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INFLUENCE OF VARIOUS EXPOSURE PERIODS ON THE BIOMASS AND CHLOROPHYLL *A* OF *CLADOPHORA GLOMERATA* (CHLOROPHYTA)[1]

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ABSTRACT

The biomass of Cladophora glomerata *(L.) Kütz. was estimated at selected sites in the Colorado River between Glen Canyon Dam, Arizona, and River Kilometer 354.* C. glomerata *biomass was significantly higher at sites above Lees Ferry (25 km downstream from the Dam) than sites below the Ferry. Biomass and chlorophyll* a *were significantly reduced when* C. glomerata *was subjected to one-time exposures to the atmosphere for 12 daylight h or more. Repeated 12/12 h and 24/24 h (exposure/submergence) cycles over a two-week period also showed a significant reduction in biomass. The adaptations of* C. glomerata *to "stranding" during regulated flows are discussed.*

Key index words: biomass; chlorophyll a; Cladophora glomerata; *Colorado River; desiccation; regulated rivers; tailwaters*

Several studies have addressed the changes in tailwater algal communities that result from modified physico-chemical features below reservoirs (Lawson and Rushforth 1975, Lowe 1979, Marcus 1980, Holmes and Whitton 1981, Ward 1982, Dufford et al. 1987, Blinn et al. 1989). However, the impacts of stranding (i.e. exposure to the atmosphere during reduced flows) on algal populations in regulated rivers has received little attention. Lowe (1979) indicated that widely fluctuating flows decrease algal standing crop. Recently, Peterson (1987) examined the influence of flow regime on diatom communities and found that communities in sheltered habitats were less resistant to desiccation than communities in more rigorous flows.

In marine systems, algae stranded during intertidal fluctuations possess adaptations to resist desiccation. Commonly, plants that thrive in the intertidal zone have thicker cell walls, produce more mucilage, and increase their saturated lipid content (Zaneveld 1937, 1969, Johnson et al. 1974, Wiltens et al. 1978, Schonbeck and Norton 1979, Jones and Norton 1979, Dromgoole 1980, Lobban et al. 1985). Intertidal marine plants likely possess adaptations to tolerate stranding because they have been exposed to a regular submergence-emergence regime over evolutionary time. However, because the construction of dams on major rivers is a relatively recent human activity (Smith 1971), one might predict severe impacts on the resident freshwater algal populations in regulated rivers.

Cladophora glomerata (L.) Kütz. is a common fila-

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mentous green alga in the tailwater systems of dams (Lowe 1979, Dufford et al. 1987, Blinn et al. 1989). *Cladophora* serves as an important food source, either directly or indirectly, and provides a substrate for epiphyton, and a refuge for a variety of stream invertebrates (Whitton 1970, Bancroft and Sylvester 1978, Carothers and Minckley 1981, Leibfried and Blinn 1986, Blinn et al. 1989). The clear, cool, nutrient enriched waters of hypolimnetic discharges below Glen Canyon Dam, Arizona (Stewart and Blinn 1976) promote dense stands of *C. glomerata* throughout the year (Usher et al. 1986).

The objectives of this study were to examine the distribution of *C. glomerata* in the Colorado River, Arizona below Glen Canyon Dam from Lees Ferry to River Kilometer 354 and to experimentally test the influence of stranding (exposure to air) on the biomass and chlorophyll *a* concentration of *C. glomerata* in a simulated stream environment.

MATERIALS AND METHODS

Cladophora glomerata was sampled at seven locations between Glen Canyon Dam, Arizona, and Kilometer 354 in the Colorado River during July 1985. Fifteen random samples (4 cm^2 area) were taken at 12 km below Glen Canyon Dam, at Lees Ferry, above Nankoweap Creek, and below the tributaries of Bright Angel, Tapeats, National, and River Kilometer 354. These locations were selected because they provide suitable habitats for *Cladophora*, i.e. submerged rock substrata in shallow water. In every case random samples were collected according to standard random number tables and predetermined grids. Water transparency was determined with a Secchi disc at each site (n = 3 per site) during July 1985.

Cladophora glomerata samples were air dried on wire mesh screens at each site. *Cladophora* filaments were then separated from silt and sand in the laboratory and oven dried (100–104° C) to a constant weight.

