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Direct and indirect effects of UV radiation on benthic communities: epilithic food quality and invertebrate growth in four montane lakes

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The direct harmful effects of ultraviolet radiation (UVR) on benthic and planktonic organisms have been well studied in aquatic systems. Less clear, however, is how UVR might affect aquatic communities through its effects on trophic interactions. The focus of this study was twofold: first, to examine the direct effect of UVR on benthic invertebrates and epilithon, the rock-dwelling matrix of algae, bacteria, viruses, fungi and detritus, and second, to examine the indirect effect of UVR-mediated shifts in epilithic food quality on epilithic consumers. Food quality was assessed by measuring carbon to nutrient ratios and the concentration of polyunsaturated fatty acids (PUFA) in the epilithic matrix; the effect of its change on epilithic consumers was measured using a feeding experiment. The study was conducted in four montane lakes, where downwelling UVR can be intense. Of these lakes, the benthic community of only one was strongly affected by UVR. In this lake, exposure to UVR decreased epilithic accrual and invertebrate colonization, and, contrary to our expectations, increased food quality in the shallows through decreased carbon to phosphorus ratios and increased PUFA concentrations. In another of the four study lakes, the feeding experiment showed no significant difference in growth rates between invertebrates fed UVR-exposed and UVR-shielded epilithon, or invertebrates directly exposed to or shielded from UVR. This study demonstrates that although UVR can play an important role in structuring the trophic dynamics of benthic communities, its effects will not be constant across systems, or important in all environments.

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In aquatic systems, the direct, deleterious effects of ultraviolet radiation (UVR) on algal photosynthesis (Helbling et al. 1992, Watkins et al. 2001) and growth (Jokiel and York 1984, Xenopoulos et al. 2002), and invertebrate abundance (Bothwell et al. 1994, Kiffney et al. 1997a) and survivorship (McNamara and Hill 1999) have been well documented. To fully understand the role of UVR in structuring aquatic ecosystems, however, it is imperative to also consider its indirect, food-web-mediated effects. Although these effects can be great (Bothwell et al. 1994, Xenopoulos and Bird 1997), the manner in which UVR-mediated changes to one trophic level might affect another has been poorly documented. In particular, there is little evidence to show how UVR might affect the nutritional quality of primary producers as food for their consumers, especially in situ.

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In this study, we experimentally tested how ambient UVA and UVB radiation affect the quantity and nutrient qualities of the epilithon (the rock-dwelling matrix of algae, bacteria, fungi, viruses, detritus, and multicellular benthic animals) in four montane lakes of Jasper National Park, Alberta, Canada. We further examined how these changes in nutrient content might affect epilithic consumers. Specifically, we hypothesized that: (1) UVR would decrease the quantity of epilithic algae and animals, (2) UVR would decrease the quality of epilithon as a food source for invertebrate grazers, and (3) decreases in the quantity and quality of their food source would decrease growth rates of epilithic grazers.

There are several mechanisms through which the composition of producer communities may affect consumer growth. Variations in producer elemental ratios (i.e. stoichiometry), most notably increases in C:P, reduce the growth rates of consumers (e.g. Sterner and Schultz 1998). Although most often documented in pelagic systems, stoichiometric imbalances are also expected to occur and limit consumer growth in the benthos (Frost and Elser 2002a, Hillebrand and Kahlert 2001). A number of theories have been advanced to explain how the stoichiometry of algal cells in particular might be affected by UVR stress. Most directly, UVR may induce changes to nutrient uptake rates. Both ammonia and nitrate are incorporated more slowly into UVR-stressed algae in the laboratory (Döhler and Biermann 1987, Döhler and Kugel-Anders 1994). Conversely, phosphorus uptake in laboratory algae has been shown to increase under low levels of UVR, but be severely inhibited at higher UVR doses (Hessen et al. 1995). Changes in algal growth rates may also alter elemental composition. Light-induced increases in growth (at constant nutrient supply rates) have long been known to increase the carbon to nutrient ratio in algal cells (Goldman 1986). More recently it has been shown that slow growing, UVR-stressed phytoplankton exhibit lower C:P ratios than non-UVR exposed assemblages (Xenopoulos et al. 2002).

In addition to stoichiometric considerations, certain biomolecules can also be important for consumer growth. Specifically, concentrations of some long-chain polyunsaturated fatty acids (PUFAs) may limit the growth of organisms at higher trophic levels because many consumers are unable to manufacture these compounds (Goulden and Place 1990, Müller-Navarra 1995). UVR-mediated changes in cellular stoichiometry can be expected to affect cellular biochemistry (Healy and Hendzel 1979, Kilham et al. 1997). For example, internal stores of carbohydrates have been shown to increase under UVR stress in phytoplankton (Van Donk and Hessen 1995), while proteins can increase at low, and decrease at higher UVR dosage rates (Buma et al. 1996). Although these patterns are not universal (Hessen et al. 1997), and can be variable between species (Arts and Rai 1997), long chain PUFAs in particular are expected to decrease under UVR stress. UVR is a powerful inducer of cell peroxidation, to which longer chain PUFAs are particularly susceptible (Girotti 2001). Laboratory studies have shown that exposure of algal cells to UVR often results in a decrease in two fatty acids (FA) considered to be essential for consumer growth: eicosapentaenoic (EPA, 20:5ω3; Goes et al. 1994) and docosahexaenoic (DHA, 22:6ω3) acids (Wang and Chai 1994).

More generally, UVR-induced changes in algal morphological characteristics, such as increased cell wall thickness (Van Donk and Hessen 1995) and increased cell size (Karentz et al. 1991, Bothwell et al. 1993, Van Donk and Hessen 1995) may decrease food quality by decreasing digestibility. However, in contrast to the fairly large body of work focused on sestonic algal food quality, relatively few studies have examined how UVR might affect the nutrient status of the epilithic matrix. UVR-induced changes in grazing pressure might be expected to affect nutrient composition because decreases in epilithic C:P ratios can occur with increasing benthic herbivory, through increases in grazer-excreted P (Hillebrand and Kahlert 2001, Frost et al. 2002). UVR-mediated shifts in epilithic community structure have also been suggested to alter the nutritional value of the epilithic community (nitrogen content; Watkins et al. 2001).

Most of the above were short-term laboratory studies. Although field studies have examined the effect of UVR stress on nutrient ratios (Watkins et al. 2001, Xenopoulos et al. 2002), we know of no previous in-situ studies that have examined the effect of UVR on fatty acid composition in freshwaters. To our knowledge, the degree to which UVR-mediated changes in food quality might affect higher trophic levels remains largely untested in the epilithon.

Methods

Study lakes

We conducted our experiments in four oligotrophic lakes of Jasper National Park. Honeymoon, Leach, Hibernia and Saturday Night Lakes were chosen for their range of UVR transparency, comparable elevations, and ease of access. We worked in multiple systems to better understand how ubiquitous the response to our experimental manipulations is at the ecosystem level. The lakes lie in the main ranges of the Canadian Rocky Mountains, are underlain by calcareous till, and surrounded by brunisolic and luvisolic soils (Holland and Coen 1983). Surrounding vegetation is dominated by lodgepole pine (*Pinus contorta*; Holland and Coen 1983). Leach, Hibernia, and Saturday Night Lakes are located in the montane ecoregion, while Honeymoon Lake lies in the lower subalpine (Holland and Coen

1983). Leach and Honeymoon Lakes are relatively transparent to both ultraviolet and photosynthetically active radiation (PAR), while Hibernia and Saturday Night Lakes are much less so (Table 1). Common limnological parameters for the four study lakes are given in Table 2.

Experimental design: direct effects of UVR on epilithon and invertebrates

Three UVR screening treatments (Cadillac Plastics, Edmonton, Canada) were employed to test the effect of UVR on epilithic communities. The first, our "PAR + UVA + UVB" treatment, allowed penetration of the full solar spectrum (Acrylite OP4®, 70% cut-off at 280 nm). The second, our "PAR + UVA" treatment, blocked UVB radiation (Mylar-D®, 70% cut-off at 320 nm). The third, our "PAR" treatment, blocked all UVR (Acrylite OP3®, 100% cut-off at 400 nm). Wavelength-specific absorbance scans for the screening materials used here are described in Watkins et al. (2001). The Plexiglas® and Mylar-D® sheets were suspended centimeters below the water surface using a frame of ABS plastic piping. Acid-washed, unglazed, ceramic tiles (104 tiles, each 4.8×4.8 cm) were placed on the lake bottom below the screens so that epilithon could colonize the tiles over the experimental period (110 d; late May – early Sept.). Tiles were initially deployed at a depth of 30 cm; however, normal water level fluctuations occurred throughout the summer and were monitored at 10 d intervals. Tiles were not pre-colonized in the study lakes to allow community succession to occur under the three optical treatments. The size and positioning of the screens was such that radiation incident upon the tiles was always filtered, despite daily and seasonal shifts in solar angle.

