

DESICCATION AND RECOLONIZATION OF PHYTOBENTHOS IN A REGULATED DESERT RIVER: COLORADO RIVER AT LEES FERRY, ARIZONA, USA

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ABSTRACT

We tested the recolonization of the phyto-benthic community in the tailwaters of Glen Canyon Dam following long- and short-term experimentally induced desiccation. The response of *Cladophora glomerata*, *Oscillatoria* spp., miscellaneous phyto-benthos species and periphyton was studied over 18 weeks using three treatments: (1) undisturbed control cobbles from the submerged zone; (2) cobbles desiccated and replaced into the submerged zone; and (3) cobbles desiccated and replaced into the varial zone. Periphyton density and compositional response resulting from these treatments were also examined.

Desiccation treatments were significantly different in biomass from controls throughout the study. The biomass of desiccated and replaced river cobbles averaged < 30% of the controls for *C. glomerata* and periphyton during the 18-week recolonization period. In contrast, the biomass of the control *Oscillatoria* and miscellaneous phyto-benthos species averaged only 3 and 50% of that in the desiccation treatments, respectively. *Cladophora*, the dominant alga, comprised 77% of the phyto-benthic biomass. A significant positive relationship between discharge, *Cladophora* and periphyton biomass was present in all treatments, while there was a negative relationship with discharge for *Oscillatoria* and miscellaneous phyto-benthos species.

There was a significant inverse correlation, as well as a pattern of separate biomass dominance, between *C. glomerata* and *Oscillatoria*. *Cladophora* was the dominant phyto-benthos species on cobbles below the baseflow and *Oscillatoria* was dominant on cobbles in the varial zone. In general, the *Cladophora* biomass decreased under intermittent drying conditions, while *Oscillatoria* declined under permanently wet conditions.

Diatom composition was not significantly different between treatments; however, their density was lower on desiccated cobbles. Diatom density on desiccated cobbles in the submerged and varial zones averaged 69 and 42% of that of the controls, respectively.

Recovery and maintenance of benthic resources are hindered by fluctuating flow regimes driven by electricity and irrigation requirements. Repeated desiccation of the phyto-benthos has major effects on the bottom-up interactions in the Colorado River ecosystem. © 1998 John Wiley & Sons, Ltd.

KEY WORDS: *Cladophora*; *Oscillatoria*; diatoms; cyanobacteria; desiccation; periphyton; phyto-benthos; recolonization; discharge; regulation; Glen Canyon Dam

INTRODUCTION

The diel and seasonal fluctuating flows characteristic of hydroelectric peaking power facilities can have detrimental effects on the growth and survival of downstream benthos. Benthic communities below dams often show depleted species diversity, density, or biomass in varial zones subject to periodic stranding and desiccation (Fisher and La Voy, 1972; Hardwick *et al.*, 1992; Stanford and Hauer, 1992; Blinn *et al.*, 1995; Humphries *et al.*, 1996; Stevens *et al.*, 1997).

Most studies examining the effects of river regulation on downstream biota concentrate on macroinvertebrates or fisheries (Fisher and La Voy, 1972; Ward, 1976; Gislason, 1985; Perry and Perry, 1986; Layzer *et al.*, 1989; Armitage and Blackburn, 1990; Dessaix *et al.*, 1995), while few studies emphasize the effects

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on the phytobenthos (Lowe, 1979; Dufford *et al.*, 1987; Hardwick *et al.*, 1992) and little has been reported on phytobenthic colonization below hydroelectric dams (Peterson, 1986; Blinn *et al.*, 1995).

The operation of Glen Canyon Dam and the presence of Lake Powell have modified the Colorado River benthic food base in Grand Canyon since 1963. Prior to impoundment, production in the muddy Colorado River was driven primarily by allochthonous input, with occasional clear-water periods and limited algal growth, including taxa such as *Cladophora*, *Spirogyra* and *Zygnema* (Flowers, 1959; Blinn and Cole, 1991; Haden, 1997). The once seasonally influenced river now flows under relatively thermally constant and clear conditions that provide enhanced habitat for algal communities in the permanently submerged channel (Blinn and Cole, 1991; Carothers and Brown, 1991; Stanford and Ward, 1991; Stevens *et al.*, 1997). However, productivity has decreased in the varial zone owing to periodic atmospheric exposure resulting from fluctuating flows (Angradi and Kubly, 1993; Shannon *et al.*, 1994; Blinn *et al.*, 1995).

Benthic algae, especially *Cladophora glomerata*, are critical to the Colorado River food web, because they serve as: (1) a food source for macroinvertebrates, owing to epiphytic diatom growth; (2) a refugium from river currents and fish predation for macroinvertebrates (primarily chironomid larvae); and (3) an important food host for fish, owing to the high density of associated macroinvertebrates (Shannon *et al.*, 1994). The phytobenthos in the submerged channel is dominated by the green, filamentous alga *C. glomerata*, while cobbles in the upper varial zone are covered by the crustose cyanobacteria, *Oscillatoria*.

Periods of short-term desiccation occur (10–15 h) within the varial zone, owing to a diel tide associated with the daily electricity demand. Repeated events of long-term desiccation (1–3 months) and loss of algal biomass result from varial zone exposure during designated low-release months, when downstream agricultural demand decreases (Usher and Blinn, 1990; Hardwick *et al.*, 1992; Angradi and Kubly, 1993; Blinn *et al.*, 1995). A critical area of impact is the 'lower varial zone' (flow stage, 142–340 m³/s) that becomes submerged and colonized with *Cladophora* and associated biota during high-discharge months, then experiences exposure and desiccation when the flow regime changes. This can lead to a significant loss of benthic substrate area (64000 m²), since it nearly equals the entire submerged channel zone (68000 m²). Atmospheric exposures of only 10 h can result in a 43% decrease in the chlorophyll *a* of *Cladophora* (Angradi and Kubly, 1993). Blinn *et al.* (1995) reported > 60% reduction in *Cladophora* and epiphyton biomass after five consecutive days of 12-h exposures in the Glen Canyon Dam tailwaters. Macroinvertebrate mass in the varial zone was found to be 4-fold lower than that in the permanently submerged channel of the Colorado River.

