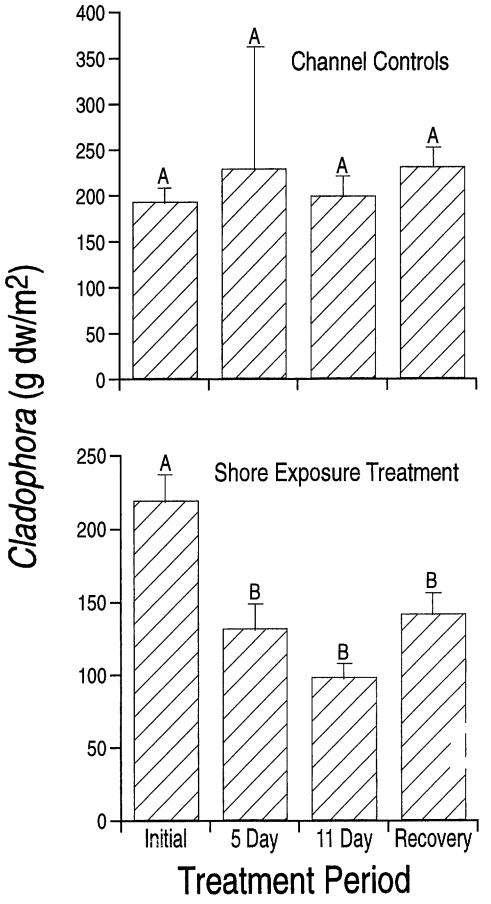

FIG. 7. Mean biomass (+1 SE) of *Cladophora glomerata* for channel controls and shore exposure treatment for 5-d, 11-d, and 5-d recovery at Lees Ferry, Arizona, 30 June–16 July 1991 (Experiment III). Bars with different letters are significantly different at $p < 0.05$ for univariate contrasts.

We estimated the amount of available energy (joules) in the Lees Ferry channel as epiphyton, *G. lacustris*, and chironomid larvae at various discharge stages calculated from mass data from various treatments in Experiment I (Fig. 9). This reach supported approximately 12.0 × 10^9 j of epiphyton mass below stage discharge of 142 m^3/s, 18 × 10^9 j below 227 m^3/s, 23.5 × 10^9 j below 425 m^3/s, and 26.1 × 10^9 j of epiphyton mass below stage discharge of 793 m^3/s (Fig. 9). Available energy estimates for secondary producers (*G. lacustris* and chironomid larvae) common in fish diets at Lees Ferry were approximately 6.6 × 10^9 j below a discharge of 142 m^3/s, 11.1 × 10^9 j below 227 m^3/s, 14.2 × 10^9 j below 425 m^3/s, and 15.2 × 10^9 j below an unregulated discharge of 793 m^3/s (Fig. 2). Therefore, the highest available energy for native and nonnative fish could potentially be supported at base discharge of 793 m^3/s when the greatest area of river channel was inundated. Nearly two times more potential community energy would exist with a base discharge of 793 m^3/s than at 142 m^3/s, and 1.6-fold more energy would exist with a base discharge of 227 m^3/s than at 142 m^3/s.

