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Abstract. Flow variation associated with hydropower production causes periodic exposure of zones along the banks of regulated rivers. These zones have reduced algal biomass and lower productivity. We investigated whether algal assemblages in regulated rivers differed in tolerance to aerial exposure because understanding such tolerance could be used to alter water releases to improve downstream productivity. In field experiments, we tested algal tolerance to aerial exposure in 3 assemblages: green filamentous and cyanobacterial assemblages in Thailand and a mixed (filamentous green + cyanobacteria) assemblage in New Zealand. Algae-bearing stones were exposed at night, during the day (in sun or shade, with or without simulated rain), or continuously, or were continuously submerged (with a handling control). Exposure reduced cyanobacterial chlorophyll *a*, and reduction was greater with day than with night exposure. Mixed algal assemblages showed a similar pattern in chlorophyll *a*, but ash-free dry mass (AFDM) did not change (bleached algae remained). In contrast, green filamentous algae survived better when exposed than when submerged, and when exposed during the day than at night. Snails consumed green filamentous algae, and submersion resulted in high grazing loss of filamentous algae but not cyanobacteria. Grazing pressure was presumably lower at night during water release. For cyanobacteria, shade and rain slightly increased chlorophyll *a* retention. For filamentous green algae, shade had no effect, and rain was beneficial in the shade but not the sun. Our experiments demonstrated an interaction among variable hydraulic conditions, activity of grazing snails, and availability of grazing-susceptible algae. A longer wet–dry cycle, daytime water release, and a shaded riparian zone reduced aerial exposure effects on algal assemblages, indicating that water releases can be regulated to improve productivity in the downstream exposed zone.

Key words: hydropower peaking, varial zone, regulated rivers, stream drying, benthic algae, periphyton ecology, algal grazing.

Frequent water-level change occurs naturally in marine intertidal zones and unnaturally because of water regulation by humans in streams and rivers. The regular, predictable pattern of water-level change in intertidal zones contrasts sharply with the changing, much less predictable pattern of water-level fluctuation in regulated rivers. Temporary, intertidal water-level changes have existed over geological and evolutionary time scales, whereas water-level fluctuation in regulated rivers is a much more recent phenomenon.

Rocky intertidal zones are highly productive (Littler and Murray 1974, Bustamante et al. 1995) with a suite of exposure-tolerant algae, but frequent aerial exposure of the banks and channels in rocky streams and rivers produces a shoreline zone of low productivity (Angradi and Kubly 1993, Blinn et al. 1998). Freshwater algae are apparently much

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less tolerant of aerial exposure caused by fluctuating flow than marine intertidal algae are of tidal water levels.

The health of the periphyton in periodically exposed river margins affects the local stream food web. Periphyton forms the main autotrophic base of stream food webs and is especially important in regulated river tailwaters where upstream sources of detritus are interrupted (Blinn et al. 1998). If algae tolerate drying conditions poorly, banks that are periodically exposed might add little to aquatic productivity. Indeed, in the Colorado River, Blinn et al. (1998) found that periodically exposed zones had 10-fold lower productivity than permanently wet areas. The periodically exposed zone produced by these changing flows can be extensive (e.g., Blinn et al. 1995). Understanding the mechanisms that cause the low algal biomass and productivity in wet–dry zones of regulated rivers requires understanding the tolerance of freshwater benthic algae to conditions during aerial exposure. Better understanding of exposure tolerance could lead to ways to alter flow releases to protect aerially exposed algae.

Studies of aerial exposure of algae in regulated rivers have centered on a single large river, the Colorado River below Glen Canyon Dam (Arizona, USA). These studies focused on *Cladophora glomerata* and examined short-term and long-term desiccation (Blinn et al. 1995), day–night differences in aerial exposure (Usher and Blinn 1990), regrowth and colonization upon resubmersion (Benenati et al. 1998), fragmentation of exposed mats (Blinn et al. 1995), effects of suspended sediment (Shaver et al. 1997), and the ecological role of *Cladophora* in the Colorado River (Shannon et al. 1994, Blinn et al. 1995, 1998).

Our 1st objective was to investigate factors affecting tolerance of aerial exposure by algal assemblages occurring in tailwaters. We approached this objective by moving algae-covered stones in and out of the water to emulate the rapid exposure and submersion conditions in fluctuating flows. We tested algal tolerance in 3 different assemblages in 2 rivers (Thailand and New Zealand) and several exposure conditions (full sun, shade, simulated rain) and durations. We used results to address our 2nd objective, which was to suggest conditions of water release that might better protect algae in zones with fluctuating flow. The experiments in Thailand were of special interest because of the paucity of studies on the effects of impoundments in the country combined with current plans for new impoundments in northern (the location of our study) and northeastern Thailand (Dudgeon 2000).

Methods

New Zealand: study site

The 8-km long Monowai River is in the Southland District on the South Island of New Zealand. The river is the outflow of 31-km^2 Lake Monowai, which is just inside the mountainous terrain of Fiordland National Park. Water release from Lake Monowai is regulated for hydropower production in a down-river facility. The Monowai River flows out of the national park and transverses a shrubby plain before its confluence with the Waiau River. The Monowai River has a narrow, densely wooded riparian zone. The substrate is dominated by quartz-rich sandstone cobbles and boulders. Upper rock surfaces had a dense coat of periphyton dominated by filamentous green algae. Globose colonies of cyanobacteria were also present.

