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EFFECTS OF ATMOSPHERIC EXPOSURE ON CHLOROPHYLL *a*, BIOMASS AND PRODUCTIVITY OF THE EPILITHON OF A TAILWATER RIVER

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ABSTRACT

Field experiments were conducted to determine the effects of atmospheric exposure on the chlorophyll *a* content, biomass and gross primary productivity (GPP) of littoral epilithon in the Colorado River below Glen Canyon Dam, Arizona. The chlorophyll *a* content of the epilithon was much more sensitive to exposure than the biomass. The epilithon was rapidly bleached during summer daytime exposures, but algal filaments remained attached for several weeks after reinundation. The percentage of initial chlorophyll *a* remaining after one day of exposure was not different from the percentage remaining after two days of exposure. However, significant reductions in chlorophyll *a* content were detected for day-time exposures as short as six hours. Overall, there were close inverse relationships ($r^2 \geq 0{\cdot}73$) between the time exposed or cumulative solar radiation (400–700 nm) and the percentage of initial chlorophyll *a* remaining after reinundation. The GPP of *Cladophora glomerata*-dominated epilithon from the permanently inundated channel was 10 times higher than the GPP of epilithon from the zone of daily water level fluctuation. Experimental atmospheric exposure of the epilithon from each zone reduced the GPP, but not the assimilation ratio (GPP per unit of chlorophyll *a*) of the epilithon.

The Glen Canyon epilithon has low resistance to exposure disturbances, and recolonization is slow under hydropower peaking flow regimes. *Cladophora glomerata* has an important structural role in Glen Canyon, the disruption of which is likely to precipitate effects at higher trophic levels.

KEY WORDS Epilithon Periphyton *Cladophora glomerata* Stranding Chlorophyll *a* Biomass Disturbance Primary Production Colorado River Flow Dam

INTRODUCTION

Most studies of the effects of flow-related disturbance on periphyton have examined changes resulting from floods in unregulated streams (e.g. Fisher *et al.*, 1982; Biggs and Close, 1989; Grimm and Fisher, 1989). Stranding and desiccation of periphyton resulting from a decrease in flow is a more likely cause of disturbance in regulated streams, particularly those used for irrigation storage and hydroelectric power generation (Petts, 1984). Although flow regulation may produce physical and chemical conditions which enhance periphyton growth (reviewed by Lowe, 1979), periphyton is generally not well adapted to conditions of stranding caused by large unnatural fluctuations in stage (Neel, 1963; Kroger, 1973; Steinman and McIntire, 1990).

This paper describes a study of the effects of stranding on the epilithon (phytobenthos growing on cobbles) of the Colorado River downstream from Glen Canyon Dam, Arizona, USA. Epilithon in the Glen Canyon tailwater is dominated by the filamentous chlorophyte, *Cladophora glomerata* (L.) Kutz. (Blinn and Cole, 1991), which often attains a high biomass (> 200 g ash-free biomass m^{-2}). The significance of the epilithon to other trophic levels in Glen and Grand Canyon has been recognized (National Research Council, 1991), but the effects of dam operations on the ecological role of the epilithon are not well understood (Blinn and Cole, 1991).

In Glen Canyon, *Cladophora* provides habitat for trout and macroinvertebrates. The tailwater macro-

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invertebrate community relies on epiphytic diatoms and detritus associated with *Cladophora* filaments for food (Pinney, 1991; Blinn *et al.*, 1992). The effects of dam operations on Glen Canyon epilithon may also have consequences for downstream ecosystems. For example, *Cladophora* sloughed from the substrate in Glen Canyon is exported downriver to the seasonally turbid and light-limited Marble and Grand Canyons (Kubly and Cole, 1979; M. D. Yard, Bureau of Reclamation, unpublished data), where it enters detrital pathways (Angradi and Kubly).

Flow releases from the Glen Canyon Dam determine the exposure regime for littoral epilithon. Although routine night-time exposures do not appear to greatly affect the epilithon (Usher and Blinn, 1990), daytime exposures such as those resulting from periodic low flows associated with dam operations or which could result from future dam operations have the potential to greatly influence the epilithon. This study was motivated by a lack of information on the relationships between atmospheric exposure, especially during the day, and epilithon characteristics.

Controlled studies of the effects of stranding on lotic epilithon are few. Usher and Blinn (1990) examined the effects of laboratory-simulated stranding on Colorado River *Cladophora* from a site 25 km below Glen Canyon Dam. Peterson (1987) examined the effects of short-term desiccation on diatom communities below Hoover Dam on the same river. No data exist on the effects of stranding on lotic *Cladophora*-dominated epilithon *in situ*, nor for the relationship between stranding and primary productivity.

Our study consisted of five field experiments conducted in the summers of 1991 and 1992. Specific objectives were: (1) to quantify the effects of exposure duration on the chlorophyll *a* and biomass of epilithon (experiments I–V); (2) to compare the effects of exposure to solar radiation on these variables among epilithon communities with different previous exposure histories (experiments IV–V); and (3) to examine the effect of exposure on epilithon primary productivity (experiment V).

STUDY AREA

Glen Canyon Dam (36° 56′ N, 111° 29′ W) is a large peaking power hydroelectric facility operated by the Bureau of Reclamation. The dam forms Lake Powell, a long (300 km), deep (average depth 51 m), warm monomictic reservoir. Water releases from the reservoir are hypolimnial, perennially cold (7–10°C), chemically stable and transparent (Stanford and Ward, 1991). Total oxidized nitrogen ($NO_2^- + NO_3^-$) average about $0{\cdot}3\ \mathrm{mg\,l^{-1}}$; orthophosphate concentrations are very low, rarely exceeding $0{\cdot}01\ \mathrm{mg\,l^{-1}}$ and N : P is typically > 30 (Angradi *et al.*, 1992).

The algal material used in this study was collected at 14 Mile Bar, a 300 m long cobble bar located 2 km downriver from the dam which is representative of the upper half of the 25 km Glen Canyon reach. Cobbles were collected from two littoral zones at 14 Mile Bar: the permanently inundated zone and the fluctuating flow zone. For the purposes of this study, the littoral zone was defined as the zone that could be sampled without scuba diving (< 0·5 m depth) at flows of $\geqslant 142\ \mathrm{m^3\,s^{-1}}$. The permanently inundated zone was defined as the littoral habitat (< 0·5 m) inundated at flows of $142\ \mathrm{m^3\,s^{-1}}$. This zone only could be sampled during early morning flows. Flows < $142\ \mathrm{m^3\,s^{-1}}$ did not occur during the study. The fluctuating flow zone was defined as the habitat inundated at flows > 142 and $\leqslant 226\ \mathrm{m^3\,s^{-1}}$. Flows > $226\ \mathrm{m^3\,s^{-1}}$ occurred throughout the study, but epilithon development above the $226\ \mathrm{m^3\,s^{-1}}$ level was almost non-existent (Angradi *et al.*, 1992).

