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DIFFERENTIAL RESPONSES OF LITTORAL COMMUNITIES TO ULTRAVIOLET RADIATION IN AN ALPINE LAKE

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Abstract. Differential sensitivities of benthic and planktonic communities to UV radiation may involve differences in habitat conditions (e.g., availability of physical refuge), taxonomic composition, UV-A (320–400 nm) and DNA-damaging UV-B (280–320 nm) irradiances, and potential indirect effects via food-web processes. These hypotheses were tested using 18 enclosures (corrals) within an alpine lake. The factorial design consisted of three UV treatments (+UV, −UV-B, −UV) and two macroinvertebrate densities (ambient, 3×). High performance liquid chromatography was used to quantify changes in periphyton and phytoplankton abundance and composition in response to UV radiation and macroinvertebrates over a period of 1 mo.

Algal and invertebrate responses to UV radiation were habitat- and taxon-specific. Epilithic standing crop was significantly suppressed by UV radiation, primarily due to UV-B radiation inhibiting diatoms by 40%. In contrast, standing crop of epipelic (sediment-dwelling) organisms was significantly enhanced by UV-A radiation, which increased the abundance of cyanobacteria by 50%. UV radiation also significantly altered the taxonomic composition of both epilithon and epipelon. In comparison, picocyanobacterial phytoplankton were unaffected by UV radiation. Zoobenthos (*Gammarus lacustris*, Chironomidae) and zooplankton (*Hesperodiaptomus arcticus*, Rotifera) did not significantly alter periphyton or phytoplankton biomass or taxonomic composition. Although total zoobenthos and zooplankton biomass were unaffected by UV radiation, UV-B significantly suppressed the final density of rotifers but not that of heavily pigmented calanoid copepods.

These results show that UV radiation affects shallow-water communities in cold and unproductive systems mainly through direct effects, rather than by indirect effects mediated by food-web processes. Access to physical refuges was evidently a key factor determining habitat-specific responses to UV radiation. UV radiation did not adversely affect motile epipelon and zoobenthos that could seek refuge in sediments, but it did suppress attached epilithic taxa. In habitats devoid of physical refuge, UV tolerance was associated with photoprotective pigmentation (i.e., *H. arcticus*), and possibly a capacity for DNA repair (i.e., epilithic filamentous cyanobacteria and planktonic picocyanobacteria). Our findings suggest that UV exposure can affect abiotic regulation of littoral food webs in extreme environments, such as alpine, polar, and anthropogenically acidified ponds and shallow lakes.

Key words: algal pigments; alpine lake; epilithon; epipelon; littoral food web; phytoplankton; Rocky Mountains, Canada; ultraviolet radiation; zoobenthos; zooplankton.

INTRODUCTION

The direct effects of ultraviolet (UV) radiation on aquatic food webs may be mediated by community- and species-specific sensitivities that result from differences in adaptive strategies and habitat conditions. UV radiation can inhibit algal photosynthesis (Moeller 1994), especially when phytoplankton are trapped in shallow epilimnetic waters (Vincent et al. 1984, Milot-Roy and Vincent 1994) without the opportunity for active avoidance (see Häder 1993). However, algae from different habitats show a wide range of sensitivities to UV radiation (Jokiel and York 1984, Xiong et al. 1996) with certain species producing photoprotective pigments (Carreto et al. 1990, Garcia-Pichel and Castenholz 1991). Similarly, epilimnetic zooplankton can be adversely affected by damaging solar radiation (Williamson et al. 1994) with differential sensitivities existing between heavily pigmented and pale species (Hairston 1980, Byron 1982, Ringelberg et al. 1984). UV radiation can also suppress benthic invertebrates (Bothwell et al. 1994) and the development of periphyton on hard surfaces (Bothwell et al. 1993, Vinebrooke and Leavitt 1996), such as on rocks (epilithon), as they lack adequate refuge from UV radiation. In comparison, UV radiation may not adversely affect sediment-dwelling algae (epipelon) that are capable of active avoidance via vertical migration through the sediments (Vincent et al. 1993).

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The ecological impacts of UV-B (280–320 nm) and UV-A (320–400 nm) radiation can also differ. Recent research on the biological effects of UV-B radiation (see Vincent and Roy 1993, Karentz et al. 1994, Williamson 1995) show that the damaging effects of UV radiation increase exponentially as wavelengths decrease (Cullen et al. 1992). However, because total UV-A irradiance exceeds that of UV-B, UV-A radiation can have a greater overall impact on physiological processes (see Karentz et al. 1994). For example, Bothwell et al. (1994) reported that UV-A radiation suppressed periphyton more than shorter wavelengths, while UV-B radiation was more damaging to herbivorous chironomids. Moreover, UV-A radiation can counteract the adverse effects of UV-B radiation by activating repair processes (Quesada et al. 1995).

UV radiation may indirectly affect communities by altering biotic interactions, such as competition, herbivory, and predation. For example, phytoplankton that are outcompeted by periphyton for nutrients (Hansson 1988*a*) may benefit from suppression of periphyton by UV radiation. Alternately, inhibition of periphyton by UV radiation can be offset if grazers are more sensitive to UV radiation than are algae (Bothwell et al. 1994). In addition, herbivores may experience reductions in food availability because UV radiation can suppress algal abundance and promote the growth of less edible, thick-walled taxa (van Donk and Hessen 1994, Xiong et. al. 1996). Photoprotective pigments in prey species may increase their susceptibility to visually feeding predators (Morgan and Christy 1996). However, many indirect UV effects may be weak in unproductive systems where predator limitation is expected to be minimal (Menge and Sutherland 1987).

The ecological effects of UV radiation are also mediated by dissolved organic matter (DOM) content and lake morphometry. DOM is the primary attenuator of UV radiation in lakes (Scully and Lean 1994, Morris et al. 1995, Schindler et al. 1996). Low concentrations of DOM cause a spectral shift with increasing water depth owing to stronger attenuation of UV-B radiation (Kirk 1994). As well, photolysis of DOM by UV radiation can produce toxic byproducts, such as peroxides (Scully et al. 1996), and enhance the availability of resources to algae and bacteria (Wetzel 1992). Lake morphometry may set the limits on the effects of UV radiation as organisms are expected to exploit depth refugia in deep lakes (Williamson 1995). UV radiation might have a more pronounced impact in shallow waters where a higher proportion of biota are exposed to high UV irradiances.

The purpose of this study was to experimentally test for differential responses of shallow-water periphyton and phytoplankton to the direct and indirect effects of natural UV radiation. Our primary hypothesis was that sediment-dwelling periphyton (epipelon) should show higher tolerance of UV radiation than either phytoplankton or periphyton on hard surfaces (epilithon) because many epipelic taxa can potentially exploit a depth refuge from UV radiation. We also hypothesized that the effects of UV radiation would be wavelength- and taxon-specific with UV-B radiation damaging to small, translucent organisms more than large, pigmented species. Finally, we tested whether the magnitude of indirect UV effects on algae depended on the abundance of higher trophic levels, or on differential sensitivities between algae and invertebrates to UV radiation (see Bothwell et al. 1994).

TABLE 1. Select ice-free limnological conditions of Pipit Lake (an alpine lake in Alberta, Canada) in 1995. Weekly measurements were taken from the epilimnion during July and August.

Feature	Value
Total chlorophyll (μg/L)	0.4–0.8
TDN (μg/L)	50–90
TDP (μg/L)	3–5
Surface water temperature (°C)	3.2–9.2
1% UV-A radiation depth (m)	4.1–12.4†
Percentage of lake bottom exposed to >1% UV-A irradiance	15.0–37.7
1% UV-B radiation depth (m)	1.2–3.9†
Percentage of lake bottom exposed to >1% UV-B irradiance	5.7–14.5
Secchi depth (m)	6.5–9.5
Maximum lake depth (m)	20.6
Mean lake depth (m)	12.6
DOC (mg/L)	0.5–1.3
Turbidity (NTU)	0.62
Conductivity (μS/cm^2)	195
pH	8.1

† Estimates are based on 380-nm (UV-A) and 305-nm (UV-B) wavelengths and were derived from model equations that predicted diffuse attenuation coefficients from measured DOC concentrations (see Morris et al. 1995).