New Zealand: experiment

This experiment tested the short-term tolerance of a mixed algal assemblage to aerial exposure at night vs during the day. We used 4 exposure treatments: (continuously) submerged, exposed at night, exposed during the day, and a handling control. We collected 24 cobbles with a visible periphyton mat from the unshaded center of the river. The experiment was sited along the shore of the Monowai River in the reach where we collected the stones. The site had little canopy cover. Stones were randomly assigned to treatments and placed on the stream bed. Submerged stones were left alone for 3 d. Handled stones were picked up, agitated underwater, and removed from or replaced back into the water at dawn and dusk. Night-exposed stones were removed from the water at dusk, placed on an open grassy area just beyond the shaded riparian zone, and returned to the water at dawn, whereas day-exposed stones were removed from the water at dawn and replaced at dusk. The experiment ran from 14 to 17 February 2000. Pioneer Generation supplied flow data from the Monowai River below the control gates at the Lake Monowai dam (site 79712).

Thailand: study site

Mae Ngad Reservoir is located in Chiang Mai Province in northern Thailand. The upstream section of Mae Ngad River runs through a densely populated valley, but the reservoir and several smaller tributaries are located within Sri Lanna National Park. The 16-km^2 reservoir is used for irrigation via a concrete canal and for hydropower, which releases into the downstream Mae Ngad River. During hydropower production, 10 m^3/s of hypolimnetic water is

TABLE 1. List of treatments used in experiments in New Zealand and Thailand on the effects of aerial exposure on epilithic algal assemblages. Dawn to dusk = ~0700–1700 h, dusk to dawn = ~1800–0700 h.

Treatment name	Description	New Zealand	Thailand
Exposed (continuously)	Exposed on the unshaded bank during the entire experiment		X
Submerged (continuously)	Submerged during the entire experiment	X	X
Night	Exposed on the bank from dusk to dawn	X	X
Sun (= day)	Exposed on the unshaded bank from dawn to dusk	X	X
Shade	Exposed under the riparian canopy from dawn to dusk		X
Sun + rain	Sun exposure as described above, with simulated rain at ~1300 h		X
Shade + rain	Shade exposure as described above, with simulated rain at ~1300 h		X
Handling	Fully submerged stones that were handled 2× daily (at dawn and dusk)	X	X

released; no water is released when power is not being produced. Hence, discharge alternates between negligible flow and 10 m³/s.

The habitat directly below the dam is highly modified, and consists of a sloped, brick-sided channel with a concrete bottom overlain with native sandstone cobbles and introduced larger, rough granitic boulders. Patches of coarse sand were downstream of some boulders. During our experiments, a mat of filamentous green algae covered the tops of submerged stones. When water was not released, the area was a shallow pool with many emergent rocks in the shallower edges. Scattered surface-dwelling hemipterans were the only apparent macroinvertebrates. Introduced mimosa trees dominated the riparian zone.

Approximately 0.5 km downstream from the dam, the river widens and opens into an extensive lateral wetland that reduces the speed of water-level change. Downstream substrates in the river ranged from coarse sand to fine gravel with scattered sandstone cobbles, which were concentrated in the riffles. In February, algal assemblages appeared as 0.5-mm-thick, bumpy dark green mats dominated by cyanobacteria. Snails were abundant on the streambed, planarians were common on the undersides of rocks, and crabs and a variety of aquatic insects were also present. The riparian zone was narrowed by farming and was scrubby with a row of mimosa trees on one side.

Thailand: experiments

We tested the effects of aerial exposure on 2 algal assemblages: the filamentous green algal assemblage found directly below the dam and the cyanobacterial assemblage found 0.5 km downstream. The study design called for separate side-by-side experiments for each assemblage. We ran experiments at the downstream site because of greater accessibility and safety, and because the smaller, more gradual changes

in water level reduced the likelihood of stone displacement. The extensive pool used in the experiment had a fine gravel substrate, negligible current (during periods when water was not released), and a depth of 30 to 40 cm.

We used 7 treatments to mimic the effects of aerial exposure at night vs day, in sun vs shade, and with rain vs dry relative to submerged controls (Table 1). We selected 2 bank sites for aerial exposure. The sun site lacked upright riparian vegetation, but the upper bank shaded the site in the late afternoon. A row of riparian mimosa trees shaded the shade site, but shade was partial because of leaf drop during the dry season. We applied rain to sun and shade stones by distributing ~1-L of river water onto each set of stones with a bucket that had small holes in the bottom. An 8th control treatment (handling) allowed us to check for effects of the twice-daily handling of substrates. In the handling treatment, we shook stones side-to-side underwater and lifted them above water at both dawn and dusk during the periods when we moved other stones in and out of the water.

We collected ~80 small cobbles from each site. Cobbles from the upper site were kept wet during transport to the downstream experimental site. We left stones on the river bed overnight and started the experiment the following morning (10 February 2008). We originally placed each set of stones in a grid pattern and randomly assigned treatments by grid position. However, once the experiment started, we placed the stones in adjacent treatment clusters in the stream bed. Using clusters prevented us from putting rocks in the wrong treatment and facilitated rapid rock movement.

At dawn (~0600 h) and before dusk (~1700 h, with dusk at 1800 h), we moved the stones, as specified for each treatment. Water was released from the dam between 1700 h and 0200 h, so we applied dusk treatments before water rose at the experiment site. The treatment most affected by this predusk schedule

Tᴀʙʟᴇ 2. Comparisons of chlorophyll *a* concentrations in algae on stones in selected pairs of treatments in each experiment. *p* values are for Fisher's Protected Least Significant Difference tests. The treatment with the higher chlorophyll *a* concentration is shown in parentheses when the test was statistically significant. The mixed assemblage experiment (New Zealand) had fewer treatments than the 2 experiments in Thailand. See Table 1 for explanation of treatments. Data are shown in Fig. 4. – = not tested, NS = not statistically significant.