Algae in the fluctuating flow zone had, in the year before the beginning of this study, been subjected to daily exposure, mostly at night (about eight hours a night), and to protracted continuous emersion (two to three days) on some weekends and during controlled special releases. In the second year of this study (summer 1992) epilithon in the original fluctuating flow zone was rarely exposed during the day or at night due to a new operating criteria at the dam. However, during this period cobbles in the permanently inundated zone still supported two to three times more epilithic chlorophyll *a* than did cobbles in the original fluctuating flow zone (cobbles in the new fluctuating flow zone in summer 1992 had almost no epilithon and were not included in this study). *Cladophora* filaments in the permanently inundated zone were dark green and had high epiphyte loads (Angradi *et al.*, 1992). Epilithon on cobbles in the fluctuating flow zone was dominated by diatoms and the crustose blue–green algae *Oscillatoria* spp. (T. Angradi, personal observation). Colonization by *Cladophora* of cobbles in this zone was very slow and was probably reset by occasional exposure (T. Angradi, personal observation).

METHODS

General

Five field experiments were conducted. A single method for collecting epilithon samples was used throughout: cobbles were removed from the river and a randomly located 4·15 cm^2 circular area was isolated on the upper surface of each cobble with a template. Algal filaments, including those attached outside the sample area, and other material within the template were sheared off, scraped loose with a chisel-shaped knife (#17 X-acto) and placed in a vial. Our method probably resulted in slight overestimates of epilithon biomass and chlorophyll content per m^2 of the river bottom in the littoral zone because we only sampled cobbles that could be removed from the river bottom, whereas occasional gaps in the epilithon occur naturally on cobble bars. Also, we made an effort to collect cobbles of a similar size to reduce variability within and among replicates. Substrate size has been shown to affect the biomass of attached *Cladophora* (Dodds, 1991).

Two methods were used to determine chlorophyll *a*. In experiments I–III (1991) samples were ground with a Teflon pestle and chlorophyll *a* was extracted for 24 hours in 90% acetone. In experiments IV–V (1992), chlorophyll *a* was extracted from unground samples by boiling in methanol. The pheophytin-corrected chlorophyll *a* concentration of extracts was determined by spectrophotometry (Spectronics 21) using the method of the APHA (1989) for acetone and of Tett *et al.* (1977) for methanol. More chlorophyll *a* could be extracted in methanol, so comparisons of absolute chlorophyll *a* content among experiments using different methods were not made. The ash-free dry mass (AFDM) of samples was determined from loss on ignition (550°C, two hours).

In experiments I–IV, treatment manipulations were performed on replicate experimental units which consisted of open-sided plastic boxes (modified utility crates, 40 × 40 × 10 cm), each containing four cobbles. In experiment VI, individual cobbles were tested. The tops of cobbles protruded above the sides of the boxes and there was no evidence for an effect of the boxes on the water velocities to which the cobbles were exposed.

Ambient photosynthetically available radiation (PAR, $\mu mol\ s^{-1}\ m^{-2}$; 400–700 nm) was measured with quantum sensors (Li-Cor). Cumulative PAR ($mol\ m^{-2}$) was used as an index of the total amount of solar radiation to which exposed cobbles were subjected. Meterological data (air temperature and relative humidity) for periods of exposure were obtained from sensors located at the dam (Table I).

Experiment I: Continuous atmospheric exposure

In experiment I we evaluated the rate of chlorophyll *a* decomposition on cobbles subjected to prolonged continuous exposure to the atmosphere. Twenty cobbles were collected from the permanently inundated zone at 14 Mile Bar, placed, in groups of four, into five boxes and exposed to the atmosphere. The geometric mean diameters, $(l \times w)^{0.5}$, of cobbles used in experiments I, II and III were 161, 147 and 152 mm; all cobbles were collected in the same vicinity and the mean diameter did not differ among treatments or experiments. A single sample was collected from a randomly located point on the upper surface of each cobble in each replicate box at 0, 10, 24, 58, 130 and 336 hours (two weeks).

The chlorophyll *a* content and AFDM of all samples were determined and the individual values for the four cobbles in each replicate unit (plastic box) were averaged. The cumulative PAR ($mol\ m^{-2}$) received by the exposed cobbles was calculated from 15 minute averages.

Experiment II: Reinundation following exposure

In experiment II we examined epilithon chlorophyll *a* and AFDM as a function of exposure duration and time since reinundation of the cobbles after exposure. The experiment was conducted in a 30 m section of a concrete sluiceway channel at the base of Glen Canyon dam. The channel conveys seepage from within the dam to the river. It has a trapezoid profile, is 0·5 m deep, 0·6 m wide at the bottom and 0·9 m wide at the top. Discharge in the sluiceway is regulated by a sump and was about 0·03 $m^3\ s^{-1}$. A 0·2 m high weir was installed

Table I. Meteorological data for experiments I–IV. Dates and times refer to periods of epilithon exposure. Values are means based on hourly records. PAR refers to maximum (full sun) photosynthetically available radiation (400–700 nm) during exposure. Temperature and relative humidity data are from sensors located at Glen Canyon Dam

Experiment No.	Date(s)	Time	Temperature (°C)		Relative humidity (%)		PAR (μmol s^{-1} m^{-2})
			Day	Night	Day	Night	
I	4–11 July 1991	NA*	33·1	28·3	23	30	2300
	15–12 July 1991	NA	34·6	30·0	17	20	2200
II	11 July 1991	NA	NA	28·7	NA	25	NA
	12 July 1991	NA	34·0	29·4	20	25	2240
	13 July 1991	NA	34·1	NA	22	NA	2240
III	22 August 1991	NA	33·3	29·0	19	24	2140
	23 August 1991	NA	33·7	28·5	20	33	1920
IVa	24 June 1992	1000–1100	31·1	NA	29	NA	1800
		1100–1200	32·3	NA	23	NA	1900
		1200–1400	34·2	NA	19	NA	1460
		1400–1600	31·4	NA	21	NA	720
		1600–1800	30·0	NA	23	NA	900
IVb	11 August 1992	1000–1100	32·6	NA	28	NA	1850
		1100–1200	34·4	NA	26	NA	2075
		1200–1400	35·6	NA	22	NA	2020
		1200–1600	35·6	NA	20	NA	1380
		1600–1800	32·0	NA	28	NA	864

*NA = not applicable.

at the half-way point and at the downstream end of the 30 m section to create two sections (blocks) of nearly equal depth and velocity. Before the experiment, the flow was diverted from the sluiceway and the attached algae were removed.