The experiment was conducted in an ultraoligotrophic clearwater alpine lake in which high ambient UV irradiances can influence a large proportion of the aquatic food web. Incident UV-B irradiance increases ~20% per 1000 m of lake elevation (Caldwell et al. 1980, Blumthaler et al. 1992). Furthermore, UV-B irradiances have progressively increased at alpine sites over the last decade (Blumthaler and Ambach 1990). Incident UV irradiance is poorly attenuated in alpine lakes due to low DOM concentrations (Baron et al. 1991, Scully and Lean 1994, Morris et al. 1995). In Banff National Park, DOM concentrations in alpine lakes average 0.9 ± 0.7 to 4.7 ± 4.4 mg/L (mean ± 1 SD) in lakes below treeline (Leavitt et al. 1997).

MATERIALS AND METHODS

Study site

Pipit Lake (51°37′ N, 116°51′ W) is a remote ultraoligotrophic alpine lake situated at treeline (2217 m above sea level) between the Vermilion and Bare ranges of the Rocky Mountains in Banff National Park, Alberta, Canada (Table 1). The ice-free season typically lasts from early July to late September. During cloudless conditions at solar noon in mid-July, maximum

integrated UV-B (280–320 nm) and UV-A (320–400 nm) irradiances at the lake surface can reach ~3.0 W/m^2 and ~60.0 W/m^2, respectively (N. M. Scully and D. R. S. Lean, York University, North York, Ontario, Canada; *unpublished data*; but see Vinebrooke and Leavitt 1996). Incident UV-B and UV-A irradiances penetrate through ~25% and 40% of the entire lake volume, owing to consistently low DOC concentrations (<1.5 mg/L).

Pipit Lake was stocked with rainbow trout (*Salmo gairdneri*) during the 1960s, but had recovered to its natural fishless state by 1990 (Donald 1987, Leavitt et al. 1994). Presently, the zooplankton community mainly consists of calanoid copepods (*Hesperodiaptomus arcticus*) and low densities of *Daphnia middendorffiana* and rotifers (*Keratella* spp., *Lepadella, Notholca*). Adult *Hesperodiaptomus* prey on rotifers (Paul and Schindler 1994, Paul et al. 1995), but are omnivorous as juveniles and young adults (A. K. Hardie and D. W. Schindler, University of Alberta, Edmonton, Alberta, Canada; *unpublished data*). The zoobenthos primarily consists of the amphipod *Gammarus lacustris* and midges (Chironomidae). The amphipods are also omnivores, consuming copepods, cladocerans, periphyton, detrital material (Anderson and Raasveldt 1974; F. Wilhelm and D. W. Schindler, University of Alberta, Edmonton, Canada; *unpublished data*), and the diapausing eggs of calanoid copepods (Parker et al. 1996).

Experimental design

We conducted a factorial experiment to test for direct and indirect effects of UV radiation and macroinvertebrates on periphyton and phytoplankton in littoral enclosures. Three UV treatments (+UV, −UVB, −UV) and two macroinvertebrate densities (ambient, 3×) were each replicated three times for a total of 18 enclosures. Rectangular enclosures (1.2 × 0.6 × 0.7 m depth; 360 L) were installed in mid-July 1995 along the 0.5-m depth contour ~10 m from the eastern shoreline of Pipit Lake. Enclosure walls were embedded 10 cm into the lake sediments and extended to 10 cm above the water surface. At a depth of 0.5 m, benthic communities received ~75% and ~50% of incident midday UV-A (380 nm) and UV-B (305 nm) irradiance, respectively. A UV-exclosure design was selected to enable us to test if natural UV irradiance regulates shallow-water food webs, and since park regulations against the use of electrical generators in this area of a UNESCO World Heritage Site (Banff National Park) prevented augmentation of UV irradiance. This design emphasized the importance of periphyton and zoobenthos relative to planktonic communities, and focused on the effects of UV radiation on littoral-dominated systems such as ponds and shallow lakes, which represent the predominant types of freshwater lentic systems in the world (Wetzel 1992).

Enclosure walls were made of Dura-Lite (CIL Industries, Calgary, Alberta, Canada) greenhouse sheeting fastened to a wooden frame. Dura-Lite is an unwoven polyethylene sheeting material that transmits ~60% of PAR and ~2% of UV radiation (50% cutoff = 390 nm) in water (Fig. 1). The use of UV-opaque walls enabled us to manipulate the underwater UV environment within the enclosures by choosing different aerial UV filters (see below). Although shading by walls reduced UV exposure during crepuscular periods, this effect was uniform among enclosures and could not account for treatment effects of UV radiation or grazers.

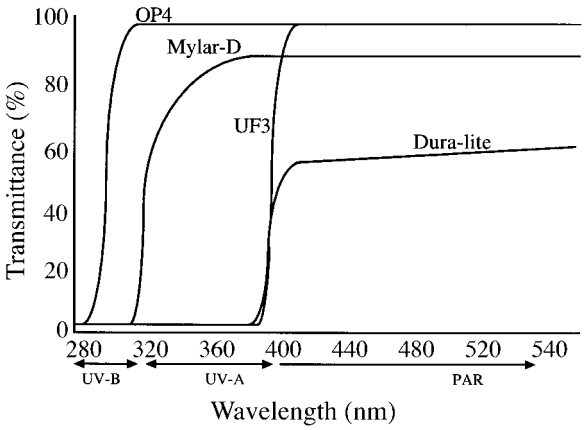

FIG. 1. Spectral transmittance of enclosure walls (Duralite) and aerial UV filters used to transmit total UV (+UV [Acrylite OP4]), UV-A only (−UV-B [Mylar-D]), or no UV (−UV [Plexiglas UF3]) irradiance.

UV radiation treatments were achieved by covering enclosures with acrylic or polyester canopies fastened to the frames ~10 cm above the water surface (Fig. 1). The +UV treatment had acrylic sheets (Acrylite OP4; CRYO Industries, Mississauga, Ontario, Canada) that transmitted 98% of total UV radiation (<400 nm). Mylar D (E. I. Dupont de Nemours, Wilmington, Delaware, USA) polyester sheets were used to filter out most of the UVB radiation (50% cutoff = 318 nm). UV-transparent OP4 sheets were used to help secure the Mylar D sheets to the enclosures. Plexiglas UF3 (Rohm and Haas, West Hill, Ontario, Canada) was used to block out UV radiation (50% cutoff = 405 nm) in the −UV treatment. Spectral transmittance (280–750 nm) characteristics of enclosure materials in air (UV filters) or water (Duralite) were confirmed before and after the experiment using a Hewlett-Packard photodiode array spectrophotometer and 1-cm quartz cuvettes.

Daily UV irradiance forecast data for the central Alberta region were obtained from the Environment Canada UV-monitoring station located in Edmonton, Alberta (World Ozone and UV Radiation Data Centre, Environment Canada, Downsview, Ontario, Canada). UV irradiance was measured at 0.5-nm intervals (290–325 nm) using a Brewer ozone spectrophotometer (SCI-TEC Instruments, Saskatoon, Saskatchewan,

Canada). This information is used to calculate the daily Canadian UV index, an international standard that is derived from an erythemal action spectrum-weighted formula that incorporates forecast total ozone, solar elevation and zenith angle, and cloud opacity (Burrows et al. 1994). The UV index represents the maximum observed daily value, which can be multiplied by 25 mW/m^2 to obtain an estimate of the biologically effective UV-B flux (Kerr 1994). Edmonton is a prairie city located ~250 km northeast of Pipit Lake, and therefore, these irradiance data represent only approximations of the daily UV-B flux during the experiment. UV-A irradiances cannot be determined directly from the Canadian UV Index.

Macroinvertebrates were added to nine enclosures to achieve an ~3× increase in ambient densities. Zooplankton were collected using midlake vertical hauls with a 350-μm mesh conical plankton net with a 3:1 length : width ratio. This mesh size enabled the capture of adult and copepodite stages of *Hesperodiaptomus arcticus* and *Daphnia middendorffiana,* but not smaller nauplii, rotifers, and algae. *Daphnia* were scarce in Pipit Lake at the start of the experiment. Thus, zooplankton amendments consisted of additions of *H. arcticus* to achieve final densities of 2.25 individuals/L. Zoobenthos were obtained from lake sediments using standard kick-sweeps with a 243-μm mesh D-frame net. Sediments were passed through a 500-μm sieve to concentrate natural densities of benthic macroinvertebrates. Juvenile amphipods and chironomids were added to achieve densities of 136 and 39 individuals/m^2, respectively.

