



---

Reservoir-River Linkages: Lake Powell and the Colorado River, Arizona

Author(s): Emma P. Benenati, Joseph P. Shannon, W. Blinn, Kevin P. Wilson, Susan J. Hueftle  
Source: *Journal of the North American Benthological Society*, Vol. 19, No. 4 (Dec., 2000), pp. 742-755

Published by: The North American Benthological Society

Stable URL: <http://www.jstor.org/stable/1468131>

Accessed: 16/07/2009 21:13

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=nabs>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).



The North American Benthological Society is collaborating with JSTOR to digitize, preserve and extend access to *Journal of the North American Benthological Society*.

<http://www.jstor.org>

## Reservoir–river linkages: Lake Powell and the Colorado River, Arizona

EMMA P. BENENATI<sup>1</sup>, JOSEPH P. SHANNON, DEAN W. BLINN, KEVIN P. WILSON,  
AND SUSAN J. HUEFTLE

*Department of Biological Sciences, Northern Arizona University, P.O. Box 5640,  
Flagstaff, Arizona 86011 USA*

**Abstract.** The effect of lotic–lentic interactions on the phytobenthic community was studied in the Colorado River below Glen Canyon Dam (GCD), Arizona. Major compositional changes in river phyto-benthos occurred following high snowmelt inflows that filled the Lake Powell reservoir and resulted in high, steady discharges from GCD. *Cladophora glomerata*, the previously dominant alga, was partly displaced by a mixed mucilaginous phytobenthic assemblage consisting of miscellaneous algae, macrophytes, and bryophytes (MAMB). Relationships between abiotic parameters (discharge, conductivity, nutrient concentration, and season) and biotic responses (composition and biomass of filamentous and epiphytic algae, and invertebrate biomass) were analyzed from 1995 to 1998. In addition, the response of the phytobenthos to an experimental flood (1275 m<sup>3</sup>/s) was examined in the tailwaters below GCD. Significant compositional changes occurred within 3 mo of lake filling and the onset of elevated discharges in June 1995. Relative phytobenthic composition by biomass prior to June 1995 was: *Cladophora glomerata* = 91.5%, MAMB = 3.5%, and cyanobacteria = 5.0%, compared to 49.6, 47.9, and 2.5%, respectively, after the initiation of high discharges. *Cladophora* and MAMB had an inverse relationship that fluctuated seasonally. *Cladophora* was positively associated with increased nutrient concentrations and lower discharge during summer–autumn, whereas MAMB was positively correlated with decreased nutrients and higher discharge during winter–spring. *Cladophora* was positively associated with invertebrate biomass and also had greater epiphyton biomass and density than MAMB. The 1996 experimental flood resulted in a significant loss of MAMB biomass, in contrast to a minimal decrease in *Cladophora* and invertebrates. Interactions between inflow patterns, reservoir chemistry, and discharge regime have an important effect on benthic community structure below dams. Resource managers need to consider these relationships and regard water resources above and below impoundments as a connected system when making management decisions.

**Key words:** regulation, reservoir, algae, *Cladophora*, diatoms, nutrients, discharge, invertebrates, tailwaters, experimental flood, mucilage, conductivity.

River benthic communities are more often shaped by a combination of conditions rather than a single factor. High discharge and fast current can affect the biomass and composition of lotic algae because of increased physical stress or changes in hydraulic characteristics of the stream bed (Peterson 1987, Statzner et al. 1988, Biggs and Close 1989, Duncan and Blinn 1989, Poff et al. 1990, Biggs 1996). Nutrient availability and delivery under different flow regimes play a primary role in phytobenthic composition and accrual (Horner and Welch 1981, Biggs and Price 1987, Dodds 1991, Leland 1995, Biggs 1996). Reservoir characteristics must also be considered as a key factor in the combination of variables influencing impounded rivers (O'Keefe et al. 1990, Puig et al. 1990).

Lotic communities below dams are structured

by the combination of discharge regimes and the chemical nature of water released from the reservoir (Stanford and Ward 1979, Byren and Davies 1989, Blinn et al. 1998). Dams dramatically change natural discharge patterns by dampening the frequency and magnitude of flood disturbance. The upstream supply of bed sediments and allochthonous C sources are trapped above the dam, which results in greatly increased light penetration into water and a changeover to autochthonous production of benthic algae on stabilized substrata of cobbles downstream (Lowe 1979, Ward et al. 1986, Dufford et al. 1987, Blinn et al. 1998, Haden et al. 1999). The presence of a reservoir and the depth in the lake from which water is drawn can have profound effects on both nutrient and thermal regimes (Stanford and Ward 1979). Watershed events such as precipitation and inflow changes can disrupt reservoir water quality, volume, and

<sup>1</sup> E-mail address: emmap.benenati@nau.edu

hydrologic outflow patterns (Hannan 1979, Rada and Wright 1979). Thus, reservoir water release regimes have the potential to cause major temporal and spatial changes in phytoplankton communities of downstream rivers.

In the spring of 1995, high snowmelt delivered from Lake Powell's tributaries filled the reservoir to capacity for only the 2nd time in its 33-y existence. This filling resulted in a freshened or diluted reservoir and subsequent high-flow releases from Glen Canyon Dam (GCD) to facilitate lake drawdown. Within 3 mo, >50% of the once-dominant nonmucilaginous chlorophyte *Cladophora glomerata* (L.) Kütz was replaced with a mixed, mucilaginous phytoplankton assemblage consisting of miscellaneous algae, macrophytes, and bryophytes (MAMB) in the tailwaters. *Cladophora glomerata* became the dominant alga below GCD within 6 y of the 1963 closure (Czarnecki et al. 1976, Mullan et al. 1976, Carothers and Minckley 1981, Blinn et al. 1989) and remained dominant until August 1995 (Blinn and Cole 1991, Blinn et al. 1995, Benenati et al. 1998). *Cladophora* is considered important to the Colorado River food web below GCD because of its keystone role as a host, refugium, and provider of food to upper trophic levels throughout the river corridor (Blinn and Cole 1991, Shannon et al. 1994, Blinn et al. 1998). Other algal constituents provide lower epiphytic diatom biomass and inadequate refugia for invertebrates (Shaver et al. 1997, Benenati et al. 1998).

The major compositional change in phytoplankton following a filled reservoir and increased water releases illustrates the need for greater understanding of lentic-lotic interactions. The aim of our study was to improve understanding of the roles that reservoir discharge and nutrient regimes play in controlling benthic composition in downstream reaches. Specific objectives of our study were: 1) to quantitatively assess selected chemical parameters below GCD, 2) to monitor and quantify the compositional change in the phytoplankton community below GCD and potential trophic ramification, and 3) to test the response of the altered phytoplankton community to extreme discharges ( $1275 \text{ m}^3/\text{s} \times 7 \text{ d}$ ).

## Methods

### Study area

The Colorado River is impounded by GCD (Fig. 1), a hypolimnetic-release hydroelectric

dam completed in 1963 near Page, Arizona. Releases from GCD are clear (Secchi depth >6 m) and cold (range = 8–10°C), averaging  $412 \text{ m}^3/\text{s}$  with a maximum discharge capacity of  $937 \text{ m}^3/\text{s}$  (Stanford and Ward 1991, Blinn et al. 1995). GCD, a peaking power facility, is governed by daily electricity demands of the western United States (US Bureau of Reclamation 1995). As a result, normal post-dam releases have had high daily fluctuations ( $226\text{--}750 \text{ m}^3/\text{s}$ ) except on rare occasions of meteorological or political mandate. Above GCD is Lake Powell, the 2nd largest reservoir in the United States with an area of  $653 \text{ km}^2$  and a capacity volume of  $33.3 \text{ km}^3$ .

Prior to GCD, the Colorado was a turbid river with wide ranges in annual peak flows and temperature. The highly erodible sediments of the basin resulted in annual sediment loads averaging 126 million metric tons between 1925 and 1957, 12-fold greater than post-dam measurements (Andrews 1991). Spring snow-melt flows averaged  $2450 \text{ m}^3/\text{s}$  with 10-y floods of  $3540 \text{ m}^3/\text{s}$ , which gradually decreased to winter lows of  $<100 \text{ m}^3/\text{s}$  (Howard and Dolan 1981). Seasonal temperatures ranged from 0°C in the winter to 30°C highs in the summer (Stanford and Ward 1991).