For the experiment, 48 cobbles were collected from the permanently inundated zone at 14 Mile Bar, transported to the dam in river water, randomly placed in 12 boxes, and the boxes were placed, six each, into two 15 m sluiceway sections. Cobbles were sampled and exposed for 0, 24 (one day and night), or 48 hour (two days and two nights; $n = 4$ for each treatment), reinundated in the sluiceway, and resampled after one day, one week and two weeks. Each sample was equal to about 2% of the upper surface of each cobble. We observed no effect of sampling on the subsequent condition of the remaining epilithon. Chlorophyll *a* content and AFDM were determined as in experiment I.

To quantify the rate of algal colonization in the sluiceway during the experiment, 25 sandstone tiles (approximately 15 × 15 × 2 cm) were placed in each sluiceway section. Five tiles were collected from each section at five day intervals. The accrued material was removed from each tile with a stiff brush, homogenized, subsampled and analysed for chlorophyll *a* and AFDM as in experiment I.

Experiment III: In situ *reinundation after exposure*

In experiment III we attempted to verify the findings of experiment II *in situ*. Four cobbles from 14 Mile Bar were placed in each of nine boxes and exposed for 0, 24, or 48 hours ($n = 3$ for each treatment), reinundated in the permanently inundated zone at 14 Mile Bar, and resampled after one day, one week and two weeks. The water velocity *in situ* (0·3–0·8 m s^{-1}, depending on flow) was higher than in the sluiceways (0·1 m s^{-1}).

Experiment IV: Short-duration exposures

In experiment IV we examined the effects of short duration (up to eight hours) daytime exposure on epilithon from the permanently inundated (experiment IVa) and fluctuating flow zones (experiment IVb). For each experiment, four cobbles, collected at 14 Mile Bar, were placed in each of 24 boxes, sampled, exposed for 0, 1, 2, 4, 6, or 8 hours ($n = 4$ for each treatment), reinundated in the permanently inundated zone, and resampled after one, two and four weeks. The four samples from each replicate were combined, homogenized and subsampled. One subsample was extracted in methanol for chlorophyll *a* determination, and a second subsample was ashed for AFDM. PAR data were collected at 15 minute intervals while the cobbles were exposed.

Experiment V: Primary productivity

In experiment V we examined the effect of exposure on the primary productivity of epilithon from the permanently inundated and fluctuating flow zones. Primary productivity was measured in a Plexiglass photosynthesis-respiration chamber (37 × 23 × 12 cm; after Bott *et al.*, 1978). An electric pump circulated water in the chamber at 10–15 l s^{-1}. Chamber water was circulated past a probe (Hydrolab Datasonde III) which measured dissolved oxygen and temperature. The chamber, pump and probe were submerged in a 150 l bath at the river's edge. Fresh river water was continuously circulated through the bath by a pair of diaphragm pumps. This allowed the water temperature within the chamber to be held within 2°C of the river during incubations.

Incubations were made using cobbles in four treatment groups: unexposed and exposed cobbles from the permanently inundated and fluctuating flow zones. Cobbles were exposed for one or two days. Exposed cobbles were tested after 6–10 days of reinundation (cobbles were exposed in groups, but tested individually, which accounts for the variation in reinundation time; other experiments indicated only small effects for differences in reinundation time of this magnitude). Before incubation, a circular template (35 cm^2) was used to isolate one (cobbles from the permanently inundated zone) or two (fluctuating flow zone) patches of epilithon on the upper surface of the cobble; epilithon outside the template was removed with a wire brush without disturbing the remaining algae. The mean geometric diameter of cobbles was 170 mm, and did not differ significantly among treatments.

Net primary productivity (NPP, $g\,O_2\,m^{-2}\,h^{-1}$) measurements were made between 1000 and 1400 hours. To allow the examination of the effect of exposure on the photosynthesis-irradiance relationship, the light intensity during incubations was varied using greenhouse shading. Incubations at each light intensity lasted 20–60 minutes, depending on the rate of dissolved oxygen change; chamber water never became supersaturated with O_2. The PAR at the water surface was recorded at five minute intervals. Community respiration for each cobble (R_c, $g\,O_2\,m^{-2}\,h^{-1}$) was measured during the night of the day on which the NPP was estimated. The gross primary productivity (GPP, $g\,O_2\,m^{-2}\,h^{-1}$) was calculated as NPP + R_c (Bott *et al.*, 1985). The chlorophyll assimilation ratio (AR; $mg\,O_2$ mg chlorophyll $a^{-1}\,h^{-1}$) provides an estimate of photosynthetic activity per unit of algal pigment.

After the incubations, the cobbles were scraped and the material was analysed as in experiment IV. For exposed cobbles, samples were collected before and after exposure to allow the determination of the reduction in chlorophyll *a* content.

Statistical analysis

In experiment I, the rate of chlorophyll *a* decomposition and rate of biomass loss were calculated as the slope of a linear regression of $\log_{10}$ of the percentage of the initial chlorophyll *a* or biomass remaining as a function of time and cumulative PAR. For all experiments, residual plots indicated heteroscedasticity; appropriate logarithmic transformations were performed (Zar, 1984). In experiments II–IV, one-way ANOVA was used to examine the effect of treatment (duration of exposure) on the $\log_{10}$ transformed percentage of initial chlorophyll *a* and biomass remaining on each sample date after reinundation; Tukey comparisons ($\alpha = 0{\cdot}05$ experimentwise error rate) revealed treatments that were significantly different. A preliminary analysis indicated no block (sluiceway section) effect for any dependent variable in experiment II, so data for blocks were combined. In experiment V, analysis of covariance was used to examine the effects of treatment on GPP and AR; PAR was the covariate. Photosynthesis–irradiance relationships were examined with linear regression of $\log_{10}$-transformed variables.