Sampling protocol and analyses

Enclosures were sampled every 10 d for 1 mo. Phytoplankton was collected with a Van Dorn water bottle, and algae from 2 L were concentrated onto Whatman GF/F filters. Filters were wrapped in aluminum foil, stored in black 35-mm film canisters, and immediately frozen in a nearby snowfield until transport to the laboratory for pigment extraction (1–3 wk). This procedure minimized pigment degradation and photochemical adaptation of filtered algae (Leavitt et al. 1994, Vinebrooke and Leavitt 1996). Water samples were preserved with Lugol's solution for algal identification. Invertebrates were sampled only on the final date to avoid depletion of their naturally sparse populations during the experiment. Zooplankton from 100 L were concentrated with a 10-μm mesh and preserved in a formalin–sucrose solution (Prepas 1978). Zoobenthos from each enclosure were isolated from three sediment cores (pooled to form a single replicate), each core taken with a 4.7-cm wide plexiglass corer. Total area sampled was 52 cm^2. Invertebrates were sieved (500-μm mesh) from the upper 1 cm of sediment and preserved in 95% ethanol.

Periphyton communities were sampled using unglazed ceramic tiles (epilithon) and surface sediments (epipelon). Acid-washed tiles had been preconditioned at a 0.5-m depth for 2 wk in Pipit Lake. Epilithon was sampled in each enclosure by retrieving three tiles at random using a tight-fitting container that minimized the loss of loosely attached taxa (Vinebrooke 1996). Epilithon was removed from tiles using a hard bristle toothbrush, pooled, and concentrated onto a Whatman GF/C filter. Epipelon was sampled by combining three surface sediment samples each collected using the top of a plastic Petri dish (4.7-cm diameter × 0.5-cm depth). This plate was slowly embedded into surface sediments and then sealed by inserting the bottom plate 1 cm into the sediments beneath the sampled area. The enclosed sample was immediately compressed between the two plates and retrieved from the sampled area. Only the upper 5 mm of surface sediment was retained within the top plate, including a visible greenish band of epipelic algae. This sample mainly represented pigments from the euphotic layer, as indicated by the low proportion of chlorophyll (Chl) degradation products (i.e., pheophytins) that are indicative of more deeply buried fossil pigments (Leavitt et al. 1994). Periphyton samples for pigment analyses were transferred to black film canisters and frozen following standard phytoplankton procedures. Duplicate tiles and sediment samples were preserved with Lugol's solution for taxonomic identifications.

High performance liquid chromatography (HPLC) was used to quantify algal abundances and composition of periphyton and phytoplankton (Leavitt and Carpenter 1990). This technique enabled us to compare algal communities across different habitats by circumventing difficulties in microscopic quantification of small fragile cells (i.e., picocyanobacterial phytoplankton) and detection of cells obscured by detritus and lake sediment (i.e., periphyton). Epipelon samples were freeze-dried for 72 h at 10 mPa to remove water and maximize the efficiency of pigment extraction (Hansson 1988*b*). Pigments from all samples were extracted in acetone : methanol : water (80:15:5 by volume) for 24 h in the dark at 10°C (Leavitt and Findlay 1994). Extracts were filtered through 0.2-μm Acropore membrane filters, dried, and stored under nitrogen gas. Dried extracts were dissolved in a precisely known volume (500–1000 μL) of injection solvent (70% acetone : 25% ion-pairing agent reagent : 5% methanol) containing Sudan II dye as an internal reference (Leavitt and Findlay 1994). Dissolved pigments were separated on a Hewlett Packard (HP) Model 1050 HPLC equipped with a Rainin C-18 column, an in-line HP 1040 photodiode array spectrophotometer, and an HP 1046A fluorescence detector programmed using an excitation wavelength of 435 nm and a detection wavelength of 667 nm.

Changes in total algal biomass and community composition were inferred from accrual of undegraded chlorophyll (Chl *a, b, c*) and carotenoids (Table 2). These pigments include compounds that allow discrimination of cryptophytes (alloxanthin), diatoms (diatox-

TABLE 2. Distributions of chlorophylls and carotenoids among the major freshwater algal groups found in Pipit Lake (modified from Leavitt [1993]).

Pigment	Algal group
Chl *a*	all algae
Chl *b*	chlorophytes
Chl *c*	chrysophytes, diatoms, dinoflagellates
β-carotene	all algae
Alloxanthin	cryptophytes
Diatoxanthin	diatoms, few chrysophytes
Fucoxanthin	chrysophytes, diatoms, some dinoflagellates
Lutein	chlorophytes, euglenoids
Zeaxanthin	cyanobacteria
Oscillaxanthin†	filamentous cyanobacteria
Peridinin	dinoflagellates

† Includes oscillaxanthin, 4-keto-myxoxanthophyll, and aphanizophyll.

anthin), dinoflagellates (peridinin), cyanobacteria (zeaxanthin), filamentous cyanobacteria (myxoxanthophyll, oscillaxanthin), chlorophytes (lutein, Chl *b*, and derivatives), as well as chromophytes (chrysophytes, diatoms, some dinoflagellates; fucoxanthin, Chl *c*). Filamentous cyanobacteria were estimated from the sum of oscillaxanthin, 4-keto-myxoxanthophyll, and aphanzophyll, characteristic cyanobacterial carotenoids that could not be separated on our HPLC system (Leavitt and Findlay 1994). Similarly, lutein from chlorophytes could not be separated from the cyanobacterial carotenoid zeaxanthin, and direct microscopic examination was combined with HPLC analyses of Chl *b* and derivatives to determine whether green algae or cyanobacteria predominated. Identification of pigments was confirmed by comparison of their light absorbance characteristics and chromatographic mobility with carotenoids from algae of known pigment composition (Leavitt and Findlay 1994) and with authentic standards provided by the US Environmental Protection Agency.

Light microscopy was used to verify the presence of major algal groups as inferred from pigment analyses. Algae were identified using Utermöhl chambers and an Olympus Model TO41 inverted microscope, and the taxonomic reference of Prescott (1982). In particular, taxonomic surveys of periphyton and phytoplankton communities sampled at the end of the experiment were made by randomly inspecting ten fields of each settled sample at a 400× magnification. Algal surveys were used solely to aid in the identification of source organisms in cases where algal carotenoids were distributed over more than one taxonomic group (e.g., fucoxanthin). Many researchers have shown linear correlations between estimates of algal abundance and community composition based on light microscopy and those based on carotenoid concentrations (e.g., Ridout and Morris 1985, Gieskes and Kraay 1986, Quiblier-Llobéras et al. 1996). For example, we have shown that the magnitude of the algal response to UV radiation is independent of whether algal abundance is measured by pigment content, cell biovolume, or ash-free dry mass (Vinebrooke and Leavitt 1996), as found in studies from other shallow-water habitats (e.g., Bothwell et al. 1994) and during whole-lake experiments (Leavitt et al. 1997).

All invertebrates were identified and enumerated from zoobenthos and zooplankton samples. Zooplankton were counted using Utermöhl chambers, whereas zoobenthos were counted with a Wild M3 dissecting microscope. Invertebrates were identified using keys from Ruttner-Kolisko (1974) and Pennak (1989). Biomasses of amphipods, chironomids, and copepods were estimated directly from ≥30 unpreserved individuals that had been air-dried in the field and subsequently oven-dried (60°C) to constant mass. Rotifer biomass was calculated based on animal volumes estimated from genus-specific geometrical formulae (Bottrell et al. 1976) and by assuming 1.0 as the tissue specific gravity and 0.1 as the dry : wet mass ratio (McCauley 1984).

Statistical analyses

Temporal patterns of total pigment (Chl, carotenoids) standing crop were analyzed by repeated-measures analysis of variance (RM-ANOVA) with fixed effects using Systat Version 6 (Wilkinson and Hill 1994). All data were $\log_{10}$ transformed prior to statistical analyses to stabilize and normalize variance (Zar 1996). Repeated-measures multivariate analysis of variance (RM-MANOVA) of taxonomically diagnostic carotenoid concentrations was used to test whether periphyton and phytoplankton community compositions were altered by UV radiation or macroinvertebrates (Scheiner 1993). Statistically significant MANOVA results were further investigated with RM-ANOVA of individual carotenoids to identify which algal groups had been significantly affected. Invertebrate biomass on the final sampling date was analyzed using two-factor ANOVA with fixed effects, followed by multiple comparison testing using Tukey's test (Zar 1996). Zoobenthos and zooplankton biomass were separately analyzed.