Experimental studies on the tolerance of *C. glomerata* to various exposure periods were conducted with laboratory "Living Stream" tanks (Frigid Unit, Model #LSW-700) in Flagstaff, AZ. In each experiment, rocks (150–200 cm^2) with attached *Cladophora* were collected at Lees Ferry, Arizona, and placed into stream tanks filled with river water collected at Lees Ferry. Water in the experimental stream tanks was maintained at a temperature similar to the water temperature at Lees Ferry (11° C ± 1° C) with light conditions at 240–300 $\mu E \cdot m^{-2} \cdot s^{-1}$ on a 12:12 h LD cycle. Exposure periods were conducted in direct sunlight in trays with standing water to simulate natural "stranding" conditions under regulated flow. For each experiment, rocks were numbered and a random numbers table was used to assign rocks to specific treatments. Three random samples were harvested from each treatment rock, according to a standard random numbers table, from numbered grids on the rocks. Air temperature was monitored during each exposure period. The average air temperature during the experimental periods was 17.8° C (SE ±2.3, n = at least 12 for each experiment) with relatively clear skies.

Estimates of biomass after one-time exposure. The effects of one-time exposures on the biomass of *Cladophora* were tested by exposing three experimental rocks with *Cladophora* to the atmosphere on a one-time basis for each of four treatments. Rocks in treatment 1 were exposed for 12 h in the dark; treatment 2, 12 h in the light; treatment 3, one day; and treatment 4, two days. These exposure treatments were selected to simulate the potential field conditions of regulated flow. Three rocks were also left submerged for control treatments. Three random samples (4 cm^2) of *Cladophora* were taken from each of the three experimental rocks prior to the exposure period to obtain an initial dry weight biomass (oven dried to a constant weight at 100–104° C) for each treatment. The experimental rocks were returned to the stream tank following each exposure treatment and submerged for a two-wk period. After this submergence period three random samples (4 cm^2) of *Cladophora* were taken from each rock, including control rocks, to determine dry weight biomass. The three samples taken from each rock were averaged. These experiments were conducted on three dates: 5 March 1985, 28 March 1985, and 16 July 1985. The difference in *Cladophora* biomass between control and exposed rocks was determined for each exposure treatment, and a two-way ANOVA (5 × 3 design) was conducted. Two-way ANOVAs (2 × 3 design) also were run to determine significant differences between paired treatments.

Estimates of chlorophyll a after one-time exposure. The loss of chlorophyll $a \cdot g^{-1}$ dry weight of *Cladophora* was tested following various exposure periods. Rocks with *Cladophora* were taken from two stream tanks on 15 March 1987 and subjected to four treatments (n = 4 rocks for each treatment from each stream tank) including a 1-d exposure, 2-d exposure, 3-d exposure, and a 5-d exposure. At the end of each exposure period, the rocks were returned to the stream tank and incubated for a 2-wk period. After this submergence period three random samples (4 cm^2) of *Cladophora* were taken from each rock for each exposure treatment and from control rocks that were continually submerged. Each of these samples were analyzed for chlorophyll *a* and corrected for phaeophytin *a* following the procedures of Wetzel and Likens (1979). The chlorophyll *a* values for the three samples taken from each rock were averaged. Two-way ANOVAs were conducted to determine differences between all treatments (5 × 2 design) and between any two treatments (2 × 2 design). The relationship between wet and dry weights of *Cladophora* was determined with a linear regression for control and treatment rocks in order to convert chlorophyll *a* values (calculated from mg wet wt) to mg chlorophyll *a* per gram dry weight.