Our study was conducted in the Colorado River near Lees Ferry, Arizona (lat  $36^{\circ}52'03''\text{N}$ , long  $111^{\circ}35'40''\text{W}$ ), a tailwater site 25.3 river kilometers (RKM) downstream from GCD that is designated as RKM 0.0 and is the legal boundary between the upper and lower Colorado River basin states (Fig. 1). The clear, cold, 26-km-long tailwater section, dominated by *C. glomerata* for 3 decades, supports prolific benthic algal growth, and contained >50% of the algal and invertebrate biomass of the entire 400-km-long river corridor below GCD during 1991 (Stevens et al. 1997). *Cladophora* became dominant below GCD and other deep-release dams in the Colorado River basin because of tailwater conditions that allowed the alga to thrive (Blinn et al. 1998). *Cladophora* is a problem taxon in many small streams but, in the Colorado River through Grand Canyon, the combination of river depth, current velocity, and the hydraulic grinding action of rapids eliminates any nuisance characteristics.

The filling of Lake Powell as a result of high snowfall in the Green and Colorado River basins in 1993 and 1995 resulted in an emergency departure from the normal pattern of widely fluctuating

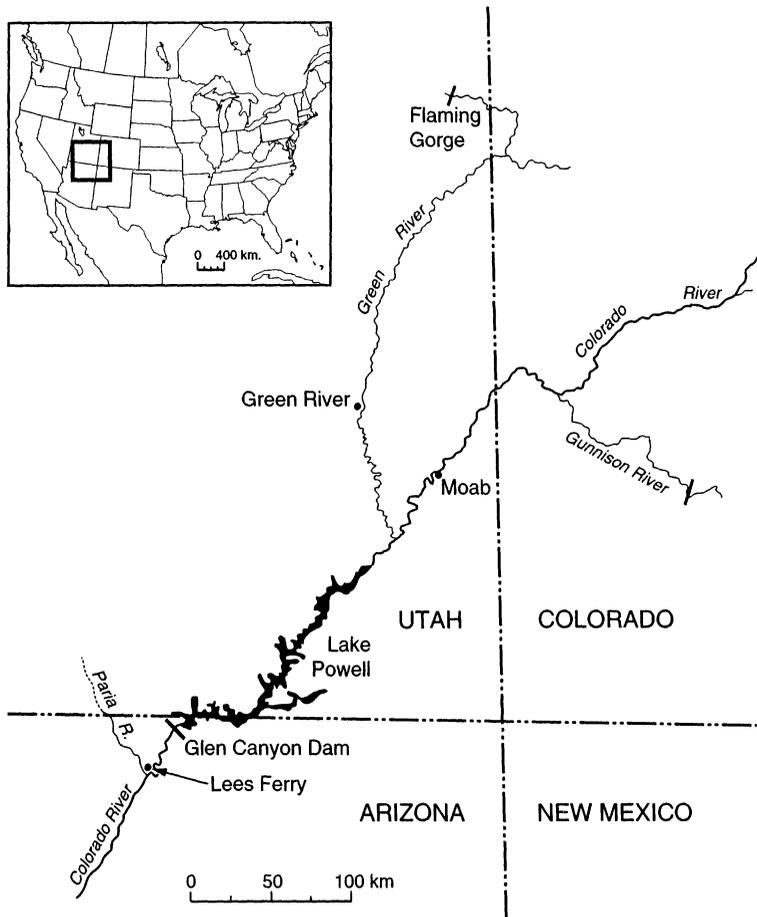


FIG. 1. The Colorado River system in Colorado, Utah, and northern Arizona. The study area is located in the Colorado River at Lees Ferry, Arizona, 25.3 km below Glen Canyon Dam and the reservoir, Lake Powell.

tuating reservoir releases in the summer of 1995. Relative to the previous 3 decades, the discharge regime changed to high and steady flows beginning in June 1995, and this pattern continued throughout the study period (June 1995–January 1998).

#### Discharge

Discharge means were monitored on a monthly basis at the Lees Ferry US Geological Survey gaging station during the period of phytobenthic change (June 1995–January 1998) to coincide with monthly benthic collections during this same period. The new steadier flow regime resulted in a decreased *varial zone* (the area of river channel above baseflow subject to intermittent wetting and drying) and an increased

*submerged zone* (the area of permanently wetted river channel) (Stanford and Hauer 1992).

#### Water quality

Water samples for nutrient and cation analyses were taken in the Colorado River at Lees Ferry from June 1995–January 1997 for 13 of the 23 benthic collection intervals. Replicate samples ( $n = 3$ ) were collected in acid-cleaned polyethylene bottles, fixed with  $H_2SO_4$  to a pH  $< 2.0$ , and refrigerated until processing ( $\leq 1$  wk). Filtered samples (Whatman® GF/C 0.45- $\mu m$  glass microfiber filters) were analyzed for  $NH_3$ ,  $NO_3^-$ ,  $O-PO_4$ ,  $Ca^{++}$ ,  $Mg^{++}$ ,  $Na^+$ , and  $K^+$ . Unfiltered samples were analyzed for total organic N (TKN) and total P (TP). The TKN and TP samples were digested and analyzed on a Technicon

Auto Analyzer II<sup>®</sup> (US Environmental Protection Agency 1979). Levels of NH<sub>3</sub>, NO<sub>3</sub>-N, and O-PO<sub>4</sub> were also analyzed by the Technicon Auto Analyzer II<sup>®</sup> with the Berthelot reaction used for determination of NH<sub>3</sub>, copper-cadmium reduction for NO<sub>3</sub>-N, and the molybdenum-blue reaction for O-PO<sub>4</sub> (US Environmental Protection Agency 1979). Concentrations of Ca<sup>++</sup>, Mg<sup>++</sup>, Na<sup>+</sup>, and K<sup>+</sup> were determined by flame atomic absorption spectrometer instrumentation (US Environmental Protection Agency 1979).

Conductivity was measured with a Scout II Hydrolab<sup>®</sup> at each monthly benthic collection in the Colorado River at Lees Ferry and at the penstock intake (depth of lake withdrawal) in the forebay of Lake Powell. Conductivity, which may be used as a surrogate of nutrient levels in freshwater systems (Biggs and Price 1987, Biggs and Close 1989), was compared between the monthly collection intervals and also with conductivity measurements dating back to 1991.

#### *Benthic collections*

Twenty-three collections were made at approximately monthly intervals from June 1995 through January 1998, which yielded 216 phytobenthic samples from the Lees Ferry cobble bar in the Colorado River at RKM 0.8 (Fig. 1). From June 1995 through January 1997, 12 replicate benthic samples were taken at each collection interval, and from February 1997 through January 1998 six replicate benthic samples were taken at each collection interval. All samples were randomly taken along established transects with a covered Hess sampler for a 30 s duration using SCUBA at or below baseflow ( $\leq 226 \text{ m}^3/\text{s}$ ). Collection intervals were designed to capture change in monthly discharge patterns and allow for a detectable response in the benthos (Shaver et al. 1997, Benenati et al. 1998).

Benthic samples from the 23 collections were sorted into 5 main categories: 1) *C. glomerata*, 2) MAMB, 3) filamentous cyanobacteria (crustose and non-crustose *Oscillatoria* spp., *Tolythrix*), 4) miscellaneous invertebrates, and 5) detritus. The MAMB category was further sorted into 4 subgroups: a) miscellaneous bryophytes and macrophytes, b) Rhodophyta, c) Chromophyta (miscellaneous diatoms in a mucilage matrix dominated by *Cymbella* spp. and *Gomphonema* spp.), and d) Chlorophyta (filamentous green algae other than *Cladophora*). All categories were

oven-dried (60°C for >48 h) and ashed (500°C for 1 h to obtain ash-free dry mass (AFDM). The miscellaneous invertebrate category included *Gammarus lacustris*, various Chironomidae (e.g., *Cricotopus annulator*, *C. globistylus*; Sublette et al. 1998), gastropods (*Physella* spp., *Pisidium* spp.), megadrile worms (Lumbricidae and Lumbriculidae), and oligochaetes (Naididae and Tubificidae).

Ashed phytobenthic material of *Cladophora*, filamentous cyanobacteria, and MAMB subgroups a to d from 12 collections were processed to examine epiphyton composition and cell density. Ashed samples were diluted with distilled water and the epiphyton suspension was mounted onto microscope slides in replicates of 3 using Hyrax<sup>®</sup> medium. A minimum of 200 diatoms per slide was counted and identified to species to determine number of cells/g algal AFDM for each category.