| | New Zealand | Thailand | |
| | Mixed assemblage | Cyanobacteria | Green algae |
Treatment comparison			
Initial vs submerged	–	NS	<0.0001 (initial)
Initial vs exposed	–	0.007 (initial)	0.002 (initial)
Initial vs sun	–	<0.0001 (initial)	0.003 (initial)
Initial vs night	–	0.045 (initial)	<0.0001 (initial)
Handling vs submerged	NS	NS	0.037 (handling)
Submerged vs exposed	–	NS	NS
Sun vs night	0.005 (night)	0.028 (night)	0.024 (sun)
Sun vs fully submerged	<0.0001 (submerged)	0.0001 (submerged)	NS
Sun vs fully exposed	–	0.121 (exposed)	NS
Night vs submerged	0.037 (submerged)	NS	NS
Night vs exposed	–	NS	0.025 (fully exposed)
Sun vs shade	–	NS	NS
Sun vs sun + rain	–	NS	NS
Shade vs shade + rain	–	NS	NS
Sun vs shade + rain	–	0.017 (shade + rain)	NS

was the night treatment. To avoid daytime exposure of the night treatment, we moved these stones to shaded tubs of water on the bank at 5 pm, and then to the dry bank at dusk. The experiment was scheduled to last 4 d; but was reduced to 2 full days because of an unexpected change in the water-release schedule (to a 24-h release for several days).

We secured a Hobo® combination temperature and light data logger (Onset, Bourne, Massachusetts) at each of 3 sites: 1) the streambed between the upstream and downstream stone clusters, 2) the sun bank site, and 3) the shade bank site. The streambed data logger was stolen. As a replacement, we measured water temperatures on day 2 with a thermometer.

We quantified canopy cover at sun, shade, and experimental pool sites with a convex spherical densiometer (Forest Densiometers, Bartlesville, Oklahoma). We used upstream, right-bank, downstream, and left-bank measurements to calculate % cover.

Algae collection

We collected algal samples from stones in all experiments by holding a bottle cap template (diameter = 40 mm in New Zealand and 33 mm in Thailand) against the upper surface of the stone, removing algae around the template, then collecting the algae under the template by scraping, scrubbing, and rinsing. We kept algal samples in a cooler in the field and stored them frozen. We blended thawed samples with a handheld blender and subsampled

volumetrically for chlorophyll *a* analysis and sampled nonquantitatively for taxonomic analysis.

Laboratory methods and data analysis

We filtered subsamples for chlorophyll *a* analysis onto glass-fiber filters and extracted chlorophyll with the ethanol procedure of Sartory and Grobbelaar (1984). We measured chlorophyll *a* with a spectrophotometer in New Zealand and a fluorometer in Thailand.

We determined ash-free dry mass (AFDM) of samples in the New Zealand experiment, but were unable to include this variable in the Thailand experiments because the necessary equipment was not available. Subsamples for AFDM were filtered onto precombusted glass-fiber filters, dried, weighed, combusted at $500°C$ for 4 h and reweighed.

We used 1-way analysis of variance (ANOVA) to analyze the chlorophyll *a* data in each of the 3 experiments and the AFDM data in the New Zealand experiment. We used Fisher's Protected Least Significant Difference (PLSD) multiple comparison tests to indicate significantly different treatment pairs in each ANOVA analysis. The 8 treatments in the 2 Thailand experiments, plus the initial chlorophyll *a* values (a 9th treatment) produced 36 treatment pairs; however, we considered only the 15 treatment pairs of interest (listed in Table 2). Because initial chlorophyll *a* levels were much higher in the filamentous algal experiment, we used 2 levels of analysis in this experiment:
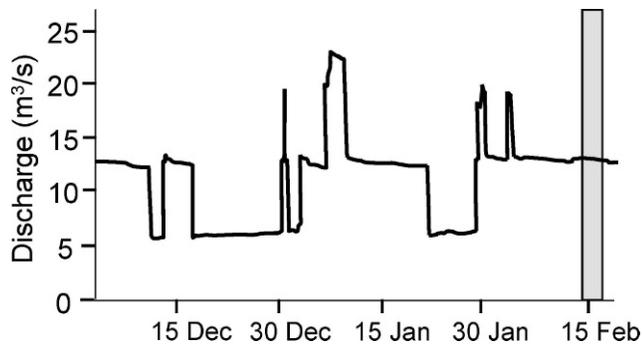
FIG. 1. Partial 2000 hydrograph of Monowai River (New Zealand) illustrating the 3 river stages in this regulated river. The gray vertical bar shows the experimental period.

1) initial vs the 8 experimental treatments and 2) comparisons among the 8 treatments. We $\sqrt(x)$-transformed data prior to analysis, but graphs and tables show untransformed data.

We characterized the taxonomic composition of algal assemblages by examining algal samples at 100× and 400× and identifying the dominant taxa. We visually determined the dominant taxa for New Zealand samples, whereas for the Thailand samples, we recorded the presence/absence of each taxon in 25 random fields at 100× magnification. We used assemblage data to describe the assemblages in the 3 experiments; no further statistical analysis was used.

Results

New Zealand: habitat characteristics

Hydropower production schedules dictated discharge in the Monowai River. In the 3 mo prior to the experiment (14 November 1999 to 14 February 2000), discharge occurred at 3 alternate levels (low: 6.3–6.7 m³/s; mid: 11.8–13.7 m³/s; and high: 19.4–22.6 m³/s), with abrupt changes among levels (Fig. 1). Discharge was most frequently at the mid-level (59% of the time) and was at this level for 10 d before and throughout the experiment. At this flow, the channel was full, with no obvious exposed bank and no flooding of bank vegetation.

