

Experimental increases and reductions of light to streams: effects on periphyton and macroinvertebrate assemblages in a coniferous forest landscape

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Abstract Increased light reaching streams as a result of riparian vegetation management is often thought to be responsible for enhanced algal productivity. However, concomitant changes in nutrients and other physical processes confound that interpretation. We manipulated light in two separate experiments to test the role of light as a controlling factor for periphyton productivity and biomass, and to observe invertebrate responses in small streams in central British Columbia, Canada. We did this by adding artificial light to reaches of three forested streams, and in a second experiment we used shade cloth to cover reaches of two streams flowing through clearcuts. Periphyton growth, productivity and composition, and macroinvertebrate benthic densities were contrasted with control reaches within the same streams. Gross primary production (GPP) was increased at least 31% by light addition to forested streams. Periphyton

biomass was higher under light additions, but only significantly so in one of the streams. In one stream grazers increased along with the periphyton response, whilst in the other two lit streams invertebrates, including grazers, decreased with increased light. The shading significantly reduced GPP to about 11% of that in clearcut sections, but failed to produce any significant responses in either periphyton standing stock or invertebrates in the clearcut streams. Measures of algal production and biomass responded as predicted; however, invertebrate responses to increased and decreased light were idiosyncratic amongst streams, perhaps indicating lagged responses and limitation by other resources.

Keywords Experiment · Forest harvesting · Light · Macroinvertebrates · Periphyton · Photic response

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Introduction

The two major basal resources in stream food webs are detritus and algae. Stream periphyton communities are controlled by a number of factors, including grazing, discharge, temperature and nutrients (see Stevenson et al., 1996), but light has often been cited as the primary factor limiting periphyton growth (Gregory, 1980; Hill & Knight, 1988; Steinman, 1992; Kiffney et al., 2004). With forest harvesting and other land-use activities that reduce riparian

forest canopy, a switch from a detritus-based to an algae-based system can occur, as solar radiation reaching the stream bed increases and leaf litter input decreases. Productivity of algae can respond rapidly to changes in available light, on hourly, daily and longer time scales (Mulholland et al., 2006). Although the increased solar radiation reaching the stream bed following forest harvesting is likely to be a major factor influencing periphyton growth (Kiffney et al., 2003), a number of other factors confound interpretation of responses of algae. For instance, reductions in forest cover through logging can lead to increased temperatures, sedimentation, and nutrient inputs, and reduced organic matter inputs, as well as changes in the behaviour of consumers (Kiffney et al., 2004; Richardson, 2008). In addition, the biofilm in which algae is included is a diverse assemblage of bacteria, algae and other organisms, each of which may respond differentially to changes in abiotic and biotic conditions (e.g. Fuller et al., 2004). All of the above processes may complicate the interpretation of the mechanisms leading to changes in biomass and productivity of algae and biofilm due to land use, such as forest harvesting.

Responses of grazers may track changes in production or biomass of algae, but the specific response depends on the mechanisms (e.g. movements, growth and reproduction), and could involve substantial time lags. For instance, consumers may respond to increased resources with a numerical response, a functional response, or both (e.g. Dudgeon & Chan, 1992; Mallory & Richardson, 2005) if they are limited by their resource supplies (e.g. food) and have time to respond. Grazers are expected to show a response most closely following their food source. Other groups of benthic invertebrates might respond to light itself or perhaps be attracted to patches of higher prey densities. The rate and magnitude of response to changes in algal productivity depends on the time scale, and in the short term most responses would be behavioural, i.e. a functional response (e.g. Dudgeon & Chan, 1992; Fuller et al., 2008). Responses to increased versus decreased light may be asymmetrical in kind and magnitude. It is unclear whether light reduction and addition would produce comparable opposite responses in periphyton and benthic macroinvertebrate communities, and whether the response would happen over short time scales. The interactions of changes in resources (light) and

consumption rates can lead to complex outcomes (e.g. Kiffney et al., 2004; Mallory & Richardson, 2005) because of differences in the rates of response and partial refuge for algae from grazing by changes in morphology or in crevices on rocks. Moreover, algae are capable of acclimation to changes in the light regimes at very short time scales (e.g. hours to days); this might result in rapid changes in productivity but not biomass (Rier et al., 2006).

In these experiments, we sought to isolate the effects of light on algae and consumer responses in small streams dominated by conifer forests. Our hypothesis was that changes in light (increased or decreased), controlling for other factors, would result in changes in the same direction in algal productivity, along with responses by consumer populations. We experimentally manipulated light by augmenting light (addition) in naturally forested reaches and by diminishing it in open reaches (reduction). We artificially added light to forested stream segments using commercial grow lights, and significantly lowered light reaching the stream bed in harvested streams using shade cloth. We predicted an increase in periphyton productivity and biomass in the lit treatments and a corresponding increase in the grazers (scrapers), and decreases in the shaded treatments of a magnitude comparable to that of the light addition.