In addition, 30 benthic samples were obtained using a Hess sampler to compare epiphyton biomass on *Cladophora* and MAMB. Invertebrates were removed and each sample was separated into *Cladophora* or MAMB, placed in a Whirl-Pak<sup>®</sup> containing 100 mL of filtered (0.45  $\mu\text{m}$ ) Colorado River water, and shaken for 1 min to remove epiphyton. This procedure removed at least 80% of diatoms, based on microscopic analysis, and was the most effective technique for separating intact epiphytic diatoms from *Cladophora* filaments (Blinn et al. 1995). The suspension was filtered onto Whatman<sup>®</sup> (GF/C) glass microfiber filters, which were oven-dried for 48 h (60°C), and ashed for 1 h (500°C) to obtain AFDM.

#### *Experimental flood*

An experimental flood (1275 m<sup>3</sup>/s) was released from GCD from 26 March to 2 April 1996 to test the effect of reservoir drawdown in high snowmelt years and for beach replenishment using displaced riverbed sediments (Webb et al. 1999). Benthic samples were collected, as described above, 2 d prior (24 March) and 12 d after (14 April) the flood to determine algal response to extreme discharge levels. Water samples also were collected in triplicate at the same pre- and postflood intervals as described above and analyzed for nutrient and ion concentrations.

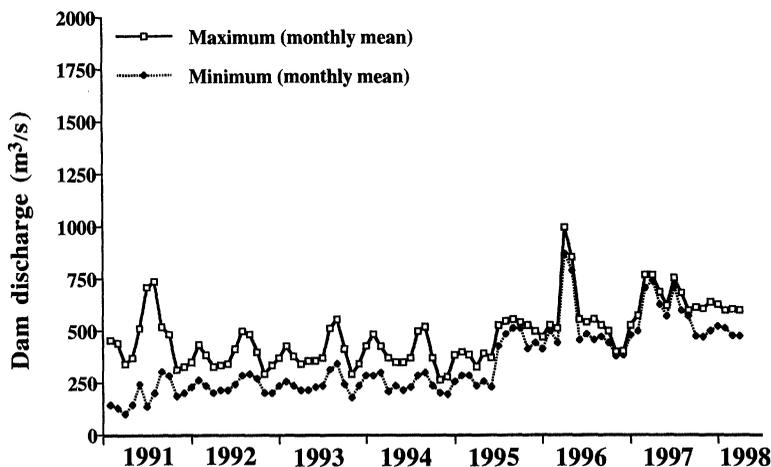


FIG. 2. Mean monthly minimum and maximum discharge ( $\text{m}^3/\text{s}$ ) released from Glen Canyon Dam into the Colorado River from January 1991 through March 1998.

#### Data analyses

All data were log-transformed to ensure constancy of variance. Multivariate analysis of variance (MANOVA) was performed to determine significant differences in biomass among and between benthic categories during the 23 collection intervals. Hotelling's  $T^2$ -tests were used to detect overall seasonal biomass differences among and between the benthic groups. We tested relationships between phyto-benthic biomass and abiotic factors (discharge, water-quality components, season) using multiple regression analysis. Multiple Pearson correlation analysis with Bonferroni-adjusted probabilities was used to describe correlations among and between phyto-benthic groups and abiotic factors. All calculations were performed using SYSTAT® (Statistics, version 5.2 edition, SYSTAT, Inc., Evanston, Illinois).

In addition, MANOVA was used to test differences between data collections prior to the change in benthic composition (January 1991–March 1995) and afterward (June 1995–January 1998). In this comparison, the pre- and post-benthic change periods will be referred to by the above dates.

Discharge was analyzed using Hotelling's  $T^2$ -tests to detect differences during the study period, and differences between the study period and the preceding 5-y period (January 1991–May 1995). When discharge was tested against algal response, flows for the preceding month

were used to allow for a biomass response period (Shaver et al. 1997, Benenati et al. 1998).

## Results

### Discharge

Discharge increased 28% from June 1995 to January 1998 compared to January 1991 to May 1995, from mean flows of  $412 \text{ m}^3/\text{s}$  ( $\pm 1.8 \text{ SE}$ ) with large daily fluctuations to higher, steadier flows of  $570 \text{ m}^3/\text{s}$  ( $\pm 0.8$ ) with little daily fluctuation (Fig. 2). Mean velocity also increased 43% from  $0.31 \text{ m/s}$  ( $\pm 0.02$ ) to  $0.54 \text{ m/s}$  ( $\pm 0.01$ ) between these same periods. The varial zone, which was previously desiccated for prolonged periods, shrank in size; most of the zone became inundated because of the steady flows initiated in June 1995.

During the high-flow period, discharge was positively correlated with MAMB (Pearson multiple correlation,  $p < 0.01$ ) and had a significant negative relationship ( $p < 0.01$ ) with *Cladophora*. Also, discharge was significantly ( $p < 0.001$ ) higher in the winter–spring season compared to other seasons. Although variability between maximum and minimum flows was reduced during our study, compared to normal dam operations, the summer–autumn period had, on average, 48% greater daily fluctuation in discharge than winter–spring (Fig. 2).

TABLE 1. Mean nutrient concentrations (mg/L  $\pm$  SE,  $n = 3$ ) from Colorado River mainstem samples taken at the Lees Ferry cobble bar from June 1995 to January 1997. Detection limits (DL, mg/L): 0.001—Ca<sup>++</sup>, Mg<sup>++</sup>; 0.002—Na<sup>+</sup>; 0.01—total organic P (TP), NH<sub>3</sub>, orthophosphate (O-PO<sub>4</sub>), K<sup>+</sup>; 0.05—total organic N (TKN), NO<sub>3</sub><sup>-</sup>(NO<sub>3</sub>-N). \* = nutrient was below DL.

Date	TKN	TP	NH <sub>3</sub>	O-PO <sub>4</sub>	NO <sub>3</sub> -N	Ca <sup>++</sup>	Mg <sup>++</sup>	Na <sup>+</sup>	K <sup>+</sup>
11 June 1995	0.10 (0.02)	*	0.01 (0.00)	*	0.36 (0.04)	67.4 (3.0)	24.1 (2.0)	67.3 (4.0)	3.3 (0.2)
29 Aug. 1995	0.12 (0.02)	*	0.01 (0.00)	*	0.29 (0.05)	61.1 (4.0)	20.8 (3.0)	59.4 (6.0)	3.1 (0.4)
10 Nov. 1995	0.08 (0.02)	*	0.01 (0.00)	*	0.30 (0.01)	64.0 (4.0)	20.8 (4.0)	60.8 (3.0)	3.1 (0.5)
30 Jan. 1996	0.08 (0.01)	0.10 (0.02)	0.02 (0.01)	0.06 (0.03)	0.23 (0.01)	55.0 (3.0)	20.1 (2.0)	52.1 (3.0)	2.8 (0.3)
29 Feb. 1996	0.20 (0.05)	0.02 (0.00)	0.04 (0.01)	0.01 (0.00)	0.30 (0.04)	57.1 (1.0)	20.4 (2.0)	58.8 (4.0)	2.8 (0.2)
24 Mar. 1996	0.19 (0.04)	0.02 (0.01)	0.01 (0.005)	0.01 (0.01)	0.30 (0.05)	63.3 (3.0)	22.4 (2.0)	67.3 (3.0)	2.8 (0.5)
14 April 1996	0.27 (0.05)	0.02 (0.01)	*	0.01 (0.005)	0.37 (0.08)	62.7 (1.0)	20.8 (2.0)	61.1 (2.0)	2.9 (0.3)
12 May 1996	0.26 (0.03)	0.01 (0.00)	0.01 (0.00)	*	0.26 (0.02)	57.1 (2.0)	19.1 (1.0)	56.1 (1.0)	3.0 (0.1)
30 July 1996	0.20 (0.03)	0.02 (0.01)	0.03 (0.01)	*	0.30 (0.04)	55.1 (2.0)	19.1 (2.0)	52.1 (3.0)	2.8 (0.2)
10 Sept. 1996	0.14 (0.02)	0.02 (0.05)	*	*	0.31 (0.01)	77.0 (5.0)	23.0 (2.0)	54.3 (4.0)	2.6 (0.1)
20 Oct. 1996	0.14 (0.03)	*	*	*	0.35 (0.08)	65.6 (3.0)	24.0 (1.0)	59.4 (3.0)	2.9 (0.3)
24 Nov. 1996	0.21 (0.04)	0.02 (0.01)	0.03 (0.01)	0.01 (0.00)	0.26 (0.06)	54.0 (1.0)	20.6 (0.5)	50.3 (1.0)	2.9 (0.1)
10 Jan. 1997	0.29 (0.05)	*	*	*	0.18 (0.03)	54.7 (2.0)	19.6 (1.0)	47.3 (2.0)	2.5 (0.2)

### Water quality

Conductivity decreased 38% at Lees Ferry and 32% at the penstock intake of Lake Powell between January 1991 and January 1998. Conductivity levels prior to June 1995 ranged from 750 to 1010  $\mu$ S/cm, but dropped to 590 to 850  $\mu$ S/cm from June 1995 to January 1998. A multiple regression showed a significant and positive relationship ( $p < 0.001$ ,  $r^2 = 0.96$ ) between conductivity and Lees Ferry nutrient/ion concentrations during water-quality collections (June 1995–January 1997). In addition, a significant positive relationship occurred between conductivity and *Cladophora*, in contrast to a significant inverse association with MAMB (Pearson multiple correlation,  $p < 0.01$  for both).