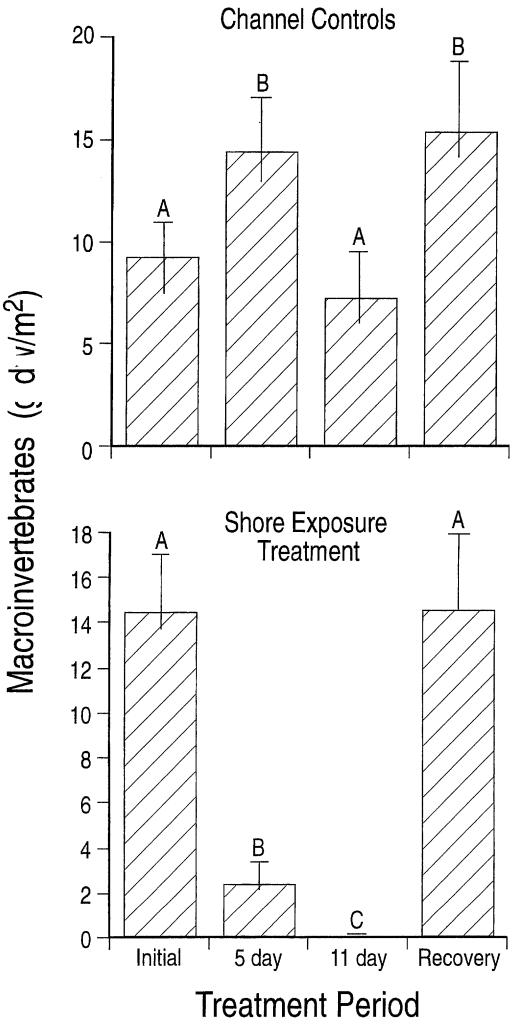

FIG. 8. Mean biomass (+1 SE) of macroinvertebrates for channel controls and shore exposure treatment for 5-d, 11-d, and 5-d recovery at Lees Ferry, Arizona, 30 June–16 July 1991 (Experiment III). Bars with different letters are significantly different at $p < 0.05$ for univariate contrasts.

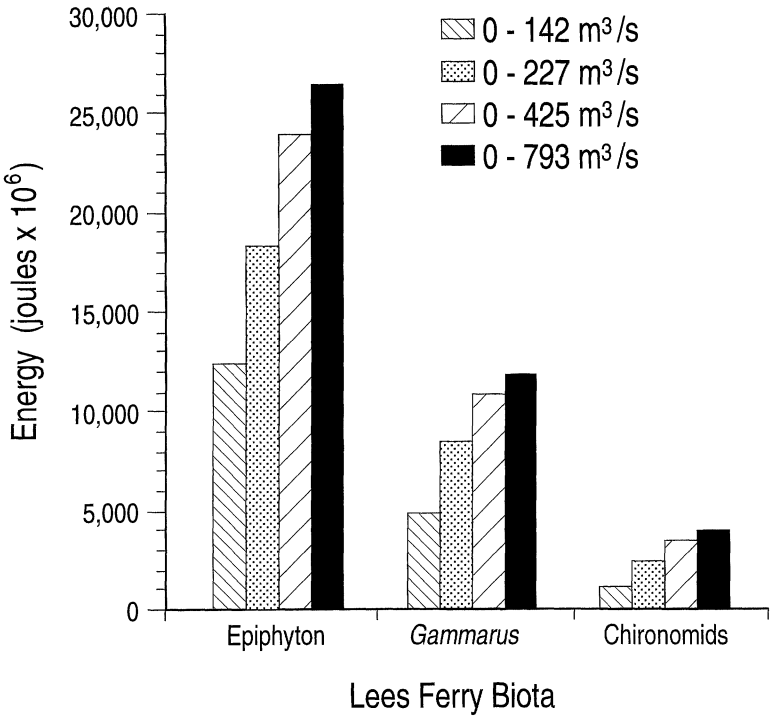

FIG. 9. Estimated community energy content of epiphytic diatoms, *Gammarus lacustris*, and chironomid larvae in the Colorado River at Lees Ferry, Arizona at various discharge stages.

Discussion

Discharge fluctuation effects of summer and winter exposure of the varial zone exert major impacts on benthos in the Colorado River tailwaters. Our results support Grimm's (1993) suggestion that atmospheric exposure in lotic environments is a more severe disturbance than flash flooding because daily exposure quickly eliminates the benthos, and recovery of algae and macroinvertebrates is a protracted process. Incremental effects of increasing base discharge on the benthos is likely to affect local fisheries and, through transport of organic drift, the Colorado River ecosystem downstream in the Grand Canyon.

