J. N. Am. Benthol. Soc., 2005, 24(4):820–831

Limitations on the effects of ultraviolet radiation on benthic algae in a clear boreal forest lake

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Abstract. We examined the effects of ultraviolet radiation (UVR) (280–400 nm) on epilithic algal metabolism, biomass, and taxonomy from early June to mid August 1999 (66 d) in Lake 224, an oligotrophic lake in the Experimental Lakes Area, northwestern Ontario, Canada. Epilithon colonized bare clay tiles placed under UVR-transparent (UVR+) and UVR-shielding (UVR−) acrylic filters, at depths of 0.5, 0.8, and 1.4 m. Filamentous chlorophytes and cyanophytes were the dominant algal taxa at 0.5 and 1.4 m depths, respectively, on day 28. Biovolumes did not differ between UVR treatments for any major algal class. We measured epilithic metabolism on days 28, 45, and 66 after the tiles were deployed. Photosynthesis was not affected by UVR on any date. On day 28, dark respiration was 33 to 49% greater in UVR+ than in UVR− treatments at all depths. On day 45, respiration was 11% greater in UVR+ than in UVR− treatments only at 0.5 m, and by day 66, respiration did not differ between treatments at any depth. Thus, the effects of UVR on respiration diminished with depth and over time and were strongest when epilithic biofilms were least developed. UVR probably has little impact on naturally colonized, fully developed epilithon deeper than 0.5 m in Lake 224, i.e., UVR affects <6% of the littoral zone. Comparison of our findings with those of an earlier study in Lake 224 suggests that the intensity and specific nature of UVR effects depend on the taxonomic composition of the benthic algal assemblage.

Key words: benthic algae, boreal forest lakes, epilithon, Experimental Lakes Area, littoral zone, periphyton, ultraviolet radiation.

Climate change and acidification can increase the exposure of biota to ultraviolet radiation (UVR) in boreal lakes by decreasing levels of dissolved organic C (DOC), thereby increasing UVR transmission (Schindler 1998). As a result, the total area of littoral surfaces and total lake volume exposed to UVR can increase (Schindler et al. 1996). Epilithic biofilms in the shallows of the littoral zone are especially vulnerable to increased UVR exposure in lakes because their positions in the water column are fixed (Vinebrooke and Leavitt 1996). Therefore, biofilms could be good indicators of the potential effects of increased UVR on littoral primary productivity. Direct exposure to UVR can reduce epilithic photosynthesis (Watkins et al. 2001), alter algal taxonomic composition (Vinebrooke and Leavitt 1996), and increase respiration of UVR-sensitive algal species (Beardall et al. 1997). Benthic primary productivity can contribute significant amounts of C to pelagic food webs (Hecky and Hesslein 1995). Therefore, the potential impacts of increased levels of UVR on whole-lake productivity may be significant.

The effects of UVR on epilithic biofilms are highly variable and often interact with other environmental factors such as grazer effects (Hill et al. 1997, Kelly et al. 2003) or the nutrient status of the algae (Bothwell et al. 1993, Higley et

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al. 2001). Moreover, some algal taxa, particularly diatoms, appear more sensitive to UVR than other taxa (Vinebrook and Leavitt 1999, Tank et al. 2003). For example, UVR did not influence the effects of invertebrate grazing on epilithon in shallow water in an Alberta alpine lake (Vinebrook and Leavitt 1999), but algal pigment concentrations in UVR-exposed epilithon were reduced by 40% when diatoms predominated and increased by 50% when cyanophytes predominated. Bothwell et al. (1993) showed that UVR negatively affected the rate of chlorophyll accrual in periphyton dominated by diatoms in very shallow experimental streams regardless of P enrichment. On the other hand, Higley et al. (2001) showed that P enrichment increased total algal biovolume regardless of exposure to UVR on nutrient-diffusing agar substrates in a California, montane lake. UVR affected the biovolume of the 2 most common cyanophytes in opposite ways; *Anabaena circinalis* decreased 2×, whereas *Chroococcus limneticus* increased 13× (Higley et al. 2001). Tank et al. (2003) found that epilithic chlorophyll concentration was 4.3× lower in UVR-exposed treatments in a lake with diatom-dominated epilithon than in UVR-exposed treatments in a lake with chlorophyte- and cyanophyte-dominated epilithon.

Work in the Experimental Lakes Area (ELA) in northwestern Ontario strongly suggests that diatoms are particularly sensitive to UVR. Xenopoulos et al. (2002) showed that P enrichment increased the negative effect of UVR on the rate of phytoplankton chlorophyll accrual in mesocosm experiments in Lake 224 (our study lake). Moreover, the effect of UVR on phytoplankton chlorophyll was greatest in spring and decreased throughout the summer, probably because phytoplankton composition shifted from UVR-sensitive diatoms in spring to UVR-resistant cyanophytes later in summer (Xenopoulos et al. 2002). Photosynthetic rate and biovolume of diatom-dominated epilithon were strongly reduced by UVR in Lake 224 (Watkins et al. 2001), and the dominant epilithic algal group changed from diatoms to filamentous chlorophytes as a function of decreasing water depth and increasing UVR flux in 8 lakes, including Lake 224 (Donahue et al. 2003).

Most research on the effects of UVR on littoral-zone communities has focused on biofilms in shallow water, where effects are likely to be most severe. However, in a 2-wk survey in Lake 224, Donahue et al. (2003) found correlations between UVR flux and epilithic algal taxonomic composition in water 0.1 to 1.5 m deep. We used an experimental approach to assess the effects of UVR on epilithon over a wide range of depths (0.5 to 1.4 m) in Lake 224. Our objective was to determine the spatial (with respect to water depth) and temporal scales of UVR effects on the metabolism and taxonomic composition of epilithon.