RESULTS

UV irradiance

Maximum daily UV-B flux in central Alberta averaged 108 mW/m^2 during the experiment, and ranged from 5 to 173 mW/m^2 (Fig. 2). Biologically effective UV-B irradiance was greatest during the first 10 d of the experiment (late July), and declined thereafter. Reductions in UV-B flux corresponded to increased overcast and precipitation both over central Alberta and at Pipit Lake during August 1995 (R. D. Vinebrooke, *personal observations*), as well as a decline in solar elevation.

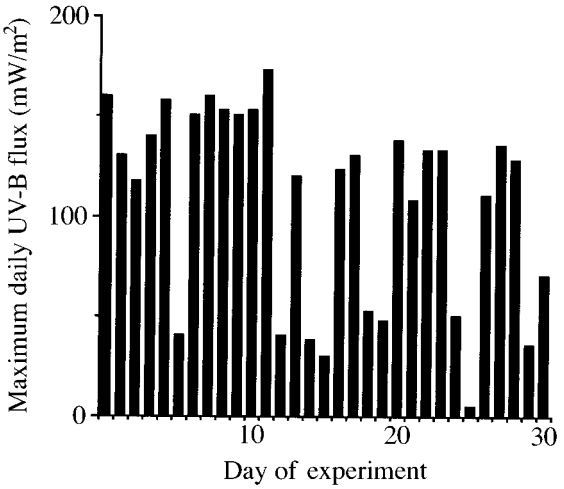

FIG. 2. Forecast maximum daily UV-B flux during 23 July–23 August 1995. Erythemal action spectrum-weighted UV-B flux data were calculated by multiplying the daily Canadian UV Index readings for Edmonton, Alberta, Canada, by 25 mW/m² (see Burrows et al. 1994).

Periphyton and phytoplankton community composition

Each of the three algal communities in Pipit Lake had a distinct taxonomic composition, as determined by indicator carotenoids and confirmed by direct microscopic examination (Fig. 3, Table 2). Epilithon was dominated by diatoms (diatoxanthin, fucoxanthin). The most common epilithic diatoms were *Cymbella, Navicula, Neidium, Pinnularia,* and *Synedra,* while the epilithic cyanobacteria (oscillaxanthin, zeaxanthin) were represented by *Merismopedia* and *Phormidium.* In contrast, epipelon contained mostly chrysophytes (represented by fucoxanthin), along with higher abundances of chlorophytes (lutein/zeaxanthin, chl *b*), filamentous cyanobacteria (oscillaxanthin), and cryptophytes (alloxanthin). Epipelic chrysophytes and cyanobacteria were primarily represented by *Ochromonas* and *Gloeocapsa,* respectively. *Rhodomonas minuta* was the most abundant epipelic cryptophyte. Phytoplankton consisted mainly of picocyanobacteria (lutein/zeaxanthin, *b*-phorbins absent), along with lower abundances of chrysophytes (fucoxanthin), cryptophytes (alloxanthin), and dinoflagellates (fucoxanthin, peridinin). *Synechococcus*-like cells comprised the picocyanobacteria, while *Kephyrion* was the most abundant chrysophyte and *Gymnodinium* represented the dominant dinoflagellate. Diatoms were absent from the phytoplankton.

Effects of UV radiation and macroinvertebrates on algae

Periphyton and phytoplankton communities differed in their responses to UV radiation (Table 3). Macroinvertebrates did not significantly affect periphyton or phytoplankton standing crops, and therefore, these treatments were pooled (producing $n = 6$ replicates) before examination of the effects of UV radiation (Table 3). By day 30, UV-B radiation had significantly suppressed the abundance of epilithon, as total epilithic carotenoid content was 30% higher in the −UV and −UV-B enclosures than in the +UV treatment (Fig. 4). UV radiation did not have a significant inhibitory effect on epilithic chlorophyll (Fig 4; Table 3). In contrast, UV-A radiation significantly stimulated the abundance of epipelon by increasing both carotenoid levels by 40% and chlorophyll concentrations by 30% (Fig. 4, Table 3). UV radiation did not significantly affect total

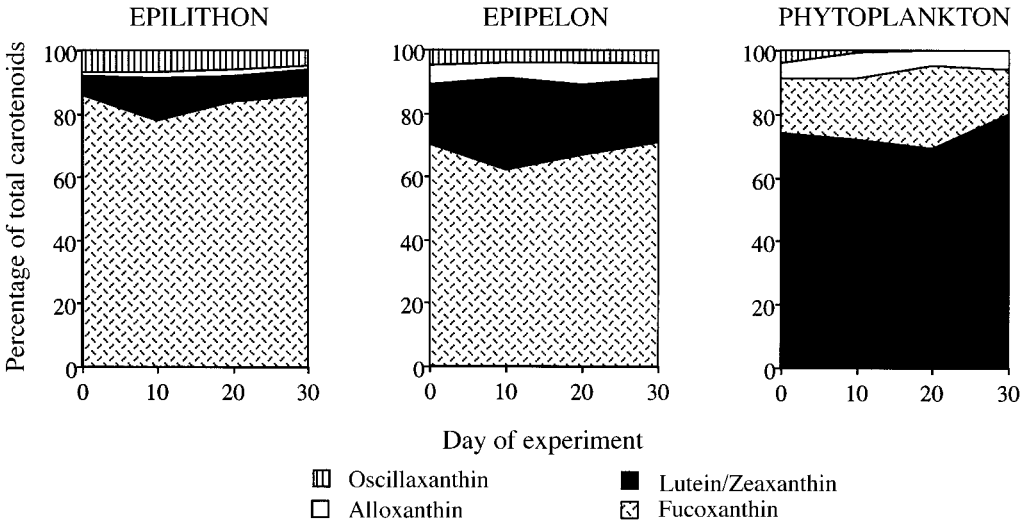

FIG. 3. Relative abundances of major taxonomically diagnostic carotenoids (concentrations measured in nmol/m²) in epilithon, epipelon, and phytoplankton from control (+UVR, −Zoo) enclosures in Pipit Lake following ice break in 1995. Taxonomic affinities of individual carotenoids are presented in Table 2.

TABLE 3. Repeated-measures ANOVA results of the effects of ultraviolet radiation (UV) and macroinvertebrates (Zoo) on log-transformed carotenoid and chlorophyll standing crops in epilithon, epipelon, and phytoplankton in an alpine lake. Values given are F statistics for $n = 3$ replicates.

Source	df	Epilithon		Epipelon		Phytoplankton	
		Carotenoids	Chlorophylls	Carotenoids	Chlorophylls	Carotenoids	Chlorophylls
UV							
Zoo	2	6.09*	1.90	6.20*	9.40**	0.10	0.11
UV × Zoo	1	1.18	2.19	0.47	0.07	0.01	0.27
Time	2	1.50	0.75	0.89	0.66	1.94	1.81
Time × UV	3	40.52***	18.36***	1.73	4.51*	16.19***	53.94***
Time × Zoo	6	1.76	1.55	0.58	0.62	0.11	0.55
Time × UV × Zoo	3	0.22	0.73	0.52	0.19	0.51	1.98
Error	6	0.61	0.49	0.23	0.28	0.98	2.47
MSE	12						
MSE (Time)	36						

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

phytoplankton carotenoid or chlorophyll, which began to decline after day 20 (Fig. 4, Table 3). On an areal basis, epipelon was ~10× and ~100× more abundant than epilithon and phytoplankton, respectively.