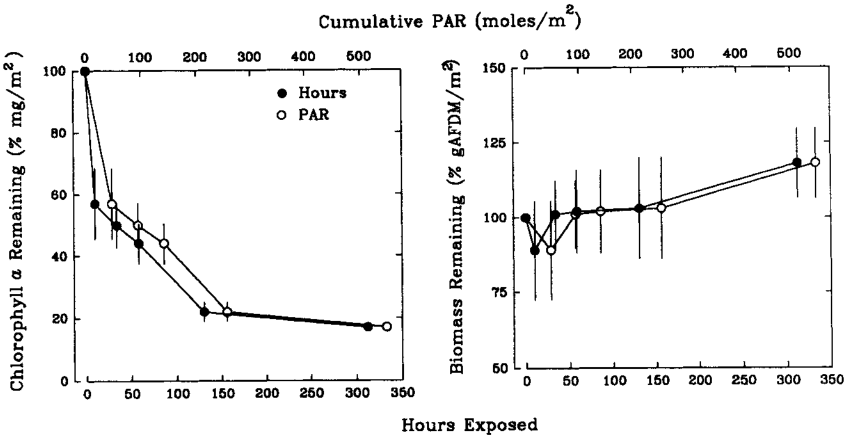

Figure 1. Mean (SE) percentage of initial chlorophyll *a* (chl *a*) and biomass remaining after exposure (Experiment I). Initial values [chl *a* (mg m^{-2}), biomass (g AFDM m^{-2})] are 655(94) and 201(22). Regression models are: $\log_{10}$ percentage chl *a* remaining = 2·05 – 0·31$\log_{10}$ hours exposed (r^2 = 0·73; n = 30); $\log_{10}$ percentage chl *a* remaining = 2·08 – 0·27 $\log_{10}$ cumulative photosynthetically available radiation (PAR) (r^2 = 0·66; n = 30)

RESULTS

Experiment I: Continuous atmospheric exposure

Epilithon was rapidly bleached from dark green to tan brown during exposure. After 10 hours of exposure, 57% of the initial chlorophyll *a* remained; after two weeks, 16% remained (Figure 1). Linear regression functions (dependent variable = $\log_{10}$ percentage initial chlorophyll *a* remaining) were significant for both time exposed and cumulative PAR (Figure 1). The percentage biomass remaining did not change with time exposed or cumulative PAR (r^2 < 0·04).

Experiment II: Reinundation following exposure

In experiment II, and in all subsequent experiments, exposed epilithon started to turn brown within a few days of reinundation. Epilithic chlorophyll *a* decreased by 40–70% after 24 hours of reinundation, and 65–80% after one week, depending on treatment (Figure 2). The percentage of initial chlorophyll *a* remaining on exposed cobble increased by about 17% in the second week. The effect of exposure was significant on all sample dates (after one day, $F_{2,9}$ = 11·8, p < 0·01; after one week, $F_{2,9}$ = 45·2, p < 0·001; after two weeks, $F_{2,9}$ = 9·4, p < 0·01), although at one day after reinundation, only the 48 hour exposed and 0 hour exposed

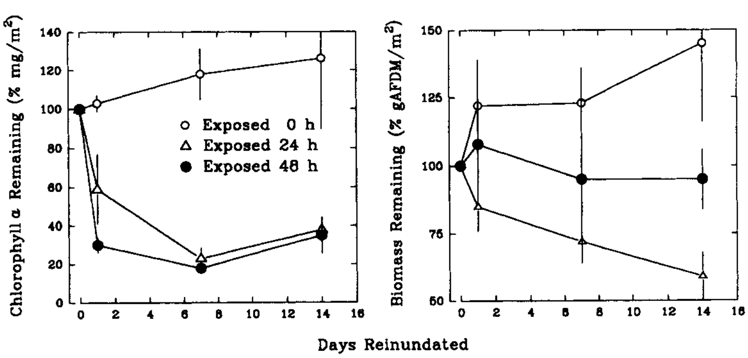

Figure 2. Mean (SE) percentage of chlorophyll *a* (chl *a*) and biomass remaining after exposure and reinundation in a sluiceway at Glen Canyon Dam (Experiment II). Initial values [chl *a* (mg m^{-2}), biomass (g AFDM m^{-2})] are: exposed 0 hours 634(85), 221(31); exposed 24 hours 877(102), 253(21); exposed 48 hours 784(102), 356(63). The apparent recovery of chlorophyll *a* in the second week of the experiment represents colonization by *Ulothrix tenuissima* on previously exposed cobbles

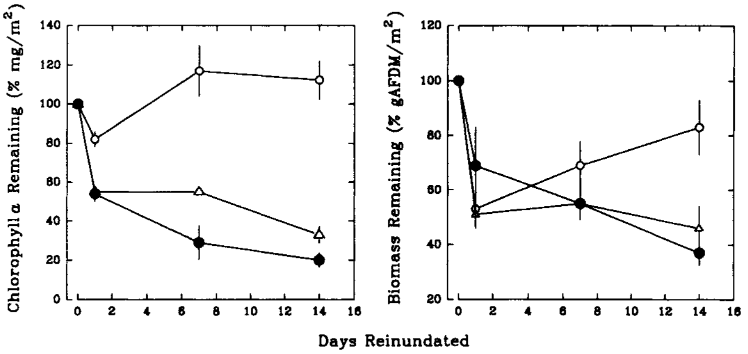

Figure 3. Mean (SE) percentage chlorophyll *a* (chl *a*) and biomass remaining after exposure and reinundation at 14 Mile Bar (Experiment III). Initial values [chl *a* (mg m^{-2}), biomass (g AFDM m^{-2})] are: exposed 0 hours 573(36), 459(24); exposed 24 hours 781(60), 535(42); exposed 48 hours 610(53), 591(103). Symbols as in Figure 2

(control) treatments differed. The mean percentage of initial chlorophyll *a* remaining did not differ significantly between the two exposure treatments (24 or 48 hour exposed) on any sample data ($p > 0{\cdot}05$, Tukey test).

Despite a dramatic loss of chlorophyll *a* in exposed epilithon, the gross physical structure appeared largely intact. The effect of treatment on the percentage biomass remaining was significant only after two weeks when epilithon that had been exposed for 24 hours had 40% less biomass than cobbles not exposed (after one day, $F_{2,9} = 1{\cdot}4$, $p = 0{\cdot}3$; after one week, $F_{2,9} = 2{\cdot}3$, $p = 0{\cdot}16$; after two weeks, $F_{2,9} = 7{\cdot}1$, $p < 0{\cdot}05$). As with chlorophyll *a*, the effects of the 24 and 48 hour exposure treatments were not significantly different.

