THE ROLE OF TURBIDITY AND DESICCATION IN STRUCTURING BENTHIC COMMUNITIES IN THE COLORADO RIVER, ARIZONA

by Michael L. Shaver

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Approved:

Dean W. Blinn, Ph.D., Chair

Lawrence E. Stevens, Ph.D.

Stephen T. Jackson, Ph.D.

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ABSTRACT

TURBIDITY AND DESICCATION STRUCTURING OF BENTHIC COMMUNITIES IN THE TAILWATERS OF GLEN CANYON DAM, ARIZONA

MICHAEL L. SHAVER

I tested the effects of water transparency and desiccation on the colonization of Cladophora glomerata and Oscillatoria spp. and consequent effects on invertebrates within each algal community in the regulated Colorado River. One hundred C. glomerata colonized cobbles from the clear-water habitat at Lees Ferry were placed in seasonally turbid habitats at Cathedral Island. Reciprocally, one hundred Oscillatoria colonized cobbles from the turbid habitat at Cathedral Island were translocated to the clear-water habitat at Lees Ferry. One hundred desiccated cobbles were also placed in the permanently wetted and varial zones at both the Lees Ferry clear-water site and the turbid site of Cathedral Island.

The turbidity and desiccation experiments revealed distinctly different ecological requirements for C. glomerata and Oscillatoria. C. glomerata, a highly branched filamentous green alga, competes well in the continuously submerged, clear-water habitats of the Colorado River ecosystem (165 g m^{-2}, SE $\pm$ 31). The cyanobacterium, Oscillatoria, forms mat-like matrices of filaments and sand that may allow it to succeed in the harsh environments of elevated suspended sediment and in sections of the channel that undergo diel drying and wetting (59 g m^{-2}, SE $\pm$ 13).

Chironomid recruitment appeared to be less dependent on C. glomerata than recruitment by Gammarus lacustris, and chironomid larvae were less effected by seasonal turbidity at Cathedral Island than G. lacustris. Macroinvertebrates were negligible in varial zone habitats undergoing desiccation. I estimate the energy incorporated in macroinvertebrates associated with C. glomerata communities to be an order of magnitude higher than energy (1 g AFDM $\approx$ 1800 j) derived from macroinvertebrates in Oscillatoria communities (1 g AFDM $\approx$ 270 j). Therefore, loss of C. glomerata habitat and replacement by habitat more suitable for Oscillatoria reduces the energy made available by the phytobenthic community to higher trophic levels.

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The financial support for this study and technical assistance was provided by Glen Canyon Environmental Studies Program (GCES) as part of a National Park Service Cooperative Agreement. This work is dedicated to the memory of all canyons to be seen nevermore.

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CHAPTER 1

INTRODUCTION

River ecosystems in the southwestern USA undergo extended periods of turbidity due to the seasonal input of suspended sediments from surrounding xeric watersheds (Blinn & Cole, 1991). Sediment loads limit photosynthetically available radiation (PAR) for benthic algae, which results in lower benthic algal biomass (Davies-Colley et al., 1992). Reductions in light have been found to be associated with a significant decrease in all functional ecological properties of a stream (Steinman et al., 1990). Suspended sediments also increase scouring and impede respiration for macroinvertebrates, resulting in reduced biodiversity and abundance (Quinn, 1992). Futhermore, suspended sediment loads alter substrate size and degrade food quality available to benthic fauna (Culp et al., 1986; O'Conner & Lake, 1994).

Phytobenthos communities are periodically exposed to desiccation in regulated rivers (Lowe, 1979; Lillehammer & Saltveit, 1984; Ward

& Stanford, 1989; Usher & Blinn, 1990). Aquatic biota of freshwater systems typically are not adapted to the sub-seasonal stranding of a varial zone, in contrast to their marine intertidal counterparts. Protective coverings and high mucilage allow marine intertidal macroalgae to tolerate periodic desiccation (Sze, 1993). Intermittent lotic systems are exposed to seasonal desiccation similar to, however lower frequency than the varial zone in regulated rivers (Stanely, 1993). Both intermittent streams and regulated river varial zones have been shown to be devoid of aquatic fauna during drought (Jourdonnais & Hauer, 1993; Petts & Bickerton, 1994).

I studied the influence of turbidity and the recovery of the benthic community to desiccation in an arid lands regulated river, the Colorado River below Glen Canyon Dam (Fig. 1). Reciprocal translocation experiments with cobble and associated biota were conducted between Lees Ferry and Cathedral Island on the Colorado River (Fig. 1) to measure the rate of accommodation among Cladophora glomerata and Oscillatoria communities in high- and low-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

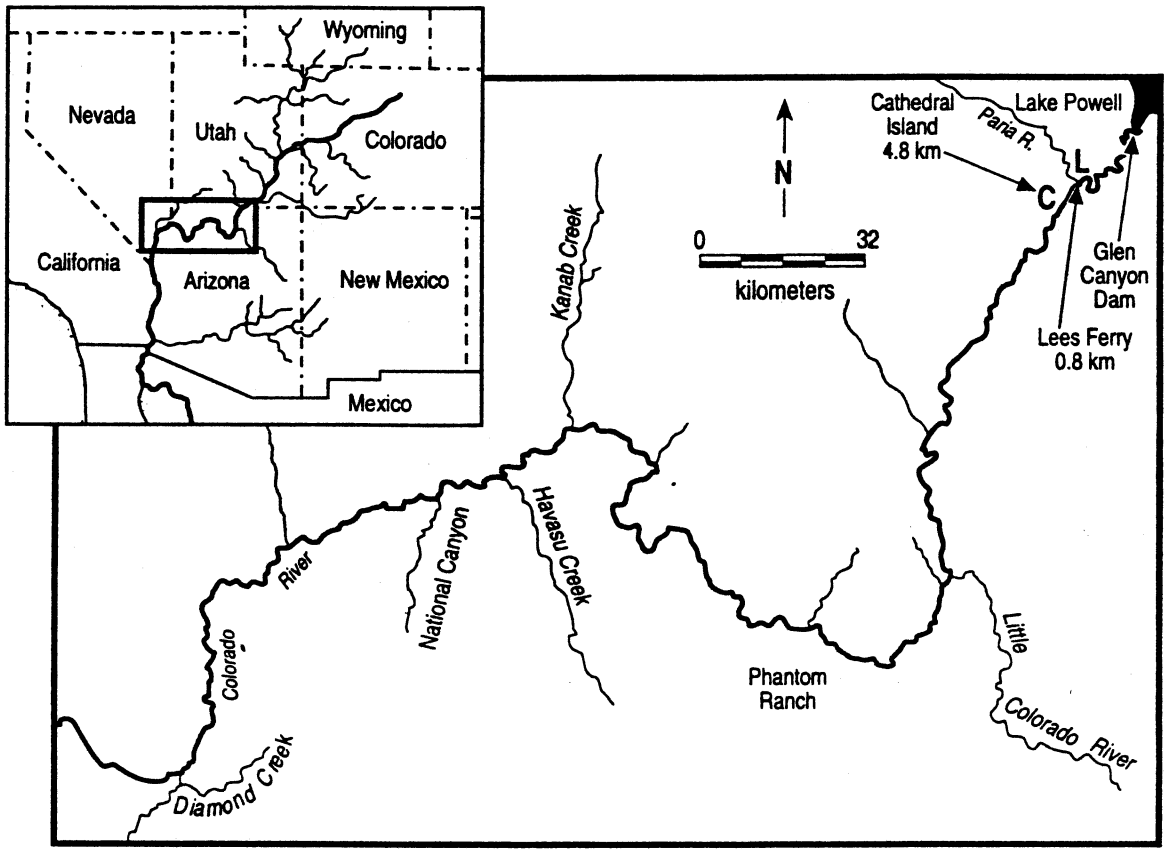

Figure 1. Study sites at Lees Ferry (0.8 km) and Cathedral Island (4.8 km) in the Colorado River.

recolonization of desiccated cobbles by benthic communities in continuously submerged and varial zones at Lees Ferry and Cathedral Island. "Recolonization" rate indicates the resilience, the ability of a community to recover from a disturbance such as desiccation (Yount & Niemi, 1990).

The conditions of the tailwaters of Glen Canyon Dam allowed the simultaneous testing of tributary sediment load and varial zone desiccation in a regulated river. 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 following Glen Canyon Dam (Fig. 1). Input of suspended sediments by the Paria River results in a contrasting turbid habitat at Cathedral Island in comparison to the clear-water habitat at the Lees Ferry in the tailwaters of Glen Canyon Dam. Glen Canyon Dam releases are fluctuated to provide peaking power during periods of high energy demand by Southwestern consumers. Discharge drops to a managed baseflow of 142 $m^3 s^{-1}$ to conserve water during periods of low power demand and ranges to as high as 566 $m^3 s^{-1}$ to provide peaking power. The habitat of the permanently wetted channel below the baseflow contrasts with the temporary induation and desiccation of the varial zones.

CHAPTER 2

METHODS

In-Situ Reciprocal-Translocation Turbidity Experiments

On May 17, 1993, 100 cobbles (20-50 cm diam) with associated biota were collected from the permanently wetted channel (<142 $m^3 s^{-1}$ stage) in the clear-water reach of Lees Ferry (River Kilometer, RKM 0.8) and transplanted into a seasonally turbid reach at Cathedral Island (RKM 4.8; Table 1). Cobbles were placed in a 10 x 10 grid beneath the varial zone (<142 $m^3 s^{-1}$ stage). Likewise, 100 cobbles with associated biota from Cathedral Island were translocated upstream to the clear-water reach at Lees Ferry.

At the start of the experiment, 20 control submerged cobbles were sampled by scraping a circular 20 cm^2 quadrat of algae and macroinvertebrates at Lees Ferry and Cathedral Island. Also, one quadrat sample was collected from each of 20 randomly selected cobbles in each grid at approximate monthly intervals for three mo, and at 9

Table 1. Experimental question, design and analysis for both the testing of turbidity and desiccation.

Reciprocal-Translocation Turbidity Experiment

QUESTION:

How will continuous water clarity or seasonal turbidity structure a stream benthic community?

DESIGN:

Benthic cobbles were reciprocally translocated from the turbid site (Cathedral Island, 4.8 RKM) and the clear-water site (Lees Ferry, 0.8 RKM).
Monthly Intervals: 1, 2, 3, 9 and 11 N = 20

ANALYSIS:

Lilliefors test for normality, the Kruskal-Wallis one way analysis of variance, and the sequential Bonferroni technique.