Fluctuations in nutrient and cation concentrations (Table 1) matched fluctuations in algal biomass. Multiple regression showed *Cladophora* biomass to have a significant positive ( $p < 0.001$ ,

$r^2 = 0.41$ ) association with nutrient and cation concentration, whereas MAMB had a significant negative ( $p < 0.001$ ,  $r^2 = 0.33$ ) association. Nutrient fluctuations were seasonal, with concentrations significantly ( $p < 0.001$ ) higher during summer–autumn coinciding with *Cladophora* dominance.

### Benthic responses

There were significant ( $p < 0.001$ ) changes in the relative phytobenthic composition within 3 mo of the reservoir reaching full pool and the initiation of high flows. In previous seasonal sampling from January 1991 to March 1995 ( $n = 145$ ), the overall biomass percentages among the benthic groups were: *Cladophora* = 91.5%, MAMB = 3.5%, and cyanobacteria = 5.0% (Blinn et al. 1995, Stevens et al. 1997, Benenati et al. 1998). However, composition changed to

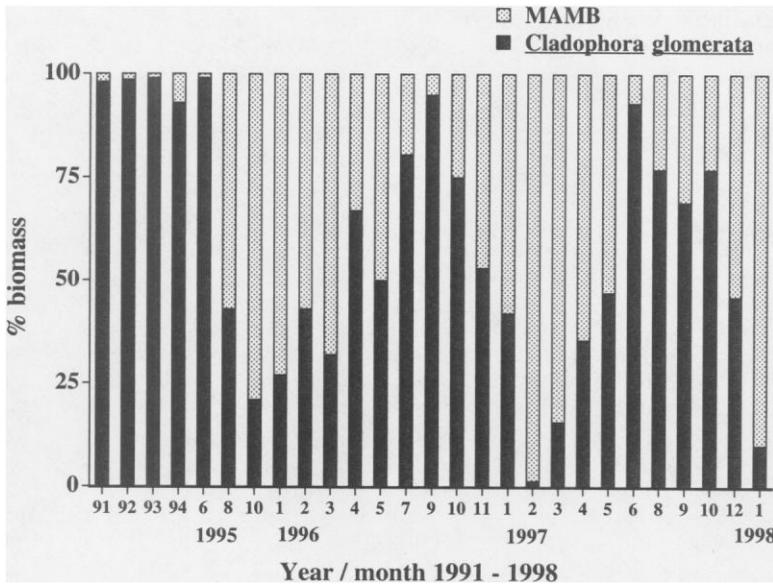


FIG. 3. Percent composition of miscellaneous algae, macrophytes, and bryophytes (MAMB) and *Cladophora glomerata* ash-free dry mass based on means of 16 seasonal collections from 1991–1994 and means of 23 monthly collections from June 1995 through January 1998 at the Lees Ferry cobble bar in the Colorado River ( $n = 384$ ).

49.6, 47.9, and 2.5%, respectively, in samples ( $n = 216$ ) taken from June 1995 to January 1998 (Fig. 3). During high flows, cyanobacteria also changed from a crustose mat previously found in the varial zone to an epiphytic filamentous form (mainly *Tolypothrix*) growing on other algae throughout the submerged channel.

Taxa in the subgroups of MAMB consisted of: a) the macrophytes *Potamogeton pectinatus* L. and *Elodea* spp., the bryophyte *Fontinalis* spp., and the alga *Chara contraria* A. Braun ex Kütz.; b) Rhodophyta (*Rhodochorton* and *Batrachospermum* spp.); c) Chromophyta (mixed diatoms in a mucilage mass); and d) Chlorophyta [*Ulothrix zonata* (Weber and Mohr) Kütz., *Ulothrix* sp., *Spirogyra*, *Mougeotia*, *Stigeoclonium* spp., and *Enteromorpha intestinalis* (L.) Grev.]. Percentages of AFDM within the MAMB subgroups changed between the January 1996 to January 1998 periods as follows: chlorophytes—42 to 69%, Rhodophytes—38 to 5%, macrophytes/bryophytes—13 to 19%, and no change in chromophytes (7%). Dominant MAMB taxa were *Batrachospermum* (90% of rhodophytes) and *U. zonata*, (80% of chlorophytes) during 1996, changing to *U. zonata* and *Spirogyra* (80% and 10% of chlorophytes) during 1997. All of these taxa except *Cladophora* are mucilage-covered.

#### Seasonal patterns

A multiple regression showed *Cladophora* and MAMB biomass to have significant opposing seasonal patterns, whereas invertebrates exhibited a significant positive association with *C. glomerata* ( $p < 0.001$ ,  $r^2 = 0.47$ ). No significant relationship occurred between invertebrates and MAMB. During winter–spring, MAMB dominated over *Cladophora*, with significantly ( $p < 0.001$ ) higher biomass than in summer–autumn ( $11.9 \pm 1.9$  SE g/m<sup>2</sup> AFDM vs  $4.8 \pm 0.5$ , Fig. 4). Conversely, *Cladophora* dominated in summer–autumn, with significantly ( $p < 0.001$ ) higher biomass than during winter–spring ( $12.6 \pm 1.0$  g/m<sup>2</sup> AFDM vs  $3.8 \pm 0.6$ ), which coincided with higher nutrient concentrations in summer–autumn. Invertebrate biomass showed the same pattern as *Cladophora* and was significantly greater ( $p < 0.001$ ) during summer–autumn than winter–spring ( $4.7$  vs  $2.4$  g/m<sup>2</sup> AFDM). Mean cyanobacteria biomass was slightly lower in the summer–autumn ( $0.9 \pm 0.1$  g/m<sup>2</sup> AFDM) compared to winter–spring ( $1.2 \pm 0.3$  g/m<sup>2</sup> AFDM). Although changes in benthic algal composition were distinct, overall biomass changed minimally between the 2 opposing seasonal periods, with summer–autumn averaging