We examined the recovery of phytobenthos following a seasonal drying disturbance while under the influence of regulated flows below the Glen Canyon Dam. Our objectives were to test and compare the recolonization rate of different components of the primary producer community on benthic cobbles in the submerged (≤ 142 m³/s) and varial zones (142–793 m³/s). We also examined the recolonization pattern of diatom periphyton in the submerged and varial zones. The questions asked were: (1) can benthic algae subjected to periodic long-term desiccation events recover in the period between these events, and how does recovery differ in submerged and varial zones?; and (2) do periodic desiccation events explain the relative distributions of different algal types?

MATERIALS AND METHODS

Study site

This study was conducted in the Colorado River on Lees Ferry cobble bar, located 25.3 km downstream from Glen Canyon Dam at Lees Ferry, Arizona (36°52'03"N, 111°35'40"W; Figure 1). Glen Canyon Dam is a hypolimnetic release (9 ± 2°C) hydroelectric dam, the flow operations of which are governed by the seasonal irrigation needs of lower basin states and daily electricity requirements of the western region (USBR, 1995).

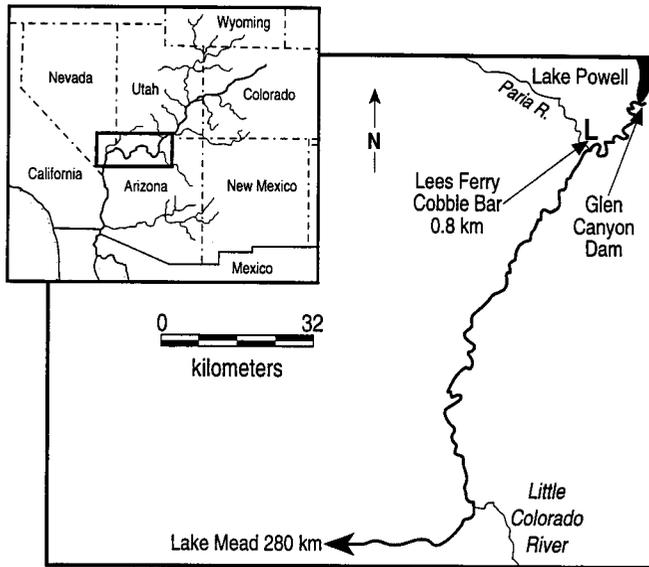


Figure 1. Map showing the region of the Colorado River; Lees Ferry, Arizona; and the study site of Lees Ferry Cobble at river km 0.8. Lees Ferry Cobble is located 25.3 km below the Glen Canyon Dam and its reservoir, Lake Powell

Dam operations have resulted in two shifting zones (Figure 2). The varial zone ($142\text{--}793\text{ m}^3/\text{s}$) is defined as the river channel area above the baseflow ($\leq 142\text{ m}^3/\text{s}$), subject to intermittent wetting and drying and experiencing hours- to months-long desiccation intervals (Stanford and Hauer, 1992). The submerged zone is the area of permanently wetted river channel at or below the baseflow ($\leq 142\text{ m}^3/\text{s}$) that experiences changing levels in water depth. However, high-discharge months (January, February, July, August) or above-average snow-melt months (May–August) can shift the submerged zone to as high as $> 450\text{ m}^3/\text{s}$ for extended periods. Designated low-flow months are from March to May and from October to November.

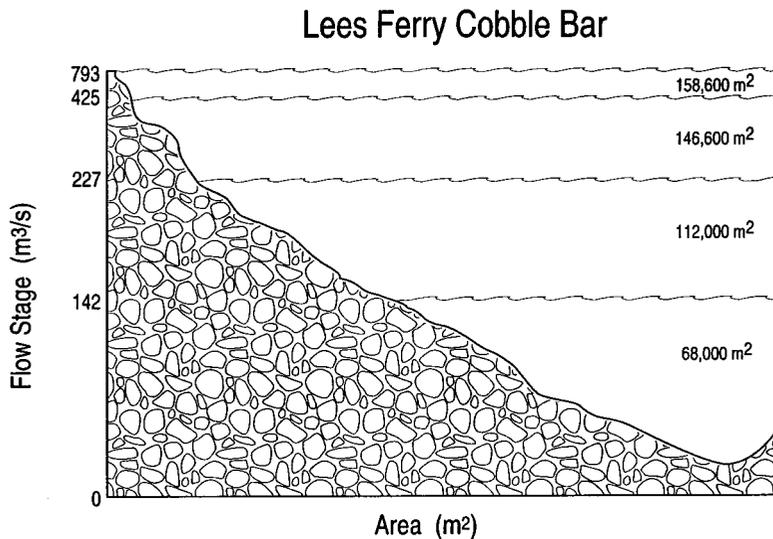


Figure 2. Diagram showing the benthic cobble areas in the river channel at the Lees Ferry study site that are inundated or desiccated at various water stages owing to fluctuating flows in the Colorado River below the Glen Canyon Dam (from Blinn *et al.*, 1995)