Estimates of biomass after regularly repeated exposures. Rocks with attached *Cladophora* were subjected to one of two exposure treatments and compared to controls that were left submerged in the stream tank for the duration of the experiment. The first treatment consisted of a 12-h exposure to the atmosphere during the day followed by a 12-h submergence at night repeated over a two week period. The second treatment was a 24-h exposure to the atmosphere followed by a 24-h submergence for two weeks. These exposure treatments were selected to simulate the field conditions of potential regulated flow regimes. The experiments were run on June 1985 and April 1987. Three random samples (4 cm^2) were taken from each of the four rocks for each exposure treatment for each date. The dry weight biomass was determined for *Cladophora* taken from each of the rocks at the 12 h and 24 h repeated exposure treatments. These values were compared to similar numbers of random samples (4 cm^2) taken from control submerged rocks for each experimental date. The biomass values obtained for the three random samples from each rock were averaged. The difference in *Cladophora* biomass between control and exposed rocks was determined for each exposure treatment and a two-way ANOVA was conducted for all treatments (3 × 2 design) and between the 12/12 and 24/24 (exposure/submergence) treatments (2 × 2 design).

RESULTS

There was a significant difference in mean standing crop of *Cladophora glomerata* in the Colorado River between sites above and below Lees Ferry, Arizona ($t = 4.99$, df = 27.1, $P < 0.001$) (Fig. 1). The sites at 12 km below the Glen Canyon Dam and Lees Ferry averaged 144 $g \cdot m^{-2}$ (SE 4.1, n = 30) *C. glomerata* during July, while the five sites below Lees

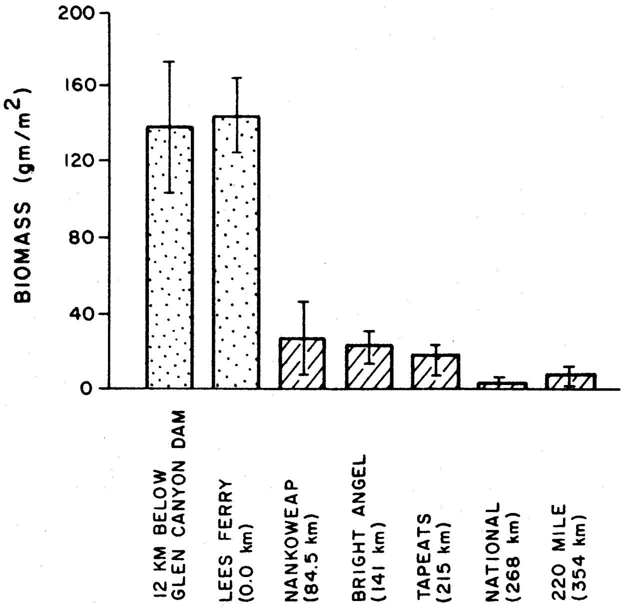

FIG. 1. Biomass of *Cladophora glomerata* at selected sites in the Colorado River through Glen and Grand Canyons, Arizona, during July 1985 (n = at least 15 samples). Bars with diagonal hatch lines represent sites with Secchi disc readings <2.0 m; vertical bar lines represent ±SE.

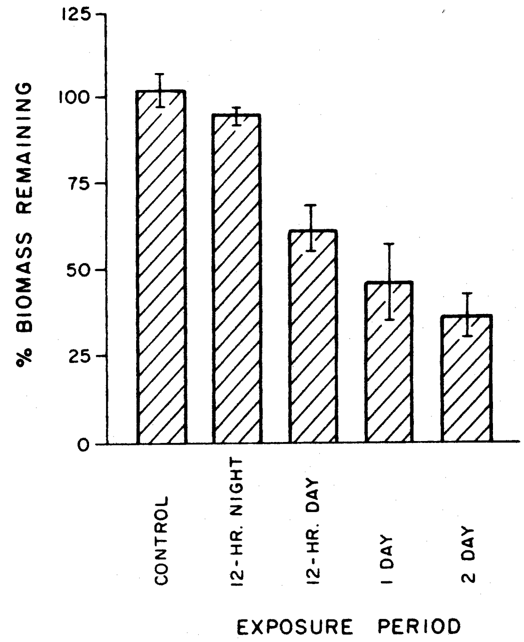

FIG. 2. Percent mean biomass of *Cladophora glomerata* remaining after various one-time exposure periods (n = 9). Vertical bar lines represent ±SE.

Ferry averaged only 17.2 $g \cdot m^{-2}$ (SE ±5.5, n = 75) during this same period. Water transparency from Secchi disc readings showed a significant positive correlation ($r = 0.957$; $P < 0.001$) with *C. glomerata* biomass during July. Secchi disc values between Glen Canyon Dam and Lees Ferry averaged 4.21 m (SE ±0.61, n = 6), whereas values below Lees Ferry averaged 1.7 m (SE ±0.35, n = 15).