One of each of the three UVR screens was set up in each of the four study lakes. Experiments were initiated between May 26 and 31, 2000. Samples were collected approximately every 10 d thereafter, by randomly selecting tiles, and scraping off the epilithic community

Table 1. Percentage of downwelling integrated UVB, UVA, and photosynthetically active radiation that penetrates to the primary, mid, and deep experiment tile depths in each of four study lakes in Jasper National Park, Alberta. Penetration was measured using a scanning spectrophotometer and is closely related to fluctuations in tile depth and water clarity on each sampling date. Measurements were calculated by averaging the penetration of the different wavelengths over: 290–320 nm (UVB), 320–400 nm (UVA), and 400–700 nm (PAR).

	Percent penetration			
	Leach	Honeymoon	Hibernia	Saturday night
UVB (290–320 nm)				
Primary	16.6–36.6	17.3–42.1	3.0–12.9	3.9–9.1
Mid	3.0–8.2	NA	0.5–1.3	NA
Deep	0.8–1.4		0.1–0.2	
UVA (320–400 nm)				
Primary	46.0–66.7	51.5–66.8	29.8–48.4	26.2–41.5
Mid	21.8–41.0	NA	15.4–25.0	NA
Deep	7.7–23.2		7.0–13.2	
PAR (400–700 nm)				
Primary	74.6–90.1	82.6–92.9	74.7–93.7	54.5–80.7
Mid	53.8–80.6	NA	73.9–90.7	NA
Deep	35.2–70.2		57.1–86.8	

Table 2. Selected parameters for four study lakes in Jasper National Park, Alberta. Measurements were taken every 10 d from early June to early September 2000.

Parameter	Leach	Honeymoon	Hibernia	Saturday night
Elevation (m a.s.l.)	1237	1405	1198	1418
Area (ha)	13.1	18.4	9.6	9.7
Z_{mean} (m)	3.1	2.1	3.4	3.3
Z_{max} (m)	11.0	7.0	8.5	8.3
DOC (mg l^{-1})	8.3–9.7	6.9–8.9	9.0–10.5	8.3–9.3
Chlorophyll (μg l^{-1})	0.4–2.1	0.7–2.4	0.7–2.2	1.0–5.5
TP (μg l^{-1})	7.7–10.2	5.5–7.9	9.1–12.5	6.9–13.3
NH_4^+ (μg N l^{-1})	1.7–49.3	5.2–41.8	1.1–23.6	4.7–25.3
$NO_2^- + NO_3^-$ (μg N l^{-1})	0.5–8.7	0.6–4.9	0.2–5.0	0.8–11.0
Conductivity (μS cm^{-1})	196–207	173–182	255–258	248–256
pH	7.9–8.5	8.1–8.5	8.1–8.5	8.1–8.5
Alklinity (mg l^{-1} HCO_3^-)	126–132	109–115	150–152	147–157
Silica (mg l^{-1})	4.7–5.3	1.5–2.2	5.6–6.3	4.2–5.1

that had accumulated on the tile surfaces. For particulate analyses (chlorophyll a [chlor a], FA, particulate carbon [C], nitrogen [N], and phosphorus [P]), four replicates were collected, each consisting of epilithon scraped from a separate whole- or half-tile. Replicates were filtered in the field on Whatman® GF/F filters, and either dried at 60°C for 24 h and frozen (C, N, and P), directly frozen (chlor a) or frozen on dry ice (FA) within 2 h. FA samples were transferred to a −80°C freezer directly from the dry ice. Filters for C, N, P and FA analyses were pre-combusted for 2 h at 475° C. Three replicate invertebrate samples were collected by gently scraping and rinsing the tiles, and were immediately preserved using 4% formalin. Water chemistry samples were also obtained on each sampling day just below the lake surface, near the center of each lake. Samples for the determination of dissolved organic carbon (DOC), chlor a, TP, NH_4^+, $NO_2^- + NO_3^-$, conductivity, pH, alkalinity and silica were analyzed using standard methods (Stainton et al. 1977, Prepas and Rigler 1982, APHA 1992, Welschmeyer 1994).

To determine how the effects of UVR might change with depth, smaller versions of the above-described set-ups were employed in Leach and Hibernia Lakes. Thirty-six tiles were attached to the bottom of wire baskets, which were covered with UVR screens large enough to block all incident solar radiation. Because of time constraints, not all incubated tiles were used for analysis. In each lake, one replicate of each of the three radiation treatments was placed at each of two depths: in Leach Lake at approximately 60 and 90 cm, and in Hibernia Lake at approximately 37.5 and 60 cm. To distinguish them from the above-mentioned primary experiment, these experiments will be referred to as "mid" and "deep".

Experimental design: indirect effects of UVR on epilithic food quality

To assess how UVR-induced changes in epilithic composition might affect epilithic grazers, a feeding experiment was performed in Honeymoon Lake. Valvatid snails (*Valvata sincera helicoidea*) were collected, measured, and incubated with epilithon-covered tiles that had been colonized for at least 6 weeks under one of the three radiation treatments discussed above. Snails were measured with calipers, at the greatest shell diameter. At the start of the experiment a sample of snails of similar length was also collected, measured as above, and dried and weighed, to obtain an initial length-weight regression. Incubation trays containing snails and tiles were then covered with one of the three UVR-screening plastics. Five combinations of previous epilithic UVR exposure, and ambient UVR shield were employed to allow us to distinguish between effects brought about by UVR-induced changes in food quality (number 1 to 3, below), and UVR incident directly on the snails (no. 1, 4 and 5). These were:

1. epilithon incubated under PAR, incubation tray covered with PAR screen;
2. epilithon incubated under PAR + UVA, incubation tray covered with PAR screen;
3. epilithon incubated under PAR + UVA + UVB, incubation tray covered with PAR screen;
4. epilithon incubated under PAR + UVA, incubation tray covered with PAR + UVA screen;
5. epilithon incubated under PAR + UVA + UVB, incubation tray covered with PAR + UVA + UVB screen.

Each treatment was replicated 5 times, and each replicate consisted of 6 snails incubated in a single container. The incubation continued for 18 d, during which tiles were replaced with new, ungrazed tiles every 3 d. Initial experiments were conducted to ensure that the consumers would not be supply-limited at this replacement rate. Tiles were also visually inspected during each replacement to ensure that the epilithic community had not been fully grazed. At the end of the experiment, snails were measured as above, dried and weighed. Initial weights were interpolated by using the initial lengths to solve for weight in the length-weight regression, and a growth rate index was calculated as:

$$\mu = \frac{[\log(b_2) - \log(b_1)]}{\text{time}}$$

where μ = growth rate, b_1 = body weight at the outset of the experiment, and b_2 = body weight at the termination of the experiment.

Determination of incident radiation and water transparency

Incident UVR and PAR were measured using a Li-Cor LI1000 data logger equipped with a quantum cosine PAR sensor (Li-Cor Instruments, Lincoln, Nebraska), and broadband UVA and UVB sensors (BW20, Vital Technologies, Toronto, Ontario). The broadband UVB sensor was calibrated against Environment Canada's Brewer spectrophotometer in Edmonton (Alberta, Canada), while the broadband UVA sensor was calibrated against 3 discrete UVA wavelengths (325, 340 and 380 nm) on a Stor-Dat radiometer (Satlantic Inc., Halifax, Canada) placed beside the broadband sensor. Because of equipment failure, the radiation flux values for certain dates were estimated using forward stepwise multiple regression with daylength, hours of bright sunshine (both provided by Environment Canada), and ozone (obtained from NASA satellite data) as input variables.

On each sampling occasion, subsurface water was collected from the center of the lake. Water samples were refrigerated in the dark until analysis (within 2 weeks), at which time light absorption in the range of 280 to 700 nm was measured through a 2-cm cuvette using a scanning spectrophotometer (Cary WinUV, Varian Instruments, California). During late summer (August 17–19, 2000) a submersible radiometer was employed to measure solar attenuation within the water column (Satlantic Stor-Dat, Satlantic Inc., Halifax, Canada). Estimates of PAR and UVR attenuation from these two methods were compared using calculated attenuation coefficients (K_d) from the closest sampling date.