New Zealand: mixed algal assemblage

The periphyton mat included 2 macroscopically different types of algae: 1) abundant stringy mats of the filamentous alga *Mougeotia* sp., with intertwining filaments of *Spirogyra* sp. and *Oedogonium* sp. and 2) less abundant rounded colonies of the filamentous cyanobacterium *Rivularia* sp. The cyanobacteria *Tolypothrix* sp. and *Scytonema* sp. also were common, as was the diatom *Tabellaria* sp.
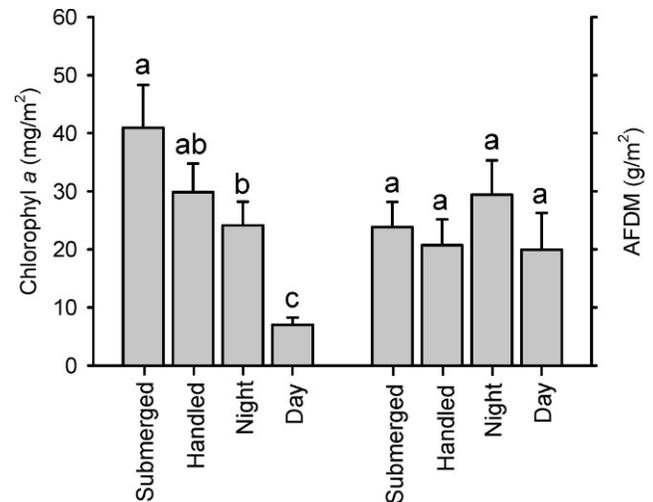

FIG. 2. Mean (+1 SE) chlorophyll *a* concentration (4 bars on the left) and ash-free dry mass (AFDM) (4 bars on the right) on rocks in the algal desiccation experiment in the Monowai River (New Zealand). Rocks were fully submerged (= Submerged), handled at dawn and dusk (= Handled), exposed to air at night only (= Night), or exposed to air during the day only (= Day). Bars for the same variable (chlorophyll *a* or AFDM) sharing the same letter are not significantly different ($p > 0.05$).

Aerial exposure reduced chlorophyll *a* concentration. After 3 d, chlorophyll *a* was 40% lower on night-exposed stones than on submerged stones, and 83% lower on day-exposed (sun) than on submerged stones (ANOVA: $F_{3,18} = 10.22$, $p = 0.0004$; Fig. 2, Table 2). At the end of the experiment, algae (cyanobacteria and filamentous green algae) on submerged and night-exposed stones remained green; in contrast, algae on day-exposed stones had bleached gray. Mean chlorophyll *a* was lower on handled than on submerged stones, but the difference was not statistically significant (Fisher's PLSD, $p = 0.20$). Despite large loss of chlorophyll *a* with aerial exposure, AFDM did not change significantly with exposure or handling (ANOVA: $F_{3,19} = 0.72$, $p = 0.55$; Fig. 2).

Thailand: habitat characteristics

Daytime light level and temperature were lower in the shade than in the sun (Fig. 3A–D), but nighttime temperatures did not differ between the shade and sun (Fig. 3D). No measurable canopy cover existed at the sun site; consequently, light level averaged 4× higher and daytime temperature averaged 11°C higher in the sun than in the shade (Fig. 3B, D). Riparian trees provided a canopy cover of 90.5% at the shade site, but this canopy cover was flecked with
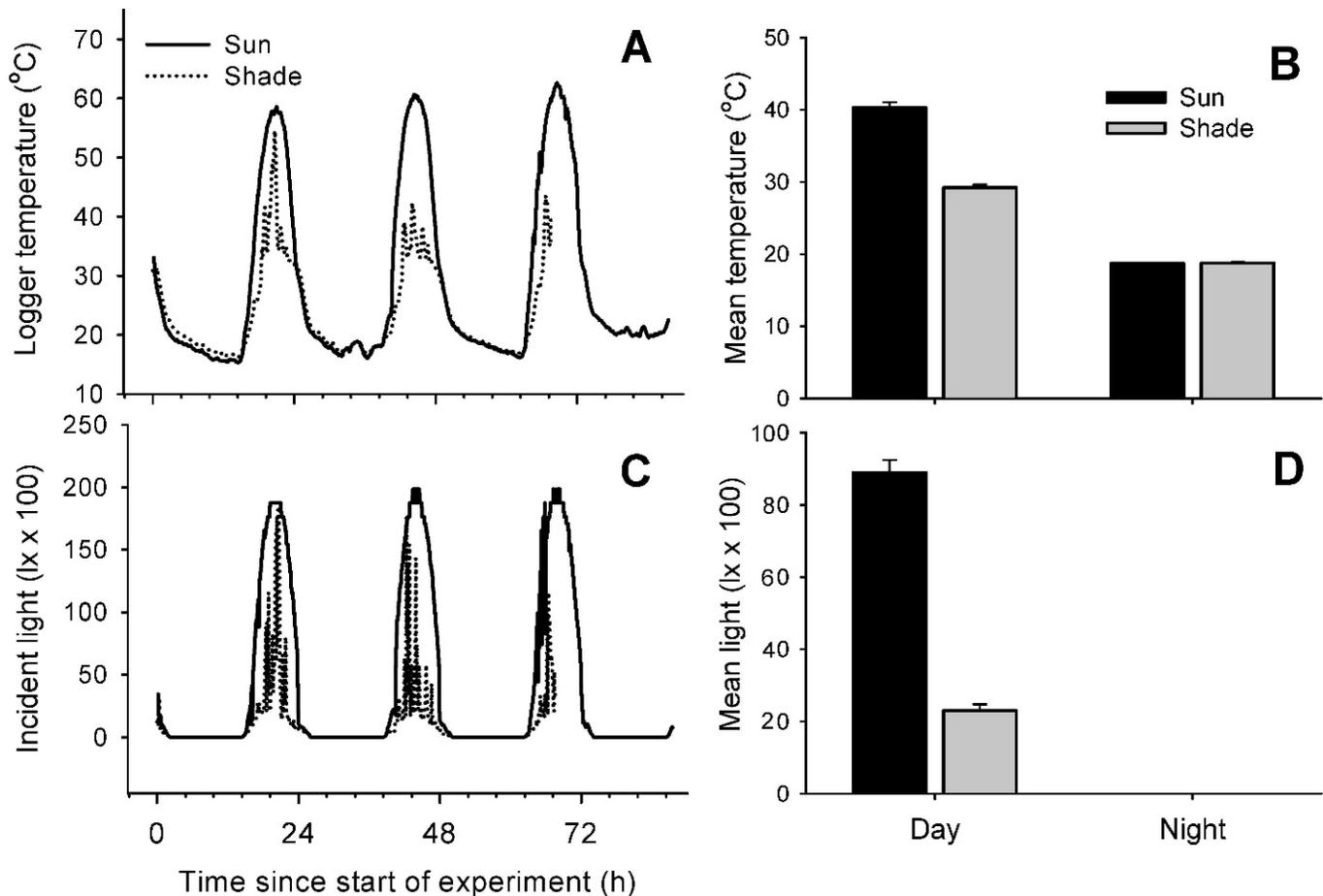
FIG. 3.   Raw (A) and mean (+1 SE) (B) temperature data and raw (C) and mean (+1 SE) (D) light data collected by data loggers in the sun and under the riparian shade during the 2008 desiccation experiments at Mae Ngat River, 0.5 km below the hydropower dam.