Desiccation-Recolonization Experiment

QUESTION:

How will benthic community structure in the submerged and varial zones recover from desiccation?

DESIGN:

Extensively desiccated benthic cobbles with negligible biota were placed in the submerged and varial zones.
Monthly Intervals: 2, 5, 9 and 11 N = 20

ANALYSIS:

Lilliefors test for normality, the Kruskal-Wallis one way analysis of variance, and the sequential Bonferroni technique.

and 11 mo. After each sampling, rocks 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. At each sampling date, 20 additional control cobbles were collected from below the 142 $m^3 s^{-1}$ stage in the channel at both sites for comparison with the translocated cobbles. Macroinvertebrates (chironomids, gastropods, lumbricids, tubificids, simuliids, and Gammarus lacustris) were sorted from each algal sample (Cladophora glomerata and Oscillatoria) and oven-dried at 60°C for 48 h to a constant mass (Greenberg et al., 1992). Established ash-free dry mass (AFDM) conversions were utilized in determining AFDM from dry weights obtained in the experiment (Blinn et al., 1994).

The algal mass was placed in a bag with 40 ml of filtered river water and agitated for 1 min. The composite was poured through a 0.5 mm screen to separate macroalgae from epiphyton. The macroalgae on the screen were rinsed with filtered river water to remove additional epiphyton from samples. This protocol removed at least 80% of the epiphyton from the macroalgae. Macroalgae were removed from the screen, sorted to genus, and oven-dried at 60°C for 48 h to a constant mass. The epiphyton solution was swirled for 3-4 s in a beaker and

filtered onto Whatman GF/C glass microfiber filters (0.45μm). Filters were oven-dried at 60°C to a constant mass. Filters were then ashed at 500°C for 1 h in crucibles and ash-free dry mass (AFDM) for epiphyton on filters were determined (Greenberg et al., 1992). Filters were saved for compositional analyses of diatom epiphyton.

In-Situ Desiccation-Recolonization Experiments

On October 10, 1992, 440 cobbles were collected from the submerged channel (<142 $m^3 s^{-1}$ stage) at Lees Ferry (Table 1). The bottoms of the cobbles were numbered with paint and placed above the high water mark (565 $m^3 s^{-1}$ stage) to allow desiccation of associated biota. Twenty additional control cobbles from the channel were sampled at Lees Ferry. On May 17, 1993 (219 d of desiccation), samples were collected with a circular 20 cm^2 quadrat from 20 desiccated cobbles prior to placement in the channel. At both sites, 100 cobbles were submerged in the channel at the <140 $m^3 s^{-1}$ stage to ensure continuous submergence. An additional 100 cobbles were placed in the varial zone (140 to 565 $m^3 s^{-1}$ stage) at 340 $m^3 s^{-1}$ at Lees Ferry and Cathedral Island. A single sample (20 cm^2) was randomly collected from each of 20 randomly selected grid cobbles at 2, 5, 9 and 11 mo.

On each sampling date, 20 control cobbles were collected from below the 142 $m^3 s^{-1}$ stage in the channel at both sites for comparison with recolonizing desiccated cobbles. Algae (C. glomerata and Oscillatoria) and macroinvertebrates (chironomids, gastropods, lumbricids, tubificids, simuliids, and G. lacustris) were sorted from each sample, oven-dried at 60°C for 48 h to a constant mass (Greenberg et al. 1992), and converted to AFDM estimates.

Statistical Analysis

The assumption of normality required for parametric tests was not met in the Lilliefors testing of the data despite a log-transformation of data (Table 1; Wilkinson, 1989). The non-parametric Kruskal-Wallis one-way analysis of variance was used to determine the significance of treatments from controls at an alpha level of 0.05 (Grim & Fisher, 1986; Wilkinson, 1989; Shannon et al., 1994). To minimize the chance of falsely rejecting the null hypothesis (Type I error) and to ensure confidence in all statements of significance the sequential Bonferroni technique was performed (Rice, 1989). All statistical analyses were performed with the SYSTAT (1992) software package.

CHAPTER 3

RESULTS

In-Situ Reciprocal-Translocation Turbidity Experiment at Lees Ferry

At the start of the translocation experiment, cobbles from Lees Ferry dominated by Cladophora glomerata had a 6-fold higher algal AFDM (165 g m^{-2}, SE ± 31) than did Oscillatoria-covered cobbles (27 g m^{-2}, SE ± 5) collected at Cathedral Island (Fig. 2). Biodiversity is limited in the consistently 8°C water at the study sites (Vannote & Sweeny, 1980; Ward & Stanford, 1982); therefore, only the dominate macroinvertebrates (Gammarus lacustris and chironomids) will be reported (Blinn et al., 1994).

Oscillatoria cover was negligible on control cobbles at the clear-water site of Lees Ferry. Accommodation by C. glomerata was slow on the Oscillatoria-covered cobbles translocated from Cathedral Island to the clear-water site at Lees Ferry (Fig. 2A). As stated in the

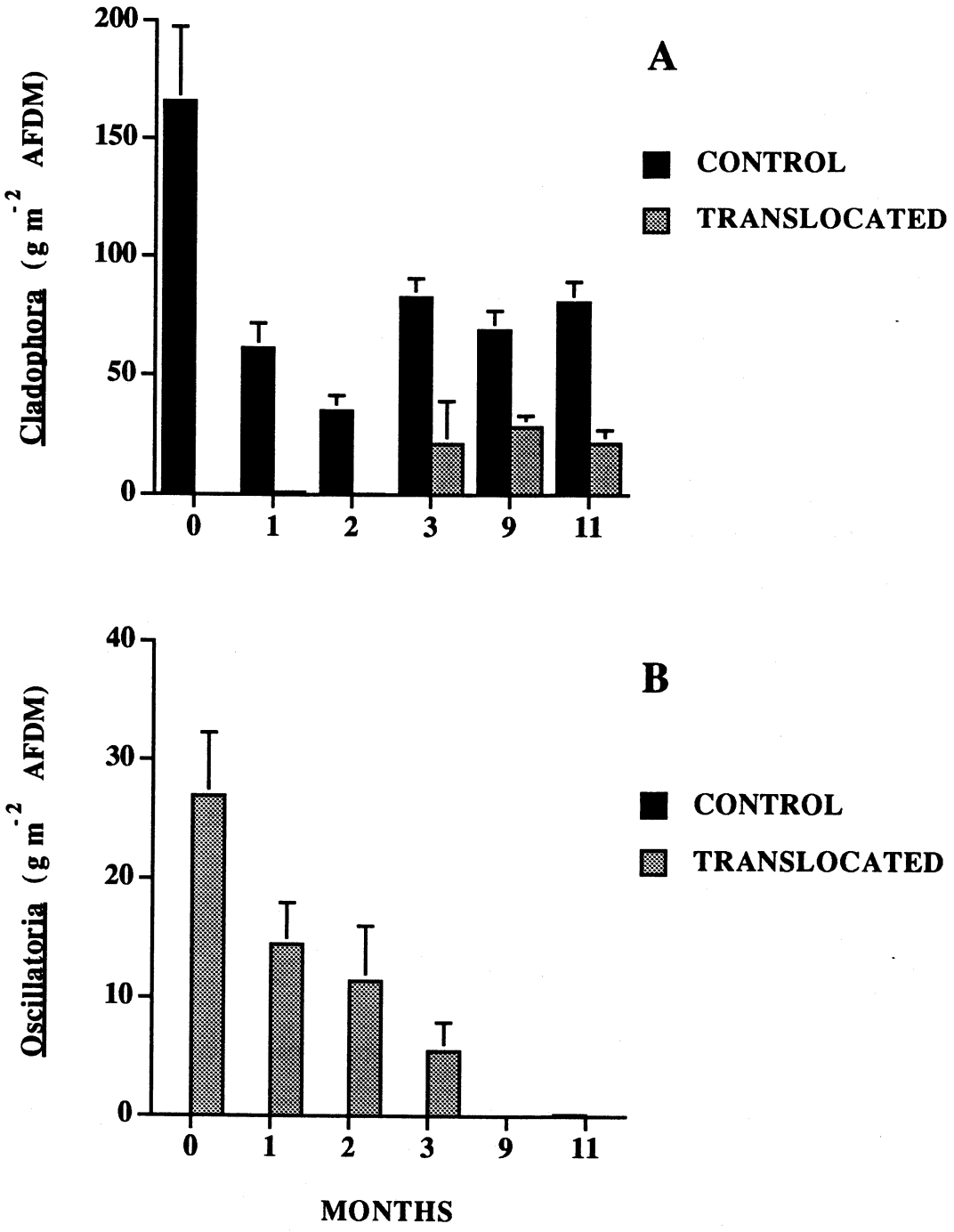

Figure 2. Accommodation as g m^{-2} AFDM for Cladophora glomerata (A) and Oscillatoria spp. (B) on the cobbles translocated from a turbid habitat at Cathedral Island (RKM 4.8) in the Colorado River to an upstream clear-water habitat at Lees Ferry, Arizona (RKM 0.8). Controls represent collections from resident submerged cobbles at Lees Ferry.

introduction, the term "accommodation" describes the adjustment of an established biotic community to a long-term incubation in an alternative environment (Yount & Niemi, 1990). Even after 11 mo, relocated cobbles at Lees Ferry had only one-third (21 g m^{-2}, SE ± 5) the C. glomerata AFDM as the control cobbles (80 g m^{-2}, SE ± 8; Fig. 2A). Oscillatoria AFDM on cobbles translocated to Lees Ferry decreased in AFDM by 20 to 50 % per mo, virtually disappearing within six mo (Fig. 2B). While translocated cobbles had significantly higher Oscillatoria AFDM than controls at the start of the experiment, both control and translocated treatment cobbles had negligible Oscillatoria AFDM after 11 mo in clear-water conditions at Lees Ferry (Table 2).