Laboratory analyses

Chlorophyll a

Samples were extracted in the dark at 80°C in 90% ethanol for 5 min. Extraction continued in darkness at 4°C for 24 h. Chlorophyll a concentration was determined spectrofluorometrically (Shimadzu Model RF-1501, Mandel Scientific, Guelph, Ontario), following the method of Welschmeyer (1994).

Carbon, nitrogen and phosphorus

To assess C content and C:N ratios, epilithic particulate C and N were measured on individual samples after combustion at 975°C in an elemental analyzer (CEC model 440, Control Equipment Corporation, Lowell, Massachusetts). To account for variation between samples, epilithic C was also estimated on samples analyzed for epilithic C:P ratios. Here, C was estimated as CO_2 after digestion in a closed vessel with potassium persulfate, using gas chromatography (Hewlett Packard 5890 with Chromosorb 102 column; Lampman et al. 2001), followed by phosphorus analysis on the same sample using the molybdate-ascorbic acid method (APHA 1992).

Fatty acids

Samples for FA analysis were extracted using a modification of the Bligh and Dyer (1959) technique. Two replicate filters for FA analysis were combined and freeze-dried prior to extraction. Dry samples were weighed, and extracted three times in chloroform: methanol (2:1 by volume). Each extracted sample was then subjected to a salt-water rinse, through the addition of 0.9% NaCl (weight per volume) at 20% of the extract's volume. Samples were vortexed and centrifuged, and the salt layer removed. Rinsed samples were then evaporated to dryness under nitrogen gas, and stored at -80°C until derivatization.

Extracted samples were derivatized using a modification of Morrison and Smith (1964). Samples were dissolved in 2 ml hexane, to which 2 ml of BF_3 methanol (10% by weight) was added. Sample tubes were purged with nitrogen, sealed, and incubated at 70°C for 2 h. Analytical blanks (2 ml of pure hexane and 2 ml of BF_3 methanol) and standards (standard concentrations of FA in 2 ml of hexane and 2 ml of BF_3 methanol) were derivatized as above. After the incubation, 1 ml of GC-grade water was added to each tube, and the hexane phase was extracted three times through repeated addition of 1 ml of hexane, which was decanted from the BF_3-water mixture. Derivatized samples in hexane were then dried to a volume of 0.2 ml, transferred into clean microvials, and stored at -80°C until analysis.

Derivatized FA were analyzed using gas chromatography (Hewlett Packard 5890, Series II), on an HP-5 column (25 m $\times$ 0.2 mm internal diameter, column head pressure = 60 kPa), using a flame ionization detector (detector at 300°C, injector at 300°C). Injection was splitless, with 1 or 2 µl of sample being injected. Oven temperature was initially set at 50°C, increased to 180°C at 10°C/min, increased to 258°C at 2°C/min, and finally increased to 300°C in 1 min, where it was held for 15 min. Individual FA peaks were identified by comparing retention times with known standards (Supelco 37-component FAME mix), and further verified using GC-MS. FA concentrations were interpolated from a four point standard curve (Supelco 37-component FAME mix; Cat. # 47885-U), and were normalized per unit dry weight.

Invertebrate taxonomy

Invertebrate samples were counted, without subsampling, under a dissecting microscope. Identifications were made to class or family. Data are presented as numbers for the most common taxa (Oligochaeta, Nematoda, and Chironomidae), as well as a total count that includes less common taxa.

Statistical analyses

Two-way ANOVAs were used to test for the effects of UVR treatment and time of sampling on the various epilithic parameters measured (JMP Version 3.2, SAS Institute, 1996). The Tukey-Kramer test was used for post-hoc comparisons where differences were significant (SYSTAT Version 8.0, SPSS Inc. 1996). Chlorophyll a, C, and area-specific FA data were $\log_{10}$ transformed in order to satisfy the assumptions of ANOVA. In Leach Lake, dry-weight specific FA data were inverted, again to meet the assumptions of ANOVA.

Invertebrate count data were first analyzed as a MANOVA before ANOVA tests were employed. Invertebrate counts were square root $(n + 1)$ transformed in order to meet statistical assumptions. When a significant difference was present in the MANOVA analysis, Dunn-Šidák adjusted contrasts were performed to in-

vestigate where differences lay (JMP, SAS Institute, 1996). For the feeding experiment, the average of all snails in a replicate was used to calculate a growth rate for that replicate. Growth rates were then analyzed using a one-way ANOVA.

Results

Incident radiation and water transparency

Incident radiation was greatest in early July, with lower values at the beginning and towards the end of the experimental period (Fig. 1). Forward stepwise multiple regressions incorporating day length and bright sunshine as independent variables explained a significant amount of variation in measured levels of PAR, UVA, and UVB (Fig. 1; $r^2_{PAR} = 0.92$, $r^2_{UVA\ (380)} = 0.85$, $r^2_{UVA\ (340)} = 0.85$, $r^2_{UVA\ (325)} = 0.85$, $r^2_{UVB} = 0.83$), and were used to estimate fluxes where data are missing. Neither breaking the regressions down seasonally, nor incorporating ozone levels into the UVB model, significantly improved model fit.

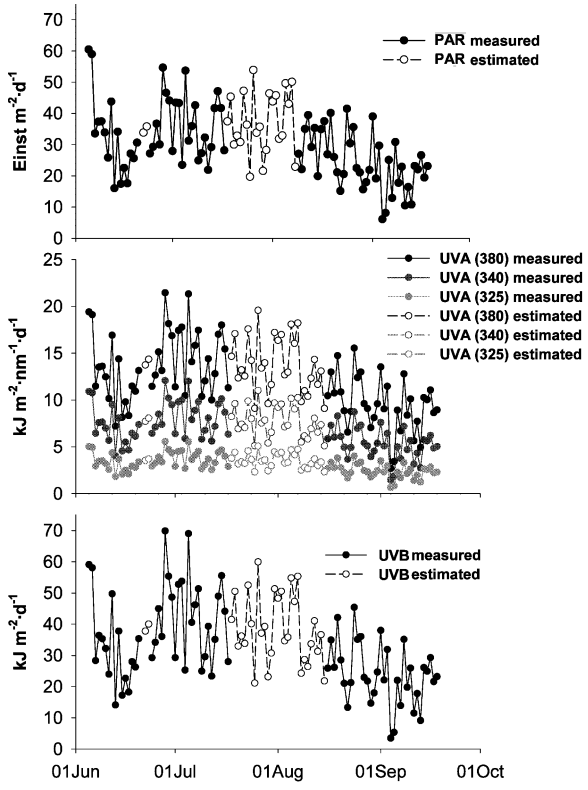

Fig. 1. Downwelling PAR, UVA and UVB radiation measured at Jasper National Park meteorological station, 1020 m a.s.l. Missing data were estimated using the following equations: $UVB = -52.600 + 3.220sun + 4.523daylength$, $r^2 = 0.83$; $UVA_{(380)} = -13.532 + 0.869sun + 1.389daylength$, $r^2 = 0.85$; $UVA_{(340)} = -7.644 + 0.491sun + 0.782daylength$, $r^2 = 0.85$; $UVA_{(325)} = -3.566 + 0.229sun + 0.361daylength$, $r^2 = 0.85$; $PAR = -36.444 + 2.833sun + 3.444daylength$, $r^2 = 0.92$. Sun = hours of bright sunshine, daylength = hours from dawn to dusk.

Spectrophotometric estimates of absorption showed that Hibernia and Saturday Night Lakes absorbed highly in the UVB range, while Leach and Honeymoon Lakes were more transparent (Table 1) despite similar concentrations of DOC, suggesting differences in DOC quality between the clear and coloured lakes (Tank 2002). In the more colored lakes, $< 15\%$ of incident UVB penetrated to the tile surface in the primary experiment. This difference in transparency amongst the lakes decreased with increasing wavelength, to the point where absorption was almost identical in the PAR region, with the exception of Saturday Night Lake. Excluding the mid experiment in Leach Lake, UVB penetration in the mid and deep experiments was negligible ($< 2\%$ of downwelling; Table 1). Penetration of UVR to the Leach Lake mid experiment was similar to that in the Hibernia and Saturday Night Lakes primary experiment, while penetration to the Leach Lake deep experiment was intermediate to that in the Hibernia Lake mid and deep experiments (Table 1).

The in situ estimation of solar attenuation using a submersible radiometer was compared to spectrophotometric measurements from the nearest sampling date. The two estimates agreed well in the UVB and UVA range. Attenuation coefficients calculated from spectrophotometric and radiometric measurements differed from each other by $< 20\%$, indicating that our spectrophotometric method may have underestimated underwater UVR penetration (data not shown).