Methods

Study site

We worked at the ELA in Lake 224 in the boreal forest of northwestern Ontario (lat 49°40′N, long 93°44′W). Lake 224 is oligotrophic, with a maximum depth of 27 m and a surface area of 25.9 ha (Brunskill and Schindler 1971). This lake is one of the clearest low-DOC lakes at the ELA (Schindler et al. 1992). In 1999, the mean concentration of DOC in the epilimnion was 3.4 mg/L, and the maximum depth of the euphotic zone (photosynthetically active radiation [PAR] $> 1\%$) was 13 m (S. E. Kasian, Freshwater Institute, unpublished data).

Experimental design

We exposed algae to 2 levels of UVR using UVR-transparent (UVR+) and UVR-shielding (UVR−) filters. The UVR+ treatment included wavelengths of ultraviolet B radiation (UVB) (280–320 nm), ultraviolet A radiation (UVA) (320–400 nm), and wavelengths that were ≥PAR (400–700 nm). The UVR− treatment excluded all wavelengths <400 nm. We did not segregate UVB from UVA and PAR because Watkins et al. (2001) concluded that UVA was largely responsible for UVR effects on metabolism of epilithon in Lake 224. We established the UVR+ and UVR− treatments using 3-mm-thick OP4 and OP3 acrylic plastics, respectively (Johnston Industrial Plastics, Mississauga, Ontario). Both plastics are ~95% transparent in the visible spectrum (400–700 nm). The UVR transmission of OP4 is 90% at 320 nm and declines to 60% at 280 nm. The UVR transmission of OP3 is 90% at 420 nm and declines to 0% at ~380 nm.

We used a blocked split-plot experimental design. We established 2 experimental blocks ~15 m apart on a rock shelf of an unshaded shore

that had a slope of ~15°. We created 3 plots in each block, 1 each at 0.5, 0.8, and 1.4 m depths. We split each plot into 2 UVR treatments (UVR+ and UVR−) to yield 12 treatment-depth-block combinations. We created the UVR treatments by covering ½ of each plot with a 1.5-m^2 square of OP3 (UVR−) and the other ½ with a 1.5-m^2 square of OP4 (UVR+) plastic. We fastened the squares to polyvinyl chloride (PVC) pipe frames, and positioned them horizontally 30 cm above the lake bottom at each water depth.

We treated 114-cm^2 unglazed clay tiles with 1% HCl, rinsed them thoroughly with lake water, and soaked them in the lake for 24 h. On 9 June 1999, we placed 40 tiles in each split plot to begin colonization. We sampled epilithon on the tiles on days 28 (7 July), 45 (21 July), and 66 (14 August). We sampled only the central 24 tiles to minimize edge effects.

We used SCUBA while deploying and sampling the UVR filters and tiles and while cleaning the top and bottom surfaces of the filters each week. We did not use diving fins to minimize disturbance of the lake bottom.

Ultraviolet radiation

UVA (mV) was recorded from early May to late August 1999 at the ELA meteorological site using a broadband UVA sensor (BW-20, 320–400 nm; Vital Technologies, Bolton, Ontario) attached to a data logger (Li1000; Li-Cor, Lincoln, Nebraska). We converted raw mV data to W/m^2 using a calibration regression ($r^2 = 0.94$, $n = 73$) that we derived by simultaneously measuring UVA with the broadband sensor and a scanning spectroradiometer (LI-1800UM; Li-Cor) over a 12-h period of daylight (Watkins et al. 2001). We calculated total daily UVA by summing daily W/m^2 from 0700 h to 1900 h and converting to kJ m^{-2} d^{-1}.

We calculated the transmission of UVA and UVB in Lake 224 using equations from Scully and Lean (1994):

$$K_{dA}(/m) = 0.299(3.4 \text{ mg DOC/L})^{1.53}, \quad r^2 = 0.95 \quad [1]$$

$$K_{dB}(/m) = 0.415(3.4 \text{ mg DOC/L})^{1.86}, \quad r^2 = 0.97 \quad [2]$$

where K_{dA} and K_{dB} are the transmission rates of UVA and UVB, respectively.

We calculated transmission at 0.2-m intervals from the water surface to the 1% transmission depth. For comparison, we calculated the 1% depths of UVA and UVB transmission using equations from Donahue et al. (2003):

$$1\% \text{ UVA depth} = 52.97(3.4 \text{ mg DOC/L})^{-2.195}, \quad r^2 = 0.97 \quad [3]$$

$$1\% \text{ UVB depth} = 24.81(3.4 \text{ mg DOC/L})^{-2.268}, \quad r^2 = 0.97 \quad [4]$$

Epilithic metabolism

We calculated rates of net photosynthesis (Pnet) and dark respiration (Rd) from in situ metabolic incubations (Turner et al. 1983, 1991). We chose cloudless sampling days, so we were able to assume that photosynthetic rates were near their maximum (Turner et al. 1983, 1991). Incubations began at ~1000 h on each sampling date. We deployed 2 transparent and 2 black acrylic 0.69-L chambers in each treatment-depth-block combination. The transparent chambers had the same UVR transmission characteristics as the shielding used in the UVR+ treatment. We placed 2 colonized tiles in each chamber and incubated them for ~1.5 h. We collected 3 ambient water samples (10 mL) from each treatment-depth-block combination for analysis of initial concentrations of dissolved inorganic C (DIC). We collected two 10-mL samples from each incubation chamber for analysis of DIC at the end of incubation.