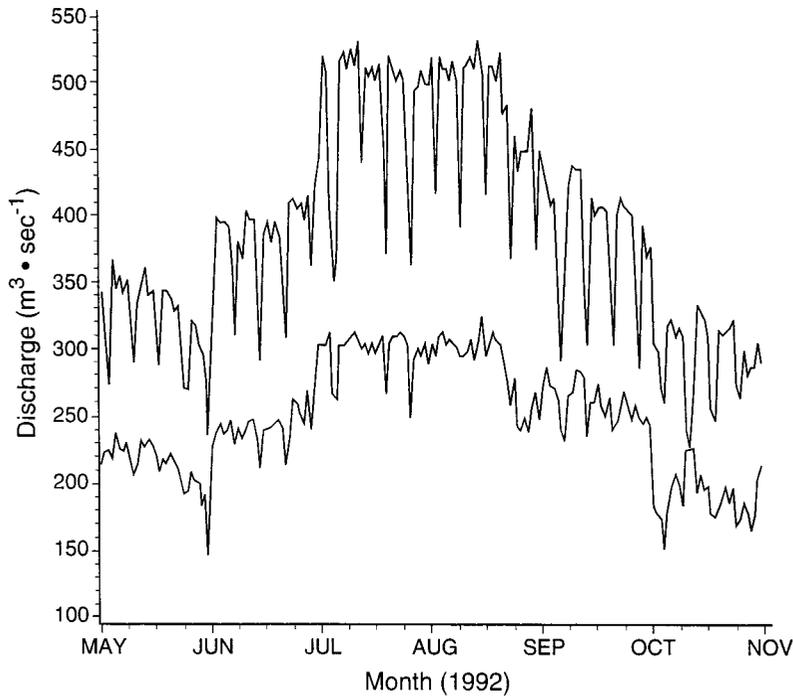


Figure 3. Minimum and maximum flows (m^3/s) in the Colorado River during the study period. Collection dates were: 24 June, 25 July, 12 August, 22 September and 21 October 1992

Sampling protocol

On 21 March 1992, 200 cobbles, (~ 80 cm in circumference) were collected from the submerged channel by snorkeling and placed on shore above the varial zone limit ($> 793 \text{ m}^3/\text{s}$ stage) for 3 months of desiccation, in order to simulate seasonal discharge patterns. Three months is a typical desiccation interval between varial zone inundations in the cycle of high- and low-flow releases below the Glen Canyon Dam (USBR, 1995). Algal material covering these cobbles was not removed, in order to simulate seasonal river conditions. On 17 June 1992, these cobbles were replaced into the river channel at two sites: (1) submerged below the $142 \text{ m}^3/\text{s}$ stage (treatment = submerged; $n = 100$); and (2) in the varial zone at the $340 \text{ m}^3/\text{s}$ stage (treatment = varial; $n = 100$). Within each site, cobbles were placed in a grid pattern of 10×10 cobbles. Control cobbles (undisturbed cobbles from the permanently submerged channel; $n = 100$) were also collected randomly throughout the study to be sampled and compared to the submerged and varial treatments.

Discharge was monitored during the 18-week study using hydrographs from the U.S. Geological Survey gauging station at Lees Ferry (Figure 3). In order to determine the effects on recolonization, the water stage range and means were documented during the five collection intervals after replacement of the cobbles into the river channel: 1 week (24 June); 5 weeks (25 July); 8 weeks (12 August); 14 weeks (22 September); and 18 weeks (21 October). At each collection interval, 60 algal patches (20 cm^2 each) were scraped from the treatment cobbles with a razor blade (submerged: $n = 20$ + varial: $n = 20$ + random control cobbles from the submerged channel: $n = 20$). Cobbles were randomly selected from the grids for scraping, then marked to prevent resampling and replaced in the grids to maintain flow patterns. A total of 300 cobbles were sampled during the five collection intervals. The samples were placed on ice and returned to the laboratory for processing within 48 h of collecting.

The phytobenthos was sorted into the categories of *C. glomerata*; *Oscillatoria* spp; and miscellaneous algae, macrophytes and bryophytes (MAMB). MAMB typically included various combinations of Rhodophytes (Batrachospermaceae, Chantransiaceae); other Chlorophytes (Ulotrichaceae, Zygnemat-aceae), *Chara* spp., *Elodea* spp., *Potamogeton pectinatus* and *Fontinalis* spp.

Cladophora was selected for the purpose of obtaining epiphyton (diatom) biomass and composition for each of the three treatments. In varial zone samples, *Cladophora* was often absent and epilithon was the only algal material present on cobbles; therefore, this was also used for diatom analysis. Because diatoms were obtained both as epiphyton from *Cladophora* and as epilithon from cobbles, the general term of periphyton shall be used in this paper. The algal material (*Cladophora* or epilithon) was placed in a Whirl-pak™ containing 100 ml of filtered (0.45 µm) Colorado River water and shaken for 60 s to remove periphyton. This procedure removed at least 80% of the diatoms, based on microscopic analysis, and was found to be the most effective technique for separating intact epiphytic diatoms from *Cladophora* filaments (Blinn *et al.*, 1995). The periphyton suspension was filtered onto Whatman (GF/C) 4.7 µm glass microfiber filters. All categories were oven-dried for 48 h (60°C), and heated at 500°C for 1 h to obtain ash-free dry mass (AFDM/m²).

Ashed periphyton was scraped from the microfiber filters and mounted onto microscope slides using Hyrax® medium. A minimum of 200 diatoms per slide were counted and identified to determine the number of cells per taxon. All reported cell numbers in this paper are cells/g periphyton.

Statistical analyses

Multivariate analysis of variance (MANOVA) was performed to determine the relationships between dependent variable groups (*C. glomerata*, *Oscillatoria* spp., miscellaneous phyto-benthos (MAMB), periphyton biomass and periphyton composition densities), and predictor variables (collection interval and cobble treatment). A square root transformation was used to insure constancy of variance (Zar, 1984). Overall patterns were determined using Wilks' lambda statistic and individual responses were detected with *post hoc* univariate tests. Tukey tests were used for multiple comparisons and Pearson correlations with the Bonferroni adjustment were used to measure associations among dependent variables and between biotic and abiotic factors. The SYSTAT statistical package was used to perform all calculations (Wilkinson, 1989).

RESULTS

Water stage

Discharge ranged from 147 to 532 m³/s, with daily fluctuations averaging 160 m³/s (S.E. ± 40) between 17 June and 21 October 1992 (Figure 3). Mean flows (m³/s) during collection intervals were as follows: week 1 = 312; weeks 2–5 = 397; weeks 6–8 = 405; weeks 9–14 = 354; and weeks 15–18 = 255. The control and submerged treatment cobbles were covered by flows during the entire period; however, changes in water depth did occur owing to fluctuating discharge. The varial treatment cobble grid was located at the 340 m³/s stage, and therefore experienced periodic exposure during the early weeks, and prolonged exposure for the last 3 weeks of the study.