UV radiation significantly altered the algal composition of epilithon and epipelon but not that of phytoplankton (Table 4). The effects of macroinvertebrate treatments were nonsignificant in all cases. Therefore, these treatments were also pooled (yielding $n = 6$ replicates) before examination of the effects of UV radiation on epilithon and epipelon community composition. In the epilithon, UV radiation suppressed diatoms (fucoxanthin; RM-ANOVA, $P = 0.02$), cryptophytes (alloxanthin; $P = 0.01$), and cyanobacteria/greens (lutein/zeaxanthin; $P = 0.02$), without significantly ($P = 0.34$) affecting filamentous cyanobacteria (oscillaxanthin; Fig. 5). In general, UV-B radiation was responsible for suppression of epilithic groups, although UV-A radiation also inhibited algal standing crop, especially in the case of cryptophytes. In the epipelon, UV-A radiation affected algal composition by stimulating epipelic chlorophytes and cyanobacteria (lutein/zeaxanthin; $P = 0.003$), including filamentous taxa (oscillaxanthin; $P = 0.002$) (Fig. 6, Table 4). UV radiation

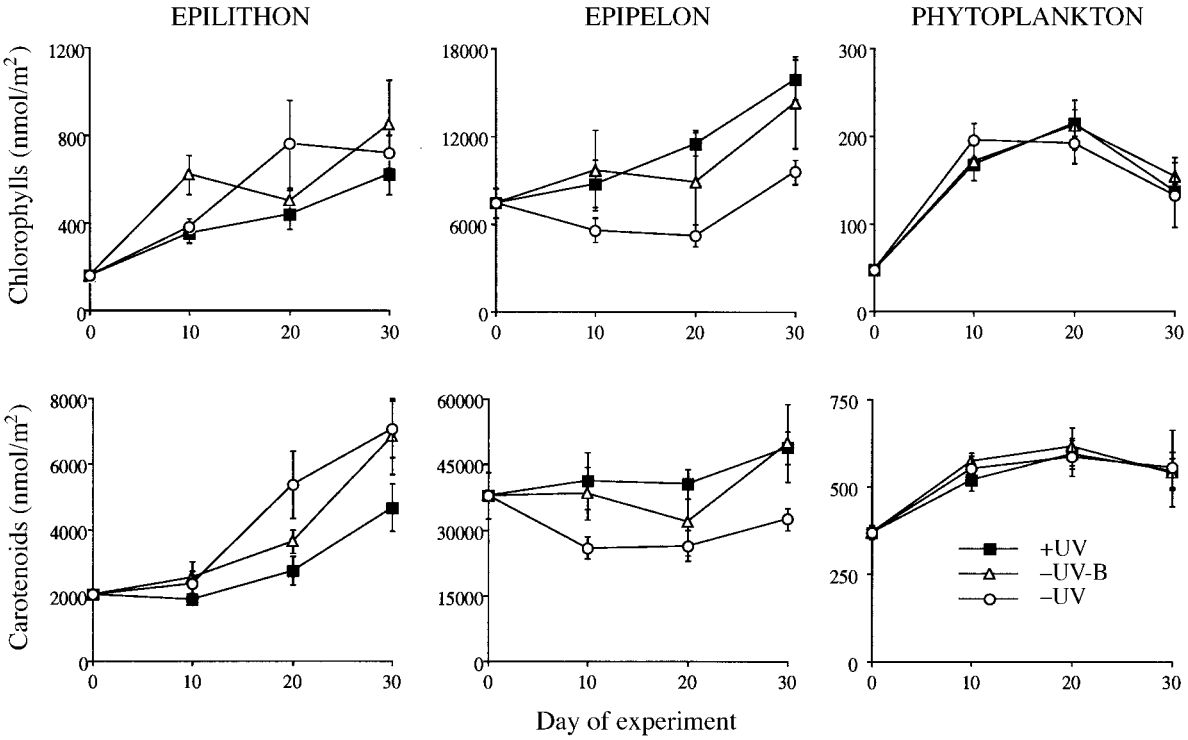

FIG. 4. Mean total chlorophyll and carotenoid concentration of epilithon, epipelon, and phytoplankton exposed to total UV (+UV), UV-A alone (−UV-B), or no UV irradiance (−UV). Macroinvertebrate treatments were pooled by UV treatment. Narrow vertical bars indicate ±1 SE ($n = 6$ replicates).

TABLE 4. Repeated-measures MANOVA results of the effects of ultraviolet radiation (UV) and macroinvertebrates (Zoo) on community composition of epilithon, epipelon, and phytoplankton in an alpine lake. Values given are *F* statistics for $n = 3$ replicates.

Source	df	Epilithon	Epipelon	Phytoplankton
UV				
Zoo	2	6.57*	6.76*	0.27
UV × Zoo	1	1.53	0.43	0.10
Time	2	1.53	0.78	2.61
Time × UV	15	160.30***	73.33***	226.12***
Time × Zoo	30	2.71**	0.76	0.57
Time × UV × Zoo	15	0.72	0.41	0.87
Error	30	0.95	0.38	1.28
MSE	12			
MSE (Time)	228			

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

also had marginally significant stimulatory effects on epipelic chrysophytes and diatoms (fucoxanthin; $P = 0.04$) and cryptophytes (alloxanthin; $P = 0.06$). In the phytoplankton, chrysophytes, cryptophytes, dinoflagellates, filamentous cyanobacteria, and picocyanobacteria were all unaffected by UV radiation (Fig. 7).

Effects of UV radiation on zoobenthos and zooplankton

Final total macroinvertebrate biomass was significantly lower in the reference than in the macroinvertebrate-amended enclosures (Fig. 8, Table 5). Final copepod densities averaged 0.5 and 1.4 individuals/L in the reference and amended enclosures, respectively. In addition, final amphipod and chironomid densities averaged 78.9 and 37.6 individuals/m^2 in the reference enclosures, and 189.3 and 75.2 individuals/m^2 in the amended enclosures. These differences show that the macroinvertebrate treatment persisted over the course of the experiment. Interestingly, zoobenthos were collected from sediment samples but were never observed on the tiles or in the water column.

UV radiation did not affect total zoobenthos and zooplankton biomass (Fig. 8) but significantly suppressed

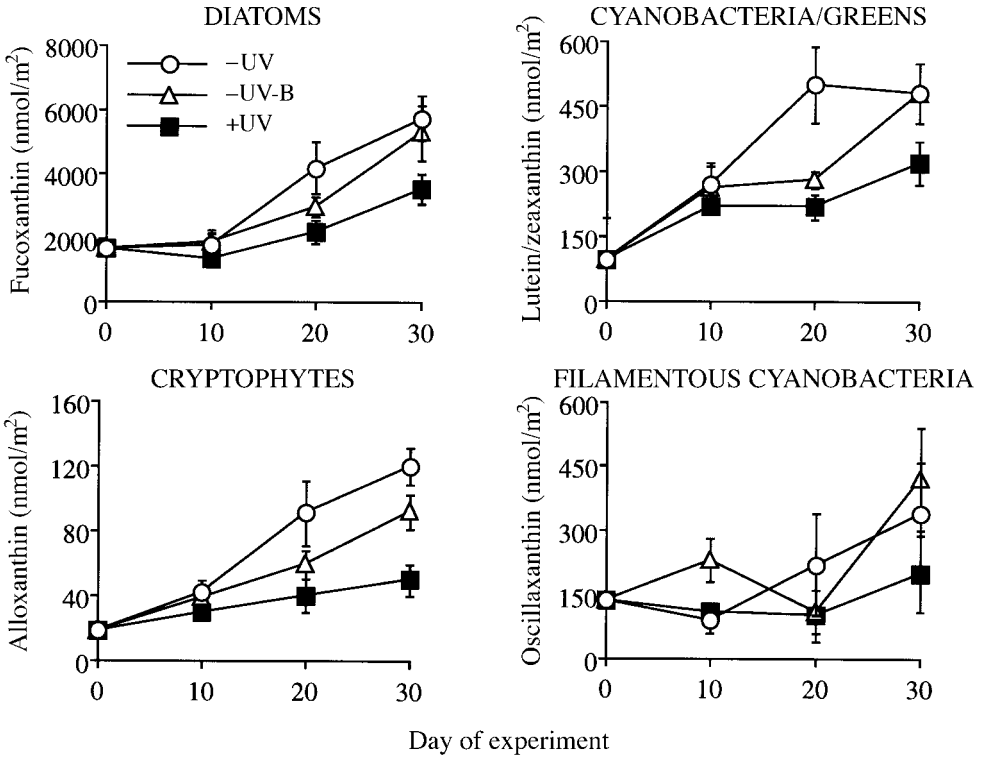

FIG. 5. Effects of total UV, UV-A alone (−UV-B), and no UV irradiance on epilithic diatoms (fucoxanthin), cyanobacteria and greens (lutein/zeaxanthin), cryptophytes (alloxanthin), and filamentous cyanobacteria (oscillaxanthin) sampled from unglazed ceramic tiles over 1 mo in littoral enclosures. Macroinvertebrate treatments were pooled by UV treatment. Pigment–algal group associations were confirmed by light microscopy. Narrow vertical bars indicate ±1 SE ($n = 6$ replicate).