We measured DIC with a CO_2 infrared gas analyzer (LI-6252; Li-Cor). We analyzed three or four 1-mL subsamples from each 10-mL water sample. The overall coefficient of variation (CV) for all DIC values was <1.3%. We calculated C flux (μM C m^{-2} h^{-1}) for Pnet and Rd during the incubation periods using the difference between DIC concentrations of initial and final samples (Turner et al. 1983, 1991). We calculated Pnet and Rd in light and dark chambers, respectively, as

$$\text{Pnet or Rd} = (DIC_i - DIC_f)\,(V/[AT]) \quad [5]$$

where DIC_i = initial DIC concentration, DIC_f = final DIC concentration, V = chamber volume, A = tile surface area, and T = time of incubation. We calculated gross photosynthesis (Pg) as:

$$Pg = Pnet + |Rd| \quad [6]$$

Mean Pnet, Rd, and Rd:Pg were calculated from the respective duplicate light or dark chambers, which we regarded as subsamples within each treatment-depth-block combination. We used these subsamples to calculate a mean metabolic rate/treatment-depth-block resulting in $n = 2$ replicates for each combination.

Rd is not necessarily a good surrogate of respiration in the light. For example, Graham and Turner (1987) observed that measuring epilithic respiration in the dark overestimated respiration in the light by ~30%. We minimized this possible bias by using the ratio Rd:Pg. Rd is included in both the numerator and denominator of the ratio. Hence, Rd:Pg better describes the relative C fluxes of epilithic respiration and photosynthesis than individually evaluating Rd and Pnet or calculated Pg.

Taxonomy of epilithic algae

We analyzed epilithic algal taxonomy only on the 1st sampling date (day 28) to determine the effects of UVR on early seral-stage colonists. We generated 12 composite algal samples (1 for each treatment-depth-block combination) by combining epilithon from the 8 tiles used in the dark and light chambers within each combination. We analyzed subsamples from composite samples from the UVR+/0.5 m, UVR+/1.4 m, UVR−/0.5 m, and UVR−/1.4 m treatment combinations in each block ($n = 8$ subsamples, 2 UVR treatments × 2 depths × 2 replicates [blocks]). We selected these samples to assess UVR effects on the composition of algal species that initially colonized the tiles at water depths with the greatest difference in UVR exposure. However, conclusions based on these data should be interpreted cautiously because the statistical power of this analysis was low.

We held epilithic samples on ice and in darkness until they were processed in the laboratory. We mixed the samples for ~3 s in a blender at low speed to break apart large clumps, diluted them with lake water, and stirred them during subsampling. We preserved taxonomic subsamples, each representing 9.8 cm^2 of epilithon, with 0.1 mL of Lugol's iodine and 0.1 mL of formalin. We also collected separate subsamples for analysis of particulate C, and filtered and froze them for later analysis using a rapid elemental analyzer (Exeter Analytical Model CE-440; Hauser 2001).

We identified and counted algae at 234× or 938× magnification using an inverted compound microscope (Wild M40). We determined genus, species (when possible), and average cell volume for each taxon using protocols described by Findlay and Kling (1998). We calculated cell density (cells/cm^2) for each taxon in each sample. We calculated the average cell volume (μm^3/cell) of each taxon from measurements on 30 to 50 cells for each taxon. We used the shape of a prolate sphere to reduce the estimated cell volume, usually by ~30%, of algal taxa, such as *Mougeotia* sp. and *Oedogonium* sp., that had large vacuoles (H. Kling, Freshwater Institute, personal communication). We calculated total algal biovolume ($\mu m^3/cm^2$) by multiplying total cell density by cell volume.

Statistical analysis

We used a 2-way nested (split-plot) repeated measures analysis of variance (RM ANOVA) to assess the effects of UVR and water depth on Rd, Pnet, and Rd:Pg over the 3 sampling dates. The 2 independent variables were UVR treatments (UVR+ and UVR−) and water depth (0.5, 0.8, and 1.4 m). We nested the UVR treatments in split-plots within each depth-block combination, and we treated blocks as replicates. We $\log_{10}$-transformed all data to correct for inequality of variances (Zar 1984). We regarded the duplicate light or dark chambers in each UVR treatment-depth combination as subsamples and used them to calculate mean metabolic rates for each block, yielding $n = 2$ metabolic replicates. We interpreted a nonsignificant UVR × depth interaction term to mean that the effect of UVR was equal in magnitude at all water depths. We interpreted a significant time × UVR interaction term to mean that the effect of UVR decreased over time. We used Bonferroni post hoc comparisons to test for differences between UVR treatments at each water depth on each day.

We used 1-way nested (split-plot) ANOVAs to compare $\log_{10}(x+1)$-transformed epilithic algal taxonomic composition between UVR treatments at 0.5 and 1.4 m water depths on day 28. We compared the biovolumes of the 16 most common algal taxa between UVR treatments when a taxon occurred in both blocks of each

treatment. A 2-way ANOVA, using UVR treatment and water depth as independent variables, was not used because not all the common algal taxa occurred in each block or at each depth. We nested the UVR treatments in split-plots as described above. To minimize the chance of a type I error during multiple comparisons, the Dunn–Sidak method was used to adjust for each comparison ($\alpha' = 1 - [1 - 0.1]^{1/k}$), where k is the k^{th} comparison (Sokal and Rohlf 1995). We also used a 2-way nested (split-plot) RM ANOVA to compare $\log_{10}$-transformed epilithic particulate C between UVR treatments at all depths and dates.

We used SYSTAT (version 10.2, SYSTAT Software, Richmond, California) for all analyses. We set $\alpha = 0.1$ to avoid making Type II errors.

Results

UVR

Total daily UVA exposure at the lake surface ranged from 332 to 1367 kJ m^{-2} d^{-1} (mean = 1013 kJ m^{-2} d^{-1}) from mid May through August 1999 (Fig. 1). Total daily UVA exposure for the same period and location in 1998 ranged from 464 to 1366 kJ m^{-2} d^{-1} (mean = 1043 kJ m^{-2} d^{-1}, data not shown). Total daily UVA on sampling days in 1999 was generally greater than weekly means because we sampled on cloudless days. Total daily UVA on day 28 (1323 kJ m^{-2} d^{-1}) was near the maximum UVA recorded during our study and was ~14% greater than on days 45 or 66 (1141 ± 4 kJ m^{-2} d^{-1}). UVR levels did not differ between days 45 and 66.