Estimates of biomass after one-time exposure. Laboratory experiments showed that one-time exposures of *C. glomerata* to atmospheric conditions can result in a significant reduction in biomass after a 2-wk period. A two-way ANOVA with *Cladophora* biomass from control and exposure treatments resulted in a significant treatment effect ($F_{4,30} = 59.1$, $P < 0.001$). There were no significant interaction effects between exposure treatments ($F_{8,30} = 1.0$, $P > 0.05$) and no significant differences between the three dates ($F_{2,30} = 1.4$, $P > 0.05$).

Our data suggests that exposures of at least 12 daylight h or longer will result in significant reductions in *C. glomerata* biomass after two weeks (Fig. 2) when compared to continuously submerged control treatments ($F_{1,12} = 93.1$, $P < 0.001$). Exposure periods of 12 daylight h or longer showed over a 1.5-fold decrease in biomass from submerged controls. The 12-h exposure at night did not show a significant difference from controls ($F_{1,12} = 3.3$, $P > 0.05$) but did show a significant difference ($F_{1,12} = 82.6$, $P < 0.001$) from the 12-h daylight exposure. This infers greater damage from day exposures than from night exposures. There were no significant differences in biomass between 1-d and 2-d treatments ($F_{1,12} = 3.27$, $P > 0.05$).

Estimates of chlorophyll a *after one-time exposure.* There were significant reductions in chlorophyll *a* concentration in the second experiment between different one-time exposure periods and submerged controls ($F_{4,30} = 84.8$, $P < 0.001$). After 1-day exposures, chlorophyll *a* was reduced to only 38.7% of the submerged controls, whereas samples from 5-day exposures were reduced to 9.4% of the controls (Fig. 3). There were no significant differences between tanks ($F_{1,30} = 0.1$, $P > 0.05$) and no significant interaction effects between exposure treatments ($F_{4,30} = 0.37$, $P > 0.05$). Also, no significant differences were measured between 3-d and 5-d exposure periods ($F_{1,12} = 0.13$, $P > 0.05$). The regression equations used for converting chlorophyll *a* ($mg \cdot L^{-1}$ wet weight) values into $mg \cdot L^{-1}$ dry weight chlorophyll *a* are provided for each treatment in Table 1.

Estimates of biomass after regularly repeated exposures. A two-way ANOVA showed a significant treatment effect on biomass for 12-h and 24-h exposure/submergence cycles over a 2-wk period when compared to controls ($F_{2,18} = 7.7$, $P < 0.01$). Both exposure cycles resulted in at least a 45% decrease in biomass from controls over a 2-wk period (Fig. 4). There were no significant interaction effects between the two experimental dates ($F_{2,18} = 2.3$, $P > 0.05$) and no significant differences between the two experimental dates ($F_{1,18} = 0.1$, $P > 0.05$). Also, there was no significant difference between the 12 h and 24

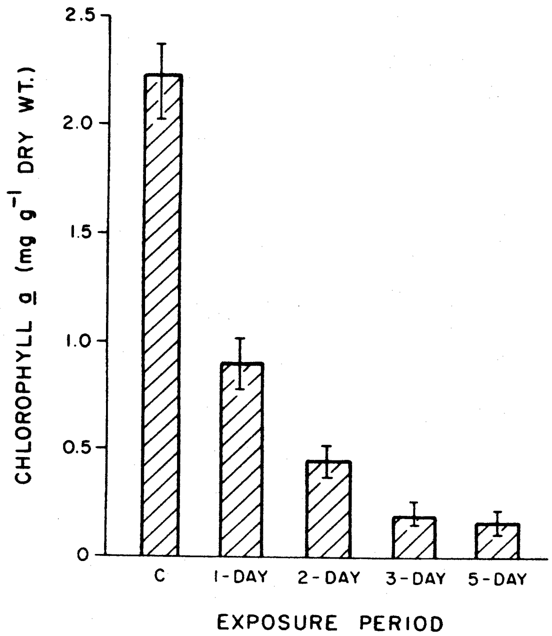

FIG. 3. Chlorophyll *a* remaining in *Cladophora glomerata* after various one-time exposure periods (n = 8). C = controls, and vertical bar lines represent ±SE.