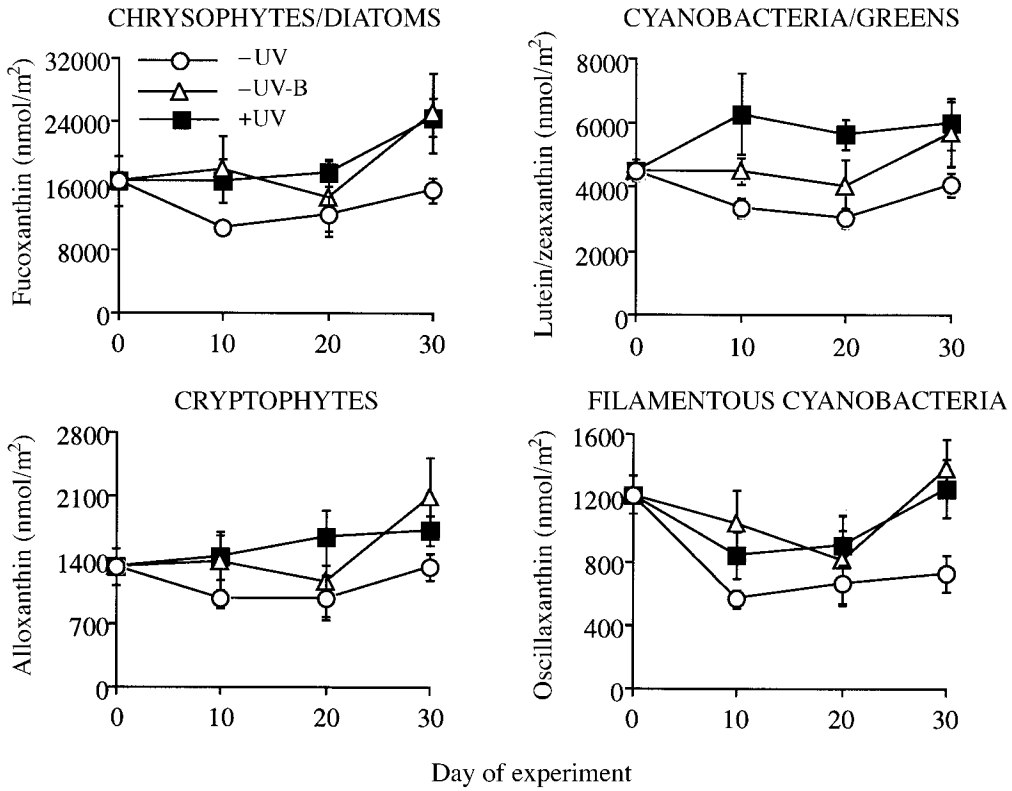

FIG. 6. Effects of total UV, UV-A alone (−UV-B), and no UV irradiance on epipelic chrysophytes and diatoms (fucoxanthin), cyanobacteria and greens (lutein/zeaxanthin), cryptophytes (alloxanthin), and filamentous cyanobacteria (oscillaxanthin) sampled from surface sediment cores over 1 mo in littoral enclosures. Errors, number of replicates (here, sediment samples), and pigment identifications are as in Fig. 5.

rotifer biomass (Fig. 9, Table 5). Zooplankton biomass was composed mostly of heavily pigmented *Hesperodiaptomus arcticus* (98% of total biomass), which was unaffected by UV radiation ($P > 0.05$). Tukey tests showed that total rotifer abundance was significantly ($P < 0.01$) suppressed by UV-B, but not UV-A, radiation. Reduction in rotifer abundance resulted from suppression of *Keratella quadrata,* whose densities declined by 3× under natural UV-B irradiance (Fig. 9). The pigmented taxon *Notholca* was the only rotifer unaffected by UV-B radiation ($P > 0.05$).

DISCUSSION

Direct effects of UV radiation on periphyton and phytoplankton

Our results showed that the direct effects of UV radiation on algae were habitat and taxon-specific. Eukaryotic epilithon was suppressed by UV radiation, particularly UV-B, while cyanobacterial epipelon was stimulated by UV-A, and all phytoplankton were unaffected by UV radiation. Differential responses of algal communities to UV radiation may involve differences in the availability of nutrients and refugia in each habitat, as well as photoprotection and photorepair capacity.

UV-B radiation suppressed the development of epilithon primarily by inhibiting the dominant diatom component (Fig. 5), consistent with reports that diatoms on hard surfaces are sensitive to natural and elevated UV-A and UV-B irradiances (Worrest et al. 1978, Bothwell et al. 1993, Vinebrooke and Leavitt 1996). Our results expand these earlier findings by showing that epilithic diatoms were more sensitive to UV radiation than were co-occurring cyanobacteria. Like those of Bothwell et al. (1994), our findings suggest that UV-A radiation suppressed epilithon; however, a high proportion of the total effect of UV radiation was also attributable to UV-B and short-wave UV-A irradiance (−UV-B treatment; Mylar-D transmittance cutoff <334 nm) (see Fig. 1). The observation that both UV-A and UV-B radiation caused photoinhibition is consistent with predictions from biological weighting functions (Cullen et al. 1992, Milot-Roy and Vincent 1994), showing that the 320-nm cutoff between UV-A and UV-B does not represent an ecologically meaningful boundary for epilithon.

The sensitivity of epilithic diatoms and cryptophytes may be linked to their inability to physically avoid the adverse effects of UV radiation. Elsewhere, we have shown that the development of periphyton on hard sur-

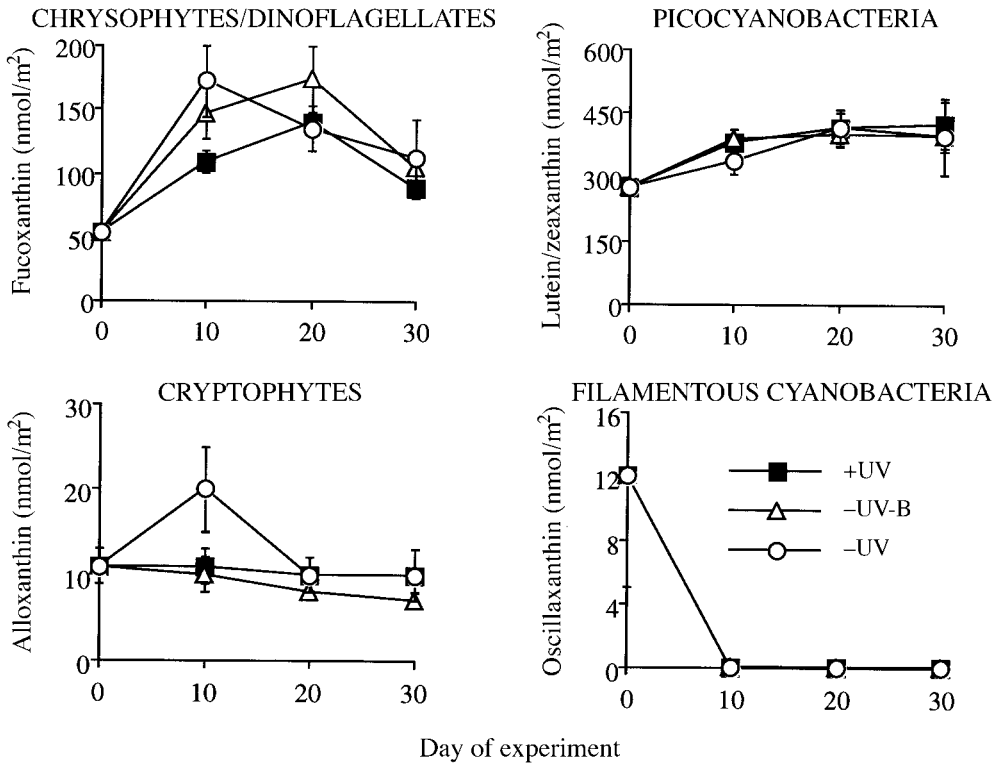

FIG. 7. Effects of total UV, UV-A alone (−UV-B), and no UV irradiance on planktonic chrysophytes and diatoms (fucoxanthin), cyanobacteria and greens (lutein/zeaxanthin), cryptophytes (alloxanthin), and filamentous cyanobacteria (oscillaxanthin) sampled from open water over 1 mo in littoral enclosures. Errors, number of replicates, and pigment identifications are as in Fig. 5.

faces consists mainly of stalked diatoms that are unable to avoid high UV irradiances (Vinebrooke and Leavitt 1996). Similarly, the sparse epilithic cryptophyte population suppressed by UV radiation in this study was in a nonmotile palmelloid phase. In contrast, the sessile cyanobacteria were unaffected by UV radiation, perhaps owing to the resiliency of their DNA (Vincent and Quesada 1994) and the production of UV-absorbing pigments such as scytonemin (Garcia-Pichel and Castenholz 1991) and mycosporine-like amino acid compounds (Garcia-Pichel et al. 1993).