Water stage effect on recolonization patterns

A significant ($p < 0.01$) drop in biomass occurred over time in all three treatments for periphyton, as well as in the control and varial treatments for *C. glomerata* (Table I). A pattern of maximum recolonization occurred between weeks 5 and 8, followed by a decrease in biomass at weeks 14 or 18 coinciding with periods of elevated and reduced river discharge, respectively (Figures 3–5).

Oscillatoria spp. did not display as uniform a pattern in their response over time and decreasing water stage. A peak in submerged treatment biomass did occur at week 5, followed by substantial loss of 83% in the remaining weeks; however, *Oscillatoria* was notably absent from control cobbles, with only one occurrence at week 14 (Figure 6). A reverse pattern occurred over time with varial *Oscillatoria*. Biomass increased across time intervals as flows decreased until the last interval, when flows fell consistently below 340 m³/s (mean 250 ± 84 m³/s), resulting in prolonged exposure and a 91% loss of biomass (Figures 3 and

Table I. MANOVA table and univariate test results of phytobenthos in the Colorado River at Lees Ferry, 24 June–21 October 1992

Source	Wilks' lambda	Approximate <i>F</i> -statistic	df	<i>p</i>	Univariate significant response variable
All intervals					
Control treatment	0.589	3.326	16, 281	<0.001	CLGL, PERI
Submerged treatment	0.586	3.366	16, 281	<0.001	PERI, MAMB
Varial treatment	0.708	2.103	16, 281	<0.01	CLGL, PERI
All treatments					
Week 1	0.399	7.861	8, 108	<0.001	CLGL, PERI, OSSP
Week 5	0.427	7.150	8, 108	<0.001	CLGL, PERI
Week 8	0.298	11.239	8, 108	<0.001	CLGL, PERI, OSSP, MAMB
Week 14	0.217	15.501	8, 108	<0.001	CLGL, PERI, OSSP, MAMB
Week 18	0.328	10.080	8, 108	<0.001	CLGL, PERI

The biomass response was tested against two abiotic predictor variables: (1) time intervals in weeks (weeks 1, 5, 8, 14 and 18); and (2) treatment (control, submerged and varial). The response variables are *C. glomerata* (CLGL), periphyton (PERI), *Oscillatoria* spp. (OSSP) and miscellaneous algae, macrophytes, and bryophytes (MAMB).

6). MAMB showed no significant biomass differences during the intervals on the control and varial cobbles, although a significant ($p < 0.001$) increase of 96% occurred on submerged cobbles at the lowest water stage during week 18.

Biomass responses related to water stage were examined after detecting significant changes in biomass in conjunction with decreased water stage. A Pearson correlation showed a significant ($p < 0.05$) and positive relationship between water stage and biomass of *Cladophora* and periphyton. Varial *Cladophora* and periphyton showed the strongest response to decreasing water stage after week 8, with 67 and 57% losses in biomass, respectively.

Both MAMB and *Oscillatoria* responded differently to water stage. *Oscillatoria* displayed a negative correlation with water stage for control and submerged cobbles throughout the collection period. Varial *Oscillatoria* also showed a negative association for all intervals except the last. MAMB biomass on submerged cobbles showed a significant ($p < 0.05$) and negative association with water stage, although no significant association was apparent on control or varial cobbles.

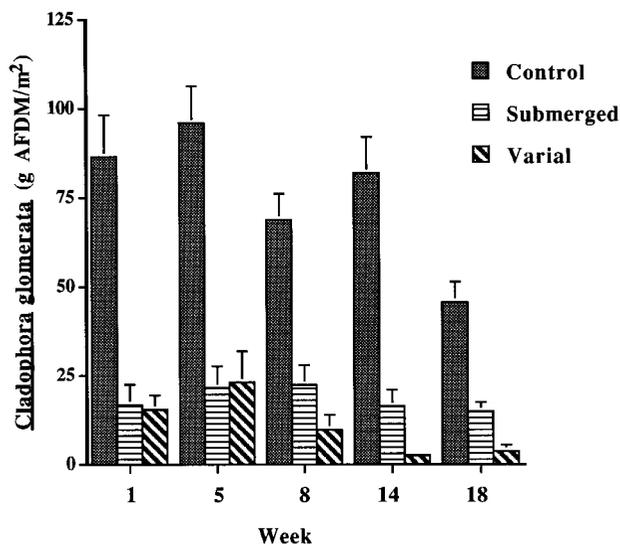


Figure 4. *C. glomerata* (g AFDM/m²; ± S.E.) for control, submerged and varial treatments from collections at weeks 1, 5, 8, 14 and 18

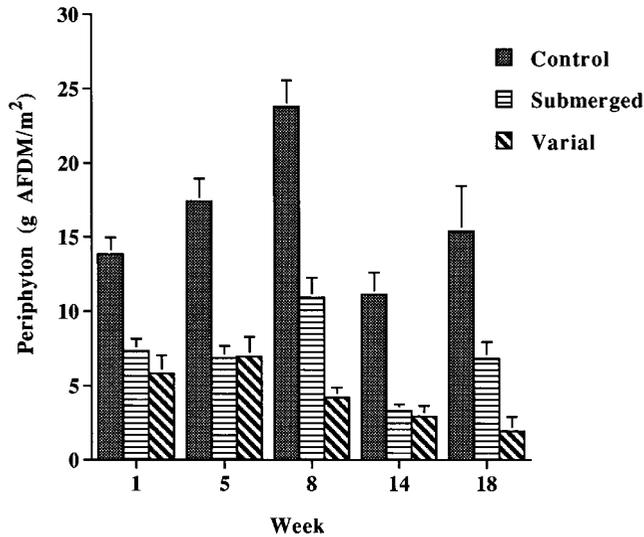


Figure 5. Periphyton (g AFDM/m²; \pm S.E.) for control, submerged and varial treatments from collections at weeks 1, 5, 8, 14 and 18

Treatment effect on recolonization

Treatment cobbles initially replaced into the river channel had a mean biomass of desiccated, bleached algal material of 10.1 g/m² (S.E. \pm 2.3). Some of this material remained on the treatment cobbles through the first collection at week 1; however, no bleached algae remained for the following collections. These results compare with previous work in the Colorado River, where 40% of bleached algae remained on river cobbles after a 48 h exposure period was followed by 2 weeks of re-inundation in the river (Angradi and Kubly, 1993).