Estimates of epilithic biomass

Both chlor a and particulate C were used to estimate epilithic biomass. Chlorophyll a concentrations increased significantly over time in the primary experiment in all lakes (Table 3, Fig. 2). In Honeymoon and Saturday Night Lakes, the elimination of UVR had no effect on chlor a concentration (Table 3). In Leach Lake, removing UVA radiation, but not UVB, significantly increased chlor a concentrations: in the PAR treatment, chlor a concentrations were significantly greater than in either the PAR + UVA or PAR + UVA + UVB treatments, which did not differ from each other (Table 3, Fig. 2). In Hibernia Lake, although chlor a concentrations differed significantly between treatments, the effect was not constant over time (Table 3, significant interaction term). Simple contrasts for this lake suggest that differences between treatments were driven by high chlor a concentrations under the PAR + UVA treatment on the 8th and 9th sampling dates ($p < 0.01$; $PAR + UVA > PAR_{(Aug.\ 20)}$, $F_{1,98} = 7.85$; $PAR + UVA > PAR + UVA + UVB_{(Aug.\ 20)}$, $F_{1,98} = 14.99$; $PAR + UVA > PAR_{(Aug.\ 30)}$, $F_{1,98} = 8.35$).

Table 3. Two-way ANOVA results for the effects of UVR on measurements of epilithic standing crop and food quality in the primary experiment for study lakes in Jasper National Park, Alberta. Reported are: degrees of freedom (df), F statistics and p-values for n = 4 replicates for chlorophyll a, particulate carbon, C:N and C:P, and n = 2 replicates for EPA. Data were transformed as stated in the text. Significant differences are highlighted as bold text. ND = not determined.

		Leach		Honeymoon		Hibernia		Saturday night	
	df	F	p	F	p	F	p	F	p
Chlorophyll a									
UVR	2	14.67	**<.0001**	1.93	0.152	3.56	**0.033**	1.17	0.315
Time	9	2.94	**0.004**	5.69	**<.0001**	58.10	**<.0001**	10.65	**<.0001**
UVR × Time	18	0.94	0.532	1.45	0.128	2.08	**0.013**	0.99	0.478
Particulate carbon									
UVR	2	8.58	**0.0007**	1.80	0.177	1.11	0.339	0.79	0.243
Time	4	13.77	**<.0001**	9.93	**<.0001**	25.95	**<.0001**	13.57	**0.002**
UVR × Time	8	2.07	0.060	3.43	**0.004**	1.35	0.244	0.79	0.613
Particulate C:N									
UVR	2	3.08	0.056	1.27	0.290	1.85	0.169	1.47	0.461
Time	4	11.21	**<.0001**	3.84	**0.009**	18.43	**<.0001**	5.34	**<.0001**
UVR × Time	8	0.94	0.493	0.80	0.603	0.82	0.586	0.79	**0.041**
Particulate C:P									
UVR	2	3.72	**0.032**	1.15	0.325	2.84	0.069	1.95	0.155
Time	4	9.05	**<.0001**	4.26	**0.006**	3.20	**0.022**	2.17	0.088
UVR × Time	8	0.34	0.946	1.56	0.165	5.06	**0.0002**	1.45	0.204
EPA ($\mu g\ g^{-1}$)									
UVR	2	13.74	**0.002**	0.60	0.563	ND		ND	
Time	4	5.21	**0.019**	0.66	0.629				
UVR × Time	8	0.82	0.601	4.26	**0.012**				
EPA ($\mu g\ m^{-2}$)									
UVR	2	1.94	0.200	0.96	0.412	ND		ND	
Time	4	25.12	**<.0001**	2.24	0.125				
UVR × Time	8	1.19	0.400	2.21	0.104				

Trends in the particulate C data from the primary experiment resemble those observed for chlor a (Table 3, Fig. 2). In Honeymoon and Saturday Night Lakes, differential UVR exposure did not significantly affect particulate C concentrations (Table 3), despite a large C increase under the PAR treatment in Honeymoon Lake on one sampling occasion. In Leach Lake, removal of UVA resulted in significant increases in particulate C concentrations (Table 3, Fig. 2). In Hibernia Lake no significant treatment effect was observed (Table 3).

Particulate C results for the mid and deep experiments in Leach Lake suggest that the UVR effect decreased with depth (Table 4, Fig. 3). The UVR effect was not statistically significant in the mid experiment (Table 4, Fig. 3) because of an interaction between UVR and time during the second sampling period. However, simple contrasts reveal that C was significantly higher in the PAR treatment on the 3rd sampling day ($p < 0.05$; PAR > PAR + UVA, $F_{1,27} = 8.13$; PAR > PAR + UVA + UVB, $F_{1,27} = 7.78$). In the deep experiment C concentrations were significantly elevated in the PAR treatment (Table 4, Fig. 3). A comparison of Fig. 2 and 3, however, clearly demonstrates the magnitude of this UVR effect to be less than that in the primary experiment.

In Hibernia Lake, C concentrations were significantly higher in the absence of UVA in the mid experiment (Table 4, Fig. 3). Although the interaction term was significant for this analysis it is marginal in comparison with the treatment effect, and will not be discussed further. There was no significant difference between radiation treatments in the deep experiment (Table 4, Fig. 3).

Invertebrate colonization

In Leach and Hibernia Lakes, invertebrate colonization differed significantly between radiation treatments (two-way MANOVA; Table 5, Fig. 4). This trend was largely driven by chironomid and oligochaete densities. In Leach Lake, colonization in the PAR treatment was significantly greater than in the PAR + UVA + UVB treatment, while other comparisons did not differ (MANOVA contrasts; Table 5). In Hibernia Lake, invertebrate colonization in the PAR + UVA treatment was significantly greater than the PAR treatment, with no significant difference occurring between the other treatments (MANOVA contrasts; Table 5). In Leach Lake, invertebrate numbers decreased significantly with time, while in Hibernia Lake they increased (Table 5, Fig. 4). The significant interaction term in the Hibernia Lake anal-