Stimulation of epipelon by UV-A radiation was primarily the result of increased cyanobacterial abundance, although abundances of chrysophytes, diatoms, and cryptophytes, were also enhanced (Fig. 6). This unexpected result may have involved phosphorus release following UV-induced photolysis of organic iron–phosphorus complexes (e.g., Francko and Heath 1982) or reactivation of phosphatase exoenzymes (Wetzel 1992). UV radiation might also stimulate heterotrophic algae through the simultaneous photolytic production of labile organics from recalcitrant humic substances (Wetzel et al. 1995) and photoinhibition of bacterial activity (Herndl et al. 1993). Other beneficial effects of UV-A radiation may include the activation of repair mechanisms that counteract the photoinhibitory effects of UV-B radiation (Quesada et al. 1995). As well, epipelic communities have the capacity to regulate their exposure to UV radiation via diel migrations through the sediments (Happey-Wood 1988, Vincent et al. 1993). Thus, motile epipelic algae may benefit from UV radiation by adjusting their position within the sediments so as to avoid high UV irradiance, yet exploit periods of photolytically enhanced resource availability.

Phytoplankton were unaffected by UV radiation (Fig. 7). Physical avoidance of UV radiation by phytoplankton via vertical migration into deeper waters was not possible in these shallow littoral enclosures. However, migrations by some epilimnetic phytoplankton into sediments (Hansson 1996) may have allowed some taxa to gain physical refuge from UV radiation. Chrysophytes were present in both the phytoplankton and epipelon in Pipit Lake, suggesting that migration could have occurred; however, the UV-tolerant phytoplankton consisted mainly of immotile picocyanobacteria. Alternately, the insensitivity of phytoplankton to UV radiation in this alpine lake may be the result of inherently high UV tolerance of algae that originate from habitats that receive high UV irradiances (Jokiel and York 1984, Xiong et al. 1996).

Picocyanobacterial phytoplankton were resistant to UV radiation in Pipit Lake, consistent with experiments demonstrating that their photosynthesis is less inhibited

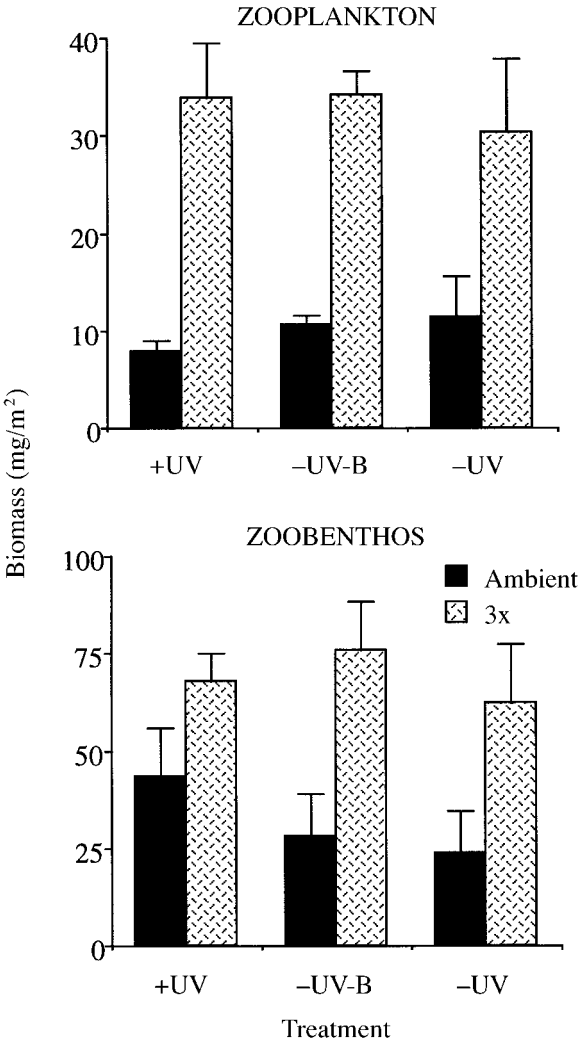

FIG. 8. Effects of total UV, UV-A alone (−UV-B), and no UV irradiance on mean areal biomasses of ambient and threefold-augmented total zoobenthos and zooplankton in littoral enclosures on day 30. Narrow vertical bars indicate +1 SE (n = 3 replicates).

by UV radiation than is that of larger algae (Milot-Roy and Vincent 1994). Picocyanobacterial resistance to UV radiation apparently does not arise from photoprotection by high concentrations of the carotenoid zeaxanthin because this pigment absorbs poorly in the UV band. While cyanobacteria may use carotenoids as antioxidants (see Vincent and Roy 1993), the cell diameter of picocyanobacteria (≤2 μm) is too small to result in appreciable attenuation of UV radiation by photoprotective pigments (Garcia-Pichel 1994). Instead, insensitivity of cyanobacteria to ambient UV irradiance may involve their capacity for photoenzymatic repair (PER) and nucleotide excision repair (NER) of damaged DNA (see Karentz et al. 1994). These adaptive strategies of cyanobacteria may reflect their evolutionary origin under previously higher UV irradiances (Castenholz 1992, Vincent and Quesada 1994).

Several lines of evidence demonstrate that changes in carotenoid and chlorophyll standing crops were attributable to algal biomass responses and not to selective pigment biosynthesis, chromatic adaptation, or degradation. First, we have shown elsewhere that the response of algae to UV radiation in alpine and temperate lakes is the same regardless of whether abundance is measured as pigment standing crop, algal biovolume, or ash-free dry mass (Vinebrooke and Leavitt 1996, Leavitt et al. 1997), corroborating earlier reports of concomitant changes in chlorophyll standing crops and other biomass estimates in shallow-water algae exposed to UV radiation (Worrest et al. 1978, Bothwell et al. 1993, 1994). In the present study, the negative effect of UV radiation on epilithon was more evidenced by the suppression of carotenoids than by chlorophyll standing crop. On this point, carotenoids exhibit less variation than do chlorophylls owing to their relative greater stability, and as a result, carotenoids are more reliable indicators of algal biomass responses to environmental factors (Leavitt 1993, Millie et al. 1993). Second, our results show that the same algal pigment exhibited unique responses to UV radiation in different habitats, despite receiving identical PAR and UV flux. For example, alloxanthin from epilithic cryptophytes increased ~450% over the 30 d following the elimination of UV radiation (Fig. 5), whereas the same pigment declined ~25% in epipelon (Fig. 6) and was unchanged within the phytoplankton (Fig. 7). Differential degradation (photobleaching, oxidation) cannot account for such differences among habitats; rather these results reflect epilithon standing crop similar to that measured using direct algal cell enumeration (Vinebrooke and Leavitt 1996). Third, although exposure to UV-A radiation can lead to nonselective degradation of pigments in detrital material (Maske and Latasa 1997), live algae increase production of carotenoids in response to UV-A radiation (Goes et al. 1994), suggesting that our experiment may actually underestimate the stimulation of epilithic algae resulting from the elimination of UV radiation (Fig. 5). Nevertheless, our

TABLE 5. ANOVA results of the effects of ultraviolet radiation (UV) and macroinvertebrates (Zoo) on final total zooplankton, rotifer, and zoobenthos biomass in the littoral enclosures in an alpine lake on day 30. Values given are F statistics for n = 3 replicate.

Community	Source	df	F
Zooplankton	UV	2	0.08
	Zoo	1	40.50***
	UV × Zoo	2	0.34
Rotifers	UV	2	7.73*
	Zoo	1	0.49
	UV × Zoo	2	0.16
Zoobenthos	UV	2	0.60
	Zoo	1	14.82**
	UV × Zoo	2	0.49

Note: Error df = 12.
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

analyses show that UV radiation can regulate algal communities more than did threefold increases in ambient herbivore densities in an alpine lake (Tables 3, 4). Finally, recent experiments demonstrate that degradation of algal pigments is not significantly affected by UV-B flux (Maske and Latasa 1997), yet UV-B irradiance significantly altered periphyton growth in Pipit Lake (Figs. 4, 5, 6). Instead, these overall patterns of periphyton and phytoplankton, as inferred from pigments, are most consistent with changes in the abundance and composition of phototrophic communities.