Percent transmissions of surface UVA were 34%, 21%, and 7% at 0.5, 0.8, and 1.4 m, respectively (equation 1, assuming 3.4 mg/L DOC; Fig. 2). Percent transmissions of surface UVB at the same depths were 11%, 4%, and <1%, respectively (equation 2). Calculated maximum depths of UVA and UVB transmission (1% of surface levels) were 3.5 and 1.5 m, respectively, based on UVR attenuation measurements made during 1996 in 8 ELA lakes (including Lake 224) (equations 3 and 4; Donahue et al. 2003). Percent transmission of UVR was probably underestimated using equations by Scully and Lean (1994) because these equations do not account for lake-to-lake differences in DOC quality (Donahue et al. 1998).

Epilithic metabolism

Rd was 30 to 50% greater in the UVR+ treatment than in the UVR− treatment at all depths on day 28 (UVR, $F_{1,2} = 5.05$, $p < 0.05$; Table 1, Fig. 3). The magnitude of this effect was similar among depths (UVR × depth, $F_{1,2} = 0.24$, $p > 0.1$; Table 1) even though UVA ranged from ~10 to 35% of surface levels. The effect of UVR diminished over time (time × UVR, $F_{2,4} = 4.60$, $p < 0.05$; Table 1). Rd was greater in the UVR+ treatment than in the UVR− treatment only at 0.5 m on day 45 (Bonferroni, $p < 0.05$; Fig. 3), and Rd did not differ between UVR treatments at any depth on day 66 (Bonferroni, $p > 0.1$; Fig. 3). Rd decreased with water depth on day 28 and 45, but not on day 66 (depth, $F_{1,2} = 5.31$, $p < 0.05$; Table 1, Fig. 3). Rd increased from day 28 to 45, but declined by day 66 (time, $F_{1,2} = 47.85$, $p < 0.01$; Table 1, Fig. 3).

Pnet did not differ between UVR treatments (data not shown). Rd:Pg was 12 to 30% greater in the UVR+ treatment than in the UVR− treatment on day 28 (UVR, $F_{1,2} = 2.58$, $p < 0.1$; Table 1, Fig. 4). Rd:Pg was significantly greater in UVR+ than UVR− treatments at all depths on day 28, at the 0.5 m depth on day 45 (Bonferroni, $p < 0.05$; Fig. 4), but not at any depth on day 66 (Bonferroni, $p > 0.1$; Fig. 4). The difference in Rd:Pg between UVR treatments decreased with time (time × UVR, $F_{2,4} = 4.44$, $p < 0.05$; Table 1). Rd:Pg decreased with water depth, and the decrease was statistically significant (depth, $F_{1,2} = 3.97$, $p < 0.1$; Table 1). Rd:Pg increased over time from day 28 to day 45 (time, $F_{1,2} = 6.46$, $p < 0.05$; Table 1, Fig. 4).

Taxonomy of epilithic algae

The biovolumes of major algal groups did not differ between UVR treatments at 0.5 m and 1.4 m depths on day 28 (1-way ANOVAs, $p > 0.1$; Fig. 5). Chlorophytes were the dominant algal group on tiles at 0.5 m. The most abundant taxa were *Botryococcus braunii*, *Cosmarium* spp., *Mougeotia* sp., *Oedogonium* sp., *Spirogyra* sp., and *Zygnema* sp. and, collectively, filamentous chlorophytes (*Mougeotia* sp., *Oedogonium* sp., *Spirogyra* sp., and *Zygnema* sp.) made up >50% of total chlorophyte biovolume. Biovolumes of individual epilithic algal taxa were highly variable between blocks, but the biovolumes of 2 chlorophytes were reduced in the UVR+ treatments.

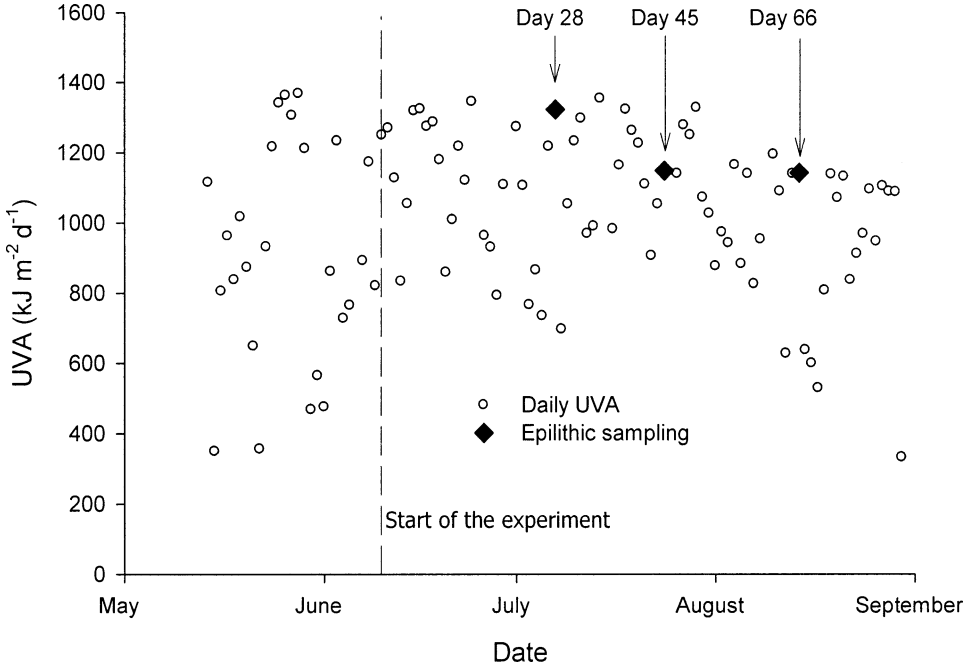

FIG. 1. Daily ultraviolet A radiation (UVA) levels at the lake surface from May to September 1999. Vertical dashed line indicates when tiles were deployed.

