

Effects of suspended sediment and desiccation on the benthic tailwater community in the Colorado River, USA

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Abstract

We demonstrated that differences in habitat requirements by *C. glomerata* and *Oscillatoria* have a profound bottom-up influence on the foodweb in the tailwaters below Glen Canyon Dam in the Colorado River through Grand Canyon National Park, USA. We examined the effects of suspended sediment and desiccation on the colonization sequence of *Cladophora glomerata* and *Oscillatoria* spp. and the consequent effects on macroinvertebrates in each algal community in a series of reciprocal transplants in the regulated Colorado River, AZ. Our experiments showed that *C. glomerata* grows best in continuously submerged, clear-water, stable habitats, whereas *Oscillatoria* forms dense mat-like matrices of trichomes and sand in varial zones and habitats with high suspended sediments typical of many southwestern USA streams. Varial zone conditions have a stronger influence on community structure than habitats with high suspended sediments. Recruitment by chironomid larvae was less dependent on *C. glomerata* and less affected by suspended sediment and periodic desiccation than *Gammarus lacustris*. We estimated the energy from macroinvertebrate biomass associated with tufts of *C. glomerata* to be an order of magnitude higher than that in *Oscillatoria* matrices. Therefore, loss of *C. glomerata* and replacement of habitat more suitable for *Oscillatoria* as a result of regulated flows indirectly reduces potential energy flow in the Colorado River foodweb.

Introduction

River ecosystems in southwestern USA undergo extended periods of turbidity due to seasonal input of suspended sediments from surrounding xeric watersheds (Fisher & Minckley, 1978; Walling & Webb, 1992; Shannon et al., 1994; Blinn et al., 1995; Stevens et al., 1997). These sediment loads limit photosynthetically available radiation (PAR) resulting in lower benthic algal mass (Blinn & Cole, 1991; Davies-Colley et al., 1992; Holopainen & Huttunen, 1992; Blinn et al., 1992). Suspended sediments also increase scouring and impede respiration of macroinvertebrates, resulting in increased drift and reduced abundance and biodiversity (Newcombe & MacDonald, 1991; Quinn et al., 1992; Shannon et al., 1994; Stevens et al., 1997). Furthermore, suspended sediment loads alter substrate size and degrade food quality available to benthic fauna (Culp et al., 1986; O'Conner & Lake, 1994).

Benthic stream communities of arid landscapes are also periodically exposed to desiccation (Boulton & Lake, 1988; Grimm & Fisher, 1991). Intermittent lotic systems are exposed to seasonal desiccation, whereas varial zones in regulated rivers are subjected to diel exposures to the atmosphere (Lowe, 1979; Lillehammer & Saltveit, 1984; Ward & Stanford, 1989; Usher & Blinn, 1990; Angradi & Kubly, 1993; Blinn et al., 1995). The varial zone is that region in the tailwaters of dams that enlarges and contracts in response to dam operations (Stanford & Hauer, 1992).

We studied the influence of suspended sediment and the recovery of benthic communities following desiccation in the tailwaters of Glen Canyon Dam in the Colorado River, AZ. Reciprocal translocation experiments with cobble and associated biota were conducted at Lees Ferry and Cathedral Island to measure the rate of accommodation of *Cladophora glomerata* (L.) Kutz. and *Oscillatoria* spp. associations in high and

low suspended sediment habitats. The term 'accommodation' has been used to describe the adjustment of an established biotic community to a long-term incubation in an alternative environment (Yount & Niemi, 1990). We additionally measured the recolonization of desiccated cobbles by benthic communities in continuously submerged and varial zones at Lees Ferry and Cathedral Island.

Study area

Our study was conducted in the tailwaters of Glen Canyon Dam, Arizona, and was part of a larger program to monitor the aquatic food base of the Colorado River in Grand Canyon National Park, Arizona (Blinn et al., 1992; Blinn et al., 1995; Shannon et al., 1994, 1996; Stevens et al., 1997). The location of the tailwaters has allowed the simultaneous testing of tributary sediment and varial zone desiccation in a regulated river (Figure 1). Glen Canyon Dam releases sediment-free waters from the hypolimnion of Lake Powell. The Paria River is the first perennial tributary to the Colorado River below Glen Canyon Dam and releases an average of 2.7 million tonnes of suspended sediment annually (Andrews, 1991). Input of suspended sediments into the mainstem by the Paria River results in a contrasting turbid-water habitat (Secchi depth <1.5 m) at Cathedral Island (4.8 River Kilometers, Rkm) with a clear-water habitat (Secchi depth >6.0 m) at Lees Ferry (0.8 Rkm), both in the tailwaters of Glen Canyon Dam (Figure 1). Average annual suspended sediment loads at Lees Ferry ranged from <0.002 g l⁻¹ to 0.03 g l⁻¹, whereas suspended sediment at Cathedral Island ranged from 0.001 g l⁻¹ to >0.1 g l⁻¹ during previous years (Yard et al., 1995; Smith et al., 1993, 1994).