light because of dry-season leaf loss. Daytime light level and temperature were much more variable in the shade than in the sun (Fig. 3A, C) because wind-induced leaf movement produced a changing shadow pattern and consequently, large variation of light level at the shaded bank site. Changes in shade produced corresponding changes in temperature, resulting in large temperature fluctuations at the shaded bank site.

Canopy cover over the experimental pool was only 0.5%, with a small amount of shade from shrubby willows on a downstream gravel bar. No light data were available because of loss of the data logger. Limited temperature measurements indicated that daytime temperatures were lower at the experimental pool (e.g., 0900 h: 23°C, 1100 h: 25°C) than at the sun and shade sites.

Water was released from the dam at ~1700 h and reached the experimental pool by 1730 h. The wide channel at the experimental site and the upstream wetland area slowed the water velocity and the rate of water-level increase at the experimental area. Water levels increased several meters in the confined channel just below the dam, but water-level increase at the study site was <1 m and none of the experimental stones moved during the experiment.

Thailand: taxonomic composition of algal assemblages

Cyanobacteria assemblages.—Larger stones in the slow-moving run used for the Thailand experiment were covered with a bumpy cyanobacteria-dominated biofilm. Two filamentous taxa formed clumps within the biofilm: the thin-filamentous *Symploca* (present in 76% of fields) and the larger *Homeothrix* (present in 56% of fields at 100×). These taxa formed a similar number of colonies, but *Symploca* also commonly co-occurred in *Homeothrix*-dominated colonies. Other common taxa were small colonies of *Aphanothece*, scattered *Phormidium* and *Oscillatoria* filaments, and the filamentous green alga *Oedogonium*.
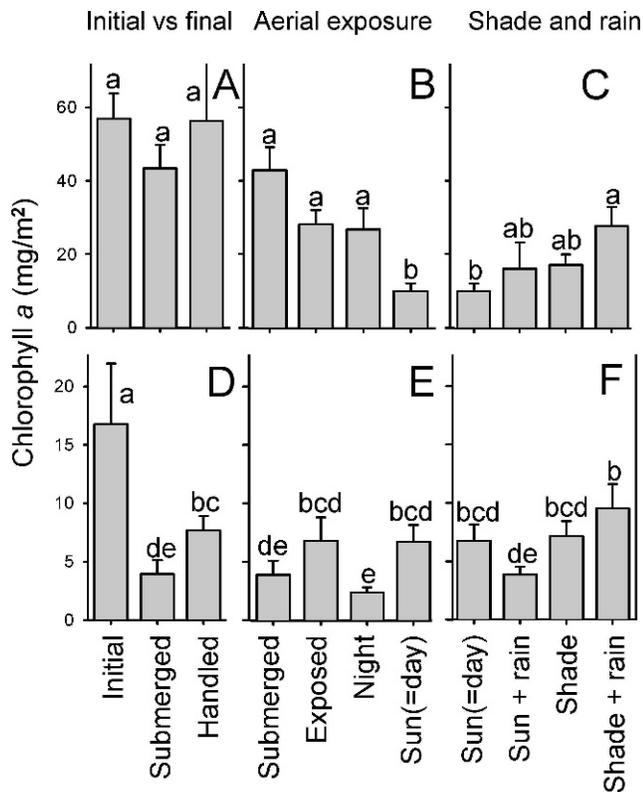
FIG. 4. Mean (+1 SE) chlorophyll *a* concentration of cyanobacteria (A–C) and *Cladophora*-dominated filamentous algae (D–F) on stones in the algal desiccation experiments in the Mae Ngad River (Thailand). Bars are grouped by treatment groups showing initial vs final (A, D), aerial exposure vs no exposure (submerged) (B, E), and conditions during daytime aerial exposure (C, F). Submerged and sun (=day) treatments occur in two treatment groups. Exposure treatments are described in Table 1. Bars sharing the same letter are not significantly different ($p > 0.05$).

Filamentous algal assemblages.—The filamentous algal assemblage in the pool just below the hydropower dam was strongly dominated by filamentous green algae (Chlorophyta), especially *Cladophora*, which formed large attached mats. *Oedogonium* and *Spirogyra* were abundant and enmeshed in the *Cladophora* mats. *Cladophora* filaments had little epiphyte cover and were bright green. The reduced mats in the experiment (discussed below) were numerically dominated by *Oedogonium* (present in 84% of fields) rather than *Cladophora* (present in 12% of fields), and *Spirogyra* was not common (present in <1% of fields). Diatoms (*Gomphonema* and *Synedra*) were fairly common.