Methods

Sites

The streams for both experiments were located in or just outside the University of British Columbia's Alex Fraser Research Forest (52°28' N, 121°44' W) near Williams Lake, BC, Canada. All streams were gravel and cobble-bottomed, and <1.2 m at bankfull width. Three small, forested streams were chosen for the light addition experiment: Cascades Creek, Gavin Creek and Fire Lake Creek. Cascades Creek ran through old-growth cedar-hemlock forest, and Gavin Creek and Fire Lake Creek ran through mature, second-growth forest of subalpine fir (*Abies lasiocarpa*), hybrid spruce (*Picea glauca* × *engelmannii*) and Douglas-fir (*Pseudotsuga menziesii*). Two additional streams flowing through areas that had been logged by clearcutting were chosen for the light reduction experiment (a third stream was initially

included but had to be abandoned when it dried up part way through the experiment). Honeybee Creek ran between two lakes, supported a population of rainbow trout, and was presumed to be nutrient rich as dense filamentous algae were present towards the end of the summer. The stream ran through an old clearcut (1970s), which was brushed mechanically 3 weeks before the beginning of the experiment to remove woody, deciduous vegetation. Frypan Creek was a small, fishless, headwater stream, which was clearcut harvested in 1997 (see Gjerløv & Richardson (2004) for a detailed description of Frypan Creek).

Light addition

Two riffle sites were chosen at each of the three streams; a light addition reach and a control section 10–20 m upstream. Commercial grow lights were suspended between 1 and 1.5 m above each stream channel in the treatment reaches from 5 June to 10 July 2000. Bulbs were 1000 W Metal Halide, which emit full spectrum light. Lights were powered by generators and shades created to protect bulbs from precipitation. Lights were powered daily from 07:00 to 19:00 during the 5-week experiment. Photosynthetically active radiation (PAR, 400–700 nm; $\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured regularly at each site (approximately 3 times per week) under the lights at water level, under the forest canopy (control sites), and in full view of the sky (no shading), using a Sunfleck Ceptometer (Model SF-80, Decagon Devices, Inc.). Due to an unknown calibration problem, we expressed light as a percentage of the maximum recorded in one of the open sites (25 June). The lengths of stream channel receiving increased radiation were about 1.5–2 m.

Six unglazed ceramic tiles (25 cm²) were placed in each stream section at the beginning of each experiment to measure periphyton growth and productivity (see below). Temperature dataloggers were placed in both control and treatment sections at each stream and water temperature recorded hourly throughout the duration of the experiment.

Light reduction

Two riffles were chosen in each of two streams, with the control section about 20 m upstream of the treatment. Shading treatment consisted of 90–95%

shadecloth (black garden weed cloth) suspended about 30 cm above the stream channel for a length of 5 m. The shadecloth was left in position for the period June 6–Aug 9, 2000 (64 days). PAR was measured approximately every 2 weeks under the shadecloth at water level and in the open clearcut at the control reach. Six unglazed ceramic tiles (25 cm²) were placed in each stream section to measure periphyton growth and productivity (see below). We used tiles as our surface for algal growth as comparisons of tiles or natural rocks over similar time periods found no appreciable difference between the two substrates (Gregory, 1980; Hetrick et al., 1998; Rosemond et al., 2000). A temperature datalogger was placed in the control section in each stream and water temperature recorded hourly throughout the duration of the experiment.

Periphyton

At the end of both experiments tiles were recovered and any visible fauna removed. Tiles were subsequently placed in sealed glass jars (250 ml) completely filled with stream water, and replaced with glass bottom facing up close to where they had been retrieved, and were left for a period of 4 to 7.5 h during daylight hours (a long period, but the field situation necessitated that). Net photosynthesis was estimated as the change in water oxygen concentration during this period. Respiration was measured in a similar way, but jars were left in a sealed darkened cooler box for 6 to 13 h (no ice added). Gross primary productivity (GPP) was estimated as net photosynthesis plus respiration, allowing for experimental time differences and changes in temperature amongst sites (Marzolf et al., 1994).

Tiles were then placed individually in sealed plastic bags in a darkened cooler box and frozen within 2 h. In the darkened laboratory tiles were defrosted, and periphyton removed from the upper surface of the tile by scraping with a razor blade, brushing, and washing with distilled water. For 3 of the tiles from each stream, 1/4 of the periphyton (biofilm) mixture was used for periphyton species identification, 1/4 for chlorophyll *a* analysis and 1/2 for biomass estimates. For the other 3 tiles, 1/2 of the sample was used for chlorophyll *a* analysis and the other 1/2 for biomass estimation.

The defrosted portion of the sample used for species identification was preserved with Lugol's

solution. The three replicates were combined to produce one composite sample for each treatment in each stream. Examination of the samples suggested that little damage had resulted from the freezing of the samples, although identification of green and Cyanobacteria could not be taken beyond genus level. Organisms were identified using an inverted microscope at 100 \times and 400 \times magnification with respect to species where possible, and relative abundances were determined.

Chlorophyll *a* subsamples were filtered through 47 mm Gelman GF/F glass fibre filters in a darkened room, extracted in 5 ml 90% acetone at 5°C for 24 h, then analysed using a fluorometer (model TD 700, Turner designs). Biofilm biomass was estimated by filtering sample fractions through pre-ashed 25 mm Gelman GF/F glass fibre filters, drying at 60°C until constant mass and ashing at 550°C for 2 h. The ash-free dry mass (AFDM) (± 0.003 mg; Sartorius M2P balance) was determined as the difference between dried and ashed filters.

Macroinvertebrates

At the end of each experiment Surber samples (0.09 m², 250 μ m mesh) were taken (three in each lighted section or five from each shade and control reach) and preserved in 70% ethanol. In the laboratory, samples were processed under a dissecting

microscope at 20 times magnification, and invertebrates identified to the lowest taxonomic level possible, usually genus.