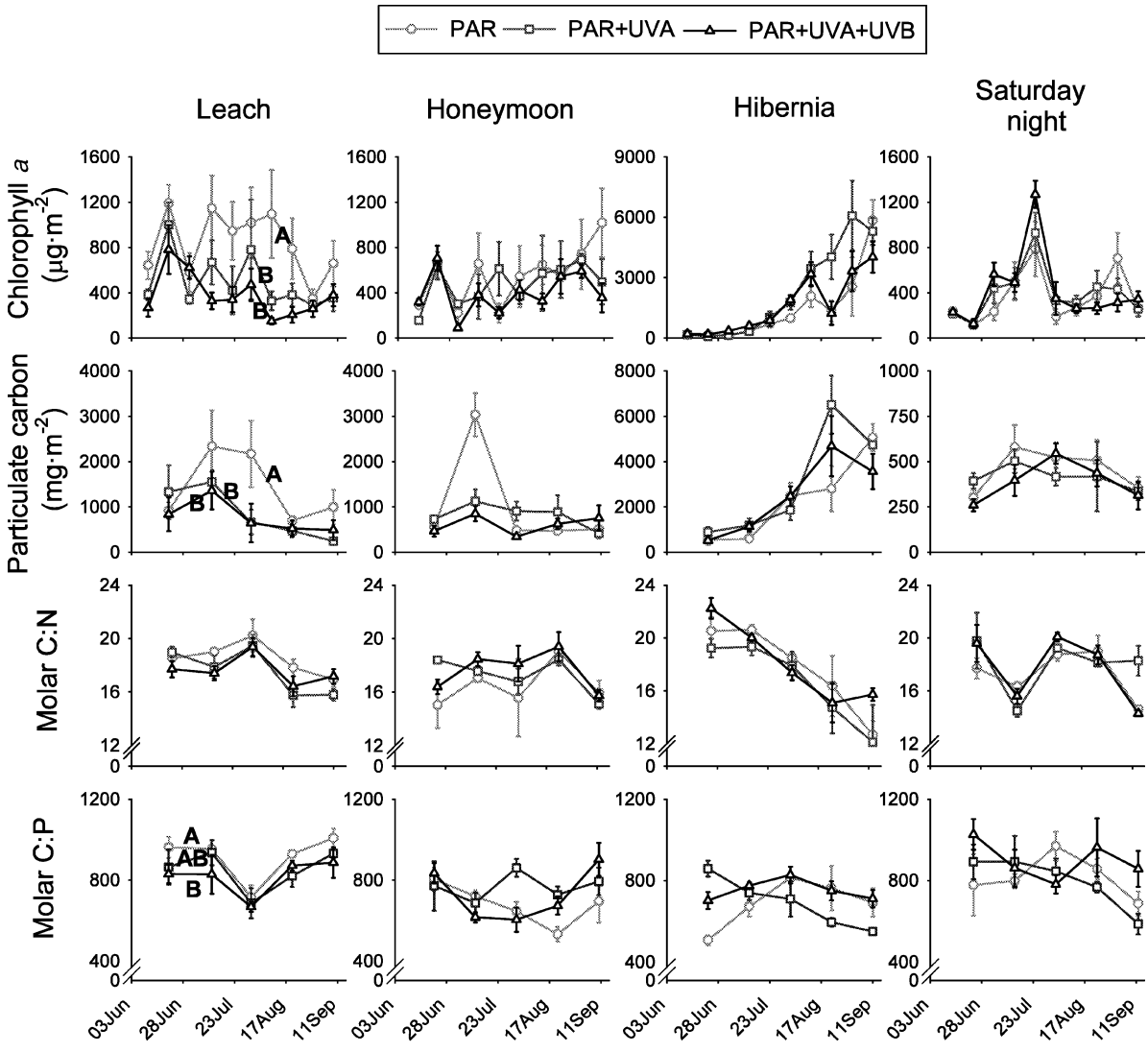

Fig. 2. Measurements of epilithic standing crop and food quality under three different UVR regimes in the primary experiment of four study lakes in Jasper National Park, Alberta. Error bars represent ± standard error for n = 4 replicates. Significant differences between treatments (for each parameter in each lake) are indicated with different letters.

ysis appears to be mediated by the large divergence of invertebrate numbers between the treatments on the last sampling day.

In Honeymoon Lake, the effect of UVR on invertebrate density was non-significant (Table 5), as assessed both by the MANOVA results ($p = 0.077$), and ANOVAs performed on individual taxa, where p-values for oligochaete ($p = 0.030$) and total counts ($p = 0.025$) fell just above the Dunn-Šidák adjusted value of 0.017. Visual inspection of the data reveals that these differences occurred largely as a result of increased abundances of these taxa in the PAR treatment (Fig. 4). No significant difference existed between treatments in Saturday Night Lake.

Epilithic stoichiometry

Manipulation of the UVR environment had no effect on C:N ratios in either Honeymoon or Saturday Night Lakes (Table 3, Fig. 2). In the Leach Lake primary experiment, there was a non-significant trend towards higher C:N ratios in the PAR treatment than in the PAR + UVA and PAR + UVA + UVB treatments ($p = 0.056$; Table 3, Fig. 2). UVR manipulation did not significantly affect C:N ratios in the mid experiment of Leach Lake. In the deep experiment, C:N ratios were significantly decreased when the epilithic community was shielded from UVA exposure (Table 4, Fig. 3); the opposite result to that seen in the primary experiment. There was no effect of light manipulation on epilithic

Table 4. Two-way ANOVA results for the effects of UVR on measurements of epilithic standing crop and food quality in the mid and deep experiments in Leach and Hibernia Lakes. Reported are: degrees of freedom (df), F statistics and p-values for n = 4 replicates. Data were transformed as stated in the text. Significant differences are highlighted as bold text.

		Leach mid		Leach deep		Hibernia mid		Hibernia deep	
	df	F	p	F	p	F	p	F	p
Particulate carbon									
UVR	2	2.07	0.146	6.173	**0.006**	24.53	**<.0001**	1.04	0.370
Time	2	13.85	**<.0001**	9.95	**0.0006**	17.68	**<.0001**	6.72	**0.005**
UVR × Time	4	3.61	**0.018**	1.69	0.182	2.749	**0.05**	2.24	0.093
Particulate C:N									
UVR	2	0.40	0.677	6.05	**0.007**	0.91	0.413	0.54	0.588
Time	2	0.72	0.496	20.49	**<.0001**	32.53	**<.0001**	6.33	**0.006**
UVR × Time	4	1.19	0.337	3.12	**0.032**	0.47	0.755	1.03	0.410
Particulate C:P									
UVR	2	1.36	0.275	1.07	0.356	5.645	**0.009**	0.41	0.668
Time	2	15.36	**<.0001**	1.53	0.236	1.11	0.344	3.64	**0.041**
UVR × Time	4	1.90	0.140	2.36	0.079	1.81	0.157	2.14	0.106

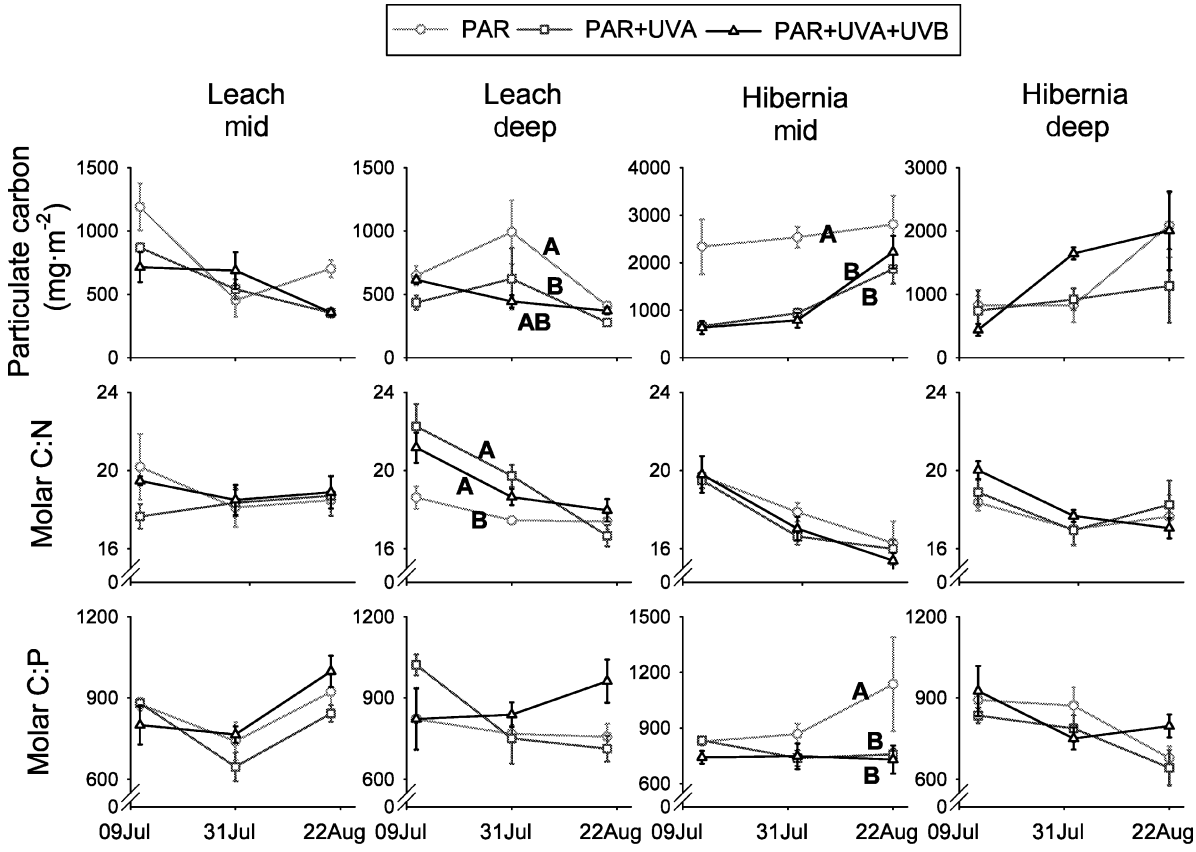

Fig. 3. Measurements of epilithic standing crop and food quality under three different UVR regimes in the mid and deep experiments of four study lakes in Jasper National Park, Alberta. Error bars represent ± standard error for n = 4 replicates. Significant differences between treatments (for each parameter in each lake) are indicated with different letters.

Table 5. Multivariate and two-way ANOVA results for the effects of UVR on square root (n+1) transformed invertebrate counts in the primary experiment in four study lakes in Jasper National Park, Alberta. Reported are degrees of freedom (df), F statistics and p-values for n = 4 replicates. The Hotelling-Lawley F statistic is used in the MANOVA test. Significance levels for the ANOVA and MANOVA contrasts have been adjusted to 0.0170 to reflect multiple comparisons. Significant differences are highlighted as bold text.