Biodiversity is limited in the constantly cold (9 °C, SE ± 0.35) tailwaters of Glen Canyon Dam. The dominant macroalgal assemblages are *Cladophora glomerata* and *Oscillatoria* spp., whereas the common macroinvertebrates are *Gammarus lacustris* and chironomids, namely *Cricotopus annulator*, *Eukiefferiella ilkleyensis* and *Orthocladia rivicola* (Blinn et al., 1992; Shannon et al., 1994; Blinn et al., 1995; Stevens et al., 1997). Diatoms are the primary algae of the epiphyton community in the tailwaters of Glen Canyon Dam and play a major role in the diets of *G. lacustris* and chironomids (Blinn & Cole, 1991; Blinn et al., 1995; Stevens et al., 1997).

Methods

Reciprocal-translocation turbidity experiments below the varial zone

One hundred cobbles (20–50 cm diam) and associated biota were collected from the permanently wetted channel (<142 m³ s⁻¹ stage) in the clear-water reach of Lees Ferry (Rkm 0.8) and transplanted into the seasonally turbid reach at Cathedral Island (Rkm 4.8). These cobbles were placed in a 10 × 10 cobble grid beneath the varial zone (<142 m³ s⁻¹ stage) at Cathedral Island. Likewise, 100 cobbles and associated biota from Cathedral Island were translocated upstream to the clear-water reach and placed in a 10 × 10 cobble grid below the varial zone at Lees Ferry.

At the start of the experiment, one sample (circular 20 cm²) of algae and macroinvertebrates was taken from each of 20 cobbles with a scapel at both Lees Ferry and Cathedral Island and deposited into individual containers. This provided an initial sample for each habitat. Also, one 20 cm² sample was taken from each of 20 randomly selected cobbles in each treatment grid at approximate monthly intervals over a 3 mo period, and at 9 and 11 mo. After each sampling, cobbles were replaced within the grid to reduce sampling disturbance. No samples were taken at 11 mo at Cathedral Island due to loss of cobbles during high flows (>566 m³ s⁻¹). On each sampling date, 20 control cobbles were also sampled from below the 142 m³ s⁻¹ stage in the channel at both sites for comparison with translocated cobbles. Macroinvertebrates (chironomids, gastropods, lumbriculids, tubificids, simuliids, and *Gammarus lacustris*) were sorted from each algal sample (*Cladophora glomerata* and *Oscillatoria*) and oven-dried at 60 °C to a constant mass. Dry mass values were then converted to ash-free dry mass estimates using the regression slope equation for each biotic category (Shannon et al., 1996).

Secchi depth measurements were taken monthly at each site during the experimental period (17 May 1993 to 19 April 1994) and used to determine attenuation coefficients (K_0) from the following equation:

$$K_0 = \log(\text{Secchi depth, m}) \cdot -0.60 + 1.13, (R^2 = 0.88, n = 164),$$

and total suspended sediments were then calculated from:

Total suspended sediment (g l⁻¹) = $K_0 \cdot 0.038 + 0.002$, ($R^2 = 0.95$, $n = 124$). The above equations were taken from a suspended sediment-light model generated

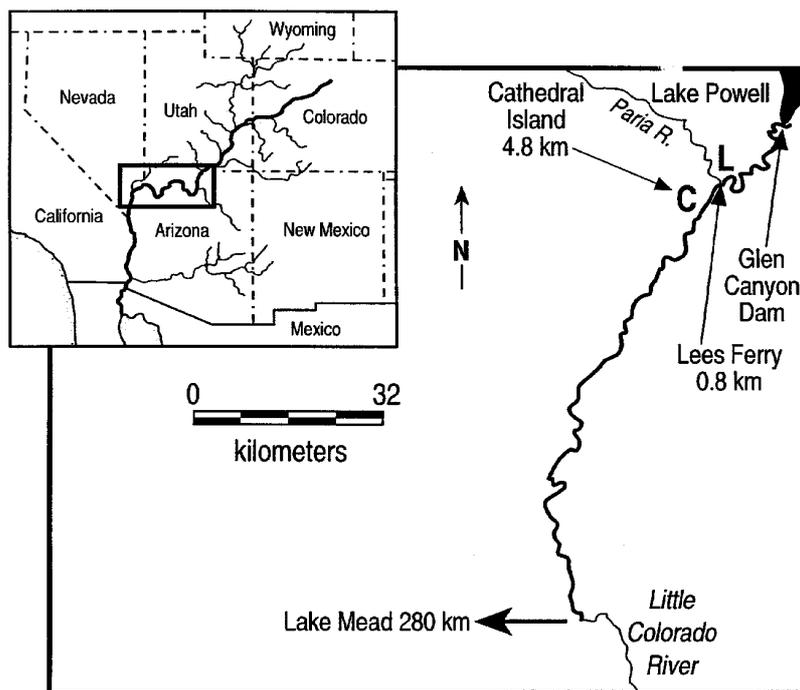


Figure 1. Study sites at Lees Ferry (0.8 Rkm) and Cathedral Island (4.8 Rkm) in the Colorado River, Arizona.

from empirical data (Yard et al., 1995). During the experiment, the Paria River discharge was above baseflow for 155 d during the 338 d period (Smith et al., 1993, 1994) which resulted in an estimated suspended sediment range of 0.007 g l^{-1} to $>15 \text{ g l}^{-1}$ (Michael Yard, Bureau of Reclamation, pers. comm.). Yard et al. (1995) estimated that negligible light enters the water column at $\geq 0.7 \text{ g l}^{-1}$ suspended sediment. Discharge from Glen Canyon Dam ranged from 142 to $566 \text{ m}^3 \text{ s}^{-1}$, with a daily mean discharge of $345 \text{ m}^3 \text{ s}^{-1}$, during the experimental period.