Cosmarium sp. was reduced ~6× at the 0.5 m depth and *Zygnema* sp. was reduced ~44× at the 1.4 m depth (1-way ANOVAs, $p < 0.05$).

Cyanophytes were the dominant taxonomic group at 1.4 m on day 28. The most common cyanophytes were *Anabaena* sp., *Chroococcus* spp., *Leiblienia* sp., *Nostoc* sp., and an unidentified colonial cyanophyte made up of spherical cells that were ≤3 μm in diameter. Biovolume of the cyanophyte taxa did not differ between UVR treatments (1-way ANOVAs, $p > 0.1$).

Particulate C did not differ between UVR treatments or depths on any date (2-way RM ANOVA, $p > 0.1$). Therefore, we calculated mean particulate C across all depths for each date and compared particulate C among dates with a 1-way ANOVA. Particulate C increased 28% from day 28 to day 45 (158 ± 69 to 219 ± 91 μg/cm², respectively, Bonferroni, $p < 0.05$), but did not increase further by day 66 (209 ± 89 μg/cm², Bonferroni, $p > 0.1$).

Discussion

Effects of UVR on epilithon

UVR disrupted epilithic metabolism by increasing Rd without affecting Pnet. Thus, the increase in Rd:Pg observed in the UVR+ treatment on day 28 occurred because Rd increased without a compensatory increase in Pnet. As a result, the fraction of Pg lost through respiration was higher in UVR+ than in UVR− treatments. However, the response of Rd to UVR decreased as UVR levels decreased and as the epilithic colonization period increased. On day 28, Rd was higher in UVR+ than in UVR− treatments at all depths, including 1.4 m, which was near the lower limits of UVR attenuation. On day 45, UVR affected Rd only at 0.5 m, and by day 66, UVR effects were not detectable.

Thickening of the epilithic biofilm over time may have increased self-shading and reduced the effect of UVR on epilithic metabolism (McNamara and Hill 2000). For example, the negative effect of UVR on chlorophyll *a* concentration declined as epilithon accrued on tiles in a 45-d study by Francoeur and Lowe (1998). We did not obtain direct measures of biofilm thickness, but areal concentrations of particulate C increased between days 28 and 45, by which time the effect of UVR on Rd was detectable only at the shallowest depth.

Our study and others that use artificial sub-

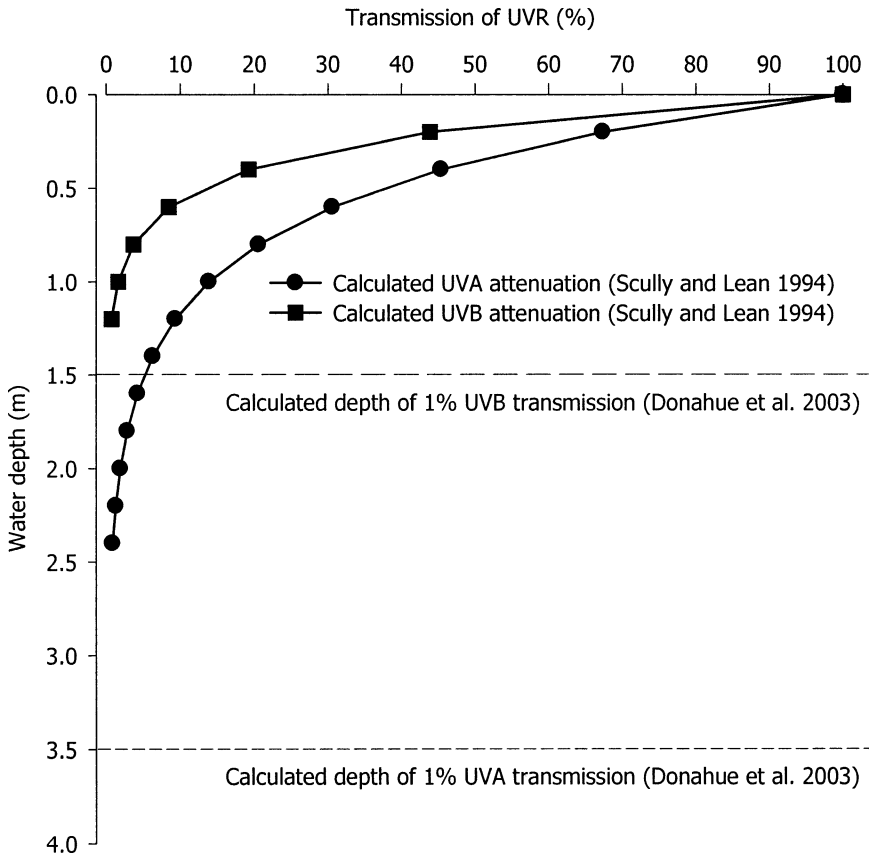

FIG. 2. Percent transmission of ultraviolet A radiation (UVA) and ultraviolet B radiation (UVB) vs water depth in Lake 224 calculated using equations from Scully and Lean (1994). Horizontal lines indicate water depths for 1% transmission of UVA and UVB calculated using equations from Donahue et al. (2003).