		Leach		Honeymoon		Hibernia		Saturday night	
	df	F	p	F	p	F	p	F	p
Chironomidae									
UVR	2	5.98	**0.013**	2.51	0.109	9.43	**0.002**	0.03	0.970
Time	2	5.86	**0.002**	0.64	0.541	0.52	0.603	0.25	0.782
UVR × Time	4	3.20	0.224	2.22	0.197	5.74	**0.004**	2.17	0.114
Oligochaeta									
UVR	2	6.68	**0.007**	4.29	0.030	5.05	0.018	1.36	0.281
Time	2	2.68	0.097	0.34	0.716	10.65	**0.001**	1.40	0.271
UVR × Time	4	0.99	0.438	0.53	0.717	6.89	**0.002**	1.47	0.254
Nematoda									
UVR	2	0.57	0.573	2.41	0.118	2.16	0.144	0.14	0.868
Time	2	3.28	0.063	3.34	0.058	23.46	**<.0001**	0.44	0.650
UVR × Time	4	0.14	0.963	1.41	0.271	3.72	0.022	1.19	0.350
Total invertebrates									
UVR	2	5.58	**0.013**	4.54	0.025	4.53	0.026	0.18	0.840
Time	2	9.17	**0.002**	1.59	0.230	23.08	**<.0001**	0.15	0.8586
UVR × Time	4	1.57	0.224	1.88	0.157	5.89	**0.003**	2.32	0.0961
MANOVA									
UVR	2	2.76	**0.030**	2.14	0.077	3.23	**0.014**	0.88	0.523
Time	2	2.90	**0.024**	1.31	0.285	8.86	**<.0001**	0.80	0.580
UVR × Time	4	1.04	0.424	1.10	0.383	2.96	**0.004**	1.45	0.180
MANOVA Contrasts									
PAR vs PAR+UVA		= 0.202		NSD		**> 0.010**		NSD	
PAR vs PAR+UVA+UVB		**> 0.007**				= 0.565			
PAR+UVA vs PAR+UVA+UVB		= 0.280				= 0.018			

C:N in Hibernia Lake (Table 3, 4, Fig. 2, 3). In the Leach deep, and Hibernia mid and deep experiments, C:N ratios decreased significantly with time (Table 4, Fig. 3).

Epilithic C:P ratios did not differ significantly between radiation treatments in either Honeymoon or Saturday Night Lakes (Table 3, Fig. 2). In the Leach Lake primary experiment, the removal of both UVA and UVB significantly decreased C:P ratios (Table 3, Fig. 2). No significant difference existed between treatments in the mid or deep experiments of Leach Lake (Table 4, Fig. 3).

In Hibernia Lake, epilithic C:P ratios did not differ significantly between treatments in the primary experiment (Table 3, Fig. 2). In the mid experiment, C:P ratios increased significantly in the absence of UVA (Table 4, Fig. 3), mediated by the large divergence between treatments on the last sampling date. The effect of UVR on the Hibernia deep experiment was not significant (Table 4, Fig. 3).

Polyunsaturated fatty acids

Because concentrations of docosahexaenoic acid (DHA, 22:6ω3) were below detection limits in several of our samples, these data are not discussed. In Honeymoon Lake, exposure to UVR did not affect area-normalized concentrations of eicosapentaenoic acid (EPA, 20:5ω3; Table 3, Fig. 5). When concentrations were normalized per unit dry weight, a significant time by treatment interaction occurred. Further analysis of these data suggests that on the last sampling day, dry weight-specific concentrations of EPA were highest in the PAR treatment (Table 3, Fig. 5; PAR > PAR + UVA, $F_{1,12} = 18.67$, $p = 0.001$). In Leach Lake, exposure to UVA significantly increased dry-weight normalized concentrations of EPA (Table 3, Fig. 5). Concentrations per unit area, however, were not significantly affected by UVR exposure (Table 3, Fig. 5).

Feeding experiment

The growth rates of incubated snails did not differ significantly among UVR treatments ($F_{4,17} = 1.38$, $p = 0.283$; Fig. 6). However, there was a non-significant trend in the data. On average, snails fed algae irradiated with the full solar spectrum had growth rates 1.55 × greater than those fed non-UVR irradiated food (Fig. 6). When both snails and their food source were exposed to the full solar spectrum, their growth rate was, on average, 2.0 × less than those exposed to PAR alone (Fig. 6).

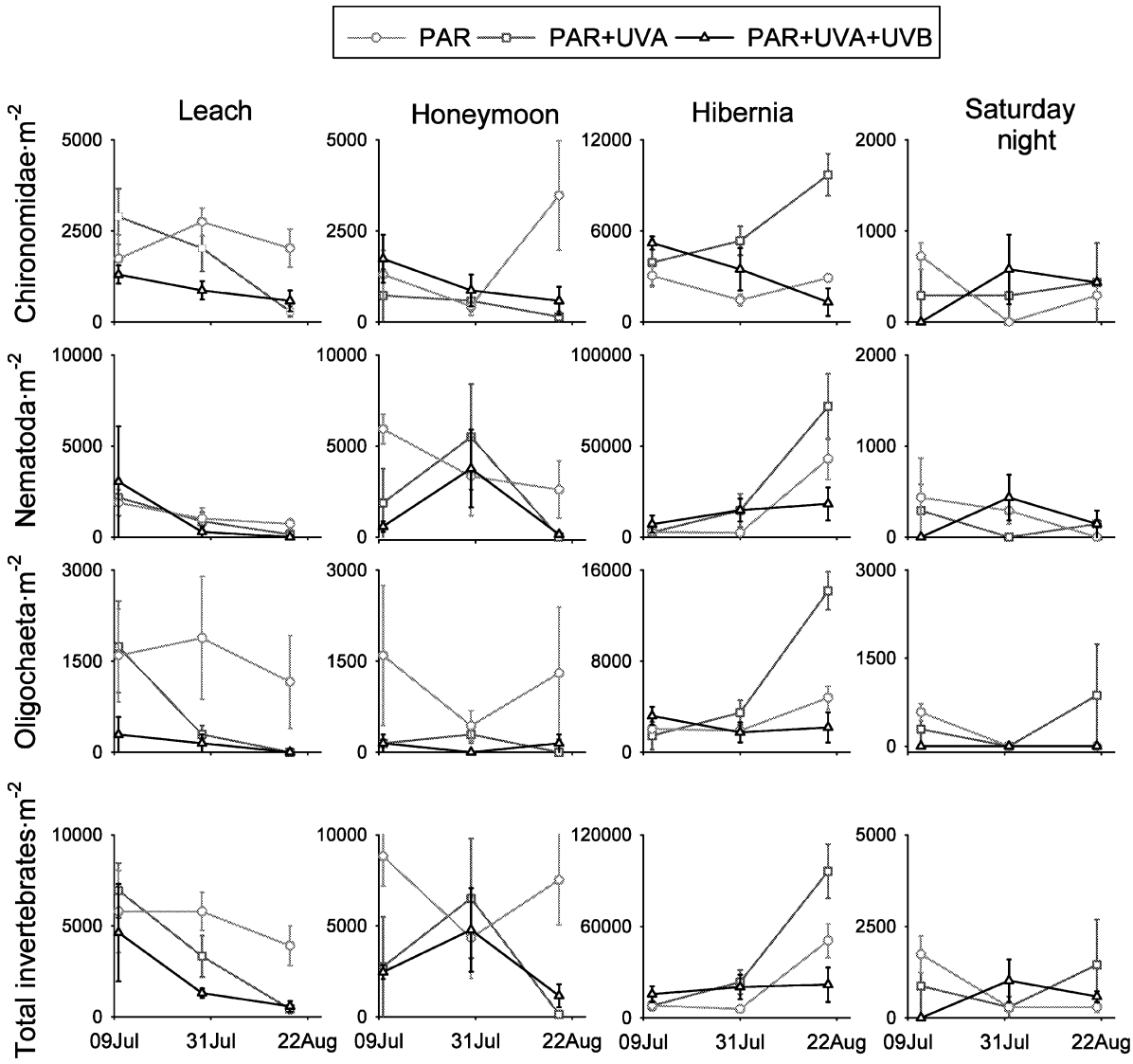

Fig. 4. Mean abundance (mean $\pm$ 1 standard error, n = 3) of Chironomidae, Nematoda, Oligachaeta, and total invertebrates under 3 different UVR regimes, in four study lakes in Jasper National Park, Alberta. Significant differences between treatments are indicated by MANOVA contrasts in Table 5.