Direct effects of UV radiation on zoobenthos and zooplankton

Zoobenthos were unaffected by ambient UV radiation, possibly as a result of adaptive avoidance strategies. Sediment-dwelling *Gammarus lacustris* and chironomids were rarely observed in the water column or on hard surfaces during the day, suggesting that they may physically avoid UV radiation. *G. lacustris* are often observed in the plankton at night in fishless alpine lakes (F. Wilhelm and D. W. Schindler, University of Alberta, Edmonton, Alberta, Canada; *unpublished data*), consistent with an active UV-avoidance strategy. Chironomids may have been insensitive to UV radiation in our corrals because their burrowing behavior removed them from direct exposure to UV radiation, unlike tube-dwelling species on hard substrates, which are inhibited by UV-B radiation (Bothwell et al. 1994).

Photoprotective pigmentation may have contributed to the insensitivity of some invertebrates to UV radiation. Zooplankton consisted primarily of large, colored calanoid copepods that were unaffected by UV radiation. *Hesperodiaptomus arcticus* may partly derive protection from UV radiation from its thick carapace. However, this species also contains high concentrations of the caroteno-protein astacene, a pigment complex known to increase the phototolerance of pigmented zooplankton, in comparison with pale morphs in mountain lakes (Hairston 1980, Byron 1982). The observation that slow-swimming, translucent rotifers were significantly suppressed by UV-B radiation, while the relatively pigmented *Notholca* was unaffected, is also consistent with the importance of photoprotective pigmentation to epilimnetic zooplankton. Pigmented rotifers (e.g., *Hexarthra bulgarica*) also inhabit other alpine lakes (Dumont et al. 1978).

Indirect effects of UV radiation on alpine littoral communities

This study suggests that UV radiation does not have substantial indirect effects on food webs in cold ultra-oligotrophic lakes. The manipulation of invertebrate densities showed that algae were not regulated by higher trophic levels. Severe resource limitation may have slowed growth by algae and invertebrates and produced a food web having weak linkages (e.g., Neill and Peacock 1980). Herbivores were also ineffective at regulating resource-limited phytoplankton in nearby Snowflake Lake despite invertebrate densities being about twice as great as those used in our experiment (Paul et al. 1995). Furthermore, the prevalence of armored loricate rotifers (e.g., *Keratella* spp.) may have reduced the efficiency of predation by diaptomids (e.g., Stemberger and Gilbert 1987, Arnott and Vanni 1993), such as found in unproductive and fishless montane lakes (Neill 1984). Thus, weak direct effects of consumers offset the possibility of strong indirect effects of UV radiation via food-web processes. Overall, the short duration of this experiment precluded the detection of potential UV-effects on the reproductive success of macroinvertebrates, many of which require >1 yr to complete their life cycles (e.g., *G. lacustris, H. arcticus*, Paul and Schindler 1994; F. Wilhelm, Edmonton, University of Alberta, *personal communication*).

Ecological significance of UV radiation in aquatic ecosystems

Our findings suggest that UV radiation may be an important environmental factor affecting food webs in translucent ponds and shallow lakes. For example, up to 35% of the benthos in Pipit Lake is exposed to UV radiation (Table 1). Similar levels of UV exposure are expected in most alpine lakes in which mean DOC concentrations are comparable to that of Pipit Lake ($\sim$1 mg/L; Leavitt et al. 1997), and in up to 200 000 boreal lakes where drought and anthropogenic acidification can reduce DOC levels and increase the depth of UV penetration (Schindler et al. 1996, Yan et al. 1996, Leavitt et al. 1997). Furthermore, the importance of benthic algae to whole-lake food webs via benthic-pelagic linkages (Hecky and Hesselein 1995, Blumenshine et al. 1997) suggests that the demonstrated effects of UV exposure may extend beyond shallow littoral habitats.

The relative importance of direct and indirect effects of UV radiation on shallow-water communities may also be influenced by system productivity. In a cold and unproductive lake, our study showed how UV radiation might affect littoral communities via direct effects on relatively slow-growing taxa. Thus, direct UV effects may be most pronounced in extreme (i.e., alpine and polar) and anthropogenically stressed (i.e., acidified lakes) systems in which abiotic regulation of communities is common (Menge and Sutherland 1987, Vinebrooke 1996, Vinebrooke and Leavitt 1996). In more productive systems, increased biotic regulation of food-web structure may reduce the importance of direct effects of UV radiation (e.g., DeNicola and Hoagland 1996, Hill et al. 1997) and hasten the onset of indirect effects (e.g., Bothwell et al. 1993, 1994).

A suite of potential adaptive strategies may help explain the differential sensitivities of organisms to UV radiation in shallow-water habitats. Active avoidance may be the most immediate option available to motile organisms. For example, we found that epipelon and

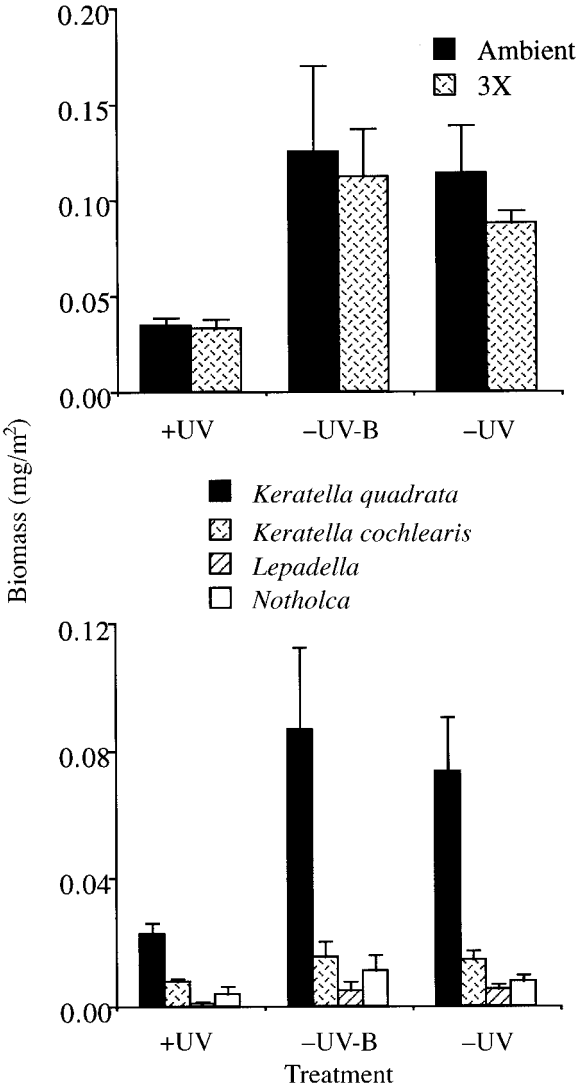

FIG. 9. Effects of total UV, UV-A alone (−UV-B), and no UV irradiance on mean areal biomasses of all rotifers (n = 3 replicates) and of individual rotifer taxa (n = 6 replicates) in littoral enclosures on day 30. Narrow vertical bars indicate +1 SE.

zoobenthos that were potentially capable of seeking refuge within sediments were not adversely affected by UV radiation. If physical avoidance is not possible, due to the absence of physical refuge (e.g., epilimnion), or the inability of taxa to migrate (e.g., attached epilithon), then photoprotective pigmentation may be an important additional adaptation against UV radiation. In Pipit Lake, taxa that had limited access to physical refuge, but that were capable of photoprotective pigmentation (epilithic filamentous cyanobacteria and *H. arcticus*), were unaffected by UV radiation. Finally, UV-tolerant organisms that were incapable of active avoidance or that lacked adequate photoprotective pigmentation may have relied on an inherently high capacity for DNA repair (i.e., picocyanobacteria). Organisms that lacked such adaptive strategies may be highly susceptible to the adverse effects of UV radiation (i.e., attached eukaryotic epilithon, translucent rotifers). Clearly, further research is required to better understand how adaptive strategies and system conditions affect the balance between the direct and indirect effects of UV radiation, and ultimately, its overall ecological impact on aquatic food webs.

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