TABLE 1. Two-way repeated measures analysis of variance of $\log_{10}$-transformed epilithic dark respiration (Rd), and Rd to gross photosynthesis (Pg) ratio (Rd:Pg) under ultraviolet radiation (UVR)-shielding and UVR-transparent filters at 3 water depths and 3 dates in Lake 224. Values are F statistics for $n = 2$ replicates. * = $p < 0.10$, ** = $p < 0.05$, *** = $p < 0.01$, and n/s = not significant ($p > 0.1$).

Source	df	Rd		Rd:Pg	
UVR	1	5.05	**	2.58	*
Depth	2	5.31	**	3.97	*
UVR × depth	2	0.24	n/s	0.09	n/s
Error	6				
Time	2	47.85	***	6.46	**
Time × depth	2	2.30	n/s	0.42	n/s
Time × UVR	4	4.60	**	4.44	**
Time × depth × UVR	4	0.18	n/s	0.40	n/s
Error	12				

strata probably overestimate the effects of UVR. The biofilms on our study tiles were much thinner than naturally occurring epilithon in Lake 224 (MAT, unpublished data). Moreover, our study may have accentuated the effects of UVR on initial epilithic colonization because we examined epilithon colonizing bare surfaces when seasonal UVR levels were high. The effect of UVR on fully developed, naturally colonized biofilms should be smaller than what we observed because of the potential for self-shading to diminish the effects of UVR.

Comparing studies in Lake 224

Watkins et al. (2001) used methods similar to ours to study UVR effects on epilithon in Lake 224 in 1998. UVR did not affect epilithic respiration and decreased net photosynthesis in 1998

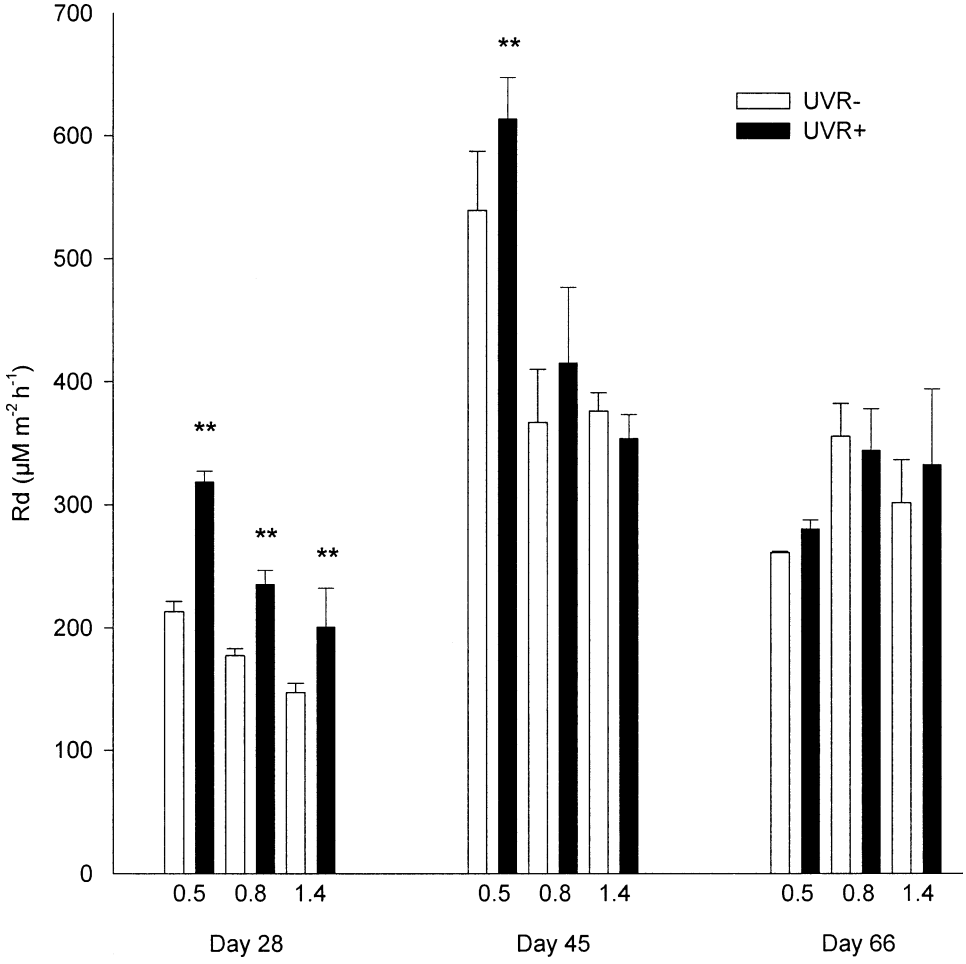

FIG. 3. Mean (+1 SE) dark respiration (Rd) of epilithon under ultraviolet radiation (UVR) filters (UVR-transparent [UVR+] and UVR-shielding [UVR−]) at 3 depths (0.5 m, 0.8 m, and 1.4 m) on 3 dates. $n = 2$. * = $p < 0.10$, ** = $p < 0.05$.

(Watkins et al. 2001), whereas UVR increased epilithic respiration and did not affect net photosynthesis in 1999 (our study). Our study and the study by Watkins et al. (2001) were conducted at nearly the same location and depth (~0.5 m). Mean UVA levels were 1043 and 1013 kJ m^{-2} d^{-1} in 1998 and 1999, respectively. However, the dates for ice-off and initial deployment of tiles were 10 to 15 d earlier in 1998 (14 April and 30 May, respectively) than in 1999 (29 April and 9 June, respectively), and mean water temperatures during the initial colonization period were ~3°C cooler in 1998 than in 1999. Abundances of chlorophytes were higher and abundances of diatoms were lower at 0.5 m in 1999 (our study) than in 1998 (Watkins et al. 2001). The dominant algal class of periphyton can shift from diatoms to chlorophytes with increased water temperatures (DeNicola 1996), and the difference in temperature between the 2 years may have caused the shift from dominance of diatoms in 1998 to dominance of chlorophytes in 1999. Biovolumes of other algal groups were generally similar between 1998 and 1999. The differences in metabolic responses to UVR may have been the result of the difference in the dominant algal taxa between years.