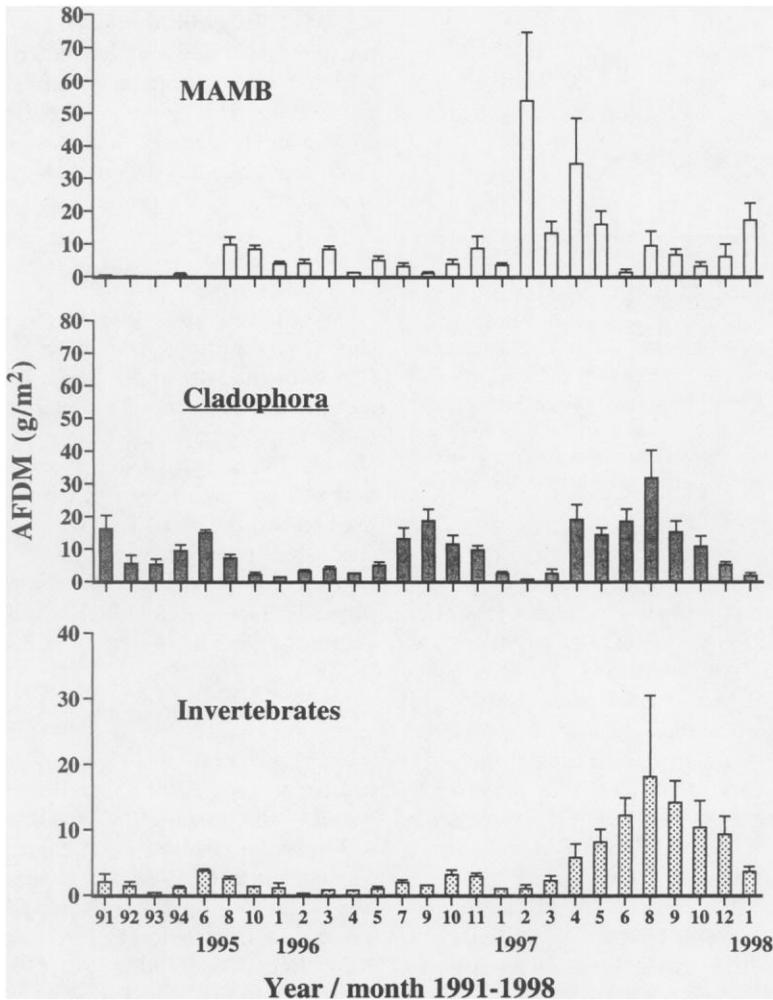


FIG. 4. Miscellaneous algae, macrophytes, and bryophytes (MAMB), *Cladophora glomerata*, and invertebrate biomass (g ash-free dry mass [AFDM]/m<sup>2</sup> + 1 SE) in 16 seasonal collections from 1991 to 1994 and in 23 collections from June 1995 through January 1998 at the Lees Ferry cobble bar in the Colorado River.

17.3 ± 1.8 g/m<sup>2</sup> AFDM vs winter–spring with 17.9 ± 2.7 g/m<sup>2</sup> AFDM.

#### Epiphyton

Comparison of epiphytic biomass between *Cladophora* and MAMB showed *Cladophora* to have significantly ( $p < 0.001$ ) greater diatom epiphyton. *Cladophora* had an average 0.3 (±0.02 SE) g epiphyton/g algal host, whereas MAMB had 0.12 (±0.04)/g host.

*Cladophora* also had higher diatom cell density than either MAMB or cyanobacteria, with respective means of 528 (±247) × 10<sup>6</sup>, 242 (±59)

× 10<sup>6</sup>, and 293 (±53) × 10<sup>6</sup> cells/g host. Of the MAMB subgroups, Rhodophyta hosts had the lowest diatom density (138 ± 72 × 10<sup>6</sup>) and the macrophyte/bryophyte hosts had the highest (341 ± 215 × 10<sup>6</sup>) cell number/g host (Fig. 5). In fact, diatom density on *Cladophora* was 40% greater than that in the diatom mucilage matrix because the matrix was largely composed of a thick mixture of sediment and mucilage. Overall diatom density on all phytobenthic categories was 35% higher during the summer–autumn season when *Cladophora* was dominant, compared to winter–spring (355 ± 80 × 10<sup>6</sup> vs 230 ± 30 × 10<sup>6</sup>).

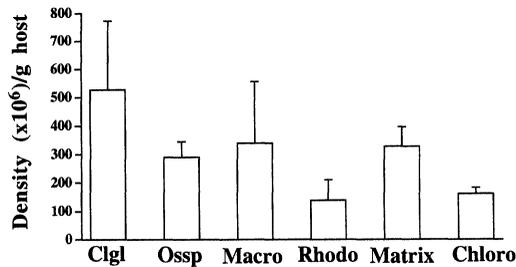


FIG. 5. Mean diatom density ( $\times 10^6$ )/g host (ash-free dry mass [AFDM] + 1 SE) for phytobenthic categories of *Cladophora glomerata* (Clgl), *Oscillatoria* spp. (Ossp), miscellaneous macrophytes (Macro), Rhodophyta (Rhodo), diatom mucilage matrix (Matrix), and Chlorophytes (Chloro). Diatom density was analyzed from monthly collections at the Lees Ferry cobble bar in the Colorado River between January 1996 and January 1998.

Relative diatom composition between phytobenthic categories was similar, although *Cladophora* had a greater percentage of large, upright diatoms (56%) than MAMB (44%) or cyanobacteria (20%). Thirteen species made up 75% of the diatom composition on *Cladophora*, MAMB, and cyanobacteria. Large ( $>35 \mu\text{m}$ ), upright diatoms (which are more available to invertebrates) of the 13 species included: *Rhoicosphenia curvata* (Kütz.) Grun. ex Rabh., *Diatoma vulgare* Bory, *Fragilaria ulna* (Nitz.) Lange-Bertalot, *F. capucina* Desm., *Gomphonema olivaceum* var. *calcareum* Cl., and *Melosira varians* (Ag.). Small, adnate diatoms (less available to invertebrates) were: *Achnanthes minutissima* Kütz., *A. affinis* Grun., *Cocconeis pediculus* Ehr., *Fragilaria leptotauroon* var. *dubia* Hust., *F. vaucheriae* (Kütz.) Peterson, *Cymbella prostrata* var. *auerswaldii* Rabh., and *Nitzschia dissipata* (Kütz.) Grun.

#### Experimental flood

There was a significant ( $p < 0.001$ ) decrease in MAMB and cyanobacteria biomass between the pre- and post-flood collections, whereas both *Cladophora* and invertebrate biomass did not show a significant decrease. MAMB dropped from  $8.4 \pm 1.0 \text{ g/m}^2$  AFDM in March 1996 to  $1.3 \pm 0.26$  after the flood in April 1996, with cyanobacteria decreasing from  $0.5 \pm 0.1$  to  $0.1 \pm 0.03 \text{ g/m}^2$  AFDM. However, only a slight decrease in biomass occurred for both *Cladophora* ( $3.9 \pm 0.44$  to  $2.7 \pm 0.36 \text{ g/m}^2$  AFDM) and invertebrates ( $0.81 \pm 0.1$  to  $0.75 \pm 0.1 \text{ g/m}^2$

AFDM). *Cladophora* dominated over MAMB in the months following the experimental flood, with a 2- to 3-fold greater biomass through October 1996. This post-flood pattern of an increase in *Cladophora* biomass was detected throughout all Grand Canyon study sites (Blinn et al. 1999).

#### Discussion

We showed that interactions of modified chemical conditions in a reservoir in combination with changes in discharge patterns can affect the composition of a previously stable tailwater phytobenthic community. *Cladophora* and MAMB biomass inversely fluctuated by 3-fold between seasons; however, overall biomass remained unchanged. The rare condition of a freshened or diluted reservoir coupled with high discharge created changes in downstream phytobenthos and potential ramifications to the present trophic food web in the Colorado River.

#### Nutrient-benthos association

A 21% decrease in  $\text{NO}_3\text{-N}$  and cation concentration at Lees Ferry from 1995 to 1997 compared to the previous 23 y (M. Dai, US Geological Survey, personal communication) likely had a major effect on the nutrient-dependent *Cladophora*. Many studies have shown *Cladophora* to be associated with elevated nutrients (Whitton 1970, Biggs 1985, Dodds 1991, Dodds and Gudder 1992). In fact, *Cladophora* is considered to be a nuisance alga under elevated nutrients in some systems (Wharfe et al. 1984, Biggs 1985). AFDM values of MAMB (*Ulothrix*, *Spirogyra*, and *Batrachospermum*) surpassed those of *Cladophora* under the reduced nutrient conditions, especially in the winter season under low light and significantly decreased nutrient concentrations released from Lake Powell. *Ulothrix*, *Spirogyra*, and *Batrachospermum* are frequently associated with decreased nutrients and conductivity, and are often present in cold streams or during the winter months (Biggs and Price 1987, Biggs 1990, Sheath and Hambrook 1990, Leland 1995).

It would be logical to do a nutrient-diffusion experiment to test the algal response to increased nutrients. We conducted 2 separate nutrient-diffusion pot experiments in the Colorado River at Lees Ferry in the spring and autumn of

1997 to determine if varying nutrient concentrations and combinations would induce compositional or biomass changes in the phytobenthos (methods according to Fairchild et al. 1985). The results of nutrient treatments on algae were inconclusive (E. P. Benenati and co-workers, unpublished data). The outcome of the nutrient-diffusion experiments highlights the difficulty in delineating the role nutrient concentrations and discharge play in determining phytobenthic composition in a large river with high discharge and velocity. Other factors such as cold water temperature and reproduction requirements may be equally important as nutrient levels in determining benthic composition. These nutrient-diffusion experiments also show the relationship between low ambient nutrient levels in this tailwater community and sustained high phytobenthic biomass, and pose the question as to whether high water velocity can compensate for low nutrient levels by delivering low concentrations at faster rates (Whitford and Schumaker 1964, Biggs and Stokseth 1996). These linkages require further examination.