Thailand: treatment effects on chlorophyll a of both assemblages

Algal biomass over time.—Change in algal biomass during the experiment was assessed by comparing chlorophyll *a* concentrations on stones collected from the river at the start of the experiment (initial) with chlorophyll *a* concentrations on the experimental stones that were submerged continuously during the 2-d experiment. Chlorophyll *a* concentration of cyanobacteria did not differ between submerged and initial stones (Table 2, Fig. 4A). In contrast, chlorophyll *a* concentrations of filamentous algae were significantly higher on initial than on submerged stones and on stones in all 7 other treatments (ANOVA: $F_{8,62} = 4.698$, $p = 0.0002$; Fisher's PLSD < 0.05; Fig. 4D–F).

Chlorophyll *a* concentration of filamentous algae was considerably lower than chlorophyll *a* concentration of cyanobacteria on initial stones (mean ± SE: 16.8 ± 5.2 for filamentous algae vs 56.9 ± 6.8 mg/m² for cyanobacteria; Fig. 4A, D). The low initial chlorophyll *a* concentration in the filamentous assemblage was inconsistent with the thick mats that occurred at the source site just downstream from the dam. Algal loss was not apparent during movement to the lower site. Instead, loss occurred when stones were placed overnight in the experimental site. Large numbers of snails (especially thiarids) moved onto the transplanted stones soon after their placement. By the start of the experiment on the following morning, little visible evidence of filamentous algae remained, presumably because of grazing by snails (snails were abundant on the transplanted stones in the morning).

Chlorophyll *a* concentration of cyanobacteria was similar between handled and submerged stones (Fig. 4A). In contrast, chlorophyll *a* concentration of filamentous algae was almost 2× higher on handled (mean: 7.7 mg/m²) than on submerged stones (3.9 mg/m²; Fig. 4D). Handling dislodged most snails from stones.

Aerial exposure.—Cyanobacteria showed the same general responses to exposure as the mixed species assemblage in New Zealand. Chlorophyll *a* concentration of cyanobacteria was significantly lower on stones exposed during the day than on submerged or night-exposed stones (Fig. 4B). Chlorophyll *a* concentration on night-exposed stones was ~½ as much as on submerged stones, but this difference was not statistically significant (Table 2, Fig. 4B). Chlorophyll *a* concentrations were similar on continuously exposed and night-exposed stones and were significantly higher on continuously exposed than on day-exposed stones.

Filamentous algal assemblages responded differently to exposure than did the cyanobacterial assemblage in Thailand and the mixed algal assemblage in New Zealand. Chlorophyll *a* concentrations were

significantly lower on night-exposed stones than on continuously exposed or day-exposed stones (Table 2, Fig. 4E). These results are opposite those found for cyanobacteria and are consistent with the grazing activity of snails. Filamentous algae exposed at night were submerged during the day when flow was low, and many grazing snails were observed on the stones and on the streambed, in general. This grazing apparently reduced algal biomass (chlorophyll a). Filamentous algae on day-exposed stones maintained relatively high chlorophyll a concentrations. Filamentous algae on these stones were submerged at night when flow was high, and grazers might have been less active (but the stream bottom was not visible). Continuous exposure prevented access to filamentous algae by grazing snails, and chlorophyll a levels were higher on continuously exposed stones (mean: 6.8 mg/m^2) than on submerged stones (3.9 mg/m^2; Fig. 4E), but this difference was not statistically significant.

Shade and rain.—Shade had a greater effect on cyanobacteria than on filamentous algae. Chlorophyll a concentration of cyanobacteria was higher on shaded (17.4 mg/m^2) than on unshaded (10.2 mg/m^2) day-exposed stones (Fig. 4C). This difference represents a 74% greater retention of chlorophyll a in the shade. However, variation in chlorophyll a concentration among stones was high (standard deviations averaged 60% of the mean for the experiment), and the difference in cyanobacterial chlorophyll a between shaded and unshaded stones was not statistically significant. In contrast, shade had little effect on the chlorophyll a concentration of filamentous algae on day-exposed stones (Table 2, Fig. 4F). Chlorophyll a concentrations of filamentous algae were only slightly higher on shaded (7.1 mg/m^2) than on unshaded (6.7 mg/m^2) day-exposed stones.

Simulated rain affected cyanobacterial and filamentous algal assemblages differently. Chlorophyll a concentration of cyanobacteria was higher on stones in the sun + rain than in the sun treatment, but chlorophyll a concentration of filamentous algae was lower on stones in the sun + rain treatment than in the sun treatment (Fig. 4C, F). These differences were not statistically significant. The combination of shade and rain produced conditions that resembled a short rain shower. Chlorophyll a concentration of cyanobacteria was significantly higher on stones in the shaded + rain treatment than on stones in the sun treatment (Fig. 4C). Chlorophyll a concentration of filamentous algae was significantly higher on stones in the shaded + rain treatment than on stones in the sun + rain treatment (Fig. 4F).

Discussion

Assemblage composition and structure

Filamentous algae formed dense growths in the regulated waters of both rivers. These mats were restricted to the permanently wetted portion of the stream bed and were apparently absent from the periodically exposed zone. Dense growths of filamentous green algae (*C. glomerata* or mixed assemblages) commonly dominate the clear waters downstream of hydropower reservoirs (Dufford et al. 1987, Angradi and Kubly 1993, Valentin et al. 1995, Chester and Norris 2006). The loss of algal cover in the periodically exposed zone certainly contributes to low productivity. Filamentous algal mats are ecologically beneficial because they provide habitat and cover for invertebrates (Power 1990, Shannon et al. 1994). In addition, *C. glomerata* can support diatom-dominated epiphytes, which are a good food source for grazers (Dodds 1991, Shannon et al. 1994). However, diatom epiphytes were not abundant on *Cladophora* or other filamentous algae in either of our study streams.