The strong nonlinear dependence of epilithic algal taxonomic composition on water depth in Lake 224 also may have caused the difference in

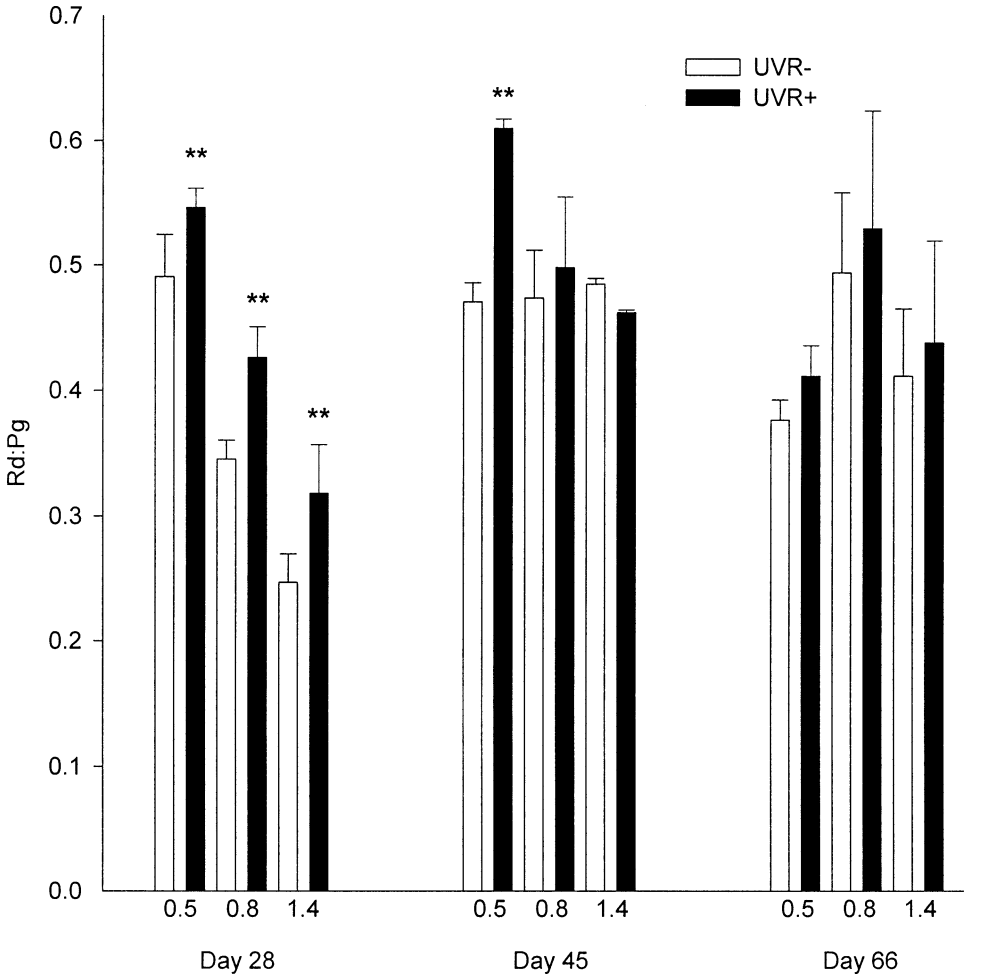

FIG. 4. Mean (+1 SE) ratio of dark respiration (Rd) to gross photosynthesis (Pg) of epilithon under ultraviolet radiation (UVR) filters (UVR-transparent [UVR+] and UVR-shielding [UVR−]) at 3 depths (0.5 m, 0.8 m, and 1.4 m) on 3 dates. $n = 2$. * = $p < 0.10$, ** = $p < 0.05$.

dominant algal taxa between 1998 and 1999. The proportion of diatoms on naturally colonized rock in Lake 224 increases from <5% at 1.5 m to 85% at 0.7 m and decreases to 15% at 0.3 m and <5% at 0.1 m; the proportion of filamentous chlorophytes on rocks increases from <5% at 1.5 m and 0.7 m to 45% at 0.3 m and 75% at 0.1 m (Donahue et al. 2003). Therefore, either filamentous chlorophytes or diatoms could be dominant at depths of ~0.5 m in any given year, and seasonal variation in lake water levels also could affect the succession of algal taxa and, therefore, the sensitivity of epilithon to UVR, at these shallow depths. In contrast, in the middle littoral zone (1.2–2.9 m), cyanophytes always are the predominant taxa on naturally colonized rock surfaces (MAT, unpublished data) and tiles (our study).

Variable metabolic responses to UVR

Variable metabolic responses of different algal taxa to UVR are not surprising (Xiong et al. 1996, Beardall et al. 1997). Beardall et al. (1994) showed that exposure to PAR and UVR together inhibited photosynthesis of the cyanophyte *Aphanizomenon flosaquae*, but increased Rd of the chlorophyte *Selenastrum capricornutum*. However, exposure to high levels of PAR alone increased Rd in both taxa because excess photosynthetic