Epiphyton AFDM associated with C. glomerata remained 25 to 70% lower on translocated cobbles compared to controls throughout the study period at Lees Ferry (Fig. 3; Table 2). When reciprocally translocated Oscillatoria spp. covered cobbles had 9.7 g m^{-2} epiphyton AFDM (SE ± 1.1), C. glomerata covered controls were almost 100% higher with 17.1 g m^{-2} epiphyton AFDM (SE ± 2.3). After 11 mo of clear-water conditions, epiphyton AFDM on translocated cobbles (15.2 g m^{-2}, SE ± 1.7) remained significantly lower than that on control cobbles (35.6 g m^{-2}, SE ± 2.8; Table 2). The pattern of slow epiphyton

Table 2. Probabilities calculated by the Kruskal-Wallis analysis of translocated clear-water treatment cobbles at Lees Ferry. Significant differences in AFDM on treatment cobbles as determined by the sequential Bonferroni technique are indicated by an * following the p. Accommodation to the clear-water habitat has occurred when there is no significant difference.

Mo	Cladophora	Oscillatoria	Epiphyton	Gammarus	Chironomid
0	0.00000*	0.00000*	0.00000*	0.00003*	0.00027*
1	0.00000*	0.00000*	0.00000*	0.00038*	0.00000*
2	0.00000*	0.00000*	0.00006*	0.31731	0.00002*
3	0.00000*	0.00006*	0.00000*	0.09596	0.02810
9	0.00009*	0.55371	0.00490*	0.65324	0.79709
11	0.00000*	0.54057	0.00000*	0.02885	0.01275*

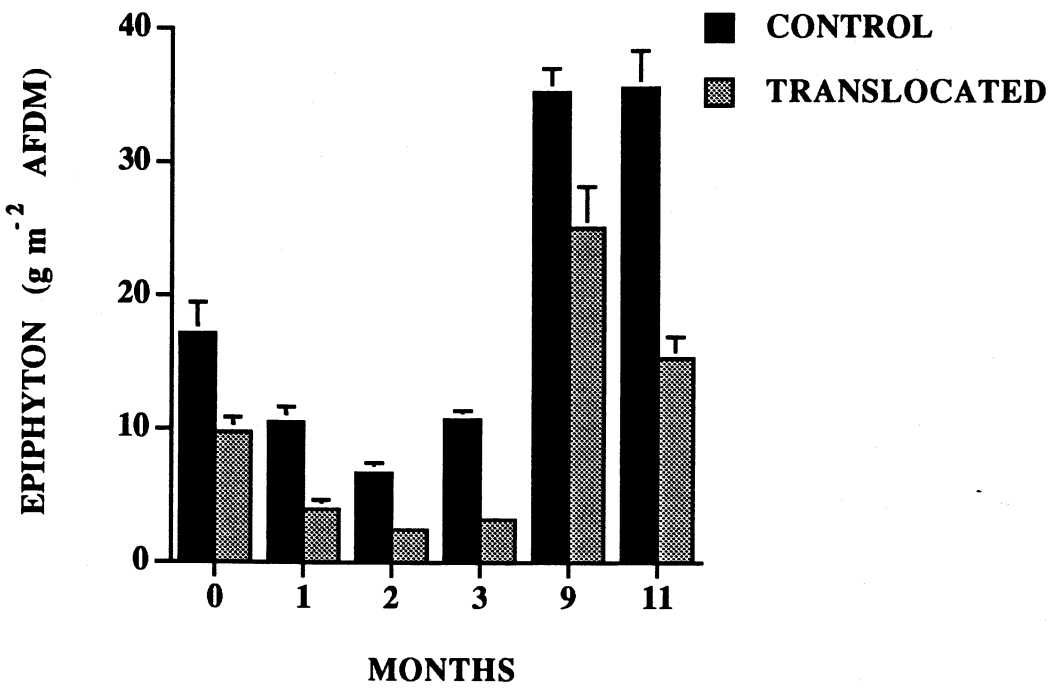

Figure 3. Accommodation as g m^{-2} AFDM for epiphyton on cobbles translocated from a turbid habitat at Cathedral Island (RKM 4.8) in the Colorado River to an upstream clear-water habitat at Lees Ferry, Arizona (RKM 0.8). Controls represent collections from resident submerged cobbles at Lees Ferry.

accommodation on relocated cobbles was similar to the pattern of C. glomerata and supports a positive correlation between epiphyton and C. glomerata AFDM.

Chironomid AFDM on accommodating cobbles increased quickly at Lees Ferry (0.058 g m^{-2}, SE ± 0.005) to comparable levels with controls (0.087 g m^{-2}, SE ± 0.012) after one mo (Fig. 4A; Table 2). G. lacustris AFDM on accommodating cobbles at the clear-water site (0.27 g m^{-2}, SE ± 0.23) did not reach control levels (0.005 g m^{-2}, SE ± 0.005) until nine mo (Fig. 4B; Table 2). Based on energy equivalents derived for the macroinvertebrate community in the Colorado River (Blinn et al., 1994), I estimate that at the start of the experiment the macroinvertebrate energy associated with C. glomerata-covered control cobbles at Lees Ferry yielded ~46,000 joules m^{-2} compared to only 2,500 joules m^{-2} in Oscillatoria benthic mats on control cobbles at Cathedral Island.

In-Situ Reciprocal-Translocation Turbidity Experiment at Cathedral Island

Benthic flora and fauna on cobbles translocated from the clear-water site of Lees Ferry to the turbid Cathedral Island site were rapidly

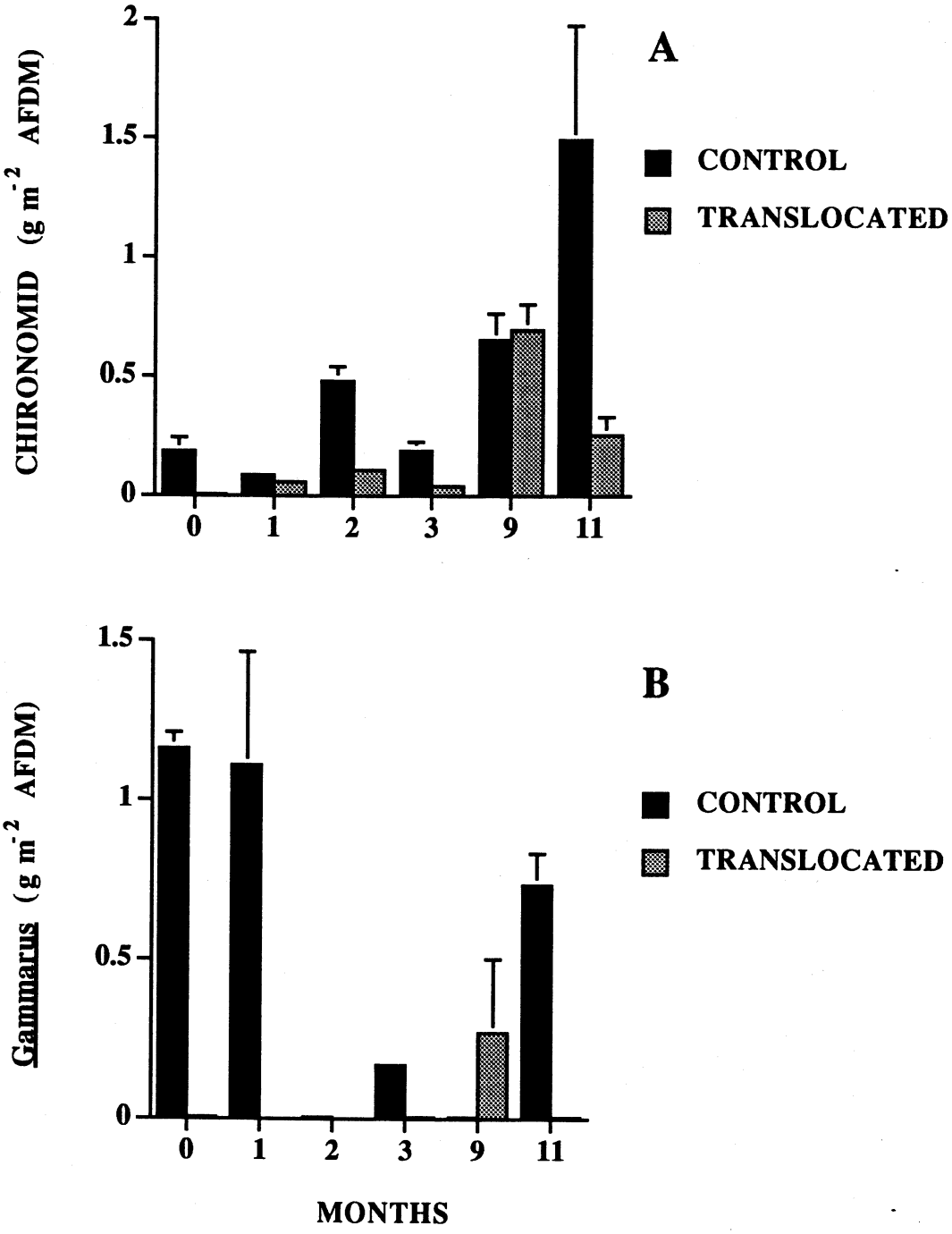

Figure 4. Accommodation as g m^{-2} AFDM for chironomid larvae (A) and Gammarus lacustris (B) on the cobbles translocated from a turbid habitat at Cathedral Island (RKM 4.8) in the Colorado River to an upstream clear-water habitat at Lees Ferry, Arizona (RKM 0.8). Controls represent collections from resident submerged cobbles at Lees Ferry.

reduced to comparable control levels. At the start of the translocation experiment, C. glomerata colonized cobbles from Lees Ferry had a 6-fold higher algal AFDM (165 g m^{-2}, SE ± 31) than did Oscillatoria-covered cobbles (27 g m^{-2}, SE ± 5) collected at Cathedral Island (Fig. 5). C. glomerata AFDM decreased by 80% on translocated cobbles within one mo and remained near control levels thereafter (Fig. 5A). By mo two, the Kruskal-Wallis test revealed no significant difference between controls and relocated cobbles (Table 3). The rapid loss of C. glomerata AFDM under high turbidity at Cathedral Island contrasted strongly with the slow increase in AFDM of C. glomerata on translocated cobbles under the clear-water conditions at Lees Ferry (Fig. 1A). Oscillatoria AFDM on translocated cobbles from the clear-water habitat at Lees Ferry was negligible compared to Cathedral Island (27.0 g m^{-2}, SE ± 5.3) at the start of the experiment (Table 3). Oscillatoria AFDM increased on translocated cobbles at Cathedral Island (7.8 g m^{-2}, SE ± 6.9) and surpassed control levels (2.4 g m^{-2}, SE ± 1.2) after nine mo under turbid water conditions (Fig. 5B).