Desiccation-recolonization experiments in the varial and submerged zones

One hundred and sixty cobbles (20–50 cm in diam) were collected from the submerged channel ($<142 \text{ m}^3 \text{ s}^{-1}$ stage) at the Lees Ferry clear water site. The bottom of each cobble was numbered with paint and all cobbles were then placed above the high water mark ($566 \text{ m}^3 \text{ s}^{-1}$ stage) and allowed to desiccate. After 219 d, 80 desiccated cobbles were submerged in the channel at Lees Ferry below the varial zone ($<142 \text{ m}^3 \text{ s}^{-1}$ stage) to ensure continuous submergence. An additional 80 cobbles were placed in the varial zone ($340 \text{ m}^3 \text{ s}^{-1}$

stage) at Lees Ferry for 1–2 h daily exposures. The 80 cobbles in each treatment were placed in an 8×10 grid in order to facilitate relocation of treatment cobbles in the river channel. Within each treatment, one sample was harvested from a circular template (20 cm^2) with a scapel from 20 cobbles that were randomly selected from the grid at 2, 5, 9 and 11 mo. Cobbles were replaced within the grid, but not resampled, to reduce sampling disturbance. Algae (*C. glomerata* and *Oscillatoria*) and macroinvertebrates (chironomids, gastropods, lumbriculids, tubificids, simuliids, and *G. lacustris*) were sorted from each sample and AFDM was estimated.

The same sequence of cobble movement and collection was conducted concurrently at Cathedral Island for comparison of recolonization under turbid conditions. Ryan thermistors were placed in the middle of the varial zone cobble grid to determine the exposure and submergence cycles from temperature; submerged periods had temperatures $\geq 11 \text{ }^\circ\text{C}$, whereas temperatures for exposed periods were $>15 \text{ }^\circ\text{C}$.

Statistical analysis

The Kruskal-Wallis one-way analysis of variance was used to determine the significance of differences between treatments and controls. To minimize the chance of falsely rejecting the null hypothesis and to ensure confidence in all statements of significance, the sequential Bonferroni technique was performed. Significant levels of >0.01 were rejected after the Bonferroni adjustment. All statistical analyses were performed with the SYSTAT (5.2.1 Wilkinson, 1992) software package.

Results

Reciprocal-translocation experiments in turbid and clear-water habitats

At the onset, cobbles translocated from the turbid ($>1.5 \text{ g l}^{-1}$ suspended sediments) Cathedral Island site to the clear-water ($<0.005 \text{ g l}^{-1}$ suspended sediments) site at Lees Ferry had negligible *Cladophora glomerata* ash-free dry mass (AFDM) compared to an average of 165 g m^{-2} (SE ± 31) AFDM of *C. glomerata* on control cobbles at Lees Ferry (Figure 2A). In contrast, cobbles from Cathedral Island averaged 27 g m^{-2} (± 5) of *Oscillatoria* AFDM mass compared to no mass of this cyanobacterium on control cobbles at Lees Ferry (Figure 2B). Accommodation by *C. glomerata* was slow on translocated cobbles from Cathedral Island (Figure 2A). Even after 11 mo of clear water, relocated cobbles at Lees Ferry had $<50\%$ of the *C. glomerata* AFDM than that of control cobbles (80 g m^{-2} , ± 8 ; Figure 2A). *Oscillatoria* AFDM on translocated cobbles in the clear-water zone at Lees Ferry showed a steady decrease in AFDM, nearly disappearing by 9 mo (Figure 2B).

Cladophora glomerata AFDM decreased by 80% within 1 mo on translocated cobbles at Cathedral Island and remained near control levels at Cathedral Island thereafter (Figure 3A). Colonization by *Oscillatoria* on translocated cobbles at Cathedral Island was slow, but surpassed controls (2.4 g m^{-2} , ± 1.2) after 9 mo (Figure 3B).