Effects on algal communities

Daily harvests from in situ experiments at Lees Ferry showed ≥38% reductions in *Cladophora glomerata* mass after 2 d and ≥70% reductions after 5 d of repeated 12-h exposures for both day and night treatments. Usher and Blinn (1990) reported similar losses of *C. glomerata* mass after repeated 12-h exposures in laboratory stream tanks. They found that repeated exposures (≤12 h) caused *C. glomerata* tufts to become stranded and bleached, holdfast systems to dry and weaken, and algal filaments to subsequently detach from cobble substrata during the rising limb of the hydrograph.

Likewise, Angradi and Kubly (1993) reported that only 57% of the initial chlorophyll *a* remained after a 10-h exposure at Lees Ferry. Differences in response rates between chlorophyll *a* and mass suggests the immediate degradation of pigment in the presence of ultraviolet light, and subsequent detachment of *C. glomerata*. Furthermore, losses in chlorophyll *a* represent significant losses of epiphyton.

Algal assemblages exposed to subzero temperatures during winter showed similar negative consequences of discharge reductions. Standing crops of *C. glomerata* and chlorophyll *a* were reduced by 50% within 1 d after a 3-h exposure to freezing temperatures (−2°C). Filaments disintegrated after a single exposure and detached from submerged cobbles.

In some lotic ecosystems, drifting *Cladophora*

contains high densities of associated organisms which enhance the nutritional value of drifting packets (Power 1990). Detachment of *C. glomerata* during discharge fluctuations in the Colorado River results in downstream export of large amounts of potential energy as tufts of coarse particulate organic matter (CPOM; Leibfried and Blinn 1986). Most of this material probably disintegrates and feeds detritivores, but some is still available for the downstream fisheries (Angradi 1994). The availability of drifting CPOM to downstream native and nonnative fish depends, in part, on water transparency. Typically, water clarity below the confluence of the Paria River (RKM 1) is an order of magnitude lower than that at Lees Ferry as a result of high suspended sediments contributed by the Paria River (Fig. 1), thereby reducing visual predation on drifting material by at least 70% (M. Yard, Glen Canyon Environmental Studies Program, Flagstaff, personal communication).

Experiment I suggested that both particulate organic carbon (POC) and dissolved organic carbon (DOC) are lost from epiphyton communities as a result of short-term emersion. The significant reduction in epiphyton AFDM and lack of significant reduction in diatom cell density after 5 d of repeated exposures suggest that dissolved organic carbon (DOC) was leached from attached cells (diatoms and bacteria). Greater losses of DOC occurred during daytime than during nighttime exposures, implying a strong negative impact of ultraviolet light on algal assemblages or perhaps greater desiccation rates. Bothwell et al. (1989) found greater adhesion of diatom cells in light than in compared dark treatments, and suggested that exposure to light may increase photosynthetic production and release of extracellular products. DOC released from epiphyton during fluctuating flows may serve as an important nutrient for the microbial loop of downstream invertebrate communities (Meyer 1993). Significantly higher densities of filter-feeding simuliid populations occur at downstream sites in the Colorado River, implying relatively high densities of bacteria in the seston (unpublished data).

Loss of epiphyton in tailwater ecosystems may have major effects on macroinvertebrate communities in the Colorado River ecosystem. Modifications in the physiognomy of epiphyton communities may determine the availability of cells for invertebrate consumption, thereby reducing or modifying energy flow in tailwater food webs (Blinn et al. 1989, Colletti et al. 1987, Steinman et al. 1987, Angradi 1994). Hardwick et al. (1992) reported a marked decrease in epiphytic upright diatom species (*Diatoma vulgare* and *Rhoicosphenia curvata*) compared with the more prostrate *Cocconeis pediculus*, resulting from fluctuations in discharge. Peterson (1987) reported similar changes in physiognomy in sheltered environments in the Colorado River below Hoover Dam.