Data analysis

Each of the two experiments was analysed separately. PAR and temperature data paired by stream were analysed using Wilcoxon tests. Periphyton and macroinvertebrate data were analysed using paired *t*-tests (the appropriate test for the level of replication, i.e. stream). Two-way analysis of variance (ANOVA) with either treatment or site as independent variables was used to explore the sources of variance (i.e. given the small number of streams, we used samples as replicates knowing this inflates the error term degrees of freedom). Macroinvertebrate data were analysed as total abundances and as functional feeding groups (FFG) (according to Merritt & Cummins, 1996, Table 1). Data were checked for normality before and after transformations using the Kolmogorov–Smirnov test. Tukey's post hoc tests were performed after significant ANOVA results. Where normality was not obtained after log ($x + 1$) transformations, non-parametric Kruskal–Wallis tests were performed using untransformed data. Mann–Whitney *U* tests were used to compare site pairs. All analyses were carried out using SAS 9.1 (SAS Inc., Cary, NC), and α was set at 0.05.

Table 1 Taxa included in each functional feeding group

| Scrapers, shredder-herbivores | Shredder-detritivores | Collector-gatherers, collector-filterers | Predators |
|-------------------------------|-------------------------|--|--------------------|
| <i>Cinygma</i> | <i>Zapada</i> | Baetidae | Tricladida |
| <i>Cinygmula</i> | <i>Visoka</i> | <i>Epeorus</i> | <i>Sweltsa</i> |
| <i>Anagapetus</i> | <i>Malenka</i> | <i>Ephemerella</i> | <i>Isoperla</i> |
| <i>Imania</i> | <i>Nemoura</i> | <i>Parapsyche</i> | Tanypodinae |
| <i>Apatania</i> | <i>Amphinemura</i> | <i>Psychoglypha</i> | <i>Rhyacophila</i> |
| <i>Neothremma</i> | <i>Despaxia</i> | <i>Ecclisomyia</i> | Ceratopogonidae |
| <i>Micrasema</i> | <i>Yoraperla</i> | Elmidae—adult | Acari |
| <i>Ameletus</i> | <i>Peltoptera</i> | Elmidae—larvae | Nematoda |
| Gastropoda | <i>Paraleptophlebia</i> | Other Coleoptera | Staphylinidae |
| | <i>Chyranda</i> | <i>Dixa</i> | Dytiscidae |
| | <i>Lepidostoma</i> | Orthoclaadiinae | <i>Seratella</i> |
| | <i>Psychoglypha</i> | Chironominae | |
| | Tipulidae | Simuliidae | |
| | | Oligochaeta | |
| | | Ostracoda | |

Results

Light addition

Photosynthetically active radiation reaching the streambed was significantly higher in the light addition treatment. Artificially lit treatment reaches received almost 25 times more PAR (average 21.24% of maximum, range 10–61%) than controls (average 1.4% of maximum, range 0.44–3.4%) (Wilcoxon two-sample test: $Z_{66} = 4.623$, $P < 0.005$). Light levels in the light treatment were not significantly different from measurements of PAR taken under open sky (average 38.95% of maximum, range 2.3–100%) (Wilcoxon: $Z_{66} = 1.298$, $P = 0.194$). Water temperatures did not differ by more than the accuracy of the data loggers between treatment and control reaches in the streams.

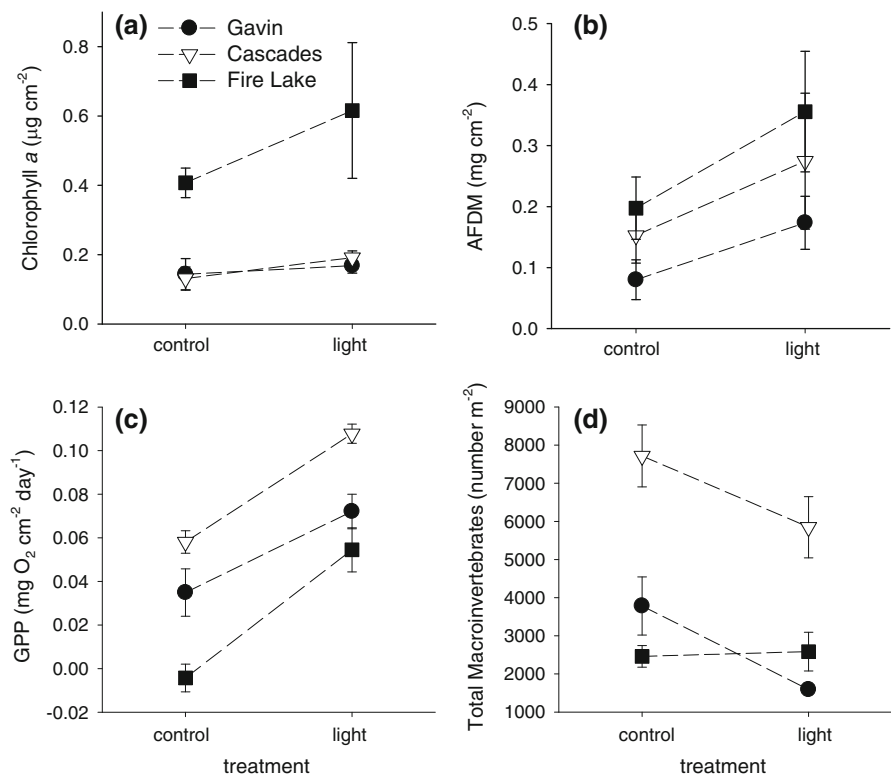
Chlorophyll *a* was higher with augmented light over controls at all sites, although not significantly so (paired *t*-test, $P = 0.225$). Periphyton chlorophyll *a* varied markedly amongst sites (Fig. 1a; two-way ANOVA: $F_{2,29} = 12.65$, $P < 0.005$), with higher chlorophyll *a* at Fire Lake than Gavin and the Cascades. None of the periphyton interaction terms