Initial AFDM values for epiphyton were significantly lower at Cathedral Island compared to epiphyton AFDM from the clear-water habitat at Lees Ferry (Fig. 6; Table 3). After one mo under turbid

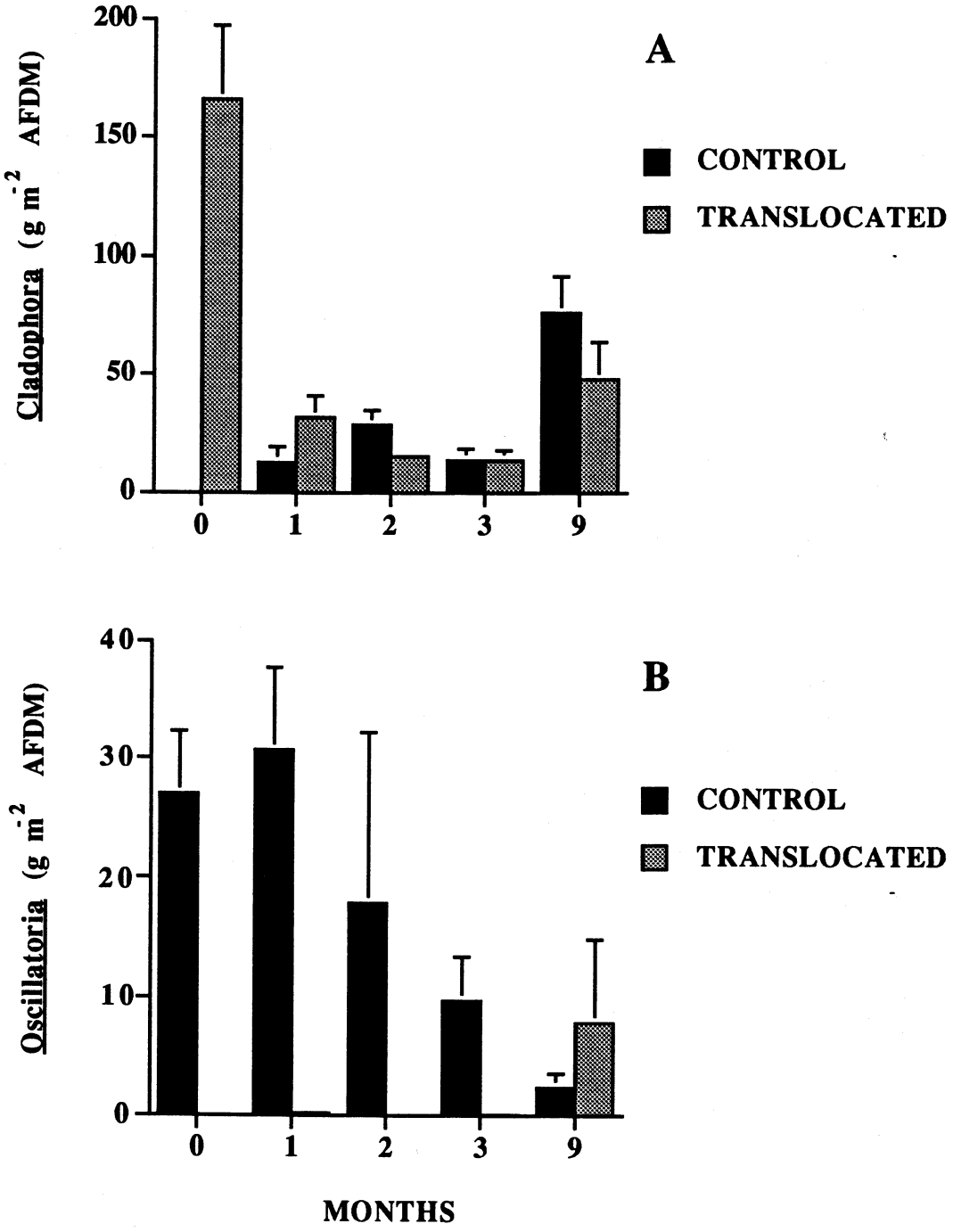

Figure 5. Accommodation as g m^{-2} AFDM for Cladophora glomerata (A) and Oscillatoria spp. (B) on the cobbles translocated from a clear-water habitat at Lees Ferry (RKM 0.8) in the Colorado River to a more turbid downstream habitat at Cathedral Island, Arizona (RKM 4.8). Controls represent collections from resident submerged cobbles at Cathedral Island.

Table 3. Probabilities calculated by the Kruskal-Wallis analysis of translocated turbid treatment cobbles at Cathedral Island. Significant differences in AFDM on treatment cobbles as determined by the sequential Bonferroni technique are indicated by an * following the p. Accommodation to the turbid habitat has occurred when there is no significant difference.

Mo	Cladophora	Oscillatoria	Epiphyton	Gammarus	Chironomid
0	0.00000*	0.00000*	0.00000*	0.00003*	0.00027*
1	0.00015*	0.00000*	0.92457	0.03726	0.00002*
2	0.11660	0.14449	0.00802*	0.51476	0.82864
3	0.20771	0.00157*	0.87107	0.97144	0.50590
9	0.01100	0.35331	0.53384	0.17541	0.64555

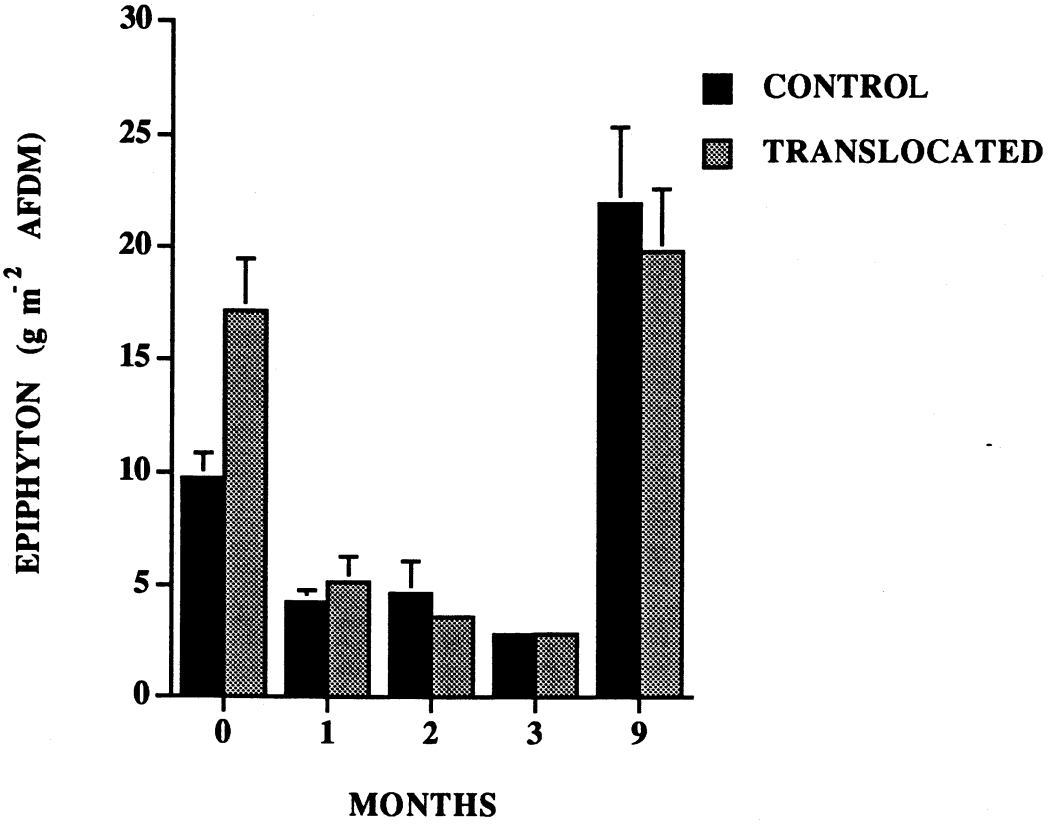

Figure 6. Accommodation as g m^{-2} AFDM for epiphyton on cobbles translocated from a clear-water habitat at Lees Ferry (RKM 0.8) in the Colorado River to a more turbid downstream habitat at Cathedral Island, Arizona (RKM 4.8). Controls represent collections from resident submerged cobbles at Cathedral Island.

conditions there was no significant difference in epiphyton AFDM between controls (4.3 g m^{-2}, SE ± 0.54) and relocated treatment cobbles (5.2 g m^{-2}, SE ± 1.2; Table 3).

Patterns in macroinvertebrate AFDM accommodation varied between chironomid and G. lacustris on translocated cobbles at Cathedral Island. Increased development of C. glomerata during periods of low precipitation and turbidity of the experiment was associated with increased macroinvertebrate mass on control cobbles at Cathedral Island. At the start of the experiment Secchi disc readings averaged 0.05 m, whereas in mo nine and eleven Secchi disc readings averaged 2.0 m. Chironomid AFDM increased on both control (1.6 g m^{-2}, SE ± 0.49) and translocated cobbles (1.0 g m^{-2}, SE ± 0.16) throughout the experiment (Fig. 7A). In contrast, G. lacustris AFDM (1.2 g m^{-2}, SE ± 0.05) decreased rapidly on translocated treatment cobbles by >80% reduction after one mo (0.17 g m^{-2}, SE ± 0.005) at the turbid Cathedral Island site (Fig. 7B; Table 3).