Chironomid AFDM increased quickly on translocated cobbles at the clear-water Lees Ferry site to equal controls (0.087 g m^{-2} , ± 0.012) by 1 mo. In contrast, *G. lacustris* AFDM on translocated cobbles at this site was highly variable throughout the experiment and did not reach control levels (0.27 g m^{-2} , ± 0.23) until

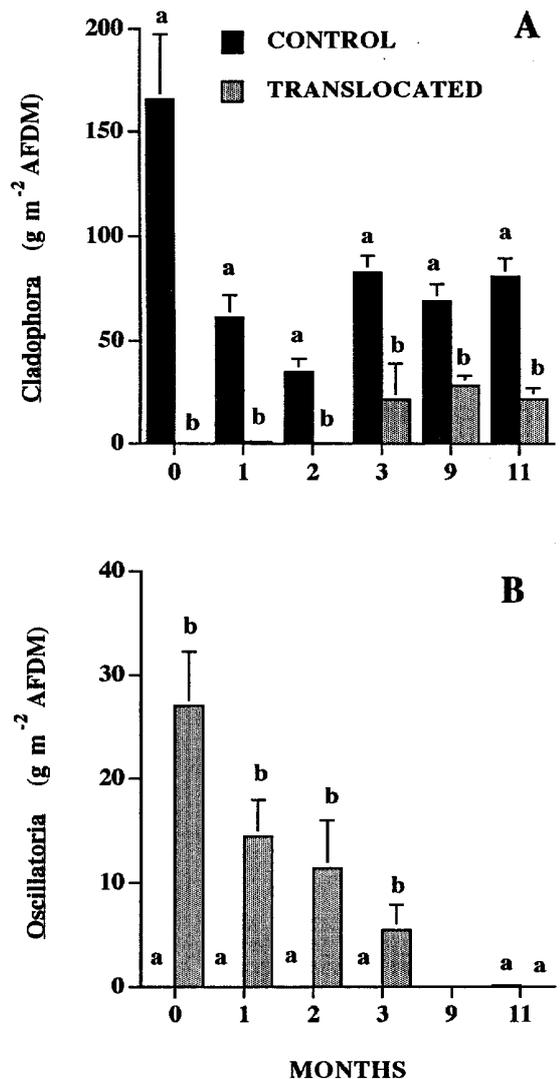


Figure 2. Accommodation as g m^{-2} AFDM of *Cladophora glomerata* (A) and *Oscillatoria* (B) on cobbles translocated from a habitat with high suspended sediment at Cathedral Island to an upstream clear-water habitat at Lees Ferry in the Colorado River, Arizona. Bars with different letters are significantly different at $p < 0.01$ within a time interval.

9 mo. Other macroinvertebrate taxa on translocated cobbles made up $<1\%$ of the overall mass during the experiment.

Patterns in macroinvertebrate AFDM accommodation varied between chironomid and *G. lacustris* on translocated cobbles at the turbid Cathedral Island site. Chironomid AFDM gradually increased from 0.2 g m^{-2} (± 0.05) to 1.0 g m^{-2} (± 0.2) on translocated cobbles during the 9 mo experiment. Controls had

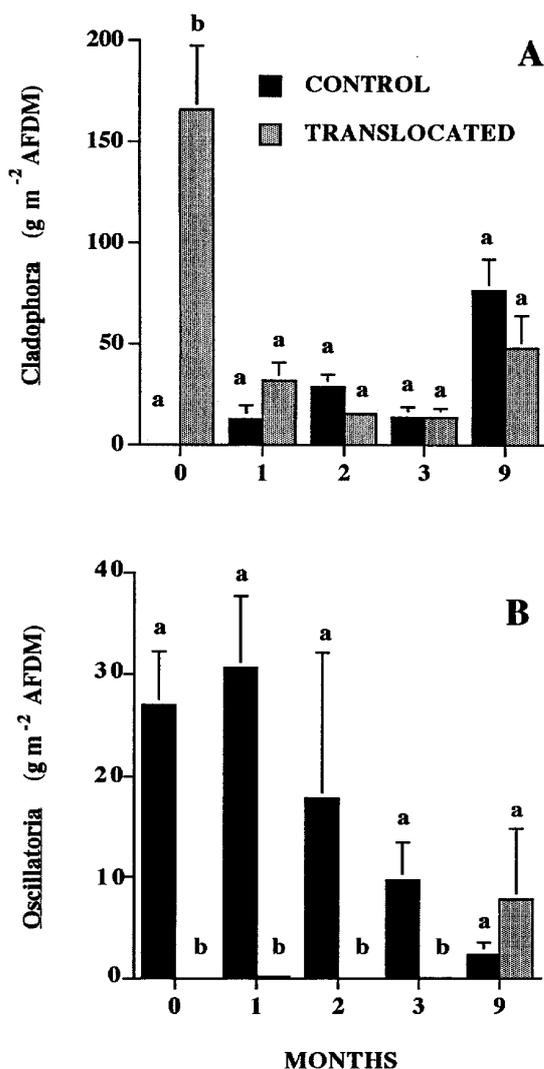


Figure 3. Accommodation as g m^{-2} AFDM of *Cladophora glomerata* (A) and *Oscillatoria* (B) on cobbles translocated from a clear-water habitat at Lees Ferry to a habitat with high suspended sediments at Cathedral Island in the Colorado River, Arizona. Bars with different letters are significantly different at $p < 0.01$ within a time interval.