were significant ($P > 0.05$). Biofilm AFDM did not differ significantly between sites (Fig. 1b; two-way ANOVA: $F_{2,27} = 2.17$, $P = 0.134$), but higher AFDM was found in the lit treatments (paired *t*-test, $P = 0.022$).

Gross primary production (GPP) was significantly higher for the periphyton grown and photosynthesising under lit treatments than those grown and measured under ambient light (Fig. 1c; paired *t*-test, $P = 0.016$). GPP was greater at Cascades than at the other two streams (two-way ANOVA: $F_{2,29} = 25.43$, $P < 0.005$). GPP estimates for Fire Lake were lower than would be expected for this high chlorophyll site, possibly due to a thunderstorm that greatly increased the amount of water and suspended particulate matter during this experiment thereby reducing the amount of light reaching the tiles.

Periphyton species compositions were dominated by diatoms (80–99% abundance), notably *Gomphonema angustatum*, with *Achnanthes* spp., *G. cf. olivaceum*, *G. cf. subclavatum*, *Synedra rumpens*, and *Meridion circulare* the common species. There were no consistent differences in species composition or number of taxa between treatments or streams. In

Fig. 1 **a** Chlorophyll *a* (mg cm^{-2}), **b** periphytic AFDM (mg cm^{-2}), **c** gross primary productivity ($\text{mg O}_2 \text{ cm}^{-1} \text{ day}^{-1}$) on experimental tiles for Cascades, Gavin and Fire Lake for control (forested) and lit treatments after 5 weeks (mean ± 1 SE). **d** Benthic densities of total macroinvertebrates for the three streams (mean ± 1 SE). Lines are for visual convenience only



Cascades Creek *G. cf. olivaceum* was more abundant and *Meridion circulare* less abundant in the lit treatment, and filamentous green and Cyanobacteria were more common in the lit treatment (10% abundance each) than the control (<1% abundance). There were minor differences between treatments in Fire Lake, where *Achnanthes minutissima* and *Navicula* spp were less abundant and *Meridion circulare*, *Synedra radians* and *Synedra rumpens* were more abundant in the lit treatment. Gavin contained larger amounts of periphyton material than the two other forested streams, but there were few differences between treatments, although *Achnanthes* spp. was less abundant and *Gomphonema cf. subclavatum* and *Synedra rumpens* were more abundant in the lit treatment.

There was no significant difference in benthic invertebrate densities (paired *t*-test, $P = 0.212$), contrary to our hypothesis. Total macroinvertebrate densities differed amongst streams, with Cascades Creek having higher densities than the other two streams (Fig. 1d; two-way ANOVA: $F_{2,20} = 32.11$, $P < 0.005$). Densities were generally lower when light was added (Table 2), with the exception of Fire Lake Creek where densities were nearly the same in treatment and control reaches (Fig. 1d). There were no significant differences by treatment for any of the 10 most common taxa (paired *t*-test, all $P < 0.05$).

Densities of macroinvertebrates declined or remained similar, and there was no relation with algae biomass (Fig. 2a). When the macroinvertebrate data were analysed as FFG further differences were found (Table 2, Fig. 2b–e). Densities varied amongst sites for all FFG, and usually it was the higher densities at the Cascades that influenced the results. Clear differences between treatments were only seen for the scraper FFG, where the lit treatment at Fire Lake had more scrapers than the control treatment (Fig. 2b; Tukey's: $P = 0.022$). There were significantly fewer collector-gatherers in the lit treatments overall, but differences were not significant at any single site (non-significant interaction term; Fig. 2c). Treatment had no effect on the shredder-detritivore densities (Table 2; Fig. 2d). Predator densities did differ between treatments (Table 2), with the significantly higher densities in Gavin Creek control reach influencing the result (Fig. 2e; Tukey's: $P = 0.025$). Overall, the trend was for a decrease in densities in the lit treatments in Gavin and Cascades creeks, and an increase or no difference in Fire Lake Creek.

Table 2 Results of two-way ANOVAs from light addition experiment of densities of macroinvertebrate functional feeding groups

| FFG | Source | SS | df | F | P |
|-----------------------|------------|-------|----|--------|------------------|
| Totals | Treat | 0.144 | 1 | 8.30 | 0.009 |
| | Site | 1.103 | 2 | 31.83 | <0.001 |
| | Site*treat | 0.142 | 2 | 4.10 | 0.032 |
| | Error | 0.346 | 20 | | |
| Scrapers | Treat | 0.002 | 1 | 0.051 | 0.824 |
| | Site | 1.251 | 2 | 15.202 | <0.001 |
| | Site*treat | 0.773 | 2 | 9.389 | 0.001 |
| | Error | 0.823 | 20 | | |
| Collector-gatherers | Treat | 0.141 | 1 | 5.178 | 0.034 |
| | Site | 1.659 | 2 | 30.430 | <0.001 |
| | Site*treat | 0.071 | 2 | 1.302 | 0.294 |
| | Error | 0.545 | 20 | | |
| Shredder-detritivores | Treat | 0.363 | 1 | 3.510 | 0.076 |
| | Site | 1.281 | 2 | 6.187 | 0.008 |
| | Site*treat | 0.365 | 2 | 1.761 | 0.197 |
| | Error | 2.071 | 20 | | |
| Predators | Treat | 0.182 | 1 | 4.412 | 0.049 |
| | Site | 1.504 | 2 | 18.203 | <0.001 |
| | Site*treat | 0.866 | 2 | 10.474 | 0.001 |
| | Error | 0.826 | 20 | | |