Sandstone tiles in the sluiceway were quickly colonized by the chlorophyte *Ulothrix tenuissima* Kutz. Accrual of chlorophyll *a* and biomass was rapid after the first week. Chlorophyll *a* accrued at a rate of *ca.* 50 mg m^{-2} day^{-1}, and biomass accrued at a mean rate of *ca.* 8 g AFDM m^{-2} day^{-1} between days 5 and 15. *U. tenuissima* filaments 1–2 m long developed on most tiles; colonization on the plastic boxes and on the bleached filaments of *Cladophora* was observed. *U. tenuissima* is also present in Glen Canyon (D. W. Blinn, personal communication), but is not abundant.

Experiment III: In situ *reinundation after exposure*

Experiment III at 14 Mile Bar confirmed the findings of experiment II (sluiceway experiment). The percentage decrease in chlorophyll *a* was similar to that of experiment II (Figure 3). The effect of exposure was significant on all sample dates (after one day, $F_{2,6} = 21{\cdot}6$, $p < 0{\cdot}01$; after one week, $F_{2,6} = 15{\cdot}2$, $p < 0{\cdot}01$; after two weeks, $F_{2,6} = 41{\cdot}1$, $p < 0{\cdot}001$), but there was no difference between the 24 and 48 hour exposure treatments ($p > 0{\cdot}05$, Tukey test). Unlike experiment II, there was no increase in chlorophyll *a* after the first week.

As in experiment II, the effect of treatment on the percentage biomass remaining was significant only after two weeks (after one day, $F_{2,6} = 1{\cdot}2$, $p = 0{\cdot}37$; after one week, $F_{2,6} = 1{\cdot}1$, $p = 0{\cdot}39$; after two weeks, $F_{2,6} = 8{\cdot}6$, $p < 0{\cdot}05$), and the effects of the 24 and 48 hour exposure treatments were not different ($p > 0{\cdot}05$, Tukey test). The reason for the decline in chlorophyll *a* and biomass on unexposed cobbles at 24 hours after reinundation is not known, but may be attributable to initial sample collection and disturbance induced by repositioning the boxes.

Experiment IV: Short duration exposure

In experiment IVa (permanently inundated zone) there was an inverse relationship between time exposed and the amount of chlorophyll *a* remaining (Figure 4). The effect of exposure was significant after one and two weeks of reinundation (after one week, $F_{5,18} = 3{\cdot}9, p < 0{\cdot}05$; after two weeks, $F_{5,18} = 4{\cdot}2, p < 0{\cdot}05$; after four weeks, $F_{5,18} = 2{\cdot}3$, $p = 0{\cdot}08$). One week after reinundation the chlorophyll *a* of the epilithon that had been exposed for eight hours had decreased more than that of the epilithon exposed for either zero, one or two hours. After two weeks, the eight hour exposure treatment differed from the zero and two hour exposure

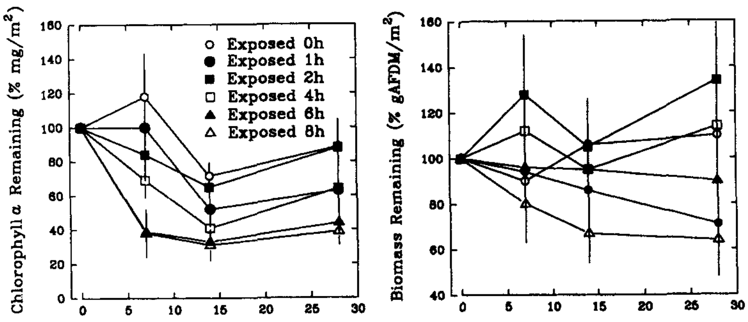

Figure 4. Percentage chlorophyll *a* (chl *a*) and biomass remaining after exposure and reinundation of epilithon from the permanently inundated zone at 14 Mile Bar (Experiment IVa). Initial values [chl *a* ($mg\,m^{-2}$), biomass ($g\,AFDM\,m^{-2}$)] are: exposed zero hours 767(148), 121(11); exposed one hour 876(78), 134(18); exposed two hours 647(92), 109(19); exposed four hours 801(202), 120(27); exposed six hours 1160(403), 127(32); exposed eight hours 1058(250), 157(19)

treatment. The exposure duration had no effect on the percentage biomass remaining on any sample data (after one week, $F_{5,18} = 0{\cdot}7$, $p = 0{\cdot}62$; after two weeks, $F_{5,18} = 1{\cdot}0$, $p = 0{\cdot}47$; after four weeks, $F_{5,18} = 2{\cdot}2$, $p = 0{\cdot}10$).

In experiment IVb (fluctuating flow zone), there was no effect of exposure duration on the percentage of chlorophyll *a* remaining after one week ($F_{5,17} = 0{\cdot}7, p = 0{\cdot}64$). After two weeks there was a significant treatment effect ($F_{5,17} = 4{\cdot}9, p < 0{\cdot}01$): the chlorophyll *a* content of epilithon exposed for six and eight hours was significantly less than that of epilithon exposed for one hour (Figure 5). After four weeks the same trend was evident, though not significant ($F_{5,18} = 2{\cdot}4, p = 0{\cdot}08$). There was no effect of exposure duration of the percentage biomass remaining of any sample date (after one week, $F_{5,18} = 0{\cdot}7$, $p = 0{\cdot}64$; after two weeks, $F_{5,18} = 1{\cdot}1, p = 0{\cdot}41$; after four weeks, $F_{5,18} = 0{\cdot}3, p = 0{\cdot}9$).

Experiment V: Primary productivity

The mean GPP was higher for unexposed cobbles than for exposed cobbles for both the permanently inundated ($F_{1,73} = 65{\cdot}8, p < 0{\cdot}001$) and fluctuating flow zones ($F_{1,46} = 20{\cdot}9, p < 0{\cdot}001$) (Figure 6). The GPP of unexposed cobbles from the permanently inundated zone was about 10 times higher than the GPP of unexposed cobbles from the fluctuating flow zone. However, the GPP of unexposed cobbles from the fluctuating flow zone approached that of exposed cobbles from the permanently inundated zone.