#### *Discharge-benthos association*

Increased discharge and velocity, because of Lake Powell approaching full capacity, may have facilitated the decline of *Cladophora* and provided favorable conditions for the rheophilic and mucilaginous *Ulothrix*, *Spirogyra*, and *Batrachospermum* (Biggs and Price 1987, Poff et al. 1990). Increased water velocities limit *Cladophora* growth and epiphyton accrual (Peterson and Stevenson 1990, Bergy 1995). Also, mucilage production is associated with increased discharge and velocity, and decreased conductivity and nutrients, and may be useful in nutrient absorption and abrasion resistance (Boney 1981, Horner and Welsh 1981, Strycek et al. 1992, Hoagland et al. 1993, Biggs and Hickey 1994). Therefore, previous work with velocity and mucilage corroborates our findings of the dominance of the mucilaginous MAMB assemblage with high discharge and decreased nutrients in winter-spring and a significant increase in *Cladophora* biomass under decreased discharge and high nutrients in the summer-autumn. Also, *Cladophora* may have competed better under the high light conditions in the summer season (Dodds 1991).

The overall decrease in epiphyton densities on all hosts in the winter-spring may be attri-

buted to high discharge because diatoms colonize more slowly in high ( $>0.4 \text{ m}^3/\text{s}$ ) velocities (Steinman and McIntire 1986, Duncan and Blinn 1989, Peterson and Stevenson 1990, Bergy 1995). Furthermore, the increased presence of mucilaginous algae in winter may have deterred diatom attachment because nonmucilaginous types of algae likely provide better surfaces for the adherence of mucilaginous diatoms.

The minor decrease in *Cladophora* and the significant loss of MAMB biomass during the experimental flood suggest that basal rhizoidal holdfasts of *Cladophora* remain more firmly attached to substrata than the cup-shaped holdfasts of *Ulothrix* and *Spirogyra* during extreme discharge events ( $\geq 1275 \text{ m}^3/\text{s}$ ). Strong holdfasts could provide *Cladophora* with a recolonization advantage immediately after a flood even if the upper filaments were removed. *Cladophora* was dominant over MAMB taxa in the months following the March 1996 experimental flood and through October 1996.

We hypothesize that mucilaginous algae found in MAMB can outcompete *Cladophora* under the combination of reduced nutrient conditions and elevated discharge regimes of  $\sim 710 \pm 142 \text{ m}^3/\text{s}$ . However, if discharge is increased to  $\geq 1275 \text{ m}^3/\text{s}$ , MAMB will be scoured out, allowing *Cladophora* to recolonize regardless of nutrient conditions because of strong holdfast attachment and lack of competition. Similar reservoir and discharge conditions in the Colorado River occurred from 1983 to 1986 with high snowmelt inflows that filled Lake Powell to capacity and resulted in extreme discharges ( $1200\text{--}2500 \text{ m}^3/\text{s}$ ) released from GCD for a 3-y period (Kearsley et al. 1994). However, prolific growth of *Cladophora* occurred during and after this time period with no invasion of other algal types (E. P. Benenati, personal observation, Usher and Blinn 1990, Blinn and Cole 1991). This perseverance of *Cladophora* during extreme flows may be advantageous to the ecosystem below GCD because periodic experimental floods are now a component in the GCD management plan, provided flood discharge exceeds  $1200 \text{ m}^3/\text{s}$ . Current reservoir criteria established by stakeholders dictate that Lake Powell must be nearly full with inflows above normal before initiation of an experimental flood. Consequently, future scenarios could include a diluted reservoir, greater than normal discharge, and benthic instability prior to future experimental floods.

### Temperature and reproduction factors

Water temperature and reproduction modes may play an important role in the seasonal competition between *Cladophora* and *Ulothrix* (Blinn et al. 1998). *Ulothrix* is able to produce zoospores under cold ( $\leq 14^{\circ}\text{C}$ ) conditions (Garwood 1982), whereas *Cladophora* prefers warmer temperatures of 15 to  $24^{\circ}\text{C}$  (Dodds 1991) that do not normally occur in the constantly cold ( $9\text{--}12^{\circ}\text{C}$ ) Colorado River. In the main channel of the Colorado River, *Cladophora* reproduces by fragmentation or regeneration of established holdfast filaments, which can result in slow turnover times of  $\leq 1$  y (Whitton 1970, Shaver et al. 1997, Benenati et al. 1998). The absence of zoospore production and the slower mode of colonization by fragmentation or regeneration of basal holdfasts in *Cladophora* may allow *Ulothrix* to quickly dominate benthic cobbles. Power (1992) observed a similar pattern in the Eel River, California. Thus, faster reproducing algal types, such as *Ulothrix*, that are able to produce zoospores under cold conditions have an advantage. *Cladophora* zoospores are virtually absent in the Colorado River or occasionally are observed in the spring or summer in the warmer splash zones on rocks and cliff walls (Shaver et al. 1997, Benenati et al. 1998). However, during the extreme flow years of 1983 to 1986, river temperatures were elevated to above  $13^{\circ}\text{C}$  because of warm reservoir conditions, which may have also facilitated increased *Cladophora* zoospore production and prolific growth in the river channel. Seasonal light also may influence changes in algal composition. *Cladophora* is often found in shallow benthic habitats with high light conditions during the summer season (Dodds 1991, Dodds and Gudder 1992). Although *Ulothrix*, *Spirogyra*, and *Batrachospermum* can be associated with high light, they are more often found in low light conditions that occur with increased turbidity or outside the summer season (Whitton 1972, Biggs and Price 1987, Sheath and Hambrook 1990).

### Importance of *Cladophora*

The critical relationship between invertebrates and *Cladophora* is evidenced by the significant decrease in invertebrate biomass during the winter–spring compositional change-over to MAMB even though overall algal biomass remained the same. In terms of diatom energy available (based on epiphyton biomass)

for invertebrate consumption on *Cladophora* alone, the summer–autumn period has  $20,700\text{ kcal/m}^2$  compared to only  $6200\text{ kcal/m}^2$  in the winter–spring, based on energy values determined by Cummins and Wuycheck (1971) and Blinn et al. (1995). An important consideration is that  $>75\%$  of MAMB biomass was composed of Chlorophyta and Rhodophyta taxa, which supported only 25% of the diatom density compared to *Cladophora*. Therefore, in winter–spring during MAMB dominance, the maximum diatom energy found on MAMB would be only  $7800\text{ kcal/m}^2$  with much less ( $1250\text{ kcal/m}^2$ ) in summer–autumn. Even the diatom mucilage matrix supported fewer diatoms than *Cladophora*. In addition, most (66%) diatoms on MAMB were smaller, adnate taxa, which would further reduce energy values relative to *Cladophora*. The crustose *Oscillatoria* spp., common in the varial zone, is also not conducive to invertebrate productivity (Shaver et al. 1997, Blinn et al. 1995). An increase in *Oscillatoria* spp. may be a good indication that daily fluctuations from GCD are too large and the quality of the food base is diminishing.

*Cladophora* is considered a keystone species in the Colorado River below GCD. With the impoundment of upstream allochthonous contributions to the food base, which served as a nutrient source or substrate for organic growth, *Cladophora* now holds a key role in supporting higher trophic levels. The multibranched, mucilage-free filaments of *Cladophora* have a large surface area and serve as a structural host for epiphytic diatoms, which provide food for invertebrates and fishes (Dodds 1990, Hardwick et al. 1992, Shannon et al. 1994, Blinn et al. 1995, Blinn et al. 1998). *Cladophora* is likely a superior structural host in the Colorado River for higher trophic levels, with nearly 3-fold greater epiphytic biomass and over twice the diatom density as MAMB. *Cladophora* also serves as a refugium for invertebrates and fishes from predation or high discharges and supports linkages to waterfowl, riparian insectivores, and birds of prey (Brown et al. 1987, Blinn and Cole 1991, Stevens et al. 1997). The dense mucilage matrix of MAMB has fewer niches for invertebrates to occupy than the loosely arranged filamentous *Cladophora*. A decline in *Cladophora* biomass and general benthic compositional instability will result in a loss of available epiphyton energy that could impact not only the invertebrates but higher trophic levels as well.