Discussion

The effect of UVR on epilithic quantity

Epilithic carbon and chlorophyll a

Decreased epilithon in the presence of UVR has been previously assessed by chlor a (Bothwell et al. 1994, Vinebrooke and Leavitt 1996, Francoeur and Lowe 1998), particulate C (Kelly 2001), and taxonomic counts (Bothwell et al. 1993, Vinebrooke and Leavitt 1999). We found variable effects of UVR exposure on epilithic standing crop in our study lakes, as assessed by chlor a and C concentrations. Of our two clear-water lakes, epilithon in Leach Lake decreased strongly with UVA exposure. Although this effect was significant at all depths tested, its magnitude decreased with depth. Conversely, Honeymoon Lake appeared to be largely unaffected by UVR. The effect of UVR exposure on epilithic C and chlor a was also largely non-significant in our more coloured lakes. These disparate responses between lakes occurred despite the fact that fluxes of UVR to the primary experiments in Leach and Honeymoon Lakes were similar, and fluxes to the primary experiments of Hibernia and Saturday Night Lakes were comparable to

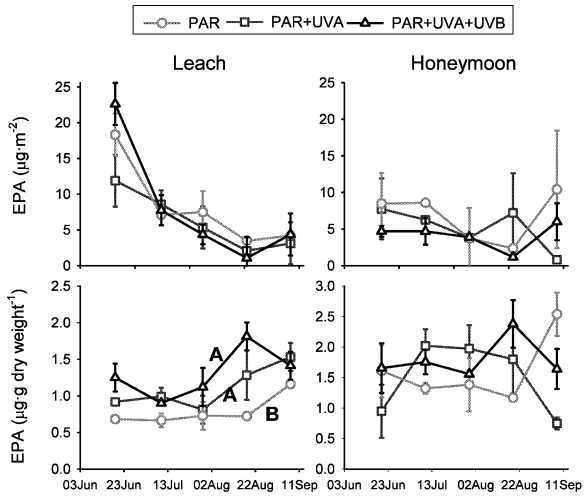

Fig. 5. Concentrations of EPA, 20:5ω3 in epilithon under 3 different UVR regimes normalized per µg dry weight, and per m^2. Error bars represent ± standard error for n = 2 replicates. Significant differences between treatments (within each panel) are indicated with different letters.

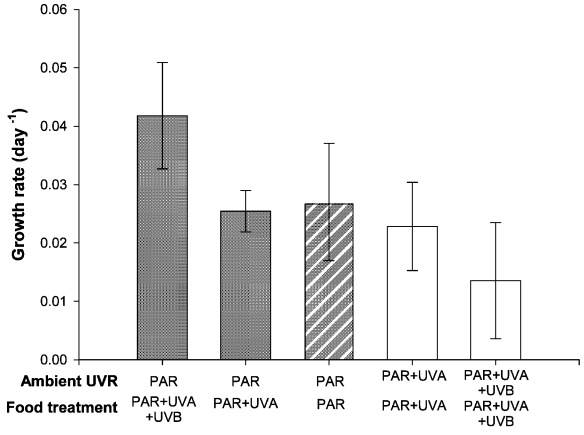

Fig. 6. Mean growth rates for valvatid snails under differing food and UVR treatments. Gray and crosshatched bars indicate trials where food exposed to differing UVR treatments was provided to snails in absence of UVR. White and crosshatched bars indicate trials where both food quality and ambient UVR was modified. Each treatment mean is an average of 5 replicates (mean ± standard error); each replicate is an average of 6 organisms.

those reaching the Leach Lake mid and deep experiments.

Invertebrates

Lower densities of benthic invertebrates as a result of UVR exposure has been shown in several stream and flume experiments (Bothwell et al. 1994, Kiffney et al. 1997a, b, Kelly 2001). In lentic systems, the effect of UVR exposure has been more poorly studied, although some results have suggested no overall effect of UVR exposure on the zoobenthos (Francoeur and Lowe 1998, Vinebrooke and Leavitt 1999). In our lakes, UVR exposure significantly decreased invertebrate colonization. Combined exposure to both UVA and UVB radiation decreased invertebrate densities in Leach Lake, while a non-significant decrease in invertebrate density with UVR exposure occurred in Honeymoon Lake. In Hibernia Lake, invertebrate density was greatest under the PAR + UVA treatment, suggesting that another unknown factor controlled invertebrate distribution in this lake.

Overall, lower invertebrate numbers were caused largely by decreases in the Chironomidae and Oligochaeta, while Nematoda densities did not change significantly between treatments. Such differential sensitivities have been shown in other studies (Kiffney et al. 1997a, b). In our lakes, the lack of significant response by nematodes to UVR exposure may have occurred because they were able to burrow within the epilithic mat on our experimental tiles. We were unable to discern whether the decreased colonization rates observed under UVR exposure occurred as a result of UVR avoidance, or direct damage. Because of their optical sensors, some invertebrates are able to detect UVR, especially in the UVA range (Tovée 1995). Migration to avoid exposure to UVR has been shown for zooplankters (Leech and Williamson 2001), and might also occur in the benthos (Kiffney et al. 1997b), although, to our knowledge, this has not been explicitly tested.

These results suggest that our first hypothesis was correct: in some of our lakes, UVR did decrease the abundance of epilithic invertebrates and algae. The decrease in invertebrate abundance in both of our clearwater lakes suggests a direct correlation between invertebrate numbers and UVR exposure. Because algal abundance (as assessed by chlor a and C) decreased in only one of our study lakes, we suggest that factors which differed between our lakes moderated the influence of UVR on standing crop. This topic is further discussed below (see Variability of response between lakes).

Epilithic food quality

The C:N (range 12 to 22) and C:P (range 500 to 1100) ratios in our epilithic communities were extremely high, and indicative of P limitation: maximal growth has been found in epilithic communities which exhibit C:P ratios of 130 (Hillebrand and Sommer 1999). These high epilithic C:P ratios are also likely to limit the growth of epilithic consumers. In pelagic systems, *Daphnia magna* fed on algae with C:P ratios > 300 were nutrient limited, and exhibited reduced growth rates (Sterner and Hessen 1994). Similar

results have also been observed in the benthos, where reductions in epilithic C:P ratios from ~600 to between 80 and 330 resulted in significant increases in grazer growth (Frost and Elser 2002b). At the high C:P ratios observed in our study, any decrease in epilithic C:P is likely to increase growth rates of epilithic consumers. The high C:P ratios in our study lakes also suggest that PUFA concentrations may not have played a key role in controlling the growth and fecundity of consumer organisms, as they do in other systems where C:P ratios are low (i.e. < 300; Müller-Navarra 1995, Boersma 2000, but see von Elert and Wolffrom 2001).

The effect of UVR

Laboratory studies have shown decreased ammonium and nitrate uptake (Döhler and Biermann 1987, Döhler and Kugel-Anders 1994) and decreased cell-specific concentrations of PUFAs in algae exposed to UVR (Goes et al. 1994, Wang and Chai 1994). Thus, we hypothesized that UVR would decrease food quality of epilithon for primary consumers by increasing C relative to nutrients and essential biomolecules in algal cells (Hessen et al. 1997). Such UVR-induced food quality decreases did not occur .

In three of our four study lakes, UVR exposure did not affect epilithic C:N and C:P ratios. In Leach Lake, both C:N and C:P ratios decreased under UVR exposure in the primary experiment, although this effect was non-significant for the N result ($p = 0.056$). Also in Leach Lake, the concentration of EPA per unit epilithic dry weight increased under UVR exposure. It was only at greater depth that any evidence for decreased food quality with UVR exposure was found. In Leach Lake, C:N ratios increased in our UVR-exposed treatments in the deep incubation.

Several factors are known to influence periphyton stoichiometry. For example, grazers have been hypothesized to change C to nutrient ratios through their excretion of nutrient-rich fecal pellets, and removal of excess detritus which is presumably C-rich (Hillebrand and Kahlert 2001, Frost et al. 2002). Although detrital removal could also affect the relative concentration of PUFAs, this effect of grazers is an unlikely explanation of the results observed in the shallows of Leach Lake: i.e. the above mechanisms both act to increase food quality in the presence of grazers. This is in direct opposition to what occurred in the high-grazer, low food quality UVR-shielded community.

Both UVR and grazers may change epilithic community structure (Bothwell et al. 1993, Hillebrand and Kahlert 2001), which might be expected to alter epilithic stoichiometry. However, this again seems unlikely to explain our results. Studies in the phytoplankton suggest that environmentally induced variation in nutrient composition within species can be greater than that between species (Healy and Hendzel 1979, Frost and Elser 2002a). Furthermore, in our study, algal taxonomic composition differed only slightly between treatments within lakes. Any variation that did occur appeared to be largely random, and unrelated to UVR (Tank 2002).