Shannon et al. (1994) reported a strong positive correlation between epiphyton biomass and abundance of *Gammarus lacustris* in laboratory and in situ experiments. They found that *G. lacustris* preferentially selected *C. glomerata* with a dense cover of epiphytes, as opposed to detritus, *Oscillatoria*, or *C. glomerata* with low epiphyte density. This preference appears to be a chemosensory response because *G. lacustris* preferred artificial substrata soaked in epiphyton extract over extract-free substrata. These results support the conclusions by Angradi (1994).

Effects on macroinvertebrates communities

Cladophora glomerata serves as an important refuge and perhaps a direct food source for macroinvertebrates in some aquatic ecosystems (Patrick et al. 1983, Dudley et al. 1986, Brönmark et al. 1991, Dodds and Gudder 1992). However, *C. glomerata* does not appear to be a direct food source in the Colorado River, but rather serves as a structural host (Shannon et al. 1994).

The tailwaters reach at Lees Ferry serves as an autochthonous energy source for the downstream portion of the river. During discharge fluctuations associated with river regulation, macroinvertebrates quickly abandon stranded *C. glomerata* and are swept downstream during the rising limb of the hydrograph (Leibfried and Blinn 1986, Blinn and Cole 1991). We observed a 90% reduction in macroinvertebrate mass within 24 h of discharge fluctuations at Lees Ferry, with no additional losses over the next 5 d of river fluctuation. Our data suggested that after 5 d of fluctuating discharges, all macroinvertebrate taxa were reduced to approximately equal levels.

Recolonization of exposed substrata by macroinvertebrates following fluctuating dis-

charges is significantly faster than that by *C. glomerata*. Re-establishment of *C. glomerata* occurs primarily by regrowth of persistent holdfasts (personal observations). Macroinvertebrate mass on cobbles that had been resubmerged following exposure to fluctuating discharges for 11 d was the same as mass on control cobbles within 5 d following resubmergence, whereas estimates for similar recovery by *C. glomerata* was >8 mo. The rapid recolonization by macroinvertebrates may result from rapid recovery of food resources (epiphyton) on remaining filaments of *C. glomerata* and cobble substrata (~50% of controls after 1 wk). Also, the rapid recolonization by macroinvertebrates may have resulted from the close proximity of a relatively large pool of macroinvertebrates at Lees Ferry (submerged channel = 6.8 ha at 142 m^3/s) which serves as a source of animals for recruitment. Other investigators have reported similar recruitment models in lotic ecosystems (Wallace 1990, Mackay 1992). Our observations revealed that gastropods recolonized cobbles within 1 d, followed by *G. lacustris* and chironomid larvae.

The frequency of fluctuations in discharge in regulated lotic tailwaters influences the rate of benthic recovery. Jensen and Jensen (1984) experimentally lowered the water level in the Gudenaa River in Denmark by 0.5 m every night for 1 mo then increased the level thereafter. These regular fluctuations in water level stimulated drift to the extent that invertebrate populations were eventually depleted and recovery of invertebrates took about 15 mo after manipulations ceased. In a second study, they lowered the water level 0.5 m within 1 h and maintained this stage for 2 wk. Drift was less than during regular fluctuations and benthos recolonized soon after the water level rose. Our data demonstrate strong effects of daily fluctuations and a protracted recovery process. Other studies have also reported slower recovery of biotic communities in lotic ecosystems with daily fluctuations than in systems with less frequent fluctuations (Perry and Perry 1986).