Cladophora and periphyton showed significant ($p < 0.001$) differences in biomass between cobble treatments (control, submerged and varial) throughout the study, while *Oscillatoria* and MAMB showed significant ($p < 0.001$) differences at weeks 1, 8 and 14 (Table I). Tukey tests showed *Cladophora* and

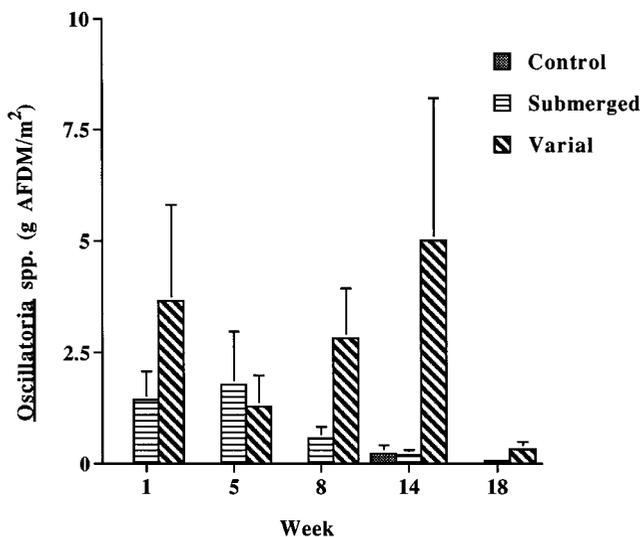


Figure 6. *Oscillatoria* spp. (g AFDM/m²; \pm S.E.) for control, submerged and varial treatments from collections at weeks 1, 5, 8, 14 and 18

periphyton control biomass to be significantly higher than that of other treatments, while varial biomass remained the lowest throughout the intervals to a significant degree (Figures 4 and 5). In contrast, the control cobbles had less overall growth of *Oscillatoria* and MAMB than the submerged or varial cobbles (Figure 6).

The biomass of control *Cladophora* averaged 76% higher than the submerged treatment, while control periphyton averaged 58% greater than the submerged treatment throughout the study. The mean biomass for control *Cladophora* was 75.8 ± 9.1 g/m² and that for periphyton was 16.8 ± 1.8 g/m² (Figures 4 and 5). In contrast, control *Oscillatoria* had 95% less biomass than the submerged test mean of 0.8 ± 0.3 g/m², while MAMB controls averaged 96% lower than their submerged treatment mean of 1.7 ± 1.0 g/m² (Figure 6).

Varial *Cladophora* and periphyton showed the lowest treatment biomass, averaging only 14 and 28% of their controls, respectively (Figures 4 and 5). The opposing pattern continued with *Oscillatoria* and MAMB. Varial *Oscillatoria* showed the highest mean biomass on the varial cobbles at 2.6 g/m² (± 1.4), which was 65-fold greater than that of the *Oscillatoria* controls (Figure 6). MAMB biomass averaged 0.1 g/m² (± 0.06) on varial cobbles, which was 30% higher than that of the controls (0.07; 0.04).

In general, *Cladophora*, periphyton and MAMB recolonization was higher on submerged cobbles than compared to varial cobbles. Tukey tests revealed significant ($p < 0.01$) biomass differences between submerged and varial treatments for *Cladophora*, periphyton and *Oscillatoria*. No significant differences in biomass occurred between MAMB submerged and varial tests. The opposite occurred with *Oscillatoria*, showing 330% greater growth on varial cobbles than on submerged cobbles.

Significant relationships and opposite recolonization patterns occurred between *Cladophora* and two variables during the study. A significant inverse correlation between *Cladophora* and *Oscillatoria* biomass was present in the submerged and varial treatments (Pearson correlation: submerged, $p < 0.01$; varial, $p < 0.05$). *Cladophora* retained consistent biomass on the submerged cobbles, but steadily lost biomass in the varial zone. In contrast, *Oscillatoria* showed initial low growth on submerged cobbles that steadily declined, while on the varial cobbles exhibited an increase through week 14. In addition, *Cladophora* was positively correlated with periphyton in both the submerged and varial treatments ($p < 0.001$).

Cladophora was clearly the dominant primary producer in this study, comprising 77% (35.0 ± 2.4 g/m²) of the total phytobenthic biomass. Periphyton, *Oscillatoria*, MAMB and detritus followed, comprising 20, 2.5, 0.4 and 0.1% of the biomass, respectively.

Recolonization rates and treatment effects on diatoms

Diatom composition and density within each treatment remained consistent throughout collection intervals, with the exception that control cobble densities were significantly ($p < 0.05$) different between weeks 1 and 5. Univariate tests showed that five of the dominant species significantly decreased in density on control cobbles, these being *Achnanthes affinis*, *Diatoma tenue*, *Fragilaria ulna*, *Rhoicosphenia curvata* and *Diatoma vulgare* (Table II). Twenty-two diatom taxa were documented, with the dominant members of each of the five collection intervals identified to species level (Table II). The total diatom density ranged from 771×10^6 to 4104×10^6 cells/g periphyton present during one collection interval for one treatment.