The downstream Mae Ngad site lacked typical tailwater filamentous algal cover despite the presence of a well developed filamentous algal mat <1 km upstream, and instead, had an adherent cyanobacterial mat. This downstream site had a high density of grazing snails, especially introduced apple snails (Ampullariidae:*Pomacea insularum* [D'Orbigny]) and native thiarids (Thiaridae:*Melanoides* spp.). Over 3000 apple snails and thiarid snails/m^2 occurred in the experimental pool, but none occurred at the tailwater site (EAB, unpublished data), where the harsh conditions apparently excluded snails but supported a thick filamentous algal mat. Thiarids congregated on *Cladophora*-covered rocks transported to the downstream experimental site, with the consequent rapid loss of most of the *Cladophora* biomass from grazing prior to the start of the experiment.

Filamentous green algal mats and cyanobacteria have physical features that might affect their rates of desiccation. The mucilage of cyanobacteria has a high water content, and during emersion, the mat structure of *Cladophora* collapses and traps water among the filaments (Usher and Blinn 1990). Greater water content might help to slow desiccation, but Dromgoole (1980) compared the desiccation resistance of several species of marine macroalgae and concluded that the surface area to volume ratio was more important than water content in affecting the rate of dehydration. In the cyanobacterial and filamentous algal mats in our experiments, mucilage and water trapping increased the surface area to volume ratio by retaining water in mucilage and in gaps among

filaments, but both cyanobacteria and filamentous green algae dried quickly.

Bleaching was evident in the day-exposed filamentous mats in New Zealand. Bleaching of the outer portion of mats might protect the inner portion and holdfasts (Usher and Blinn 1990), but bleaching extended to the base of the mat after 3 d of daytime exposure. This result suggests that protection by the outer part of the mat was ineffective. Nighttime exposure during the same period did not cause mats to bleach. Therefore, we concluded that conditions specific to daytime exposure caused the bleaching.

Some cyanobacteria have physiological mechanisms for tolerating desiccation (Potts 1999). As a consequence, cyanobacteria are common in habitats, such as soils (Campbell et al. 1989, Davey 1989, Jones 1989) and seasonally dry wetlands (Gottlieb et al. 2005), that dry naturally. However, in our study, cyanobacterial (primarily *Symploca* and *Homoeothrix*) mats were as susceptible as filamentous green algal mats to chlorophyll *a* loss during aerial exposure. This result indicates that not all cyanobacteria are tolerant to desiccation. Indeed, aquatic algae might be less tolerant of desiccation than nonaquatic algae (Alpert 2005).

Percent chlorophyll *a* loss after 2 to 3 d of 12-h aerial exposure was high and remarkably similar among the taxonomically diverse algal assemblages in our experiments. Daytime exposure resulted in 83% and 77% loss relative to submerged assemblages of chlorophyll *a* in filamentous algae-dominated assemblages in New Zealand and cyanobacteria-dominated assemblages in Thailand. This similarity is even more remarkable when the temperature differences are considered. Mean maximum temperature in February is 32°C in northern Thailand and 22°C in New Zealand (WMO 2009).

Exposure conditions: day vs night, shade, and rain

Exposure conditions can affect algal survival. The most obvious differences were between daytime and nighttime exposure in the New Zealand experiment. In comparison to the chlorophyll *a* concentration of submerged mixed-assemblage algae in the Monowai River, 40% of chlorophyll *a* remained after nighttime exposure, whereas only 20% of chlorophyll *a* remained after daytime exposure. In other studies, daytime losses of chlorophyll (Usher and Blinn 1990) and AFDM (Blinn et al. 1995) were greater than nighttime losses. These results indicate that algae in exposure zones would be better protected by daytime than nighttime power generation. Solar radiation (including UV radiation), temperature, and humidity differ between daytime and nighttime exposure. Our experiments were not designed to allow separation of the effects of these factors. However, Angradi and Kubly (1993) found strong effects of daytime exposure and suggested that solar radiation might be the primary factor because temperature and humidity did not vary much between day and night at their study site in Arizona (USA).

Riparian canopy cover is a natural feature along streams and rivers but often is altered by downstream effects of dams (see review by Nilsson and Berggren 2000). If present, riparian canopy can shade the bed in wet–dry zones of regulated rivers. In our study, canopy cover reduced solar radiation and reduced surface temperature in the riparian zone. Canopy shade can reduce evaporation from bare soils by up to 35% compared to unshaded soils (Wallace et al. 1999) and can reduce water temperatures in small streams (Rutherford et al. 2004). Despite the potential benefits of shade from canopy cover to exposed algae, chlorophyll *a* concentration of day-exposed cyanobacteria and filamentous algae was similar in the sun and in the shade in the Thailand experiments. This result might not be universal because the canopy cover in our experiments was much reduced by dry-season leaf loss, and algae were only partly shaded in the shade treatment. More complete canopy cover might have yielded stronger effects.

Unlike canopy cover, rain is often unpredictable in time and space (but see Jones 1989). Rain rewets surfaces, and the accompanying cloud cover reduces evaporation and temperature, factors that can benefit exposed algae (e.g., Jones 1989). In our experiments, the sun + rain treatments provided rewetting without rain-associated cloud cover, conditions that might arise after rainfall or from ripples, waves, or splashes that wet the shore, whereas the shade + rain treatment more closely approximated conditions during a short rain storm. The chlorophyll *a* concentration of cyanobacteria was almost 3× higher in the shade + rain treatment than in the sun treatment. In contrast, the chlorophyll *a* concentration of filamentous algae was only slightly higher in the shade + rain treatment than in the shade treatment, and was lower in the rain + sun treatment than in the sun treatment. Rewetting under conditions of heat and sun is detrimental for many algae (Gupta and Agrawal 2006, our study), although cyanobacteria can benefit from this combination (Jones 1989, our study).