In-Situ Desiccation-Recolonization Experiment at Lees Ferry

Phytobenthic composition varied dramatically between the continuously submerged and varial zone recolonizing treatment cobbles

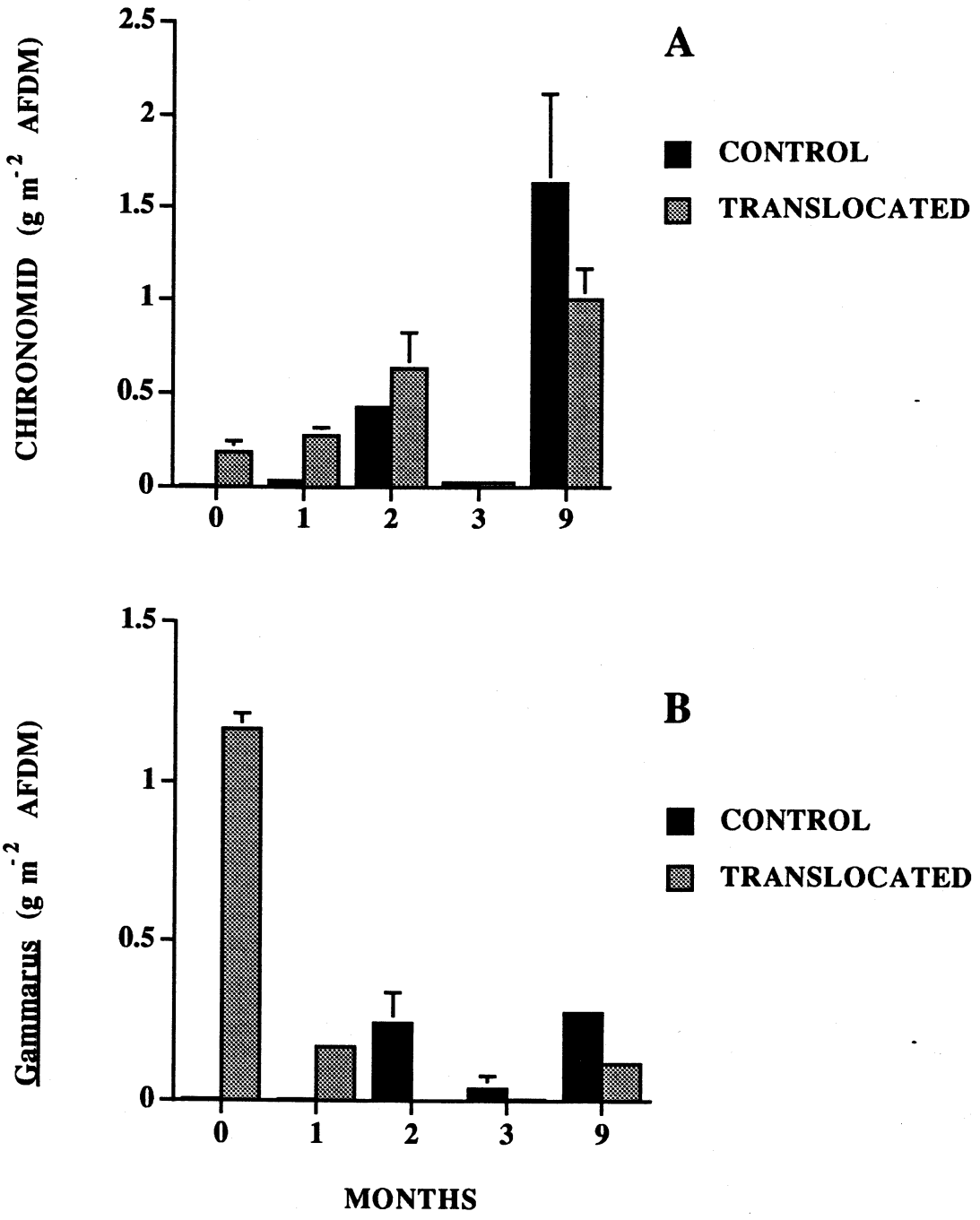

Figure 7. Accommodation as g m^{-2} AFDM for chironomid larvae (A) and Gammarus lacustris (B) on cobbles translocated from a clear-water habitat at Lees Ferry (RKM 0.8) in the Colorado River to a more turbid downstream habitat at Cathedral Island, Arizona (RKM 4.8). Controls represent collections from resident submerged cobbles at Cathedral Island.

at Lees Ferry. At the start of the experiment, biota was devoid with no living benthic algae or invertebrates occurring on cobbles desiccated for 219 d above the high water mark. After resubmergence, C. glomerata recolonized desiccated cobbles in the submerged zone, while Oscillatoria was the dominant recolonizing alga on desiccated cobbles in the varial zone (Fig. 8). C. glomerata AFDM was negligible in the varial zone at Lees Ferry through out the 11 mo experiment (Fig. 8A). C. glomerata recolonized submerged cobbles and by mo nine there was no significant difference between C. glomerata AFDM on submerged (68.8 g m^{-2}, SE $\pm$ 17.9) and control (68.7 g m^{-2}, SE $\pm$ 8.1) cobbles at Lees Ferry (Fig. 8A; Table 4). In contrast, Oscillatoria AFDM remained negligible on both control and submerged treatment cobbles at Lees Ferry through out the experiment. Oscillatoria AFDM reached the C. glomerata averages of greater than 50 g m^{-2} AFDM by mo nine in the varial zone (59.4 g m^{-2}, SE $\pm$ 13.2; Fig. 8B; Table 4).

Macroinvertebrate communities recolonized more quickly in the continuously submerged zone at Lees Ferry than did benthic algae. Chironomid mass on submerged desiccated cobbles (0.34 g m^{-2}, SE $\pm$0.27) was not significantly different from chironomid AFDM on controls (0.14 g m^{-2}, SE $\pm$ 0.04) at mo five (Fig. 9A; Table 4).

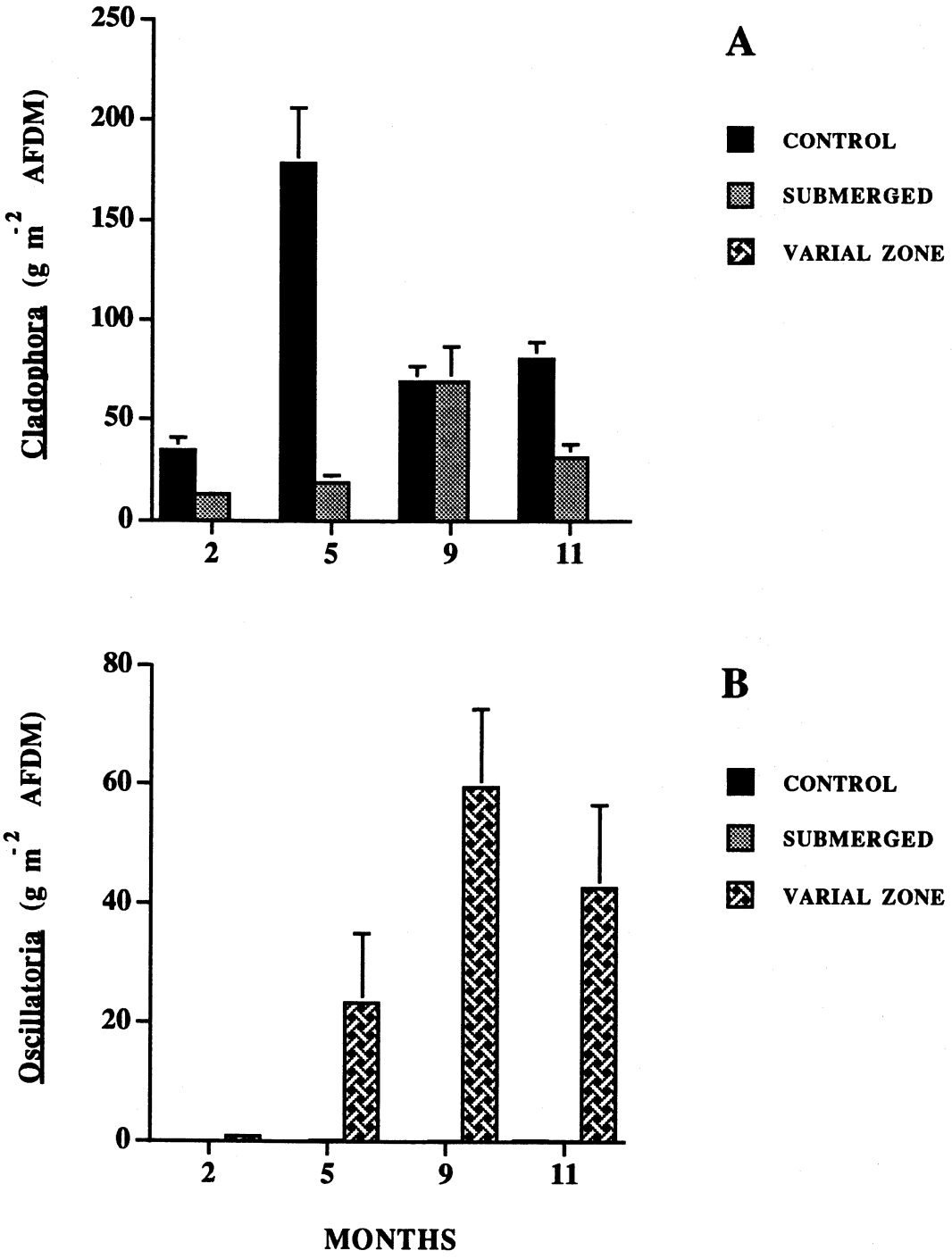

Figure 8. Recolonization as g m^{-2} AFDM for Cladophora glomerata (A) and Oscillatoria spp. (B) on desiccated cobbles placed in continuously submerged ($\leq$140 m^3 s^{-1}) and varial zones (140 to 283 m^3 s^{-1}) of the Colorado River at Lees Ferry, Arizona (RKM 0.8). Cobbles were desiccated for 219 days.

Table 4. Probabilities calculated by the Kruskal-Wallis analysis of resubmerged treatment cobbles at Lees Ferry. Significant differences in AFDM on treatment cobbles as determined by the sequential Bonferroni technique are indicated by an * following the p. Recolonization on submerged treatment cobbles has occurred when there is no significant difference.