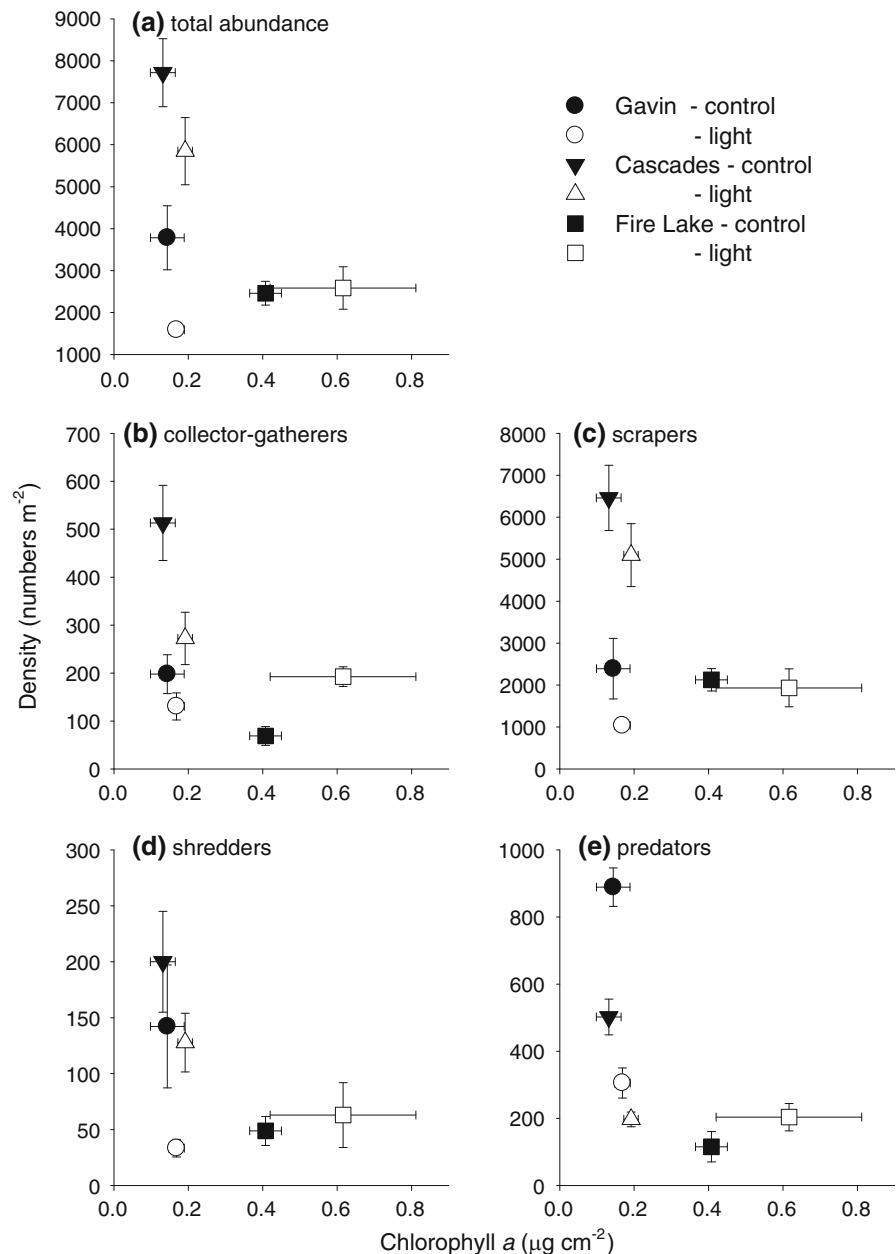
Analyses were performed on log ($x + 1$) transformed data using samples as replicates. Bold characters indicate statistical significance

Light reduction

PAR reaching the streambed was significantly decreased in the shade treatments compared to the controls in both streams (shading of 93%). Temperatures in Honeybee, the lake-outlet stream, were higher than in Frypan, where from July 6–13 water temperatures in Honeybee were 14.4°C (± 0.1) compared with Frypan's 10.0°C (± 0.06).