Frequency of wetting

Frequent cycles of exposure and submersion might be more detrimental to algae than longer, continuous

exposure. Chlorophyll *a* loss under continuous exposure was much lower than the sum of the separate losses from day exposure and from night exposure for both cyanobacteria and filamentous algae in the Thailand experiments. Changes in water level were more frequent at the site in Thailand than at the site in New Zealand. We suggest that the more frequent changes in water level at the Thailand site vs the New Zealand site would result in greater algal survival in the New Zealand site, but this hypothesis remains to be tested.

Frequency and duration of submersion often affect biofilm assemblage composition over longer time scales than we used. For example, wood exposed to a 5-d/9-d wet–dry cycle developed a heterotropic biofilm, whereas wood exposed to an 11-d/21-d wet–dry cycle developed an algae-dominated biofilm (Ryder 2004). In the Florida Everglades (USA), a shorter (<4 mo) submersion period promotes cyanobacteria, whereas longer submersion (~8 mo) produces a more diverse algal assemblage. After drying, both assemblages are dominated by cyanobacteria because of greater survival of cyanobacteria (Gottlieb et al. 2005).

Chlorophyll a vs AFDM loss

In the New Zealand experiment, AFDM remained relatively stable during 3 d of wetting and drying, whereas chlorophyll *a* was lost in both night-exposed and day-exposed conditions. Maintenance of AFDM despite loss of chlorophyll *a* and obvious bleaching has been observed for both filamentous macroalgae (Usher and Blinn 1990, Blinn et al. 1995) and diatom biofilms (Mosisch 2001). However, over longer periods than in our experiments, exposure results in loss of AFDM through fragmentation of algal mats (Benenati et al. 1998). Many cyanobacteria can regenerate directly, but other types of algae repopulate primarily by colonization (Robson 2000). Intact, bleached periphyton mats can promote algal biofilm regrowth when resubmerged because they facilitate entanglement and settlement of propagules, which enhances colonization (Robson et al. 2008).

Grazer effects

The large effect of snail grazers was an unanticipated factor in the Thailand experiments. Consumption of filamentous green algae by grazing invertebrates is not universal. Generally, grazers in tailwaters consume diatom and other epiphytes on *Cladophora* rather than the filaments (e.g., Dodds 1991, Stevens et al. 1997, Blinn et al. 1998). Nevertheless, grazers consumed nearly all of the filamentous green algae on submerged stones, and grazing pressure was so high

that algae survived aerial exposure better than they survived submersion with exposure to grazing snails. Even handling stones, which visibly displaced snails, resulted in higher chlorophyll *a* concentrations than on submerged, undisturbed stones. Snail grazing apparently was affected by the diel pattern of water release, such that grazing occurred during the day when flow was low. At night, when water was released through the dam, grazing pressure was lower. Consequently, algae exposed to the air during the day were protected from intense daytime grazing, but had to contend with drying. Thus, our study demonstrated the ecological complexity that occurs in regulated rivers. The interactions among the temporally variable hydraulic conditions, the resultant activity patterns of grazing snails, and the availability of both grazer-resistant and grazer-susceptible algae produced a change from dominance by filamentous green algae to dominance by cyanobacteria in a short stretch of river.

Concluding remarks: intertidal vs freshwater periodically exposed zones

Survival in the periodically exposed zone of regulated rivers is a challenge. Some macroalgae, such as the *Cladophora* in our study, thrive in the wetted bed of the river despite frequent changes in water velocity, but survive poorly when exposed to the air. Similarly, subtidal marine algae are adversely affected by aerial exposure (Smith and Berry 1986). In contrast to freshwater *Cladophora*, some marine *Cladophora* species commonly occur as intertidal macroalgae (e.g., Wiencke and Davenport 1987, Leliaert and Coppejans 2003, Hooper and Davenport 2006) and tolerate frequent aerial exposure.

The environmental challenges experienced by aquatic organisms in the wet–dry zone of regulated rivers are, in some ways, more pronounced than the challenges of intertidal algae. Exposure periods in regulated rivers are not dictated by predictable tides but by changing schedules of water release or withdrawal. Exposure time varies, ranging from very short periods to several days. On freshwater banks, the equivalent of the wetting sprays from waves hitting marine rocky shores and refugial intertidal pools are rare, although riparian canopy shade partially ameliorates conditions in freshwater habitats. Canopy cover from shoreline vegetation is less common in rocky intertidal zones where, in contrast, macroalgae might form a protective overstory (Dayton 1975). However, no freshwater macroalgae appear to be both common in tailwaters and preadapted to living in the wet–dry zone of rivers. Thus, no

macroalgae are available to provide the food and shelter resources that could sustain a wet–dry zone community. The filamentous cyanobacterium *Oscillatoria* sp. survives better in the wet–dry zone than *Cladophora*, especially if fine sediments are present, because *Oscillatoria* is motile and can burrow into the sediment to escape desiccation (Shaver et al. 1997) and because mucilage coating filaments of *Oscillatoria* retains water, which might slow desiccation (Shaver et al. 1997). However, in comparison to *Cladophora*, *Oscillatoria* mats provide little shelter (Shannon et al. 1994) and little epiphytic food (Blinn et al. 1995) for grazing invertebrates. Thus, invertebrate biomass is much lower in *Oscillatoria* mats than in *Cladophora* mats in the same river (Shaver et al. 1997).

Wet–dry zones in rivers are a relatively recent phenomenon and occur at aquatically isolated sites. When combined with the unpredictability of flow fluctuations, conditions are too extreme for most freshwater algae. To survive in this wet–dry zone, algae must tolerate frequent drying and rewetting and in-stream conditions, including exposure to grazers. Conditions most likely to promote tolerant algae are: longer wet–dry periods, minimal aerial exposure during the daytime, and riparian shade.

Acknowledgements

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