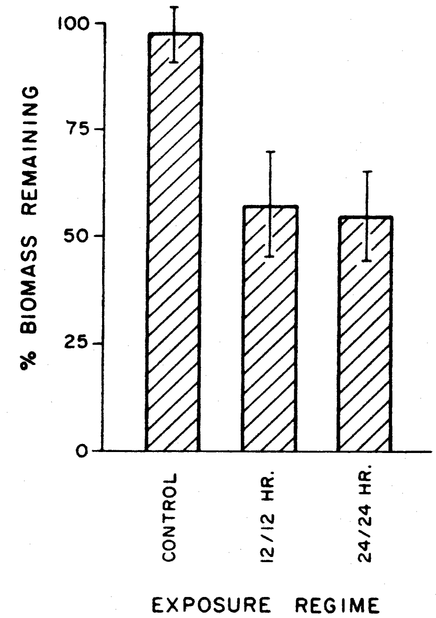

FIG. 4. Percent biomass of *Cladophora glomerata* remaining after a 2-wk period of repeated cycles of exposure and rewetting. Two experimental cycles of 12 and 24 h were compared to control (C) treatments which remained wetted in a stream tank for the entire 2-wk period (n = 8). Vertical bar lines represent ±SE.

h exposure/submergence cycles ($F_{1,12} = 0.12$, $P > 0.05$). During the course of the repeated exposure experiments many of the *C. glomerata* filaments were bleached.

DISCUSSION

A dense stand of *Cladophora glomerata* occurs in the tailwaters of Glen Canyon Dam Arizona, as far downstream as the confluence of the Paria River (ca. 30 km below Glen Canyon Dam) in the Colorado River. Below the confluence of the Paria, the standing crop of *C. glomerata* showed a dramatic decrease (Fig. 1). Also, Usher et al. (1986) reported a progressive increase in standing crop with greater depth. They reported 168.8, 203.1, and 224 $g \cdot m^{-2}$ of *C. glomerata* at the shoreline (0.0–0.3 m), intermediate (0.3–1.25 m), and deeper waters (1.25–3.0 m), respectively, for three dates at Lees Ferry. The downstream distributional patterns as well as distribution with depth for *C. glomerata* are present during all seasons (Usher et al. 1986).

The loss of *C. glomerata* biomass downstream may result from increased silt loads below tributaries that occur after summer rains in the Colorado River, including the Paria River (Cole and Kubly 1976). Secchi disc readings showed a significant positive correlation with standing crop of *C. glomerata* at selected sites through Glen and Grand Canyons during July. The lack of adequate substrata and/or reductions in nutrient levels may also be responsible for the reduced standing crop of *C. glomerata* at the downstream stations (Whitton 1970).

The results of this study suggest that fluctuations in flow (i.e. stranding) could have significant effects on the biomass of *C. glomerata*. One-time exposures of 12 h in daylight or more resulted in significant reductions in *C. glomerata* biomass and chlorophyll *a* concentrations. *C. glomerata* biomass from 12 h exposures during the night were not significantly different from continuously submerged controls. This infers that ultraviolet light during the day is harmful (Round 1981, Graham et al. 1982), and desiccation rates during darkness are slower, perhaps due to higher relative humidities and lower temperatures during the night.

The 12 and 24 h cycle exposure/submergence experiments also showed a significant reduction in *C. glomerata* biomass. Two weeks of repeated 12 h and/or 24 h exposures resulted in significant reductions in *C. glomerata* biomass. Experiments involving repeated exposures more accurately mimic natural conditions than one-time exposure experi-

TABLE 1. *Linear regression equations and associated statistics for determining the relationships between wet weight and dry weight for* Cladophora glomerata. *All treatments were significant at the 0.05 level (n = 10 for each treatment).*

Time period	Regression equation	r^2
Control	Dry (mg) = 0.012 + 0.155 wet (mg)	0.821
1-day	Dry (mg) = −0.067 + 0.612 wet (mg)	0.971
2-day	Dry (mg) = −0.009 + 0.307 wet (mg)	0.698
3-day	Dry (mg) = −0.076 + 0.629 wet (mg)	0.978
5-day	Dry (mg) = 0.035 + 0.232 wet (mg)	0.772

ments (Hodgson 1981). It is not uncommon for a section of channel bed in the Colorado River to be exposed for 12–24 h under normal operational flow regimes (Leibfried and Blinn 1986).