There was no effect of exposure on the AR of permanently inundated cobbles ($F_{1,73} = 1{\cdot}3$, $p = 0{\cdot}26$). When the effect of an outlier was eliminated (Figure 6, plot 2) there was no effect of exposure on the AR

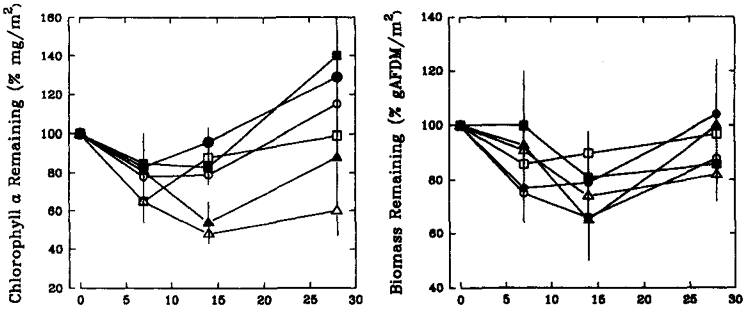

Figure 5. Percentage chlorophyll *a* (chl *a*) and biomass remaining after exposure and reinundation of epilithon from the fluctuating flow zone at 14 Mile Bar (Experiment IVb). Initial values [chl *a* ($mg\,m^{-2}$), biomass ($g\,AFDM\,m^{-2}$)] are: exposed zero hours 300(17), 118(9); exposed one hour 334(41), 139(27); exposed two hours 271(34), 99(13); exposed four hours 342(47), 131(11); exposed six hours 302(47), 120(16); exposed eight hours 307(24), 124(11). Symbols are as in Figure 4

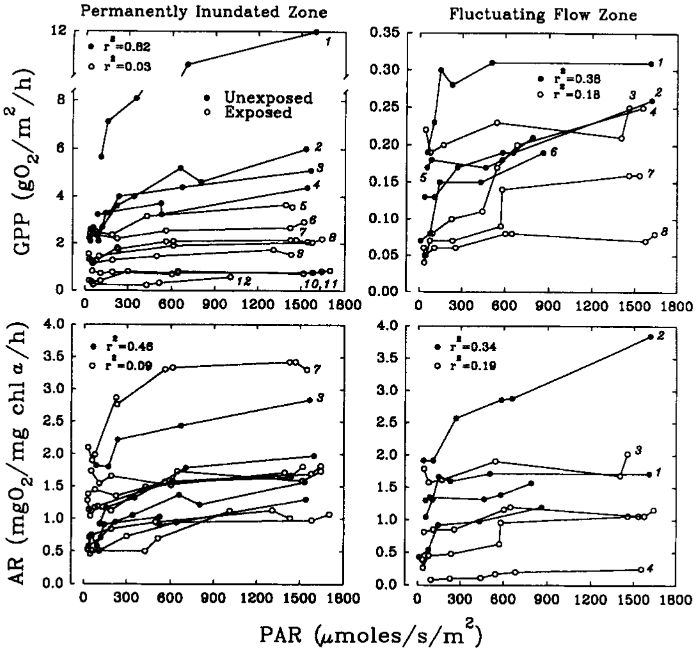

Figure 6. Relationship between gross primary production (GPP) and photosynthetically available radiation (PAR) and between assimilation ratio (AR) and (PAR) for unexposed and exposed epilithon from the permanently inundated and fluctuating flow littoral zones. Each plot is for an individual cobble. Closed circles refer to unexposed cobbles; open circles refer to exposed cobbles. Regression statistics are given for models that include all cobbles in each treatment group from each zone. Plot numbers refer to experimental parameters given in the Appendix; some plot numbers omitted for clarity

of cobbles from the fluctuating flow zone ($F_{1,40} = 2{\cdot}0$, $p = 16$), nor was there an effect of zone on AR for pooled treatments ($F_{1,122} = 0{\cdot}18$, $p = 0{\cdot}67$).

Linear regression functions for the relationship between GPP and PAR and between AR and PAR were significant ($p < 0{\cdot}05$, Figure 6) for all treatment and level combinations except for the effect of PAR on the GPP of exposed cobbles from the permanently inundated zone ($p = 0{\cdot}13$). The PAR explained more of the variation in GPP and AR on unexposed (34–82%) versus exposed cobbles (0·09–0·19%, Figure 6), probably because exposed epilithon was light-saturated at a lower PAR level. There was no apparent relationship between epilithon parameters (Appendix) and GPP except that the two samples with the most chlorophyll *a* had the highest GPP; use of AR eliminated this effect.

DISCUSSION

In experiment I, the similarity of the time and PAR functions (Figure 1) is accounted for by the relatively constant environmental conditions during the experiment (Table I). Under more variable environmental conditions, for exposures of shorter duration, and for among-site and among-season comparisons, the cumulative PAR should be a more reliable predictor of chlorophyll *a* decomposition with exposure. Exposure to solar radiation was probably the most important determinant of mortality as the relative humidity and air temperature were similar during the day and at night (Table I). Usher and Blinn (1990) showed little effect of night-time exposure of *Cladophora*.

Chlorophyll *a* was much more sensitive to exposure than biomass (Figures 2–6). This finding is partly an artifact of the duration of the experiments: bleached filaments, although chlorophyll-depleted, retained most of their ash-free biomass. On reinundation, these filaments were not immediately sloughed from the epilithon *en masse*, but appeared to fragment incrementally.

There is probably a continuous inverse relationship between exposure (time or PAR) and percentage of initial chlorophyll *a* remaining, at least in the short term (Figure 7), but the inherent variability of the epi-

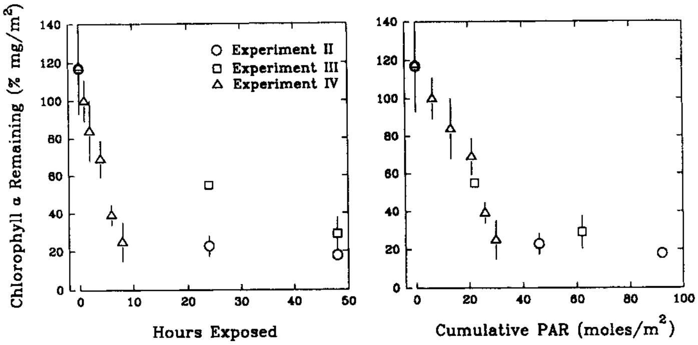

Figure 7. Percentage chlorophyll *a* remaining after exposure and reinundation for one week versus time exposed and cumulative photosynthetically available radiation (PAR). Values are means (SE). Regression models are $\log_{10}$ percentage chlorophyll *a* remaining = 2·07 − 0·43$\log_{10}$ hours exposed (r^2 = 0·79; n = 12); $\log_{10}$ percentage chlorophyll *a* remaining = 2·14 − 0·38 cumulative PAR (r^2 = 0·76; n = 12). Models for two weeks of reinundation were similar

lithon precluded detection of significant effects for exposures of less than about six hours or 10–15 mol m^{-2} (experiment IV, based on June–August conditions). Under the conditions of our experiments, the effects of one versus two days of exposure were similar. However, under less severe conditions (i.e., less PAR, higher humidity) the disturbance threshold could shift from six to eight hours to 12 daylight hours or longer.