Changes in the distribution of other, unmeasured, organisms could also account for our observed differences. Because we did not measure bacteria or other heterotrophs in our study, we cannot rule out the possibility that the abundance and distribution of these organisms influenced our results. This explanation also seems unlikely, however: if such organisms were alone responsible for our results, their abundance would have had to increase dramatically in the presence of UVR. Bacteria, for example, have been shown to be particularly sensitive to UVR exposure (Jeffrey et al. 1996, Xenopoulos and Bird 1997, Plante and Arts 2000).

Differences in the thickness of the periphytic mat between our light treatments, known to change light supply and nutrient and C uptake rates (Wetzel 1996), also seems an unlikely explanation for our results. The mats of our experimental communities remained poorly developed throughout the growing season, likely because of the harsh growing conditions typical of mountain lakes. Instead, we suggest that changes in relative C assimilation are responsible for the observed pattern. This hypothesis has been proposed previously for both epilithon and phytoplankton (Watkins et al. 2001, Xenopoulos et al. 2002). These studies suggest that lower C concentrations in UVR exposed cells, caused by decreased C acquisition, lead to decreases in C:P ratios. Our study suggests that UVR can decrease C:P ratios, PUFA concentrations, and C:N ratios in some environments. The lack of statistical significance of the N effect may reflect strong UVR-induced decreases in N-uptake counterbalancing decreases in C accumulation. These increases in food quality may be especially important in benthic systems where the effect of UVR-induced decreases in C assimilation can accrue over time, because senesced cells do not leave the community.

In contrast to the results of the Leach Lake primary experiment, C:N ratios increased in our UVR-exposed treatments in the Leach Lake deep incubation. These diametric responses at different experimental depths may have occurred because rates of N uptake and C accumulation did not change uniformly in response to variations in UVR exposure with depth. Inhibition of N uptake by UVR has been shown to extend to greater depths than the inhibition of C fixation, because N uptake is more strongly affected by the longer, more deeply penetrating, UVR wavelengths (Behrenfeld et al. 1995). Thus, although

C concentrations decreased under UVR exposure in the deep incubation, the reduction may not have been large enough to overcome decreased N uptake rates, as we suggest occurred in the shallower incubation. In addition, some of the hypotheses rejected above for their ability to explain the result in the primary experiment may be at work here. Invertebrates, for example, have been found to be highly sensitive to UVR (Bothwell et al. 1994), suggesting that their colonization could have been elevated in the UVR-shielded treatment at this depth. Increases in grazer densities in the UVR-shielded communities may have decreased C to nutrient ratios, as described above. Again, we cannot rule out the possibility that changes in the relative abundance of other, unmeasured, organisms might have accounted for the observed results. However, it is difficult to understand why these latter hypotheses would have affected C:N, and not C:P, ratios.

Variability of response between lakes

The study of ecological interactions in multiple systems is crucial to understanding how experimental and ecological perturbations might act at the ecosystem level. In our study, the benthos of four proximate lakes differed widely in their response to variations in ambient UVR. Given the similar clarity across these lakes (see discussion in "The effect of UVR on epilithic quantity" above), the fact that epilithic quantity and quality only responded to UVR manipulation in one of our four study lakes (Leach Lake) is, on the surface, surprising.

Given our apparent lack of a general unified response, it is perhaps difficult to reconcile the observed effects. However, an examination of the limnological characteristics of these lakes is possible. Although the clearwater and coloured lakes do partition for some of these variables (e.g. the clearwater lakes posses lower alkalinity, conductivity, and total phosphorus; Table 2), Leach Lake alone does not stand apart from the rest based on these characteristics. The epilithic algal community in Leach Lake, however, does differ markedly from the other three study systems. The experimental communities in Leach Lake were greater than 90% diatoms (Tank 2002). This percentage was higher than for any of our other study lakes, and contrasted most sharply with the community in Honeymoon Lake, where the composition was up to 50% chlorophytes and Cyanobacteria (Tank 2002).

The susceptibility of organisms to UVR exposure is known to vary both among taxa (Jokiel and York 1984, Karentz et al. 1991) and environments (Helbling et al. 1992, Xiong et al. 1996). It has been suggested that diatoms are the most susceptible of the freshwater algal taxa to the effects of UVR (Vinebrooke and Leavitt 1996, Xenopoulos et al. 2000). Our study supports this suggestion. However, we cannot rule out the possibility that physiological shifts in UVR-sensitive taxa (such as decreased cell-specific chlor a concentrations and C and nutrient fixation; Döhler and Buchmann 1995, McNamara and Hill 2000, Watkins et al. 2001), rather than decreases in cell numbers, might account for our observations.

The effect of UVR at the system level

The primary experiment was intentionally incubated at a shallow depth to maximize the likelihood of observing a significant response to our UVR manipulation. However, to extend our results to greater depths and thus to try and gauge the effects of UVR over broader areas of the lakes, deeper incubations were included in two of the study lakes. Of the four study lakes, three showed generally no response to UVR manipulation; although it is possible that UVR might affect these epilithic communities at extremely shallow depths, the system-wide effects in these lakes are clearly negligible. In Leach Lake, the effects of UVR were much more pronounced. Here, the presence of UVA radiation significantly affected epilithic communities in our deepest incubation, where UVA radiation averaged 20% of surface levels through the summer.

Because we have only three depth replicates, we have not attempted a statistical analysis of how the epilithic response to UVA might decrease with depth. However, we do know that much of this lake is available for epilithic growth: the 1% PAR depth was, on average, 8 m during our experimental season ($z_{mean} =$ 3.1 m; $z_{max} = 11.0$ m). Conversely, the 1% UVA penetration depth averaged only 2.2 m. Thus, even if UVA-specific changes in epilithic structure happen throughout the UVA penetration range, their occurrence is largely restricted to relatively shallow waters.

Direct and indirect effects of UVR on consumers

Significant, direct damage to invertebrates has been shown in the presence of UVR (McNamara and Hill 1999). In contrast, the effect of direct UVR exposure on snail growth rates was non-significant in our study. We did, however, observe a general decrease in growth rates with increasing UVR exposure. There are several explanations for our non-significant finding. First, snails have been shown to be more resilient to UVR than other invertebrates (McNamara and Hill 1999), possibly because their shell offers a protec-

tive shield that other invertebrate species lack. Second, food quality, as discussed below, may have increased under UVR stress. This result, acting in a direction opposite to that of the direct effects of UVR, may have dampened the significance of our observations. Finally, it is possible that we have committed a type 2 error in our analysis because our level of replication was not large enough to detect significance in our results. A post-hoc power analysis suggests that with 42 replicates spread over our 5 treatments (i.e. 8.4, rather than 5 replicates per treatment), a significant response may have been observed.

Although other studies suggest that food quality should be affected in UVR-exposed communities (Watkins et al. 2001, Xenopoulos et al. 2002), to our knowledge no study has examine the effects of UVR-mediated shifts in food quality on consumer organisms. UVR has been hypothesized to reduce the food quality of aquatic primary producers (Hessen et al. 1997). In our study, however, food quality increased at shallow depths (as assessed by C:N and C:P ratios and EPA concentrations) with exposure to UVA radiation. This effect occurred in only one of our four study lakes. Our feeding experiment, conducted in Honeymoon Lake, was carried out with epilithon that did not show significant UVR-induced changes in the measured food quality parameters. The effect of food quality on snail growth was non-significant. We did, however, see a trend towards increasing growth rates in UVR exposed food. As discussed above, power analysis suggests that this result may have been significant with greater replication.

In our study, organisms were not C (i.e. quantity) limited. Thus, a mechanism other than stoichiometric ratios, EPA content, or food availability, may explain the observed tendency towards increasing growth on UVR-irradiated food. For example, exposure to UVR, at low intensities, has been shown to increase proteins (Buma et al. 1996). Decreases in grazer density in the presence of UVR may also mean that irradiated communities are less recalcitrant, and contain nutrients and biomolecules in a form more available for consumers, having been less subjected to modification by grazing pressure. Further study focussing on the magnitude and underlying mechanisms of the indirect effects of UVR on grazer growth rates is warranted.

Clearly, UVR can affect structure and function in the benthos. In this study, where benthic communities in four lakes were simultaneously examined for their response to variations in UVR exposure, we found that this response was not constant across lakes, and was often weak. While we show that UVR exposure can decrease epilithic standing crop, increase food quality (as assessed by stoichiometric ratios and EPA concentrations), and decrease grazing pressure, we also show that the effects of UVR exposure can decrease and change rapidly with depth. Our study further demonstrates that UVR may increase the quality of primary producers as food for their consumer organisms. The mechanism for this effect, however, remains unclear.

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