Exposed filaments near the holdfast that are not protected by a neighboring plant are the first parts of the *C. glomerata* tuft to be exposed to the atmosphere and the first portion of the tuft to dry. These filaments are therefore most susceptible to desiccation and damage due to exposure. As the river begins to rise, weakened filaments are easily broken, resulting not only in the loss of the damaged portions of filaments, but in the loss of the viable terminal tufts as well. After repeated cycles of exposure over long periods of time, the long tufts in the shallower portions of the river bed may be nearly eradicated and thereby expose the basal holdfast. Continued exposure of the river bed may damage the holdfast and inhibit regeneration of *C. glomerata* in the exposed zones.

Fragmentation during fluctuating flow regimes may be a common cause for loss of standing crop. *C. glomerata* is a common constituent of stream drift in the Colorado River (Haury 1981), and Leibfried and Blinn (1986) reported higher amounts of *C. glomerata* in drift samples during periods when fluctuations in discharge were most dramatic. These findings suggest that fragmentation due to drying of holdfast systems may be responsible for reduced standing crop under regular exposure periods. Our laboratory studies also showed increased fragmentation and subsequent drift of *C. glomerata* when subjected to various exposure treatments.

C. glomerata does, however, display a few adaptions to tolerate the widely fluctuating flow regimes caused by dams. The cell walls of *C. glomerata* are relatively thick and contain cellulose and silicon (Moore and Traquair 1976, Bold and Wynne 1985). Also, as the water level drops *C. glomerata* filaments collapse on themselves, with the long filaments overlapping each other and trapping water like a sponge. Similar behavior has been described for intertidal macroalgae (Evans 1959, Jones and Norton 1979, Quadir et al. 1979, Schonbeck and Norton 1979, Dromgoole 1980, Hodgson 1981). The tufts of *C. glomerata* hold the water for long periods (at least 12 h, pers. observ.) and therefore may protect internal filaments from desiccation. Overlying filaments are subjected to the damaging effects of ultraviolet light (Round 1981) and, in some cases following prolonged periods of exposure, become matted with a thin layer of bleached filaments covering a thicker layer of green filaments. The bleached layer provides a shield for the underlying filaments; i.e. the holdfast of one tuft is generally protected by overlying filaments of a neighboring plant. Lembi et al. (1988) also observed that the outermost layers of filaments in *Pithophora* serve a function of protecting innermost filaments from high light and/or desiccation.

The dense growths of epiphytic algae, especially diatoms, that typically occur on the filaments of *Cladophora* (Chudyba 1968, Round 1981, Stevenson and Stoermer 1982, Blinn et al. 1989) may also reduce damage to the underlying filaments during periods of exposure. The numerous epiphytic cells along with associated mucilage may help reduce exposure of underlying filaments to UV light and water loss during periods of stranding in tailwater environments.

Some populations of *Cladophora* occur in the eulittoral or "splash" zones of freshwater (Bellis and McLarty 1967, Blum 1982, Lorenz and Herdendorf 1982) and marine environments (Round 1981). Adaptations to the conditions of intermittent exposure in these habitats may have pre-conditioned *C. glomerata* for the emergence-submergence regimes of regulated rivers. Furthermore, mitotic divisions in *C. glomerata* (McDonald and Pickett-Heaps 1976) and the marine *C. flexuosa* (Scott and Bullock 1975) are very similar which suggests that *C. glomerata* is a marine invader of freshwater systems (Graham 1982).

This study examined the impact of different exposure periods on the biomass and chlorophyll *a* in *C. glomerata*. Our laboratory findings suggest that repeated exposures of at least 12 h of daylight or longer will reduce the biomass and chlorophyll *a* of *C. glomerata* over short periods of time (i.e. 2 wk). Additional studies need to be conducted to determine the long term effects on *Cladophora* biomass during regulated flow.

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