1.6 g m^{-2} (± 0.49) AFDM of chironomid larvae at this time. In contrast, *G. lacustris* AFDM (1.2 g m^{-2} , ± 0.05) on translocated cobbles decreased by $>80\%$ after 1 mo (0.17 g m^{-2} , ± 0.005) and remained low over the next 9 mo, whereas *G. lacustris* associated with controls varied from <0.2 to 2.5 g m^{-2} (± 0.8) AFDM throughout the experiment.

Based on energy equivalents derived for the macroinvertebrate community in the Colorado River

(Blinn et al., 1995), we estimated that *C. glomerata*-covered translocated cobbles at the clear-water Lees Ferry site had $\sim 23\,000 \text{ joules m}^{-2}$ (j m^{-2}) of invertebrate mass compared to $<2000 \text{ j m}^{-2}$ of invertebrate mass in *Oscillatoria*-covered translocated cobbles at Cathedral Island.

Desiccation-recolonization experiments in varial and submerged zones

The composition of the phytobenthic community varied dramatically on desiccated cobbles placed in the continuously submerged and varial zones at the clear-water Lees Ferry site. At the start of the experiment, there were no living benthic algae or aquatic macroinvertebrates on the desiccated cobbles after 219 d above the varial zone. After 2 mo, the AFDM of *C. glomerata* was 13.2 g m^{-2} (± 0.1) on submerged translocated cobbles compared to 33.1 g m^{-2} (± 3.1) on control cobbles with no significant difference ($p = 0.111$) in AFDM of *C. glomerata* between control and treatment cobbles at 9 mo (Figure 4A). AFDM of *C. glomerata* was negligible ($<0.01 \text{ g m}^{-2}$) on translocated cobbles in the varial zone throughout the 11 mo experiment (Figure 4A). In contrast, *Oscillatoria* AFDM on treatment cobbles placed in the varial zone of the clear-water Lees Ferry site was 25.5 g m^{-2} after 5 mo with only negligible mass accruing on cobbles in control and submerged habitats (Figure 4B).

Desiccated cobbles placed below the permanently wetted channel at the turbid Cathedral Island site were slowly colonized by *Oscillatoria* and *C. glomerata* with no significant differences ($p = 0.283$) between controls and translocated cobbles after 5 mo for *Oscillatoria* and 11 mo for *C. glomerata* ($p = 0.162$, Figures 5A & 5B). Again, *Oscillatoria* was the dominant recolonizing alga on periodically exposed cobbles in the varial zone at Cathedral Island (Figure 5B). *Oscillatoria* colonization in the varial zone exceeded that on translocated submerged (0.92 g m^{-2} , ± 0.45) and control cobbles after 9 mo (Figure 5B).

Macroinvertebrate communities recolonized more quickly in the submerged clear-water habitat at Lees Ferry than did benthic algae. Chironomid mass (0.34 g m^{-2} , ± 0.27) on desiccated treatment cobbles was not significantly different ($p = 0.853$) from control cobbles (0.14 g m^{-2} , ± 0.04) at 5 mo. *Gammarus lacustris* AFDM was highly variable but achieved levels equal to or higher than controls in the submerged zone (0.19 g m^{-2} , ± 0.09) after only 2 mo. *Gammarus lacustris* AFDM remained negligible in the var-

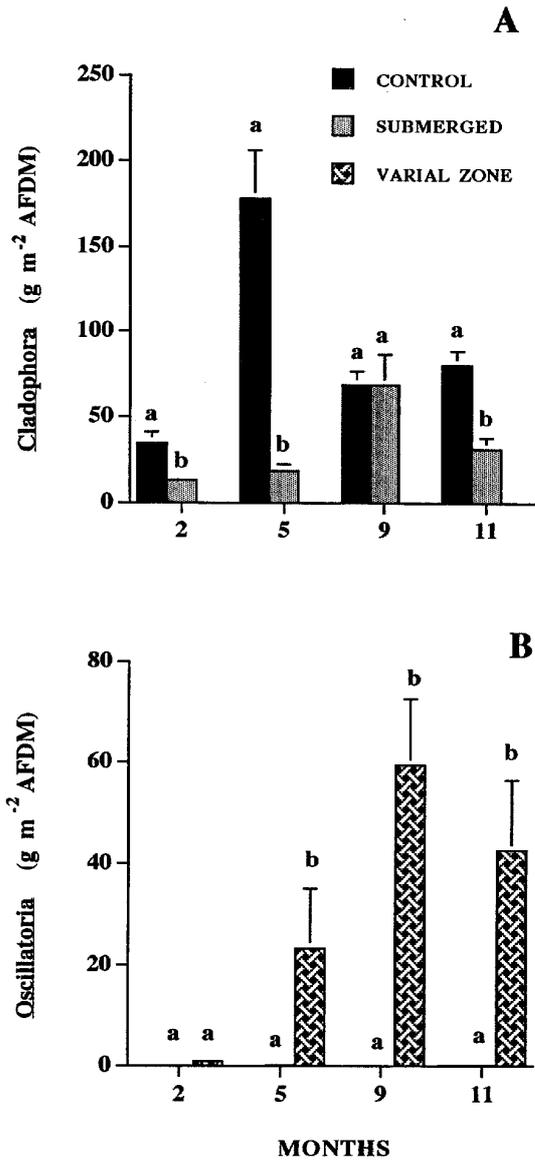


Figure 4. Recolonization as g m^{-2} AFDM of *Cladophora glomerata* (A) and *Oscillatoria* (B) on desiccated cobbles placed in continuously submerged ($\leq 140 \text{ m}^3 \text{ s}^{-1}$) and varial zone ($340 \text{ m}^3 \text{ s}^{-1}$) of the Colorado River at Lees Ferry, Arizona. Cobbles were desiccated for 219 d. Bars with different letters are significantly different at $p < 0.01$ within a time interval.