Nine species made up 75% of the total diatom assemblage in all treatments: *A. affinis* (24%); *D. tenue* (16%); *Fragilaria leptostauron* (15%); *F. ulna* (7%); *Amphora ovalis* (4%); *Cocconeis pediculus* (3%); and *R. curvata*, *Denticula elegans* and *Diatoma vulgare* each maintaining $\sim 2\%$ of the total (Table II and Figure 7). The mean percentages of these dominants were maintained with little change during the five collection intervals. *A. affinis* had the highest number of cells/g periphyton, with an overall mean of 1979×10^6 ($\pm 180 \times 10^6$), while *D. vulgare* had the lowest overall mean of 94×10^6 ($\pm 12 \times 10^6$) during the collection period. These dominant species are in contrast with past studies in the Glen Canyon Dam tailwaters. *Diatoma vulgare*, *R. curvata*, *C. pediculus* and *A. affinis* have been reported as the most common epiphytes, making up $> 80\%$ of the diatom standing crop (Czarnecki and Blinn, 1978; Hardwick *et al.*, 1992; Shannon *et al.*, 1996). Most of the 13 other taxa that comprised the remaining 25% of the density also maintained

Table II. Lees Ferry diatom recolonization by composition and density ($\times 10^6$ cells/g periphyton) after three months of desiccation

Taxa	Interval (weeks)				
	1	5	8	14	18
<i>D. tenue</i> ^a (Ag.)					
Con.	963	361	461	231	286
Sub.	258	159	651	264	227
Var.	368	127	185	68	31
<i>F. leptostauron</i> ^a var. <i>Dubia</i> (Hust.)					
Con.	289	156	381	208	234
Sub.	306	91	558	160	246
Var.	332	267	165	430	323
<i>F. ulna</i> ^a (Ehr.)					
Con.	260	93	262	178	80
Sub.	69	44	285	78	96
Var.	117	136	96	57	39
<i>D. vulgare</i> ^a (Bory)					
Con.	47	21	89	56	38
Sub.	12	7	46	18	40
Var.	20	20	26	17	14
<i>A. ovalis</i> ^b var. <i>pediculus</i> (Kutz.)					
Con.	148	46	112	104	153
Sub.	103	33	201	55	113
Var.	59	64	43	43	23
<i>C. pediculus</i> ^c (Ehr.)					
Con.	79	38	81	126	41
Sub.	37	16	72	11	42
Var.	65	61	85	55	51
<i>R. curvata</i> ^c (Kutz.)					
Con.	16	8	119	52	44
Sub.	14	3	76	22	41
Var.	44	50	35	17	16
<i>A. affinis</i> ^c (Grun.)					
Con.	1496	573	1052	669	1264
Sub.	447	291	1327	514	968
Var.	665	162	248	162	128
<i>D. elegans</i> ^d (Kutz.)					
Con.	76	9	88	41	22
Sub.	11	2	33	17	41
Var.	12	26	41	63	73
Miscellaneous ^e					
Con.	767	324	1263	565	619
Sub.	292	116	910	140	460
Var.	313	225	221	170	120

The dominant taxa are listed by treatment and collection interval. The treatments are: Con. (undisturbed controls $< 142 \text{ m}^3/\text{s}$); Sub. (desiccated and submerged $< 142 \text{ m}^3/\text{s}$) and Var. (desiccated and placed into the varial zone at $\sim 340 \text{ m}^3/\text{s}$). Miscellaneous taxa are listed at the bottom of the table.

^a Family Fragilariaceae.

^b Family Cymbellaceae.

^c Family Achnantheaceae.

^d Family Epithemiaceae.

^e Miscellaneous includes species of *Achnanthes*, *Caloneis*, *Cyclotella*, *Cymbella*, *Diatoma*, *Diploneis*, *Epithemia*, *Fragilaria*, *Gomphonema*, *Navicula*, *Nitzschia* and *Plagiotropis*.

consistent numbers throughout the collection intervals; however, a few were only intermittently present in small numbers, these being: *Caloneis* spp., *Diploneis* spp., *Epithemia* spp. and *Plagiotropis* spp. (Table II).

Between-treatment effects on diatom composition and density were non-significant throughout collection intervals, with one exception at week 18. Diatom densities were significantly higher ($p < 0.05$) on control cobbles compared to varial cobbles when discharge fell below the varial cobble grid for the last interval.

Control taxa showed the highest overall density (cells/g periphyton) and varial taxa the lowest, with overall means of 2.9 ± 0.28 billion, 2.0 ± 0.39 billion and 1.2 ± 0.25 billion for control, submerged and varial treatments, respectively. However, an exception to this pattern occurred with *F. leptostauron*, *C. pediculus* and *D. elegans*, which displayed tolerance to desiccation and repeatedly reached equal or greater numbers on the varial cobbles, compared to both control and submerged treatments, throughout the