Mo	Cladophora	Oscillatoria	Gammarus	Chironomid
0	0.00000*	0.00000*	0.00000*	0.00000*
2	0.00629*	0.97144	0.03369	0.02740
5	0.00000*	0.07563	0.31879	0.85369
9	0.11050	0.15208	0.43323	0.00007*
11	0.00000*	0.33650	0.09101	0.00032*

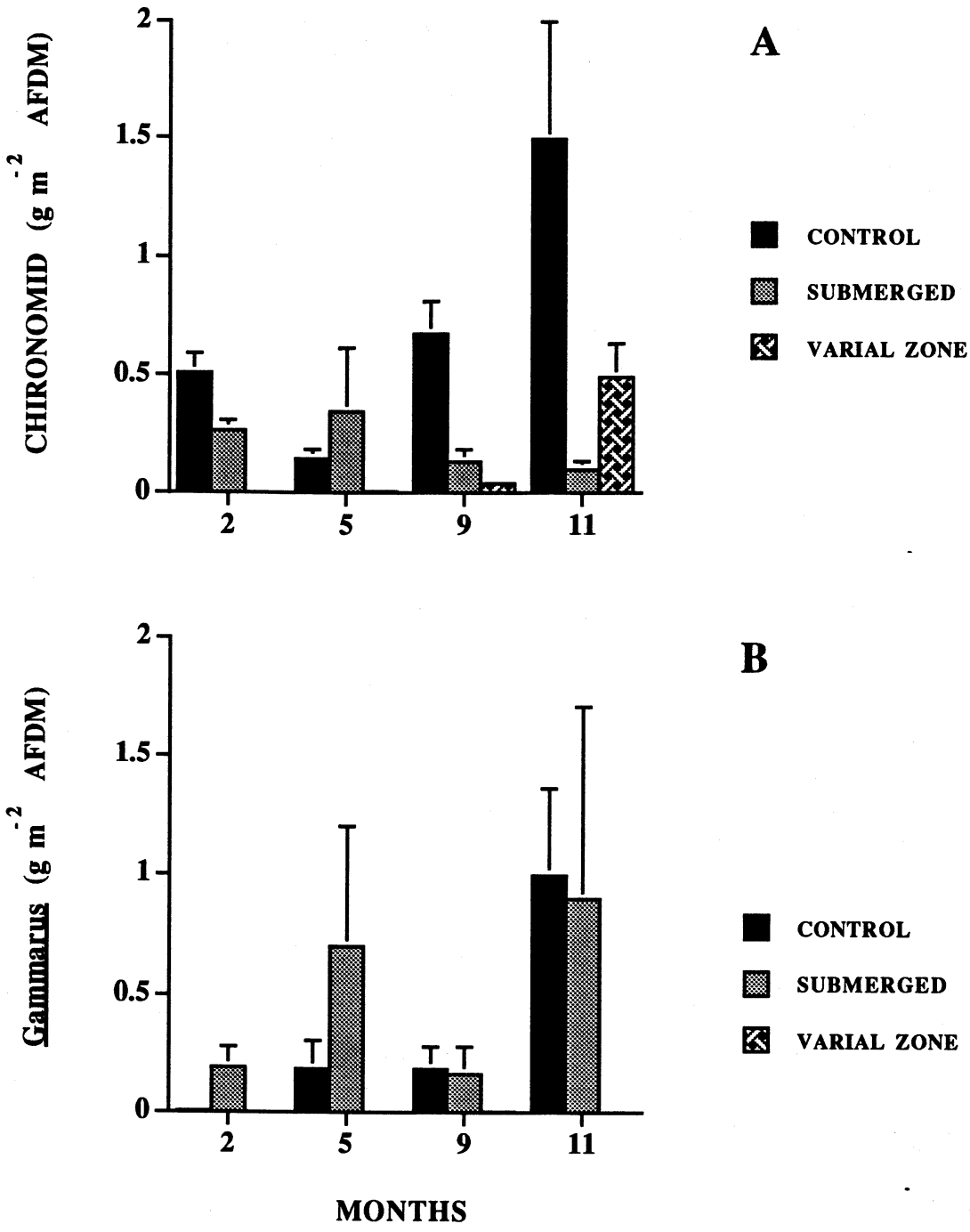

Figure 9. Recolonization as g m^{-2} AFDM for chironomid larvae (A) and Gammarus lacustris (B) on desiccated cobbles placed in continuously submerged ($\leq$140 m^3 s^{-1}) and varial zones (140 to 283 m^3 s^{-1}) of the Colorado River at Lees Ferry, Arizona (RKM 0.8). Cobbles were desiccated for 219 days.

Similarly, G. lacustris AFDM was highly variable but achieved levels equal to or higher than controls (0.006 g m^{-2}, SE ± 0.006) in the submerged zone (0.19 g m^{-2}, SE ± 0.09) by mo two (Fig. 9B; Table 4). G. lacustris AFDM remained negligible in the varial zone through the experiment. However, chironomids appeared on varial zone cobbles and AFDM exceeded submerged levels at mo 11 (0.49 g m^{-2}, SE ± 0.14). This increase in chironomid AFDM coincided with the temporary inundations of cobbles in the varial zone during the high release flows of winter (>340 m^3 s^{-1} or >12,000 ft^3 s^{-1}).

In-Situ Desiccation-Recolonization Experiment at Cathedral Island

Benthic recolonization of desiccated cobbles in the permanently wetted channel at the turbid Cathedral Island habitat was not solely dominated by C. glomerata as in the clear-water habitat at Lees Ferry. Both C. glomerata and Oscillatoria recolonized desiccated cobbles slowly in the submerged zone (Oscillatoria at five mo and C. glomerata in nine mo). Average C. glomerata AFDM on recolonizing submerged cobbles (103.3 g m^{-2}, SE ± 42.6) surpassed control levels (49.5 g m^{-2}, SE ± 13.6) by mo 11 (Fig. 10A; Table 5).

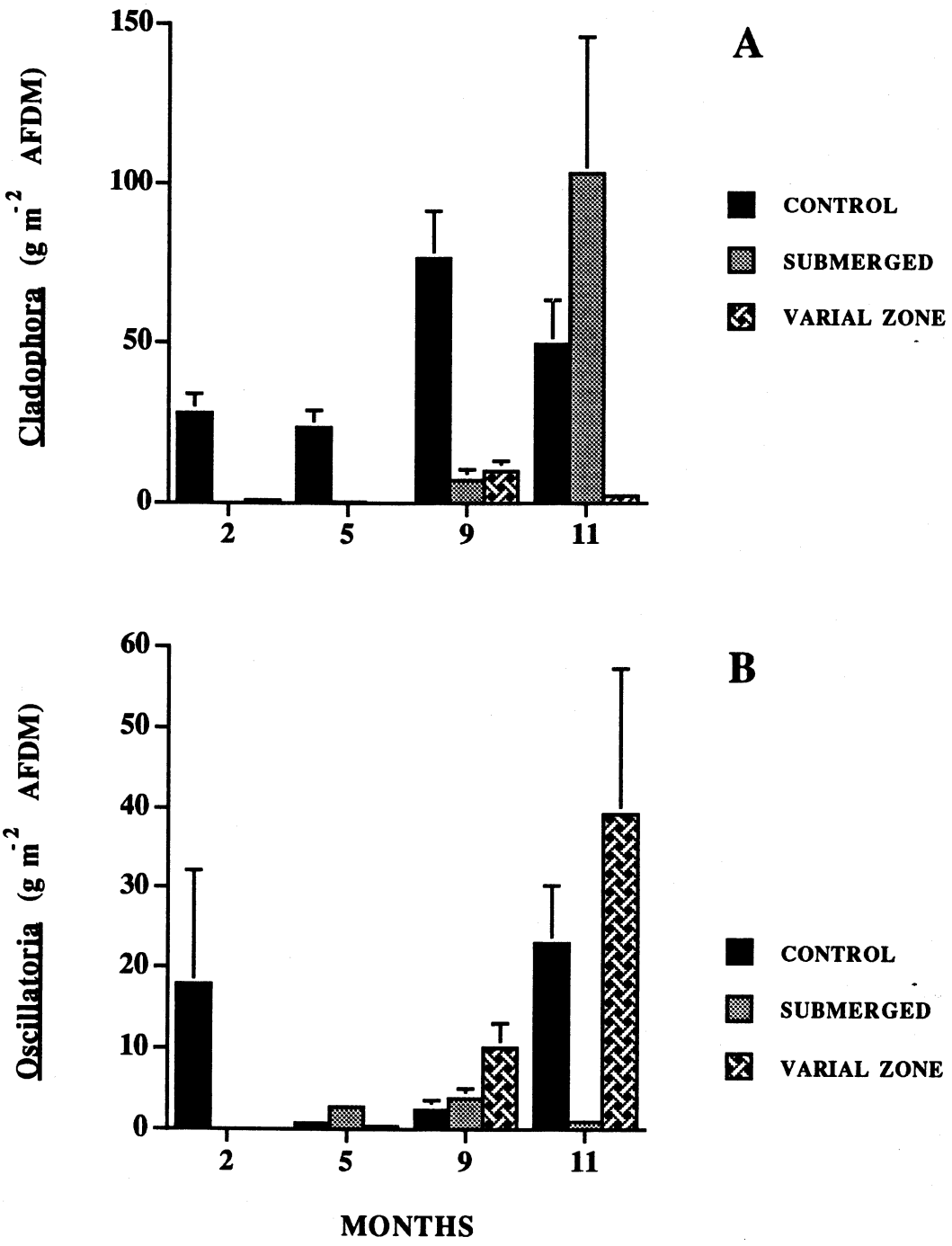

Figure 10. Recolonization as g m^{-2} AFDM for Cladophora glomerata (A) and Oscillatoria spp. (B) on desiccated cobbles placed in continuously submerged ($\leq$140 m^3 s^{-1}) and varial zones (140 to 283 m^3 s^{-1}) of the Colorado River at Cathedral Island, Arizona (RKM 4.8). Cobbles were desiccated for 219 days.

Table 5. Probabilities calculated by the Kruskal-Wallis analysis of resubmerged treatment cobbles at Cathedral Island. Significant differences in AFDM on treatment cobbles as determined by the sequential Bonferroni technique are indicated by an * following the p. Recolonization on submerged treatment cobbles has occurred when there is no significant difference.

Mo	Cladophora	Oscillatoria	Gammarus	Chironomid
0	0.00000*	0.00000*	0.00000*	0.00000*
2	0.00262*	0.28733	0.47049	0.00067*
5	0.00000*	0.00160*	0.07563	0.16034
9	0.00000*	0.12115	0.00900*	0.04102
11	0.16772	0.01293	0.59404	0.07202

Oscillatoria AFDM on recolonizing submerged cobbles (3.8 g m^{-2}, SE ± 1.3) never reached the levels of C. glomerata AFDM reported for control or submerged cobbles (Table 5). As at Lees Ferry, Oscillatoria was the dominant recolonizing alga on periodically desiccated cobbles in the varial zone at Cathedral Island (Figs. 8B & 10B). Oscillatoria colonization in the varial zone (39.3 g m^{-2}, SE ± 18.0) exceeded that on the submerged (0.92 g m^{-2}, SE ± 0.45) or control cobbles (23.0 g m^{-2}, SE ± 7.3) at mo 11 (Fig. 10B).