At the end of the experiment, biofilm AFDM on the tiles did not differ between sites (Fig. 3a: two-way ANOVA: $F_{1,41} = 2.30$, $P = 0.137$) or treatments (two-way ANOVA: $F_{1,41} = 1.47$, $P = 0.232$; using tiles as replicates). Periphytic chlorophyll *a* was higher at Honeybee than Frypan (Fig. 3b: two-way ANOVA: $F_{1,41} = 27.01$, $P < 0.05$) but did not differ between treatments ($F_{1,41} = 0.73$, $P = 0.397$). GPP did not differ between sites (Kruskal–Wallis: $P = 0.276$) but was significantly greater for control

Fig. 2 Invertebrate functional feeding group densities in relation to chlorophyll *a* concentration for **a** scrapers, **b** collector-gatherers, **c** shredder-detritivores and **d** predators. Both axes are expressed as mean \pm 1 SE. Gavin = circles, Cascades = triangles and Fire Lake = squares



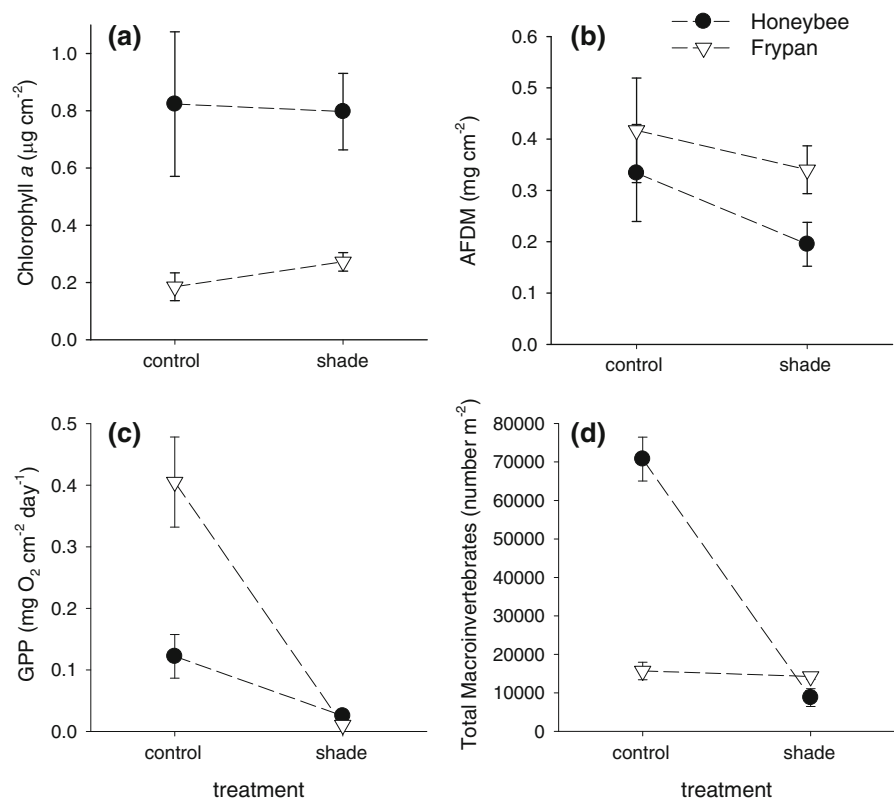
than for shaded treatments (Fig. 3c, Mann–Whitney $U = 458$, $P < 0.05$).

As in the light addition experiment, periphyton communities were dominated by diatoms (>99%), predominantly *Cocconeis placentula*, *Melosira varians*, and *Nitzschia* spp., with *Achnanthes* spp. and *Navicula* spp. common. There were only subtle differences in species composition between treatments in Honeybee, where a large *Nitzschia* sp. was less abundant and *Navicula* spp. were more abundant

in the shaded treatment. Differences between treatments in Frypan again were subtle, with *Melosira varians* and a large *Nitzschia* sp. being less abundant and *Achnanthes* spp., *Cocconeis placentula* and *Navicula* spp. more abundant in the shaded treatment.

The control reach in Honeybee had dense filamentous green algal growth by the end of the experiment. The invertebrates associated with this algal growth were heavily dominated numerically by orthocladiine chironomids and ostracods, and this

Fig. 3 **a** Chlorophyll *a* (mg cm^{-2}), **b** periphytic AFDM (mg cm^{-2}), **c** gross primary productivity ($\text{mg O}_2 \text{ cm}^{-1} \text{ day}^{-1}$) on experimental tiles for Honeybee and Frypan creeks for control (clearcut—open to the sky) and shaded treatments after 9 weeks (mean \pm 1 SE). **d** Benthic densities of total macroinvertebrates for the two streams (mean \pm 1 SE). Lines are for visual convenience only



was reflected in the analyses for total abundance (Fig. 4a, Table 3). Abundances were not different between sites, but were greater in control than shade treatments, with the significantly higher densities in Honeybee control influencing the result (Tukey's test: $P < 0.05$).