The actual mechanism of chlorophyll destruction with exposure are uncertain. Usher and Blinn (1990) hypothesized that ultraviolet (UV) radiation damages exposed basal holdfasts, which weakens the filaments enough for them to break off and become entrained. Citing studies of intertidal macroalgae, they proposed that many holdfasts are protected by overlying filaments, which provide some resistance to UV damage. Our observations do not corroborate this hypothesis as even severely damaged filaments remained attached after reinundation. We emphasize that under summer conditions of prolonged daytime exposure (≥ eight hours), most of the filaments are bleached, and the productive capacity of the epilithon is largely destroyed.

There is some evidence from our study (experiment IVb) that epilithon from the fluctuating flow zone was more tolerant of exposure than epilithon from the permanently inundated zone (Figures 3 and 4). The relative reduction of chlorophyll *a* and biomass was less and recolonization (measured as the increase in chlorophyll *a* after week two) was greater in exposed epilithon from the fluctuating flow zone. The blue-green alga, *Oscillatoria*, is reported to be tolerant of exposure (Blinn *et al.*, 1992), and may be capable of replacing *Cladophora* in the fluctuating flow zone in Glen Canyon under flow regimes that include occasional daytime exposures. The productivity (e.g. GPP, Figure 8) and surface area (discussed later) of epilithon from the fluctuating flow zone is much lower than that of the intact *Cladophora*-dominated epilithon.

Although epilithon from the permanently inundated zone was as much as 10 times more productive, it had an assimilation ratio similar to that of the epilithon from the fluctuating flow zone. Furthermore, exposure did not greatly alter the assimilation ratios of epilithon. The GPP appeared to be a constant function of the amount of chlorophyll *a* present. Changes in the GPP resulting from exposure can therefore be predicted with a simple model that includes cumulative PAR and initial chlorophyll *a* (Figure 8). The GPP range predicted by the model is in agreement with published studies of production for similar chlorophyll *a* levels (Bott *et al.*, 1985). The response of epilithon to exposure will vary among seasons as the light regime changes, but the form of the model may be general for other regulated rivers where seasonal changes in community composition, temperature and nutrient availability are small.

The reach-wide loss of GPP resulting from exposure depends on the channel morphology and the flow regime. A model incorporating channel morphology and cobble distribution (Figure 8) indicates that changes in reach-wide littoral production are an approximately linear function of minimum daytime flow (especially on weekends when daytime flows are lowest) over the range of normal water releases (140 to > 566 $m^3 s^{-1}$); loss of reach-wide GPP would increase dramatically at flows < 140 $m^3 s^{-1}$. The model overestimates the loss in GPP because it does not include the relatively small amount of GPP by recolonizing

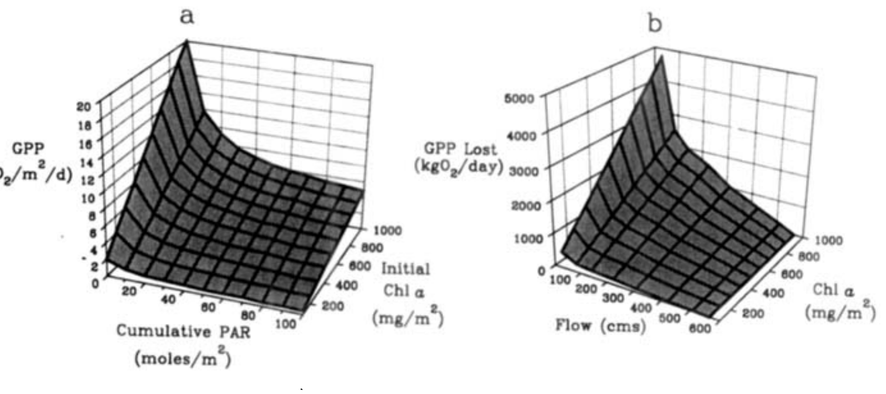

Figure 8. (a) Gross primary production (GPP) of epilithon from the permanently inundated zone as a function of cummulative PAR and initial chlorophyll *a* content and (b) loss of GPP from the first 12 km of littoral cobble habitat downstream from Glen Canyon Dam as a function of flow and the chlorophyll *a* content of epilithon. The GPP was calculated for a range of chlorophyll *a* values and the relationship between assimilation ratio (AR) and photosynthetically available radiation (PAR) for unexposed cobbles from the permanently inundated zone ($\log_{10}AR = -0{\cdot}56 + 0{\cdot}26\log_{10}PAR$; $r^2 = 0{\cdot}46$; $n = 25$). Ambient PAR data for 15–17 July 1991 were used. The GPP was then recalculated for exposure durations (cumulative PAR) using the relationship between percentage chlorophyll *a* remaining and cumulative PAR (see Figure 7 caption). An assumption of the model was that AR did not vary with exposure or chlorophyll content (see Figure 6). In (b), flow refers to the lowest discharge and resulting river surface elevation at which a viable *Cladophora*-dominated epilithon is present. Lost GPP refers to the reduction in GPP compared with summertime littoral production if a *Cladophora*-dominated epilithon were present up to the 566 $m^3 s^{-1}$ level. Estimates of littoral area were based on channel profiles from a 1990 survey of fixed rangelines (US Bureau of Reclamation, unpublished data); the distribution of cobble substrates was determined from aerial photographs. Model (b) was generated by calculating the GPP for a range of chlorophyll *a* values and ambient PAR data for 5–17 July 1991, as was carried out for model (a). The GPP was then expressed on a reach-wide basis and the lost GPP at flows lower than 566 $m^3 s^{-1}$ calculated. Estimates of partial loss due to the incomplete destruction of the epilithon without a change in flow regime can be derived by calculating the endmember chlorophyll *a* value using the relationship between the PAR and the percentage chlorophyll *a* remaining (Figure 7). An assumption of the model is that light limitation does not occur in the littoral zone at any flow $\leqslant$566 cm s^{-1} (M. D. Yard, Bureau of Reclamation, unpublished data)

algae. In effect, the model predicts the GPP immediately after a severe exposure disturbance; the relative magnitude of the overestimation of loss would increase with time since disturbance.