Recruitment of macroinvertebrates was slower in the submerged zone at Cathedral Island than at Lees Ferry. Chironomid AFDM increased slowly (0.1 g m^{-2}, SE ± 0.1) in the submerged zone, and did not achieve control levels (1.08 g m^{-2}, SE ± 0.28) after 11 mo (Fig. 11A; Table 5). Not until mo 11 did G. lacustris AFDM on submerged cobbles (0.066 g m^{-2}, SE ± 0.066) equilibrate with control levels (0.087 g m^{-2}, SE ± 0.062; Fig. 11B; Table 5). At Lees Ferry, macroinvertebrate AFDM values on recolonizing cobbles reached and surpassed controls in two months for G. lacustris and by month five for chironomids. With negligible AFDM values being reported, neither chironomid or G. lacustris recruitment developed to any extent in the varial zone at Cathedral Island.

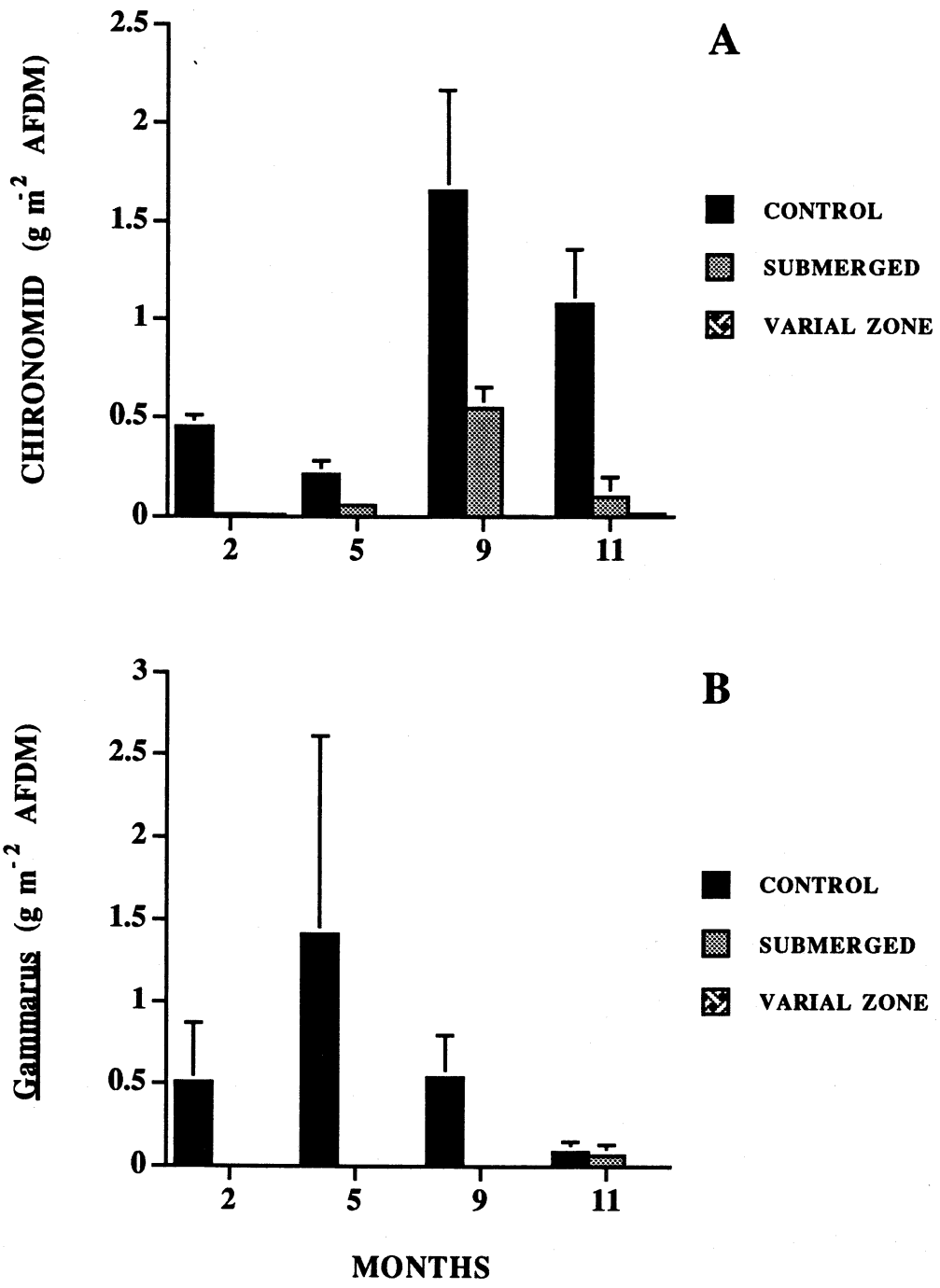

Figure 11. Recolonization as g m^{-2} AFDM for chironomid larvae (A) and Gammarus lacustris (B) on desiccated cobbles placed in continuously submerged ($\leq$140 m^3 s^{-1}) and varial zones (140 to 283 m^3 s^{-1}) of the Colorado River at Cathedral Island, Arizona (RKM 4.8). Cobbles were desiccated for 219 days.

CHAPTER 4

DISCUSSION

The turbidity and desiccation experiments conducted in the tailwaters of the Colorado River below Glen Canyon Dam revealed distinctly different ecological requirements for Cladophora glomerata and Oscillatoria spp. C. glomerata is a highly branched filamentous green alga that performs well in the continuously submerged, clear-water habitats of the Colorado River ecosystem. In contrast, the cyanobacterium, Oscillatoria, forms mat-like matrices of filaments and sand that are more successful in the harsh environments of high suspended-sediment and in sections of the channel that undergo periodic drying and wetting. Oscillatoria mats have been shown to survive desiccation, recovering rapidly upon rehydration (Vincent & Howard-Williams, 1986; Hawes, 1993), while C. glomerata has been shown to lose significant amounts of chlorophyll a after as little as six hours of atmospheric exposure in field and laboratory experiments (Usher &

Blinn, 1990; Angradi & Kubly, 1993).

Reciprocal-Translocation Turbidity Experiment

Below Glen Canyon Dam, a transition in the structure of the algal community coincides with abrupt increases in the suspended sediment load accompanied by reduced water clarity at the Paria River and subsequent tributaries (Yard, personal comm.). An average three million tons per year of suspended sediment enter from the Paria River annually (Andrews, 1991). The standing stock of C. glomerata in the Colorado River is strongly reduced below the confluence of the Paria River, whereas in varial zones of the stream channel and under turbid conditions through the Grand Canyon section of the river, Oscillatoria becomes a dominant benthic algae (Blinn et al., 1994; Shannon et al., 1994).

A comparison of the structure of the benthic communities at Lees Ferry and Cathedral Island on the Colorado River indicates the importance of turbidity. The C. glomerata colonized cobbles from the clear-water site at Lees Ferry had a 6-fold higher algal AFDM than did the Oscillatoria-covered cobbles in the seasonally turbid habitat at Cathedral Island. At Cathedral Island, translocated cobbles exhibited a

>80% reduction in mass of C. glomerata due to elevated turbidity. This reduction was even more dramatic than the 15 to 57% loss in algal mass reported in six New Zealand streams following increased turbidity (Davies-Colley et al., 1992). It has been shown that C. glomerata and epiphyton mass decreases laterally on the Colorado River with increased distance from Glen Canyon Dam (Hardwick et al., 1992; Blinn et al., 1994).

In association with the reduced C. glomerata, epiphyton mass was less than one-third that found in the upstream clear-water habitats. The high surface area of C. glomerata provides an excellent substrate for epiphytes (Sze, 1993) and has been positively correlated with epiphyton AFDM (Blinn et al., 1994). Therefore, in addition to direct physical abrasion caused by turbidity, the reduction of C. glomerata further reduces epiphyton mass. Recent studies have indicated that C. glomerata supports significantly higher epiphytic diatom and macroinvertebrate communities than the Oscillatoria assemblage (Pinney, 1991; Blinn et al., 1992; Shannon et al., 1994). Epiphytic diatoms comprise the largest proportion of diet items in the guts of chironomid larvae and Gammarus lacustris, whereas the macroalgae C. glomerata and Oscillatoria are rare or absent in macroinvertebrate guts (Pinney,

1991). Fish gut analyses at the study sites have found C. glomerata and associated macroinvertebrates (Leibfried, 1988). Therefore, replacement of C. glomerata habitats with those more suitable for Oscillatoria has major bottom-up implications on the aquatic food web in the Colorado River through Grand Canyon National Park.

Oscillatoria AFDM was negligible on cobbles translocated from Lees Ferry to the turbid site. However, after 9 mo of seasonally turbid conditions at Cathedral Island, Oscillatoria reached the AFDM of control levels. There was an overall decrease in Oscillatoria AFDM and increase in C. glomerata AFDM on control cobbles over the course of the experiment at Cathedral Island. This likely resulted from the unusually low discharge from the Paria River during the experiment. The Paria River was above a baseflow of 20 $ft^3 s^{-1}$ (0.56 $m^3 s^{-1}$) only 25% of the time during the experiment, whereas the Paria River was above baseflow 40% of the time (USGS Paria River Gauge) the year before the experiment. High suspended-sediment loads are more detrimental to the exposed filamentous streamers of C. glomerata than to the compact mucilaginous assemblages of Oscillatoria (Power et al., 1988; Newcombe & Mac Donald, 1991; Dodds & Gudder, 1992).

It has been shown that C. glomerata supports nearly ten-fold higher

mass of secondary producers than does Oscillatoria assemblages in this system. For example, one gram of C. glomerata yields ~0.1 g of macroinvertebrate mass compared to ~0.015 g of macroinvertebrates in a comparable mass of Oscillatoria (Blinn et al., 1994). The reduction in G. lacustris AFDM by >80% after one mo at Cathedral Island was consistent with the loss C. glomerata AFDM. Macroinvertebrate densities have been shown to be reduced by >50% due to catastrophic drift within 24 h of the addition of fine sediments (Culp et al., 1986). The loss of G. lacustris AFDM on translocated cobbles at Cathedral Island was most likely by similar catastrophic drift of individuals and the reduction in C. glomerata AFDM. In contrast, chironomid AFDM increased on both control and translocated cobbles throughout the experiment at Cathedral Island. This may be due to chironomid larvae being less susceptible to drift loss and/or their ability to utilize Oscillatoria assemblages. The high variability and general trend of increase of macroinvertebrate AFDM on the control cobbles of the turbid site followed the seasonally low input of suspended sediments by the Paria River and increased development of C. glomerata.