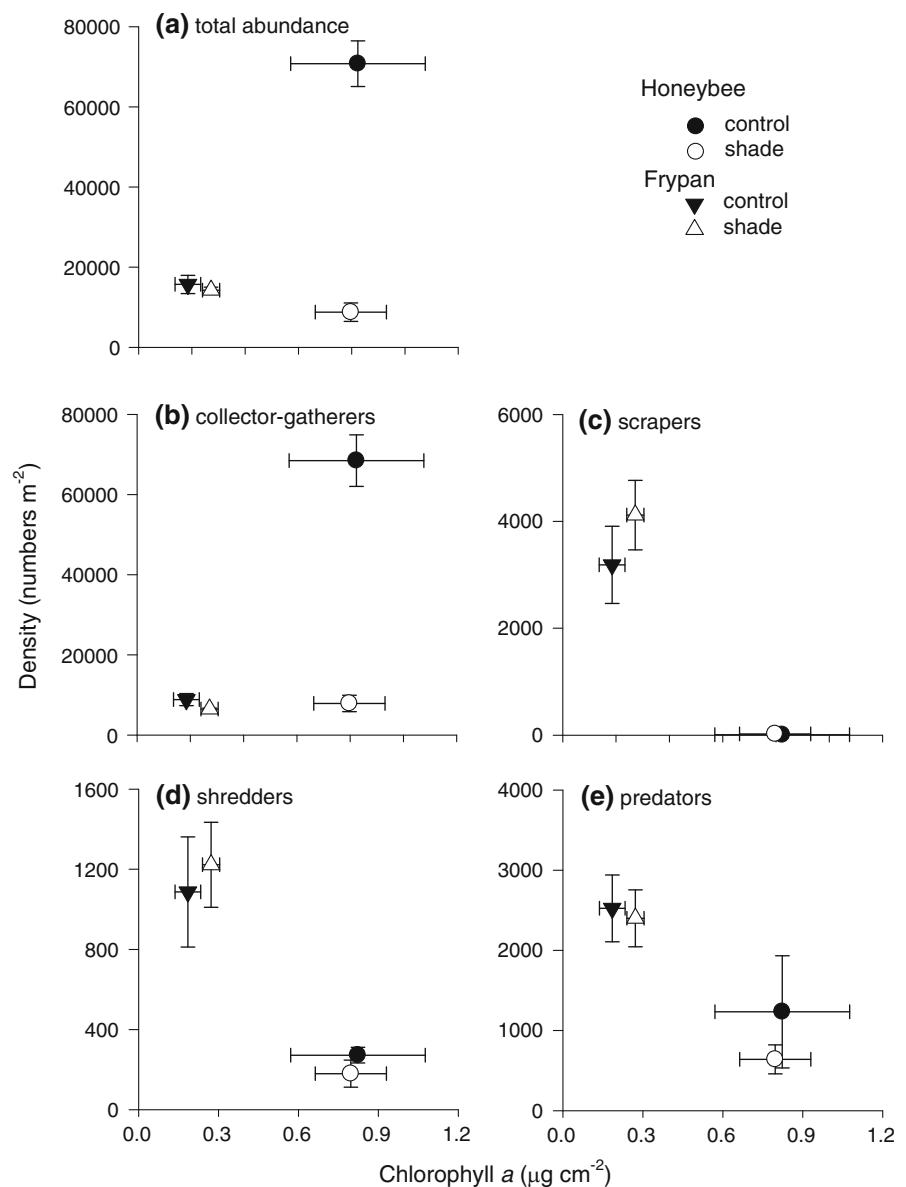
The Orthocladinae and Ostracoda were classed as collector-gatherers and, hence, this FFG showed a pattern similar to that of the total abundance (Fig. 4b). The data could not be normalised, however, and the non-parametric test indicated there were no statistically significant differences between sites or treatments (Table 3). Densities of scrapers, shredder-detritivores and predators were greater at Frypan than Honeybee (Fig. 4c–e, Table 3), but there were no differences between treatments.

Discussion

We found that rates of GPP responded strongly to either augmentation or reduction of light in small streams. The responses of algal chlorophyll *a* and

biofilm biomass were also consistent with our initial hypotheses. These responses demonstrate that light is one of the limiting factors for periphyton production that responds to riparian forest harvesting. However, the responses of benthic macroinvertebrate densities and composition were idiosyncratic and not as predicted according to our hypotheses. The effects of experimental modifications of light on algal biomass and invertebrate densities were modified by some context-dependent factors which we did not measure and were not evident. In addition, increases (e.g. aggregation) or decreases (e.g. negative phototaxis) of consumer numbers may have interacted with periphyton productivity to partly confound measurement of some effects in some streams. We have previously found inconsistent responses to riparian forest clearcutting for other streams in this region (Melody & Richardson, 2007) and others have found large site-to-site variation that is in excess of forestry-related effects (including light) on stream communities (Danehy et al., 2007; Gravelle et al., 2009). In our case we used paired reaches on the same streams to account for stream-to-stream differences.

Fig. 4 Invertebrate densities in relation to chlorophyll *a* concentration for **a** total density, **b** collector-gatherers, **c** scrapers, **d** shredder-detritivores and **e** predators. Both axes are expressed as mean \pm 1 SE. Honeybee = open circle, Frypan = downward triangle. Control are filled symbols, shaded are open symbols. Note the different y-axis scales



It is worthwhile noting that these streams flow through coniferous forests, and the seasonal changes in light are associated with sun angle and not the timing of leaf-out, as in deciduous forests (e.g. Hill et al., 2001), hence shading effects are persistent throughout the year. Thus, changes in light regimes from forest harvesting or regeneration of forest cover following clearcutting can persist for considerable time after the activity is completed. Some algae, particularly diatoms, are good at photoacclimation (e.g. Rier et al., 2006), which may have damped the magnitude of response in composition and chlorophyll in algae.