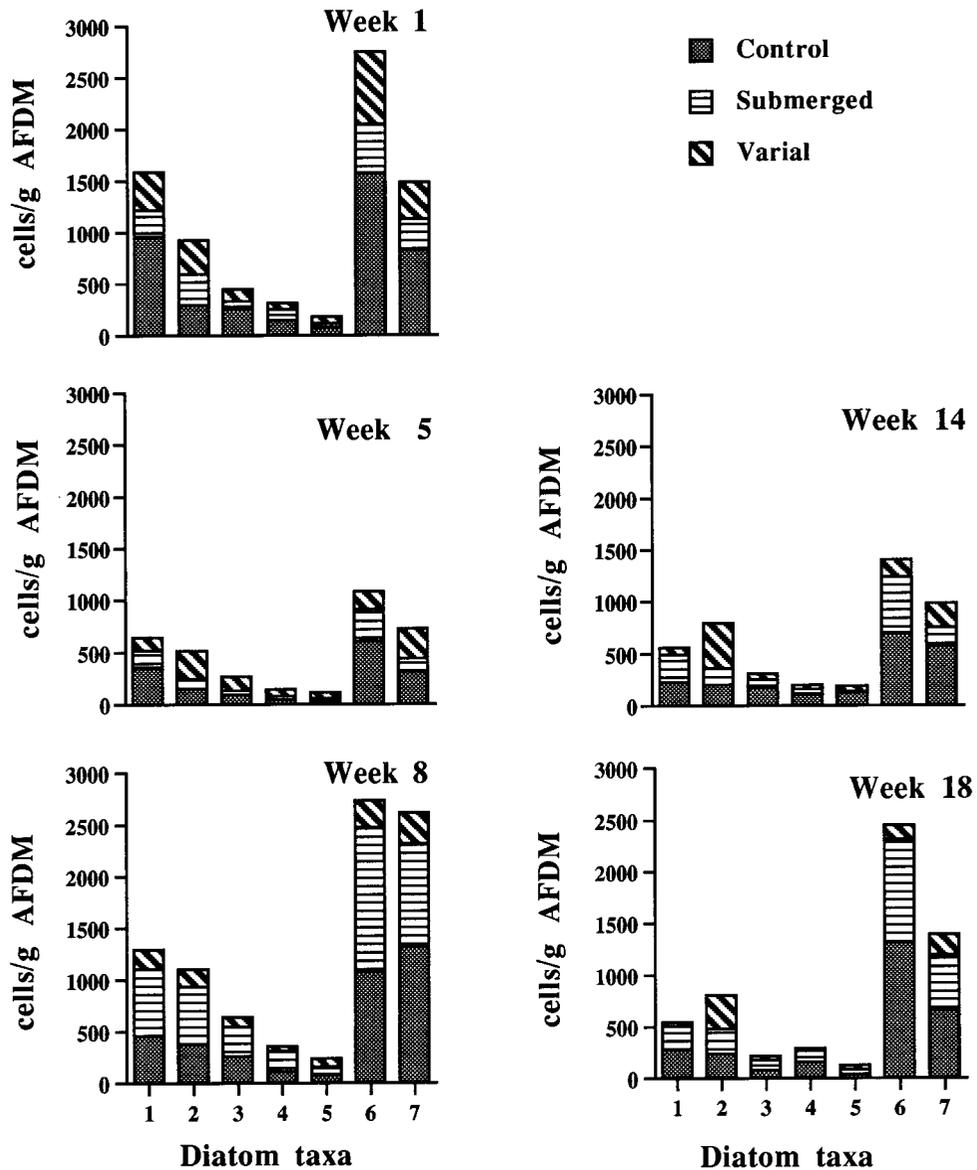


Figure 7. Dominant and miscellaneous diatom species density (10×6 cells/g periphyton) for control, submerged and varial treatments from collections at weeks 1, 5, 8, 14 and 18. Diatom taxa listed on abscissa: (1) *D. tenue*; (2) *F. leptostauron*; (3) *F. ulna*; (4) *A. ovalis*; (5) *C. pediculus*; (6) *A. affinis*; (7) miscellaneous species

collection intervals (Table II and Figure 7). Overall, varial *F. leptostauron*, *C. pediculus* and *D. elegans* averaged 134 and 300% of their respective control and submerged treatments during the 18 weeks.

DISCUSSION

Recolonization rates

Experimentally induced exposure and desiccation had a significant impact on the phytobenthic community tested. Our results demonstrate that recolonization cannot occur under the restraining influence of daily fluctuating flows in conjunction with monthly discharge changes, and confirms the negative effect of regulated flows on the biomass and density of the aquatic food base in the Colorado River.

The dependent biotic variables did not maintain either stable biomass or density, and generally followed the highs and lows of the discharge regime. Changeable patterns in the recolonization process for desiccated cobbles in the submerged and varial treatments, as well as in the control biomass, indicates an outside influence, or influences, such as variable discharge, nutrients and light. After 18 weeks, *Cladophora* and periphyton in the submerged treatment attained less than 35% of their control biomass. Recolonization in the varial zone was only 21% of the control, where the stresses resulting from decreasing water stage have the strongest effect. Fluctuating flows characteristic of regulated rivers require longer periods for biomass recolonization than do steady flows (Blinn *et al.*, 1995; Shaver *et al.*, 1998). A seasonal decline in photosynthetically available radiation (PAR) coupled with decreased discharge and nutrient delivery may be a possible explanation for the decline in the biomass and density of both control and recolonizing benthic primary producers (Dodds, 1991; Dodds and Gudder, 1992).

The pronounced decline of *Cladophora* and periphyton biomass on varial cobbles is probably a consequence of the repeated episodes of exposure and desiccation that occurred in this zone as flows decreased while daily fluctuations continued. Although the MAMB maintained low biomass throughout the collection period, an increase in biomass during lowered discharge at week 18 may indicate it to be desiccation-tolerant, or an opportunistic colonizer when conditions are not optimum for the dominant alga *Cladophora*. The algal types in MAMB (e.g. *Batrachospermum*, *Ulothrix*, *Spirogyra*) are mucilage-covered, enabling them to retain moisture longer than non-mucilaginous algal types, such as *C. glomerata* (Round, 1981). MAMB was also found to be a strong benthic invader in the Glen Canyon Dam tailwaters when *Cladophora* biomass decreased as a result of reduced nutrients (Benenati *et al.*, 1997).

The increase in *Oscillatoria* biomass as a response to declining water stage in the varial zone indicates desiccation tolerance. Higher water stages that completely submerged *Oscillatoria* and resulted in decreased biomass appear to be detrimental to growth, while the intermittent wet–dry conditions of the varial zone optimize conditions for its growth (John *et al.*, 1990; Shaver *et al.*, 1998). The absence of *Oscillatoria* on the undisturbed, permanently wet control cobbles is further evidence that varial conditions are optimal. The silt–filament matrix characteristic of *Oscillatoria* can trap and hold moisture, allowing survival and growth in marginal conditions that may not be tolerated by *Cladophora* or other algal types. In addition, *Oscillatoria* filaments are capable of vertical migration within the top few millimeters of sediment (Vincent and Castenholz, 1993).