Recolonization by macroinvertebrates onto submerged cobble substrata that were subjected to long-term drying (6 mo) varied between taxa. Gastropod densities on resubmerged desiccated cobbles equalled controls after 1 wk, whereas *G. lacustris* and chironomid larvae were only 30% of control densities after 4 mo. The high variance between samples was likely due to the mobility of *G. lacustris* and the relatively small sample area (20 cm^2). The rapid recolonization by gastropods over other macroinvertebrates may have resulted from the ability of snails to move more efficiently on smooth surfaces, whereas *G. lacustris* and chironomids require more texture for efficient movement. Differential recolonization rates among macroinvertebrate taxa may also result from different feeding habits and different degrees of mobility among animals. At Lees Ferry, gastropods feed on the rapidly recolonizing epilithon on cobble substrata, whereas *G. lacustris* and chironomid larvae feed primarily on epiphyton associated with *C. glomerata*. Therefore, slow recolonization by *C. glomerata* limits recolonization by *G. lacustris* and chironomid larvae, but not necessarily gastropods.

Effects on top trophic levels

Lees Ferry supports a trophic trout fishery (Stanford and Ward 1986), producing nearly 95 kg/ha of trout mass (Bill Persons, Arizona Game and Fish, personal communication). We estimated that discharge maintained at 793 m^3/s provided nearly twice the energy in the form of macroinvertebrate mass at Lees Ferry (15.5 ha) than flows of 142 m^3/s.

Cho (1992) reported that each kg of trout mass requires an average of 15 MJ of digestible energy. Based on Cho's conversions and a 70% assimilation efficiency for rainbow trout (Phillips and Brockway 1959), we predict that fish mass would be increased by ~42.5 kg/ha if discharge was increased from 142 to 793 m^3/s at Lees Ferry. Similarly, we predict that trout mass would be increased by 34.7 kg/ha if discharge increased from 142 to 425 m^3/s, and 18.1 kg/ha if discharge increased from 142 to 227 m^3/s. Foraging efficiencies for rainbow trout were not considered in our model. These estimates are based on combined energy losses for *G. lacustris* and chironomid larvae extrapolated from Figure 9 and assuming relatively uniform distribution of macroinvertebrates throughout the river channel.

The morphometry of the Lees Ferry reach suggests that discharges between 142 and 227 m^3/s inundate ~11.2 ha (72% of the wetted perimeter) of the river channel compared with 4.6 ha for discharges between 227 and 793 m^3/s

(Fig. 2). This contrast suggests that a 71% increase in discharge only inundates an additional 28% of the river channel.

However, the assumption that macroinvertebrates are uniformly distributed may underestimate the overall impact of discharge reductions on fish production, because numbers of benthic invertebrates typically are higher along the margins of large rivers where impacts of river regulation are most severe. Our SCUBA observations at Lees Ferry have shown greater densities of invertebrates along the margins of the Colorado River. Gislason (1985) noted that condition factors for salmon and rainbow trout were higher under periods of stable discharge than under periods of fluctuating discharge in the Skagit River, Washington. He attributed these differences to loss of shoreline insects and habitat during the fluctuations.

Management considerations

Thorp and Delong (1994) extended the predictions of the river continuum concept (Vannote et al. 1980) by recognizing that the highly productive nature of shallow fluvial habitats may increase local and reach-based ecosystem dynamics in high order streams. However, in large regulated rivers, shallow-habitat production may be limited by fluctuating discharges that expose the varial zone. In our study, the magnitude of fluctuation in base discharge and daily discharge was strongly and negatively correlated with exposure of the varial zone, resulting in reduction of shallow benthic production. Our data showed that two 12-h periods of exposure below normal base discharge (142 m^3/s) eliminated >50% of the *C. glomerata* standing mass, and recovery from this brief period of exposure required more than 4 mo. Although direct nocturnal exposures of the varial zone in the summer may not eliminate *C. glomerata*, short periods of nocturnal exposure during the winter combine the effects of freezing and desiccation on *C. glomerata* and dramatically reduce standing mass of this keystone species. Tradeoffs between the potential benefits of hydroelectric power generation versus the production of benthos and fisheries in tailwaters should be carefully considered by managers of rivers with dams, power stations, or locks that vary the discharge.

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