Light addition

Significant increases in GPP and periphyton biomass, and the trends to increased chlorophyll *a* with increased radiation followed our predictions. Chlorophyll *a* values were low, but were comparable to those found in nearby stream systems (0.1–1.3 µg cm⁻²; Melody & Richardson, 2007). Gregory (1980) found higher algae biomass, but not significantly higher, in stream reaches flowing through clearcuts than in forested reaches, a pattern similar to ours. Experiments in indoor flumes along a gradient

Table 3 Results of two-way ANOVAs and Mann–Whitney tests for the light reduction experiment of total density and densities of macroinvertebrate functional feeding groups

| Dependent variable | Source | $F_{1,11}$ | P |
|-----------------------|------------|------------|--------------|
| Total density | Treat | 15.329 | 0.002 |
| | Site | 2.315 | 0.156 |
| | Site*treat | 14.246 | 0.003 |
| Shredder-detritivores | Treat | 0.009 | 0.926 |
| | Site | 16.395 | 0.002 |
| | Site*treat | 0.247 | 0.629 |
| Predators | Treat | 0.784 | 0.395 |
| | Site | 14.173 | 0.003 |
| | Site*treat | 0.335 | 0.575 |

| Dependent variable | Source | Mann–Whitney U | Chi-square approximation | P |
|---------------------|--------|------------------|--------------------------|--------------|
| Collector-gatherers | Treat | 42 | 2.625 | 0.105 |
| | Site | 35 | 0.656 | 0.418 |
| Scrapers | Treat | 31 | 0.122 | 0.727 |
| | Site | 0 | 10.595 | 0.001 |

ANOVAs were performed on $\log(x + 1)$ transformed data. **Bold** characters indicate statistical significance

of light intensity also show a strong increase in algal biomass, but those systems lack most grazers (Hill et al., 2008). Consumption by grazers in our study may have dampened the response of algae biomass to light augmentation.

We found subtle and inconsistent differences in periphyton community compositions. Measurable periphyton responses to changes in light levels in other studies include changes in chlorophyll *a*, biomass, productivity and species composition (Hill et al., 1995; Kiffney et al., 2004). In our experiment we found significantly higher GPP from increases in light inputs, but only slight responses were observed in AFDM and chlorophyll *a* concentrations. The headwater streams used in our study were densely shaded, and clearly our experimental manipulation of light demonstrated that light was limiting to periphyton growth. It is plausible that responses of algae may have been co-limited by nutrients (Rier et al., 2006; Sanderson et al., 2009). In an experimental augmentation of light and nutrients to a forested Oregon stream, Gregory (1980) found algae in his streams to be primarily light limited and secondarily nutrient limited. Although we did not measure nutrient levels in our streams, other streams in our study region had relatively high concentrations of both N and P (Melody & Richardson, 2007).

We expected to see an increase in grazers with increased periphyton, but we observed this only at

Fire Lake Creek, the site with the highest chlorophyll *a* concentrations. The generally negative relation between grazer abundance and algal biomass suggests reduction of algae by consumers could be one mechanism involved in the resulting patterns. Similar variable associations of grazers with increased periphyton densities have been shown by other workers (e.g. Dudgeon & Chan, 1992; Danehy et al., 2007). Although the lower chlorophyll *a* levels at the two other sites may in part explain why an increase in grazers was not observed at these sites, the actual decrease in grazers and other invertebrates in the light treatments is not likely related to changes in periphyton. In a comparison of streams flowing through clearcuts versus forested sites in the same region as ours, the biomass and densities of scrapers were lower in the clearcut sites despite higher algal biomass (Fuchs et al., 2003). Invertebrates sometimes exhibit direct photic responses to increased predation risk associated with increased light levels, or perhaps UVB effects. There is no obvious explanation for the responses of the macroinvertebrates.

Light reduction

The light reduction experiment resulted in a significant reduction of GPP when the stream reaches were shaded in contrast to full sunlight. The biofilm AFDM also was lower under shaded conditions,

although the difference was not statistically significant. Other studies have shown reduced algal production under shading relative to full light (Dudgeon & Chan, 1992; Fuller et al., 2004; Kiffney et al., 2004). In contrast, another study done in the region of our experiment found no significant response to light reduction (Melody & Richardson, 2004), and Yang et al. (2009) found periphyton biomass to be lower in unshaded reaches, perhaps because of higher consumer densities in such reaches. Clearly, the responses of periphyton biomass are complex outcomes of resources (light, nutrients, etc.) and consumption (Hillebrand, 2005). In our experiment, we found no evidence of a direct photic response by invertebrates, as trends in invertebrate densities in response to experimental shading differed between streams. The differences we observed in consumers between the two sites were probably caused by the higher algal growth in Honeybee. The filamentous green algae found in Honeybee may have additionally influenced the macroinvertebrate assemblage.

Light reduction versus addition

The responses of algal productivity to light addition versus light reduction were opposite in direction as predicted. The magnitude of differences in light in each experiment was not equivalent and neither were the changes in response to the two experiments. The duration of the light addition experiment differed slightly from that of the light reduction experiment, but the main difference was that light addition did not reach levels of full sunlight input, which the clearcut streams ('controls') in the shading trials received. The suggestions of a direct photic response of invertebrates in the light addition experiment, and not in the reduction experiment, may reflect either an adaptation to increased light levels in the clearcut invertebrates, or that periphyton productivity in the clearcut was above a certain threshold at which the light levels become less important.

In summary, production of algae in our streams was limited by light. Invertebrate community responses to increased radiation, such as found after canopy removal, might vary with stream nutrient status (Gregory, 1980; Fuchs et al., 2003; Melody & Richardson, 2007). Light addition and reduction produced similar and opposite responses in algae for their rates of GPP and standing stock measured as

AFDM, as predicted. However, the reasons for the idiosyncratic responses of macroinvertebrates to these changes in light and periphyton remain unclear.

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