ial zone throughout the experiment, whereas chironomid AFDM appeared on treatment cobbles in the varial zone and exceeded the AFDM on submerged cobbles at 11 mo (0.49 g m^{-2} , ± 0.14). The increase in chironomid AFDM coincided with the temporary inundations

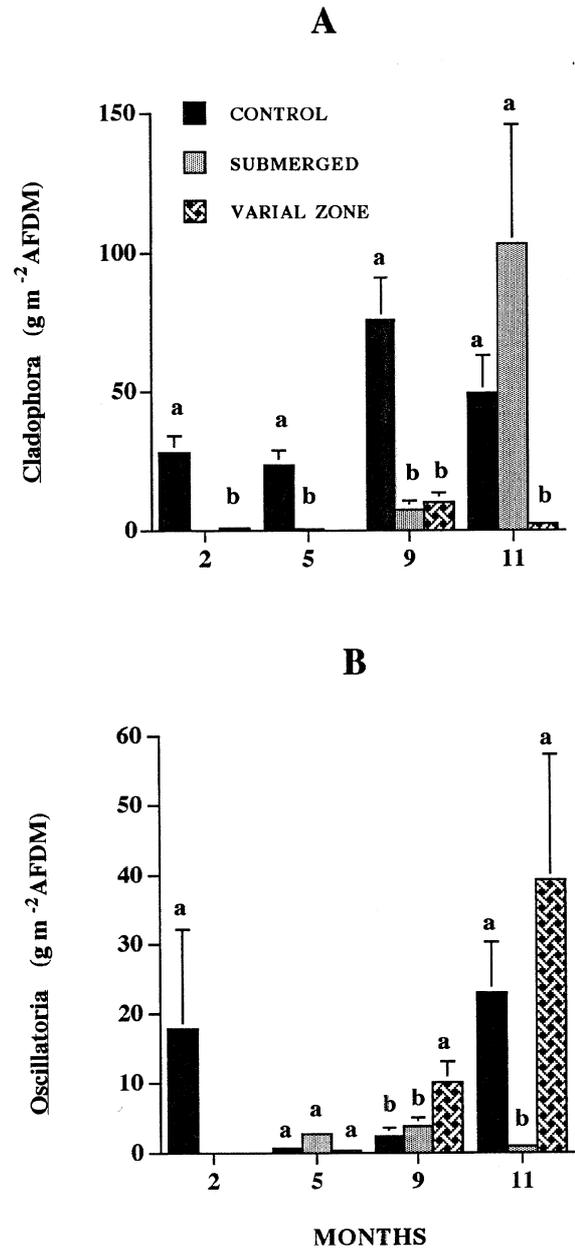


Figure 5. Recolonization as g m^{-2} AFDM of *Cladophora glomerata* (A) and *Oscillatoria* (B) on desiccated cobbles placed in continuously submerged ($\leq 140 \text{ m}^3 \text{ s}^{-1}$) and varial zones ($340 \text{ m}^3 \text{ s}^{-1}$) of the Colorado River at Cathedral Island, Arizona. Cobbles were desiccated for 219 d. Bars with different letters are significantly different at $p < 0.01$ within a time interval.

of cobbles in the varial zone during the high winter flows ($> 340 \text{ m}^3 \text{ s}^{-1}$).

Recruitment by macroinvertebrates was considerably slower and more variable at the turbid Cathedral Island site compared to Lees Ferry. Chironomid larvae first appeared on translocated cobbles in the submerged zone at low levels ($<0.001 \text{ g m}^{-2}$ AFDM) after 2 mo and increased slowly to 0.1 g m^{-2} AFDM (± 0.1) after 11 mo. *Gammarus lacustris* did not appear, or only at negligible levels ($<0.01 \text{ g m}^{-2}$ AFDM) on submerged cobbles until 11 mo ($<0.15 \text{ g m}^{-2}$ AFDM). Neither chironomid nor *G. lacustris* recruitment ($<0.001 \text{ g m}^{-2}$) developed to any extent in the varial zone at Cathedral Island.