In summary, the presence of GCD and its reservoir have generated profound effects on the Colorado River ecosystem through Grand Canyon. The food web is dramatically changed from what existed prior to dam construction. Without placing value judgements on pre- versus post-dam food webs (Schmidt et al. 1998), we suggest conservation of the alien downstream aquatic ecosystem, which is ultimately tied to native fish and other endangered vertebrates that frequent Grand Canyon. Ecosystem goals should be prioritized and implemented based on sound research that recognizes the close relationship between reservoirs, dams, and downstream habitats. There are 46 major dams in the Colorado River basin and hundreds of small diversions. As a consequence, understanding the linkage between reservoir dynamics and dam operations on downstream aquatic communities is imperative for conservation measures. Restructuring of agency boundaries may be necessary for successful integration of monitoring and research on reservoirs and rivers.

### Acknowledgements

This study was funded by the US Department of Interior through the Bureau of Reclamation, Glen Canyon Environmental Studies Program and the Grand Canyon Monitoring and Research Center. We cooperated with Grand Canyon National Park and Glen Canyon National Recreation Area. We thank Wade Albrecht, Jessica Hagan, Gaye Oberlin, Chris O'Brien, Allen Haden, Carol Haden, and Kimberly Pomeroy for assisting with field collections and laboratory processing. Mike Dai and Robert Hart of the US Geological Survey helped obtain water-quality data. Tom Huntsberger of the Bilby Research Center and Stevan Earl of Northern Arizona University provided nutrient analysis. This study was part of the Northern Arizona University Aquatic Food Base Program.

### Literature Cited

- ANDREWS, E. D. 1991. Sediment transport in the Colorado River Basin. Pages 54–75 in Committee on Glen Canyon Environmental Studies (editor). Colorado River ecology and dam management. National Academy Press, Washington, DC.
- BENENATI, P. L., J. P. SHANNON, AND D. W. BLINN. 1998. Desiccation and recolonization of phytobenthos in a regulated desert river: Colorado River at Lees Ferry, Arizona, USA. *Regulated Rivers: Research and Management* 14:519–532.
- BERGEY, E. A. 1995. Effects of water velocity on the architecture and epiphytes of *Cladophora glomerata* (Chlorophyta). *Journal of Phycology* 31:264–271.
- BIGGS, B. J. F. 1985. Algae: a blooming nuisance in rivers. *Soil and Water* 21:27–31.
- BIGGS, B. J. F. 1990. Periphyton communities and their environments in New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* 24:367–386.
- BIGGS, B. J. F. 1996. Hydraulic habitat of plants in streams. *Regulated Rivers: Research and Management* 12:131–144.
- BIGGS, B. J. F., AND M. E. CLOSE. 1989. Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biology* 22:209–231.
- BIGGS, B. J. F., AND C. W. HICKEY. 1994. Periphyton responses to a hydraulic gradient in a regulated river in New Zealand. *Freshwater Biology* 32:49–59.
- BIGGS, B. J. F., AND G. M. PRICE. 1987. A survey of filamentous algal proliferations in New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* 21:175–191.
- BIGGS, B. J. F., AND S. STOKSETH. 1996. Hydraulic habitat suitability for periphyton in rivers. *Regulated Rivers: Research and Management* 12:251–261.
- BLINN, D. W., AND G. A. COLE. 1991. Algae and invertebrate biota in the Colorado River: comparison of pre- and post-dam conditions. Pages 85–104 in Committee on Glen Canyon Environmental Studies (editor). Colorado River ecology and dam management. National Academy Press, Washington, DC.
- BLINN, D. W., J. P. SHANNON, P. L. BENENATI, AND K. P. WILSON. 1998. Algal ecology in tailwater stream communities: Colorado River below Glen Canyon Dam, Arizona. *Journal of Phycology* 34:734–740.
- BLINN, D. W., J. P. SHANNON, L. E. STEVENS, AND J. P. CARDER. 1995. Consequences of fluctuating discharge for lotic communities. *Journal of the North American Benthological Society* 14:233–248.
- BLINN, D. W., J. P. SHANNON, K. P. WILSON, C. O'BRIEN, AND P. L. BENENATI. 1999. Response of benthos and organic drift to a controlled flood. Pages 259–272 in R. H. Webb, J. C. Schmidt, G. R. Marzolf, and R. A. Valdez (editors). The controlled flood in Grand Canyon. Geophysical Monograph No. 110. American Geophysical Union, Washington, DC.
- BLINN, D. W., R. TRUITT, AND A. PICKART. 1989. Response of epiphytic diatom communities from the tailwaters of Glen Canyon Dam, Arizona, to elevated water temperature. *Regulated Rivers: Research and Management* 4:91–96.
- BONEY, A. D. 1981. Mucilage: the ubiquitous algal attribute. *British Phycological Journal* 16:115–132.
- BROWN, B. T., S. W. CAROTHERS, AND R. R. JOHNSON. 1987. Grand Canyon birds: historical notes, nat-

- ural history, and ecology. University of Arizona Press, Tucson, Arizona.
- BYREN, B. A., AND B. R. DAVIES. 1989. The effect of stream regulation on the physico-chemical properties of the Palmiet River, South Africa. *Regulated Rivers: Research and Management* 3:107-121.
- CAROTHERS, S. W., AND C. O. MINCKLEY. 1981. A survey of the fishes, aquatic invertebrates, and aquatic plants of the Colorado River and selected tributaries from Lees Ferry to Separation Rapids. Water and Power Research Service, Lower Colorado River Region, US Bureau of Reclamation, Boulder City, Nevada. (Available from: US Geological Survey, Grand Canyon Monitoring and Research Center, 2255 N. Gemini Dr, Flagstaff, Arizona 86001 USA.)
- CUMMINS, K. W., AND J. C. WUYCHECK. 1971. Caloric equivalents for investigations in ecological energetics. *International Association for Theoretical and Applied Limnology, Special Communication* 18:1-158.
- CZARNECKI, D. B., D. W. BLINN, AND T. TOMPKINS. 1976. A periphytic microflora analysis of the Colorado River and major tributaries in Grand Canyon National Park and vicinity. Colorado River Research Program Publication 6:1-106.
- DODDS, W. K. 1990. Community interactions between the filamentous alga *Cladophora glomerata* (L.) Kützing, its epiphytes, and epiphyte grazers. *Oecologia* (Berlin) 85:572-580.
- DODDS, W. K. 1991. Factors associated with dominance of the filamentous green alga *Cladophora glomerata*. *Water Research* 25:1325-1332.
- DODDS, W. K., AND D. A. GUDDER. 1992. The ecology of *Cladophora*. *Journal of Phycology* 28:415-427.
- DUFFORD, R. G., H. J. ZIMMERMANN, L. D. CLINE, AND J. V. WARD. 1987. Response of epilithic algae to regulation of Rocky Mountain streams. Pages 383-390 in J. F. Craig and J. B. Kemper (editors). *Regulated streams: advances in ecology*. Plenum Press, New York.
- DUNCAN, S., AND D.W. BLINN. 1989. Importance of physical variables on the seasonal dynamics of epilithic algae in a highly shaded canyon stream. *Journal of Phycology* 25:455-461.
- FAIRCHILD, G. W., R. L. LOWE, AND W. B. RICHARDSON. 1985. Algal periphyton growth on nutrient-diffusing substrates: an in situ bioassay. *Ecology* 66:465-472.
- GARWOOD, P. E. 1982. Ecological interactions among *Bangia*, *Cladophora*, and *Ulothrix* along the Lake Erie shoreline. *Journal of Great Lakes Research* 8:54-60.
- HADEN, G. A., D. W. BLINN, J. P. SHANNON, AND K. P. WILSON. 1999. Driftwood: an alternative habitat for macroinvertebrates in a large desert river. *Hydrobiologia* 397:179-186.
- HANNAN, H. H. 1979. Chemical modification in reservoir-regulated streams. Pages 75-94 in J. F. Craig and J. B. Kemper (editors). *Regulated streams: advances in ecology*. Plenum Press, New York.
- HARDWICK, G., D. W. BLINN, AND H. D. USHER. 1992. Epiphytic diatoms on *Cladophora glomerata* in the Colorado River, Arizona: longitudinal and vertical distribution in a regulated river. *Southwest Naturalist* 37:148-156.
- HOAGLAND, K. D., J. R. ROSOWSKI, M. R. GRETZ, AND S. C. ROEMER. 1993. Diatom extracellular polymeric substances: function, fine structure, chemistry, and physiology. *Journal of Phycology* 29:537-566.
- HORNER, R. R., AND E. B. WELCH. 1981. Stream periphyton development in relation to current velocity and nutrients. *Canadian Journal of Fisheries and Aquatic Sciences* 38:449-457.
- HOWARD, A., AND R. DOLAN. 1981. Geomorphology of the Colorado River in Grand Canyon. *Journal of Geology* 89:269-298.
- KEARSLEY, L. H., J. C. SCHMIDT, AND K. D. WARREN. 1994. Effects of Glen Canyon Dam on Colorado River sand deposits used as campsites in Grand Canyon National Park, USA. *Regulated Rivers: Research and Management* 9:137-149.
- LELAND, H. V. 1995. Distribution of phytobenthos in the Yakima River basin, Washington, in relation to geology, land use, and other environmental factors. *Canadian Journal of Fisheries and Aquatic Sciences* 52:1108-1129.
- LOWE, R. 1979. Phytobenthos ecology and regulated streams. Pages 25-34 in J. V. Ward and J. A. Stanford (editors). *The ecology of regulated streams*. Plenum Press, New York.
- MULLAN, J. W., V. J. STAROSTKA, J. L. STONE, R. W. RILEY, AND W. J. WILTZIUS. 1976. Factors affecting Upper Colorado River Reservoir tailwater trout fisheries. Pages 405-423 in J. F. Orsborn and C. E. Allman (editors). *Instream flow needs*, Vol. II. American Fisheries Society, Bethesda, Maryland.
- O'KEEFE, J. H., R. W. PALMER, B. A. BYREN, AND B. R. DAVIES. 1990. The effects of impoundment on the physicochemistry of two contrasting southern African river systems. *Regulated Rivers: Research and Management* 5:97-110.
- PETERSON, C. G. 1987. Influences of flow regime on development and desiccation response of lotic diatom communities. *Ecology* 68:946-954.
- PETERSON, C. G., AND R. J. STEVENSON. 1990. Post-spate development of epilithic algal communities in different current environments. *Canadian Journal of Fisheries and Aquatic Sciences* 68:2092-2102.
- POFF, N. L., N. J. VOELZ, AND J. V. WARD. 1990. Algal colonization under four experimentally-controlled current regimes in a high mountain stream. *Journal of the North American Benthological Society* 9:303-318.
- POWER, M. E. 1992. Hydrologic and trophic controls of seasonal algal blooms in northern California rivers. *Archiv für Hydrobiologie* 125:385-410.
- PUIG, M. A., J. ARMENGOL, G. GONZALEZ, J. PENUELAS, S. SABATER, AND F. SABATER. 1990. Chemical and