The impact of lost primary production on the Glen Canyon ecosystem is difficult to evaluate without estimates of secondary production on littoral cobble bars versus secondary production in other habitats, and a better understanding of trophic linkages in the ecosystem. Cobble bars comprise only about 16% of the total littoral habitat in Glen Canyon; the bulk of the remaining substrate is comprised of relatively unproductive (10–20 mg chlorophyll *a* m^{-2}; T. Angradi, unpublished data) sandy substrates. The importance of *Cladophora*-colonized cobble bars is disproportionate to its area, and even relatively moderate losses of epilithon GPP could have a large effect on the Glen Canyon trophic structure.

Effects of exposure disturbance on primary productivity are likely to be protracted. Recolonization of substrates in Glen Canyon is slow; studies of the algal colonization of introduced substrates at 14 Mile Bar indicated that the accrual of chlorophyll *a* to the levels found on natural cobbles would take four to six months in the permanently inundated zone, and even longer in the fluctuating flow zone (Angradi *et al.*, 1992). These findings suggest that *Cladophora* has low resilience after disturbance. This conclusion is supported by the observations of Dodds (1991) who studied *Cladophora* in an ephemeral channel, and of Fisher *et al.* (1982) who found that *Cladophora* was a late successional species after flash floods in desert streams.

The available evidence suggests the following scenario: *Cladophora*, once established, thrives in the upper Glen Canyon, even on substrates exposed to daily exposure (mostly at night). *Cladophora* appears to have a competitive advantage over other taxa under these conditions (Usher and Blinn, 1990), but is not resistant to protracted daytime exposure, especially in summer. The combination of daily night-time exposure and low dissolved nutrient concentrations results in very low post-disturbance recolonization rates of *Cladophora* (Steinman and McIntire, 1990; DeAngelis *et al.*, 1990; T. Angradi, unpublished data) and the establishment and maintenance of a non-filamentous phytobenthos.

The consequences of a shift to early colonizers and resistant taxa, such a *Oscillatoria*, to ecosytem function

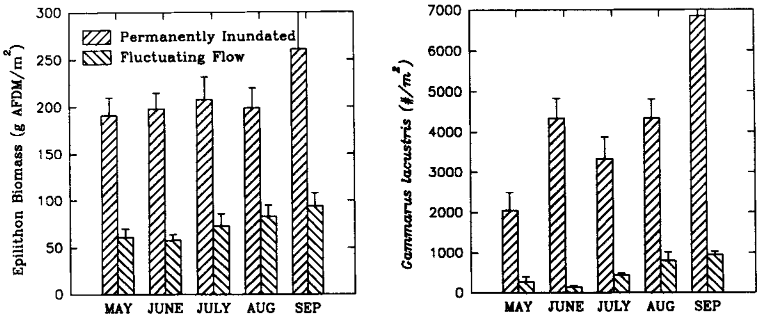

Figure 9. Epilithon biomass and density of *Gammarus lacustris* in the permanently inundated and fluctuating flow littoral zones at 14 Mile Bar in 1992. Epilithon biomass values are means (SE) values ($n = \geqslant 10$) for samples collected using the same methods as for exposure experiments. *Gammarus lacustris* densities [mean (SE); $n = 8$] are from Hess samples (0·087 m^2) collected at 14 Mile Bar (D. Parmley, unpublished data)

(e.g. trophic structure, macroinvertebrate habitat) in Glen Canyon are not known. As is often the case below dams with hypolimnetic discharge, the Glen Canyon epilithon lacks the functional redundancy and taxonomic evenness of most unregulated rivers (Ward, 1976; Petts, 1984; Dufford *et al.*, 1987). Filamentous macroalgae other than *Cladophora* are rare (Blinn *et al.*, 1992) and vascular hydrophytes are restricted to depositional areas. Thus the physical and autecological characteristics of *Cladophora* are unique to that species on Glen Canyon cobble bars.

Studies of the ecology of the amphipod *Gammarus lacustris* at 14 Mile Bar indicate a potential higher trophic level response to disturbance of the epilithon. The macroinvertebrate fauna of Glen Canyon is depauperate (Blinn and Cole, 1991) and only a few taxa, including *Gammarus*, constitute most of the diet of rainbow trout (*Oncorhynchus mykiss*), the most abundant fish species in Glen Canyon (Angradi *et al.*, 1992). *Gammarus* were, on average, eight times more abundant in the permanently inundated littoral zone where *Cladophora* biomass was high, than in the fluctuating flow littoral zone where *Cladophora* was largely absent (Figure 9). Stable isotope analyses (^{13}C, ^{15}N) revealed that assimilated C and N in *Gammarus* collected at 14 Mile Bar originated from diatoms rather than from *Oscillatoria*, terrestrial detritus, or seston exported from Lake Powell (T. Angradi, unpublished data). Intact *Cladophora* has a high surface area which supports a dense assemblage of diatoms (Blinn *et al.*, 1989). The most important ecosystem level function of attached *Cladophora* may be as a habitat for other organisms (Dodds and Gudder, 1992), and reach-wide disruption of this structural function due to exposure could precipitate higher trophic level effects within the Glen Canyon ecosystem.

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APPENDIX

Table AI. Experimental parameters for estimations of GPP and AR (Experiment VI). Plot numbers refer to Figure 7. Cumulative PAR is the total PAR to which exposed cobbles were subjected; '0' PAR denotes cobbles that were not exposed. Chlorophyll *a* and biomass values represent the epilithon sample on which incubations were run

Plot No.	Cumulative PAR ($mol\, m^{-2}$)	Chlorophyll *a* (mg $sample^{-1}$)	Percentage Chlorophyll *a* remaining*	Biomass (g AFDM ($sample^{-1}$)
Permanently inundated zone				
1	0	21·5	100	3·7
2	0	13·5	100	2·5
3	0	6·3	100	1·5
4	0	12·7	100	2·1
5	47	7·5	84	2·6
6	64	5·7	30	2·9
7	64	4·4	30	1·1
8	37	4·3	80	1·2
9	37	5·4	80	1·5
10	31	1·6	60	0·5
11	31	5·5	60	1·6
12	47	1·6	65	0·8
Fluctuating flow zone				
1	0	1·2	100	0·5
2	0	0·5	100	0·2
3	47	0·9	36	0·6
4	64	0·9	30	0·7
5	0	0·9	100	0·3
6	0	1·1	100	0·4
7	37	1·1	77	0·6
8	23	0·5	36	0·4

*Values are based on unreplicated samples; values for exposed material from the fluctuating flow zone overestimate the percentage chlorophyll *a* remaining.