Based on energy equivalents derived for the macroinvertebrate community in the Colorado River (Blinn et al., 1995), we estimated that invertebrate mass on translocated cobbles in the varial zone at Lees Ferry had $\sim 10\,700 \text{ j m}^{-2}$ compared to $\sim 19\,170 \text{ j m}^{-2}$ for submerged treatments after 11 mo incubation, whereas the varial zone at Cathedral Island had negligible energy as invertebrate mass in the varial zone and $\sim 2100 \text{ j m}^{-2}$ on submerged cobble treatments. All of the energy in the varial zone at Lees Ferry was in chironomid mass and probably did not persist after dewatering. Control cobbles at Lees Ferry and Cathedral Island had $\sim 49\,000$ and $\sim 23\,000 \text{ j m}^{-2}$, respectively.

Discussion

Our translocation experiments demonstrated that disturbances from suspended sediment loads and diel exposures to the atmosphere greatly modify the community structure of benthic communities in the tail-water zone and have the potential to exert a major bottom-up influence on the trophic ecology in the Colorado River ecosystem. We demonstrated that the filamentous green alga, *Cladophora glomerata* and cyanobacteria, *Oscillatoria* spp. respond differently to regulated flows of Glen Canyon Dam and suspended sediment input from tributaries. *Cladophora glomerata* thrived in the continuously submerged, clear-water habitats with stable cobbles, whereas *Oscillatoria* formed extensive mat-like matrices of filaments and sand and was highly successful in habitats with elevated suspended sediment and unstable varial zones.

Oscillatoria mats have been shown to survive desiccation and recover rapidly upon rehydration (Vincent & Howard-Williams, 1986; Round, 1981; Hawes, 1993), whereas *C. glomerata* loses significant amounts of chlorophyll *a* and mass after ≤ 6 h of atmospheric exposure in field and laboratory experiments (Usher

& Blinn, 1990; Angradi & Kubly, 1993; Blinn et al., 1995). *Oscillatoria* appeared in the varial zone of the regulated Colorado River after 2 mo in the clear-water Lees Ferry site and reached over 60 g m^{-2} AFDM in this zone by 9 mo. *Oscillatoria* colonization was 2–3 fold slower in the varial zone at the turbid Cathedral Island site than at Lees Ferry perhaps due to abrasion and rapid light extinction from suspended sediment. *Cladophora glomerata* mass was negligible in the varial zone at both Lees Ferry and Cathedral Island.

Our study also suggested that *C. glomerata* is more sensitive to suspended sediment than *Oscillatoria*. Translocated cobbles exhibited a $>80\%$ reduction in *C. glomerata* AFDM at the turbid Cathedral Island site and a substantial increase in *Oscillatoria*. In contrast, cobbles translocated from the turbid Cathedral Island site to the clear-water Lees Ferry site, 4 km upstream, showed a gradual decrease in *Oscillatoria* and the eventual dominance of *C. glomerata*. These changes likely resulted from differences in suspended sediment since there was no significant difference in water temperature (9°C , ± 0.35) and typically no significant differences in either total nitrogen (0.19 mg l^{-1} , ± 0.03 , $p=0.322$) or total phosphorus (0.02 mg l^{-1} , ± 0.002 , $p=0.274$) between the sites (Benenati, unpublished data).

Suspended sediment modifies the quantity and quality of light available to phytoplankton and increases the abrasive action on algal cells (Blinn et al., 1976; Roemer & Hoaglund 1979; Newcombe & MacDonald, 1991). Elevated suspended sediments selectively remove wavelengths which suggest the biliprotein pigment system of *Oscillatoria* is more efficient at using the altered light energy in turbid waters than the pigment system of *C. glomerata*. Also, suspended sediments are likely more abrasive to the exposed filamentous streamers of *C. glomerata* than to the compact mucilaginous matrices of *Oscillatoria* (Power et al., 1988; Newcombe & Mac Donald, 1991; Dodds & Gudder, 1992).

Our findings corroborate previous reports that *C. glomerata* is better suited to grow on sediment-free, stable substrata (Dodds & Gudder, 1992), while cyanobacteria are frequently associated with unstable sediment substrata (Prescott, 1978; Round, 1981; Sze, 1993). During cycles of regulated flow, *Oscillatoria* filaments undergo vertical migration to the sediment surface and down into the sediments (≤ 0.5 cm) during submerged and exposed periods, respectively (J. Shannon, unpublished observations). A similar migration rhythm has been documented for the

diatom *Hantzschia virgata* in mud flats during tidal cycles by Palmer & Round (1967). Furthermore, the mucilage produced by *Oscillatoria* trichomes forms mat-like assemblages which retains water when exposed, whereas, the mucilage-free and high surface area of the branched filaments of *C. glomerata* are more susceptible to desiccation (Usher & Blinn, 1990; Angradi & Kubly, 1993; Blinn et al., 1995).

The above habitat preferences for *C. glomerata* and *Oscillatoria* spp. corroborate the distributional pattern of these two primary producers throughout the Colorado River in Grand Canyon National Park (Shannon et al., 1994; Stevens et al., 1997). The AFDM of *C. glomerata* is typically an order of magnitude higher in the clear-water reach at Lees Ferry than below the confluence of the Paria River where suspended sediment is significantly higher (Andrews, 1991; Blinn et al., 1992; Stevens et al., 1997). The dramatic reduction in *C. glomerata* mass correlates closely to the seasonally high levels of suspended sediment that enter the Colorado River from the Paria River, as well as the Little Colorado River downstream (Figure 1). Davies-Colley and coworkers (1992) have also reported a 15 to 57% loss in algal mass in several New Zealand streams following increased turbidity.