- biological changes in the Ter River induced by a series of reservoirs. Pages 373–382 in J. F. Craig and J. B. Kemper (editors). *Regulated streams: advances in ecology*. Plenum Press, New York.
- RADA, R. G., AND J. C. WRIGHT. 1979. Factors affecting nitrogen and phosphorus levels in Canyon Ferry Reservoir Montana and its effluent waters. *Northwest Science* 53:213–220.
- SCHMIDT, J. C., R. H. WEBB, R. A. VALDEZ, G. R. MARZOLF, AND L. E. STEVENS. 1998. The roles of science and values in river restoration in Grand Canyon. *BioScience* 48:735–747.
- SHANNON, J. P., D. W. BLINN, AND L. E. STEVENS. 1994. Trophic interactions and benthic animal community structure in the Colorado River, Arizona, U.S.A. *Freshwater Biology* 31:213–220.
- SHAVER, M. L., J. P. SHANNON, K. P. WILSON, P. L. BENENATI, AND D. W. BLINN. 1997. Effects of suspended sediment and desiccation on the benthic tailwater community in the Colorado River, USA. *Hydrobiologia* 357:63–72.
- SHEATH, R. G., AND J. A. HAMBROOK. 1990. Freshwater ecology. Pages 423–453 in K. M. Cole and R. G. Sheath (editors). *Biology of the red algae*. Cambridge University Press, Cambridge, UK.
- STANFORD, J. A., AND F. R. HAUER. 1992. Mitigating the impacts of stream and lake regulation in the Flathead River catchment, Montana, USA: an ecosystem perspective. *Aquatic Conservation: Marine and Freshwater Ecosystems* 2:35–63.
- STANFORD, J. A., AND J. V. WARD. 1979. Stream regulation in North America. Pages 215–236 in J. V. Ward and J. A. Stanford (editors). *The ecology of regulated streams*. Plenum Press, New York.
- STANFORD, J. A., AND J. V. WARD. 1991. Limnology of Lake Powell and chemistry of the Colorado River. Pages 75–101 in Committee on Glen Canyon Environmental Studies (editor). *Colorado River ecology and dam management*. National Academy Press, Washington, DC.
- STATZNER, B., J. A. GORE, AND V. H. RESH. 1988. Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society* 7:307–360.
- STEINMAN, A. D., AND C. D. MCINTIRE. 1986. Effects of current velocity and light energy on the structure of periphyton assemblages in laboratory streams. *Journal of Phycology* 22:352–361.
- STEVENS, L. E., J. P. SHANNON, AND D. W. BLINN. 1997. Colorado River benthic ecology in Grand Canyon, Arizona, USA: dam, tributary, and geomorphological influences. *Regulated Rivers: Research and Management* 13:129–149.
- STRYCEK, T., J. ACREMAN, A. KERRY, G. G. LEPPARD, M. V. NERMUT, AND D. J. KUSHNER. 1992. Extracellular fibril production by freshwater algae and cyanobacteria. *Microbial Ecology* 23:53–74.
- SUBLETTE, J. E., L. E. STEVENS, AND J. P. SHANNON. 1998. Chironomidae (Diptera) of the Colorado River, Grand Canyon, Arizona, USA, I: systematics and ecology. *Great Basin Naturalist* 48:97–146.
- US Bureau of Reclamation. 1995. Operation of Glen Canyon Dam. Environmental impact statement. Upper Colorado Regional Office, US Bureau of Reclamation, Salt Lake City, Utah. (Available from: US Bureau of Reclamation, Upper Colorado Regional Office, 125 South State Street, Room 6107, Salt Lake City, Utah 84138-1102 USA.)
- US Environmental Protection Agency (USEPA). 1979. Methods of chemical analysis. EPA-600/4-79-020. US Environmental Protection Agency, Washington, DC. (Available from: US Environmental Protection Agency, 1200 Pennsylvania Avenue, NW, Washington, DC 20460 USA.)
- USHER, H. D., AND D. W. BLINN. 1990. Influence of various exposure periods on the biomass and chlorophyll *a* of *Cladophora glomerata* (Chlorophyta). *Journal of Phycology* 26:244–249.
- WARD, J. V., H. J. ZIMMERMANN, AND L. D. CLINE. 1986. Lotic zoobenthos of the Colorado system. Pages 403–423 in B. R. Davies and K. F. Walker (editors). *The ecology of river systems*. Dr. W. Junk Publishers, Dordrecht, The Netherlands.
- WEBB, R. H., J. C. SCHMIDT, G. R. MARZOLF, AND R. A. VALDEZ (EDITORS). 1999. *The controlled flood in Grand Canyon*. Geophysical Monograph No. 110. American Geophysical Union, Washington, DC.
- WHARFE, J. R., K. S. TAYLOR, AND H. A. C. MONTGOMERY. 1984. The growth of *Cladophora glomerata* in a river receiving sewage effluent. *Water Research* 18:971–979.
- WHITFORD, L. A., AND G. J. SCHUMAKER. 1964. Effect of a current on respiration and mineral uptake in *Spirogyra* and *Oedogonium*. *Ecology* 45:168–170.
- WHITTON, B. A. 1970. Biology of *Cladophora* in freshwaters. *Water Research* 4:457–476.
- WHITTON, B. A. 1972. Environmental limits of plants in flowing waters. Symposium of the Zoological Society of London 29:3–19.

### About the Authors

*Emma Benenati, Joseph Shannon, and Kevin Wilson are research associates at Northern Arizona University specializing in benthic ecology of the Colorado River above and below Glen Canyon Dam. Dean W. Blinn is a Regents' Professor at Northern Arizona University specializing in algal ecology with an emphasis on diatoms. Susan Hueftle is a limnologist with the Bureau of Reclamation, working on Lake Powell, which is above Glen Canyon Dam.*