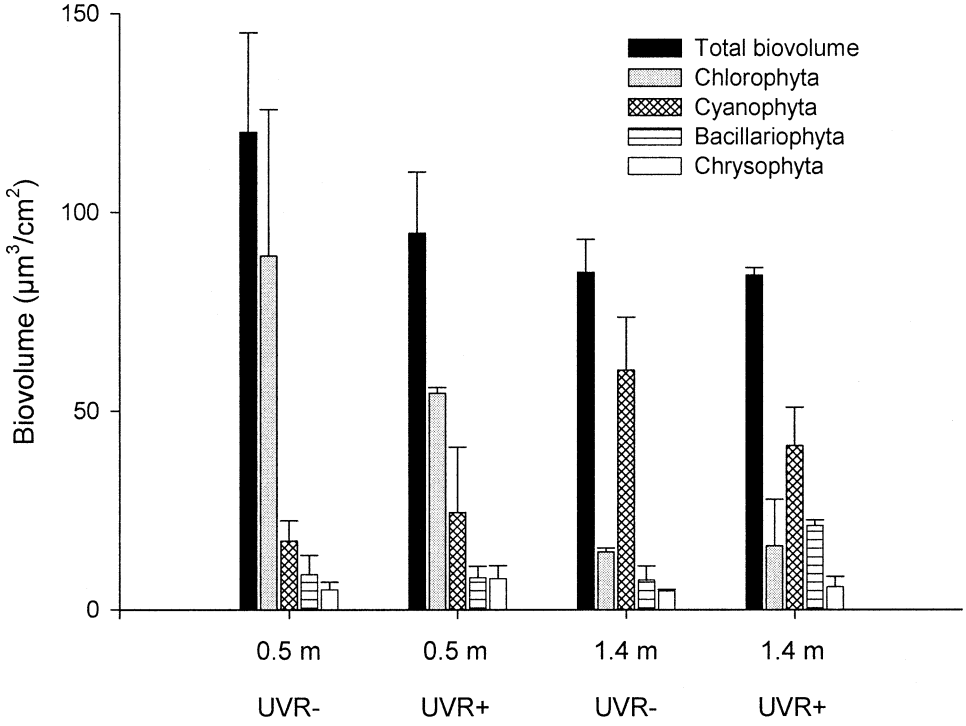

FIG. 5. Mean (+1 SE) epilithic algal biovolume of each major algal class on tiles at 0.5 and 1.4 m depths under ultraviolet radiation (UVR) filters (UVR-transparent [UVR+] and UVR-shielding [UVR−]) after 28 d. $n = 2$.

products were respired (Beardall et al. 1994). van Donk et al. (2001) found that growth rates of filamentous and colonial cyanophytes were more resistant than growth rates of diatoms to UVR. In our study, the metabolic costs associated with cellular repair of UVR damage or creating UVR-shielding pigments may have caused the increased respiration rates of epilithon dominated by filamentous chlorophytes and cyanophytes (Donahue et al. 2003).

Epilithon consists of a mixed assemblage of autotrophs and heterotrophs. The entire biofilm, not just the algal component, contributes to the metabolic responses of epilithon to UVR. In our study, particulate C was up to 3.5× greater than algal wet biomass (assuming cell-specific density was equal to 1 g/mL) on the tiles. This result suggests that most of the biofilm was not viable algae. Hence, algae, bacteria, and possibly fungi and protozoans contribute to Rd in metabolic studies of epilithon. Each of these components may respond differently to UVA and UVB.

Implications for ultraviolet radiation effects in the littoral zone

Fluctuations in the concentrations of DOC will alter the effect of UVR. In Lake 224, the euphotic zone is ~13 m deep. The area of the littoral zone <0.5 m deep is 6% of the euphotic zone, and the area <1.4 m deep is 13% of the euphotic zone (Brunskill and Schindler 1971). The portion of the littoral zone affected by UVR would increase if DOC concentrations declined in response to climate change or acidification (Schindler 1998). For example, the 1% depth of UVA penetration in Lake 224 would increase from 3.6 to 7.8 m (47%) if DOC decreased by 1 mg/L, a change that is within the range of interannual variation in Lake 224 (Donahue et al. 2003). However, most Canadian inland waters currently have sufficient DOC to be well protected (Molot et al. 2004).

UVR effects on benthic metabolism could disrupt the flow of C from benthic to pelagic food webs because these food webs are strongly

linked by benthic primary production (Hecky and Hesslein 1995). However, our results suggest that the effects of current UVR intensities on the littoral zone in Lake 224 are likely to be limited. The strongest effects of UVR on epilithon occurred when seasonal UVR levels were greatest. By mid July, the effects were limited to the shallow littoral zone (≤0.5 m), and by mid August, UVR had no statistically significant effects. Moreover, biofilm thickening may have increased self-shading and partly reduced the effect of UVR on metabolism. UVR did not inhibit epilithic C from accruing ultimately. Newly developing epilithon on shallow littoral surfaces may be the most sensitive to UVR following events such as ice scouring or periodic sloughing of the biofilm. The effect of UVR on benthic–pelagic C flow is likely to be greatest during these times. Thus, present-day intensities of UVR can affect both the function and structure of benthic algal assemblages in the shallow littoral zone, but the effects of UVR are seasonally transient and decrease with depth.

Acknowledgements

We thank R. Hazewinkle, A. Majewski, T. Laidlaw, P. Frost, and K. Peech for field assistance. M. Stainton, R. Schade, and S. Page of the Freshwater Institute Chemistry Laboratory did the chemical analyses. H. Kling provided algal taxonomy. S. Kasian provided statistical guidance. L. Hendzel and D. Findlay discussed the research. E. Watkins and M. Xenopoulos provided UVR data and materials used in this experiment. D. Rosenberg reviewed an early draft of the manuscript. Our study was funded by the Department of Fisheries and Oceans, Government of Canada through MAT and K. Kidd, a Natural Sciences and Engineering Research Council of Canada grant to LGG, and funds from the Department of Botany, University of Manitoba to RPW. This research was submitted in partial fulfillment of RPW's BSc thesis.

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Received: 8 May 2003
Accepted: 16 August 2005