Although *C. glomerata* and *Oscillatoria* eventually replaced one another on submerged cobbles in reciprocal habitats, recruitment was slow. Both developed extensive prostrate filaments on substrata which suggests some level of competition for attachment space between the filamentous matrix of *Oscillatoria* and the rhizoidal holdfast system of *C. glomerata*. Each prostrate system may physically restrict attachment by the other and therefore prolong recolonization, even in more optimum physico-chemical environments. Also, the constantly cold (9°C , ± 0.35) water in the stream channel may limit zoospore production by *C. glomerata* (Bellis & McLarty, 1967), and therefore restrict colonization to random entrapment of drifting filamentous tufts and/or development of adnate filaments. No zoospores were observed in cells of *C. glomerata* collected at monthly intervals throughout the experimental period (Shaver, 1995). Other filamentous green algae have been shown to achieve maximum standing mass in lotic habitats within 2 mo (Blum, 1982; Peterson & Stevenson, 1992), however, the condition of the substratum was not given.

The effects of suspended sediment from tributaries and regular exposure to the atmosphere during regulated discharges showed a dramatic bottom-up influence. Recent studies have indicated that *C. glomerata*

supports significantly higher epiphytic diatom communities than *Oscillatoria* assemblages (Shannon et al., 1994; Blinn et al., 1995). The extensive surface area of the branched filaments of *C. glomerata* provides an excellent substratum for epiphytes and positively correlates with epiphyton AFDM (Hardwick et al., 1992; Shannon et al., 1994; Blinn et al., 1995). Epiphytic diatoms comprise the largest proportion of diet items in the guts of chironomid larvae and *Gammarus lacustris*, whereas *C. glomerata* and *Oscillatoria* are rare or absent in macroinvertebrate diets (Stevens et al., 1997). Therefore, in addition to direct physical abrasion and reduction in solar radiation caused by suspended sediments, the loss in *C. glomerata* habitat due to regulated flows and high suspended sediments further reduces epiphyton mass.

Cladophora glomerata supports nearly a ten-fold higher mass of invertebrate consumers than does the *Oscillatoria* assemblage in the Colorado River ecosystem. The more compact matrix of *Oscillatoria* restricts the movement of macroinvertebrates and therefore limits use of this habitat, whereas the loosely arranged *C. glomerata* provides easy habitat for movement within the filamentous tuft. The dramatic reduction in *G. lacustris* AFDM after one mo at Cathedral Island closely correlated with the loss *C. glomerata* AFDM. Also, macroinvertebrate densities have been shown to be greatly reduced due to catastrophic drift upon the addition of fine sediments (Rosenberg & Weins, 1978; Culp et al., 1986). *Gammarus* appears to be considerably more sensitive to elevated sediment than the chironomid assemblage in the Colorado River. These differences may suggest that *G. lacustris* is more closely linked to the epiphytic community on *C. glomerata*, whereas the chironomid assemblage is more opportunistic. Also, the larger sized *G. lacustris* may be more vulnerable to the abrasive force of suspended sediment, while many taxa of chironomid larvae are closely associated with fine sediments and periphyton. Recent studies have demonstrated the close trophic linkage between *G. lacustris* and diatom epiphytes (Shannon et al., 1994). The high variability and general trend of increase in macroinvertebrate AFDM on the control cobbles at the turbid site followed the seasonally low input of suspended sediments by the Paria River and increased development of *C. glomerata*.

Recolonization by macroinvertebrates at the clear-water habitat at Lees Ferry occurred almost immediately with equal or greater AFDM than control cobbles within 2 mo in some instances. The rapid recolonization of treatment cobbles at Lees Ferry may have result-

ed from the close proximity of a relatively large pool of macroinvertebrates and their ability to disperse to new substrata by drift (Blinn et al., 1995). Other investigators have reported similar recruitment models in other lotic ecosystems (Hynes, 1970; Mackay, 1992).

This study demonstrates that differences in habitat requirements by *C. glomerata* and *Oscillatoria* have a profound bottom-up influence on the foodweb in the Colorado River through Grand Canyon National Park. We estimated the energy derived from macroinvertebrates associated with *C. glomerata* to be nearly an order of magnitude higher than energy derived from macroinvertebrates in *Oscillatoria* assemblages. Therefore, loss of *C. glomerata* habitat and the replacement by habitat more suitable for *Oscillatoria* may reduce the overall food value of the phyto-benthic community by several fold. The stair-step reductions in biomass at all trophic levels throughout the river corridor of Grand Canyon support these predictions (Angradi & Kubly, 1993; Shannon et al., 1994; Blinn et al., 1995; Valdez & Ryel, 1995; Stevens et al., 1997). Also, the slow colonization by *C. glomerata* on substrata occupied by *Oscillatoria* may have major implications on the role of regulated flows on the food base in the Colorado River ecosystem.

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