The replacement of *Cladophora* with *Oscillatoria* owing to decreased and fluctuating discharge would result in a dramatic loss of algal food base. *Oscillatoria* provides a poor substrate for diatoms and macroinvertebrates, owing to its reduced surface area and exposed location (Shaver *et al.*, 1998). Moreover, *Oscillatoria* spp. contribute less potential energy (4405 ± 340 kcal/g AFDM) than *Cladophora* (5170 ± 580 kcal/g AFDM) or diatoms (5470 ± 160 kcal/g AFDM) (Cummins and Wuycheck, 1971). Stevens *et al.* (1997) found only 34 organisms on cobble bars within the *Oscillatoria*-dominated varial zone in 396 bi-monthly Hess samples along 363 km of the Colorado River in 1991, compared to 3860 organisms collected on cobble bars in the *Cladophora*-dominated submerged zone below the baseflow ($142 \text{ m}^3/\text{s}$). Although there were >100-fold more animals found in *Cladophora*-dominated zones, these

numbers are substantially less than subsequent samples (Shannon *et al.*, 1996; Shaver *et al.*, 1998), owing to the highly variable flows (750 m³/s) that occurred during 1991. Therefore, varial zone *Oscillatoria* spp. have little trophic significance in the Colorado River compared to *Cladophora*, despite the fact that it is the dominant algal type in the varial zone.

Although *Oscillatoria* can endure desiccating conditions, the dramatic drop in varial biomass at week 18 after 1 month of flows below the varial zone suggests that prolonged atmospheric exposure is deleterious to growth. The clear, sediment-free tailwaters of Lees Ferry may have contributed to the overall low biomass of *Oscillatoria* throughout this experiment, since previous studies have shown turbid waters to be more conducive to the growth of *Oscillatoria* (Davies-Colley *et al.*, 1992; Blinn *et al.*, 1995).

The inverse relationship observed between *Cladophora* and *Oscillatoria* in this study has been documented by other workers (Davies-Colley *et al.*, 1992; Blinn *et al.*, 1995; Shaver *et al.*, 1998). Based on the submerged and varial zone biomass, we suggest that *Cladophora* outcompetes *Oscillatoria* in a submerged, permanently wetted environment, and *Oscillatoria* outcompetes *Cladophora* in an intermittently wetted environment in the Colorado River. This may provide an explanation for the initial appearance of *Oscillatoria* in the submerged treatment followed by rapid decline, while *Cladophora* maintained its presence throughout the period of the study. *Cladophora* can use *Oscillatoria* as a substrate to grow from, eventually covering it (personal observation). These data also demonstrate the varial zone to be inhospitable for *Cladophora*, the biomass of which rapidly diminished as the water stage dropped. The positive correlation between *Cladophora* and periphyton corroborates prior studies (Hardwick *et al.*, 1992; Blinn *et al.*, 1995), where diatoms were found to be strongly associated with *Cladophora* owing to the mucous-free algal substrate allowing easy attachment.

Diatom recolonization

Diatom density followed the same patterns as *Cladophora* and periphyton biomass. The abundance of diatoms was substantially greater in the control treatment, and decreases in varial diatom density were more pronounced in latter weeks. High water stage may have facilitated greater relative varial and submerged densities at weeks 5 and 8.

D. tenue, *D. vulgare*, *A. affinis*, *F. ulna*, *A. ovalis* and *R. curvata* generally showed greater density in the control and submerged treatments and were not tolerant of intermittently wet conditions. This group of diatoms (with the exception of *A. affinis*) is larger in size (> 35 µm) and attaches to substrate in an upright position, thus allowing easier removal under changing flows. Conversely, *C. pediculus*, *F. leptostauron* and *D. elegans* flourished under varial zone conditions. This may be because of their small size (20 µm) and the adnate nature of their attachment onto the substrate, where moisture is retained by *Cladophora*. Hardwick *et al.* (1992) found a similar pattern.

Management considerations

C. glomerata is often regarded as a nuisance alga in other rivers, and biomass levels that exceed 50 g/m² are considered to be detrimental to aquatic life, recreation and aesthetics (Wharfe *et al.*, 1984; Biggs and Price, 1987; Zuur, 1992). However, in the Colorado River below the Glen Canyon Dam, *C. glomerata* is viewed as an important keystone species (see Introduction) and is not considered a nuisance, even at 75 g/m² as reported in this study. Many of the streams that experience nuisance growth are shallow (< 1 m depth) with cobbles exposed at the surface and have low–moderate flows. In contrast, the Colorado River below the Glen Canyon Dam is deep (5–7 m), has high discharge and velocity (412–570 m³/s; 0.31–0.50 m/s) and a baseflow minimum of 142 m³/s. These characteristics preclude *Cladophora* from growing to nuisance levels in this reach of the Colorado River. However, based on the results of this study, it is suggested that periodic desiccation may be an effective control tool for nuisance proliferations of *Cladophora* in other systems.

The benthic algal assemblage covering the cobble substrate on the river bottom in the Glen Canyon tailwaters provides a primary source of organic matter and nutrients for the Grand Canyon aquatic ecosystem (Angradi, 1994; Blinn *et al.*, 1995; Shannon *et al.*, 1996). Therefore, downstream impacts of

fluctuating flows should be a management consideration for all hydroelectric facilities. A slight drop in water stage translates into a large decrease in benthic area and available energy to higher trophic levels. For example, regulated flows of 142 m³/s at Lees Ferry will inundate 68000 m² of river channel, and 227, 425 and 793 m³/s will inundate 112000, 146000 and 158000 m², respectively (Blinn *et al.*, 1995). The greatest increase in benthic area and potential energy could be attained by a small increase in water stage. Flows slightly increased above the present base level (142 m³/s) to 227 m³/s could increase the available benthic energy (periphyton and dominant macroinvertebrates) by a minimum of 1.6-fold (Blinn *et al.*, 1995). Benthic energy could double with a base level increase to 425 m³/s, regardless of continued fluctuations in the varial zone above this water stage, assuming uniform growth at all depths. Although river channel morphology varies downstream through the Grand Canyon, similar benthic area and potential energy increases could occur under low turbidity conditions. A steady regime of discharge covering the littoral zone would increase algal biomass, as well as the biomass of higher trophic levels, by providing food, shelter and refugia (Hardwick *et al.*, 1992; Angradi and Kubly, 1993; Angradi, 1994; Blinn *et al.*, 1995; Valentin *et al.*, 1995; Stanford *et al.*, 1996). The authors recommend maintaining steady flows covering the varial zone to create a larger amount of stable habitat on the river bottom. This will maximize benthic growth, essential trophic resources and the export of nutrients downstream.

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