With reduced turbidity, the benthic community on cobbles translocated to the clear-water site at Lees Ferry from the seasonally

turbid habitats at Cathedral Island accommodated to the higher, stable light availability. Development of C. glomerata was slow on cobbles translocated from Cathedral Island. Even after 11 mo of incubation in the clear-water habitat, translocated cobbles had only one-fourth the mass found on control cobbles. Other filamentous green algae have been shown to achieve maximum standing mass in lotic habitats in 33 d (Peterson & Stevenson, 1992). C. glomerata was reported in the summer of 1980 to recolonize the scoured and desiccated shoreline of Lake Michigan to maximum growth in less than two mo (Blum, 1982). A year-long bi-monthly survey found no zoospores of C. glomerata present, thus limiting colonization to random fragments in drift and/or surviving basal holdfasts (Graham, 1982; Dodds & Gudder, 1992). The slow epiphyton accommodation at Lees Ferry resembled the pattern of C. glomerata. The high mid-winter epiphyton levels for both sites during mo nine may have been due to seasonal influences such as increased nutrients from turnover of Lake Powell or less competition with other primary producers under the lower light conditions of winter.

Oscillatoria AFDM on cobbles translocated from Cathedral Island consistently dropped until AFDM values were negligible after nine mo

of clear-water conditions. Although highly variable, macro-invertebrate AFDM followed the colonization of C. glomerata and exhibited an overall trend of increase at the clear-water Lees Ferry site. The clear-water conditions of the tailwaters of Glen Canyon Dam accommodated the increased levels of C. glomerata and associated biota AFDM. The loss of Oscillatoria AFDM from the clear-water benthic community may have been due to the shading of the highly branched morphology of C. glomerata and/or competition for substrate by the rhizoidal holdfasts of C. glomerata.

Desiccation-Recolonization Experiment

Desiccation of cobbles structured the benthic community by limiting recolonization of biota in the varial zone of the channel. Cobbles that were previously desiccated above the varial zone for the extended period of 219 d had no living benthic biota. Lotic ecosystems have been shown to have no living benthic biota present during periods of drought (Stanley, 1993; Milner, 1994). Significant recolonization by C. glomerata or benthic macroinvertebrates did not occur in the varial zone at either site; however, Oscillatoria AFDM recolonized to over 40 g m^{-2} on cobbles in the varial zones at both sites. My findings

collaborate previous reports on the ability of Oscillatoria mats to tolerate periodic desiccation (Vincent & Howard-Williams, 1986; Hawes, 1993) and the ability of C. glomerata to be better suited to grow on stable substrata (Dodds & Gudder, 1993) in non-varial tailwaters with high transparency (Blinn et al., 1994). C. glomerata mass and chlorophyll a have been shown to be reduced with the exposure and desiccation experienced in the varial zone (Usher & Blinn, 1990; Angradi & Kubly, 1993). Oscillatoria filaments may migrate within the layer of sediment on colonized cobbles and escape desiccation (Prescott, 1978; Sze, 1993). Futhermore the mucilage produced by this alga and the mat-like construction of Oscillatoria assemblages retain water and prevent desiccation. In contrast, the high surface area that makes C. glomerata a good substrate for epiphyton attachment and for macroinvertebrates to reside further increases the rate of desiccation.

An increase in chironomid AFDM coincided with the 11 mo collection during the temporary inundation of cobbles in the varial zone at the Lees Ferry site. The negligible recolonization by G. lacustris on cobbles located in the varial zone during periods of temporary inundation suggests that chironomids are better adapted to utilizing resources in the Oscillatoria assemblage than G. lacustris and/or that G.

lacustris is more selective and mobile. The negligible recolonization of macroinvertebrates in the varial zone at either site agrees with previous findings that intermittent streams and the varial zone of regulated rivers have been shown to be devoid of fauna during periods of desiccation (Petts & Bickerton, 1994; Jourdonnais & Hauer, 1993).

Recolonization of previously desiccated cobbles in the permanently wetted zone differed between clear-water and turbid habitats. C. glomerata AFDM on submerged cobbles at the clear-water Lees Ferry site achieved control levels by mo nine. In contrast, recolonizing cobbles in the submerged treatment did not equilibrate with C. glomerata AFDM on control cobbles until 11 mo in the seasonally turbid Cathedral Island site. Recolonization by Oscillatoria on submerged cobbles in the permanently wetted zone did not occur at the clear-water site, whereas, Oscillatoria recolonized the submerged cobbles at the turbid site of Cathedral Island during the nine mo period. This development of Oscillatoria and the retarded recolonization of C. glomerata and macroinvertebrates at Cathedral Island supports the longitudinal pattern reported by Blinn et al. (1994) and observed in the reciprocal-translocation experiment findings of the influence of turbidity.

The slower recolonization of C. glomerata on submerged cobbles at the seasonally turbid Cathedral Island site and/or lower macro-invertebrate density on surrounding cobbles resulted in delayed recolonization of the submerged cobbles until nine mo by chironomids and 11 mo by G. lacustris. Recolonization by macroinvertebrates at the clear-water habitat of Lees Ferry occurred almost immediately with equal or greater AFDM than control cobbles by the two or five mo collections. The rapid recolonization of treatment cobbles at Lees Ferry by macroinvertebrates was most likely due to their ability to disperse by drift in lotic systems to new substrates and resources (Hynes, 1970; Mackay, 1992).

The minimum discharge of fluctuating flows from Glen Canyon Dam determines the area of channel within the permanently wetted zone. A low discharge of 142 $m^3 s^{-1}$ (5,000 $ft^3 s^{-1}$) results in an estimated 67,981 m^2 of channel substrata inundated in the Lees Ferry reach (Blinn et al., 1992). However, if the discharge was increased to 227 $m^3 s^{-1}$ (8,000 $ft^3 s^{-1}$) or 425 $m^3 s^{-1}$ (15,000 $ft^3 s^{-1}$) the permanently wetted zone would increase by 44,100 m^2 or 78,671 m^2, respectively, in the Lees Ferry reach (Blinn et al., 1992). It was also estimated that a low discharge of 142 $m^3 s^{-1}$ (5,000 $ft^3 s^{-1}$) would provide a projected

ecosystem energy of 18.1 x 10^9 joules and that increased base flows of 227 m^3 s^{-1} (8,000 ft^3 s^{-1}) or 425 m^3 s^{-1} (15,000 ft^3 s^{-1}) would support an increase of 28.5 x 10^9 or 37.6 x 10^9 joules of energy, respectively (Blinn et al., 1992).

I demonstrated that the benthic community in the varial zone never achieves the potential energy of the aquatic environment. More than five mo of continued submergence is required for recovery from extended desiccation. The Oscillatoria assemblage on translocated cobbles from Cathedral Island retarded C. glomerata colonization at Lees Ferry and resulted in lower energy made available to higher trophic levels by the aquatic foodbase. Oscillatoria colonized cobbles in the varial zones at both sites. For the reasons given above, management of discharges from Glen Canyon Dam should take into consideration the fact that benthic energy dynamics in the tailwaters contributes to downstream ecosystem function and is dependent on consistent discharge practices.

CHAPTER 5

CONCLUSIONS

This study indicates that variable flows and high suspended sediment loads are less suitable for Cladophora glomerata than Oscillatoria phytobenthic communities. Under desiccating conditions C. glomerata recolonization is negligible, while Oscillatoria filaments develop extensive matrices of sediment and mucilage on benthic cobbles in the varial zone of desiccation. C. glomerata AFDM increases under clear-water conditions and is reduced under turbid habitat conditions. In contrast, Oscillatoria AFDM decreases under clear-water conditions and recolonizes at the turbid habitat site. These observations are generally supported by patterns displayed by phytobenthic communities located downstream from Glen Canyon Dam (Angradi & Kubly, 1993; Shannon et al., 1994; Blinn et al., 1994). The loss of Oscillatoria AFDM under clear-water conditions is believed to be due to biotic interactions with C. glomerata for substrate and/or light.

Chironomid recruitment appeared to be less dependent on C. glomerata than recruitment by Gammarus lacustris, and chironomid larvae were less effected by seasonal turbidity at Cathedral Island than G. lacustris. Macroinvertebrates recolonized faster on desiccated cobbles in the continuously submerged zone than did benthic algae. As for C. glomerata, macroinvertebrate recolonization is negligible in habitats undergoing desiccation in the varial zone.

We estimate the energy derived from macroinvertebrates associated with C. glomerata communities to be nearly an order of magnitude higher than energy derived from macroinvertebrate mass in Oscillatoria communities. Therefore, loss of C. glomerata habitat and the replacement by habitat more suitable for Oscillatoria reduces the overall food value of the phytobenthic community in the Colorado River through Grand Canyon National Park. A reduction in the energy available from the aquatic foodbase of the Colorado River to higher trophic levels impacts the functioning of the complete food web.

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BIOGRAPHICAL INFORMATION

NAME OF AUTHOR: Michael L. Shaver
PLACE OF BIRTH: Rochester, New York
DATE OF BIRTH: September 2, 1965

EDUCATIONAL DEGREES OBTAINED

Northern Arizona University, M.S., 1995
State University of New York College of Environmental Science and Forestry, B.S., 1990

PROFESSIONAL POSITIONS HELD

Research Assistant, Northern Arizona University,
Flagstaff, Arizona, 1993 - Present
Lab Technician, Northern Arizona University,
Flagstaff, Arizona, 1991 - 1993
Teaching Assistant, Northern Arizona University,
Flagstaff, Arizona, 1992

PROFESSIONAL SOCIETIES

North American Benthological Society of America
Beta Beta Beta, Biological Honor Society
Arizona-Nevada Academy of Science
The Wildlife Society

SCHOLARLY PUBLICATIONS

Shaver M.L., Govedich F.G., Shannon J.P., Wilson K.P. & Blinn D.W. (1994) Reciprocal transplants in clear and turbid water habitats in the regulated Colorado River, Grand Canyon, Arizona. 38th Annual Meeting of the Arizona-Nevada Academy of Science. Glendale Community College, Glendale, Arizona.

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