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Cell size versus taxonomic composition as determinants of UV-sensitivity in natural phytoplankton communities

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Abstract

Independent evidence from cultures, field studies, and modeling suggests that cell size is a key factor determining the extent of ultraviolet radiation (UVR) damage of phytoplankton, with the greatest effects on small cells. We investigated this hypothesis in subarctic lake communities by measuring size-dependent photosynthesis under different UVR treatments. Lakewater was exposed to near-surface solar radiation in the presence or absence of UVA and UVB, and the phytoplankton was then fractionated into taxonomically distinct pico-, nano-, and microplankton size classes. The first part of the study was conducted in a large oligotrophic lake where UVA lowered photosynthesis on average by 32%, while UVB caused an additional 20% decrease. For the pooled data set, mean UVR inhibition of photosynthesis was lowest for the picoplankton and highest for microplankton, but the differences between size fractions were not significant. This photosynthetic assay was repeated in a shallow, mesotrophic coastal lake. This community was less inhibited by UVR (on average 10% inhibition); there was no difference in response between the pico- and nanoplankton fractions, whereas photosynthesis of the microplankton fraction was significantly enhanced under UVR. These results show that cell size is not a good index of UV sensitivity and that cyanobacteria-dominated picophytoplankton are less sensitive to the impacts of rising UVB in the polar and subpolar regions than would be predicted from relationships based only on cell size.

A variety of evidence in the literature indicates that the sensitivity of planktonic cells to inhibition by solar ultraviolet radiation (UVR) may be a function of cell size. This evidence includes theoretical analyses of light absorption and experimental results using natural assemblages and cultures exposed to different spectral UVR regimes. Aquatic ecosystems, particularly at high latitudes, are currently experiencing changes in their underwater UVR associated with stratospheric ozone depletion (Kerr and McElroy 1993; Rex et al. 1997) and climate-related changes in spectral UVR attenuation in the water column (Schindler et al. 1996; Vincent and Pienitz 1996). Any shift in size structure of phytoplankton communities that might occur in response to these changes has wide-ranging implications for pelagic food web processes and for interactions with the benthos via sedimentation (Häder and Worrest 1991; Kiørboe 1993).

Two related aspects of bio-optical theory imply that small cells should be more vulnerable to UVR than large cells. Firstly, pigment-specific absorption in general increases with decreasing cell size and decreasing internal molecular self-shading, the phenomenon referred to as package effect (Morel and Bricaud 1981), leading to higher exposure per unit pigment and cell volume. Secondly, one of many protective strategies against UVR is the biosynthesis of UV-absorbing substances such as mycosporine-like amino acids (Garcia-Pichel and Castenholz 1993). The protective efficiency of these natural sunscreens is a function of the cellular concentration but also cell size through its effect on molecular self-shading. Model calculations by Garcia-Pichel (1994) have indicated that while nano- and microplankton cells may contain sufficient UVR-screening pigments to confer protection, the small cell volume of picoplankton precludes this strategy (*see also* Raven 1991). This led him to conclude that the smallest phytoplankters are the most sensitive to UV exposure.

The experimental evidence of cell size effects comes mostly from oceanographic studies. The UV sensitivity of 12 species of Antarctic diatoms was highest in the smaller cells with greater surface-to-volume ratios (Karentz et al. 1991). These smaller cells sustained more damage per unit of DNA and were killed by a lower UVR flux than larger cells. These authors proposed that cell size might be a reliable indicator of UV sensitivity but also noted the potential importance of other factors such as cell morphology or the presence of photoprotective pigments. In water samples collected from the Gulf of Mexico, UVB-induced DNA damage in the bacterioplankton size fraction (<0.8 μm) was approximately twice the damage of the larger, eukaryotic size fraction (0.8–120 μm; Jeffrey et al. 1996), consistent with a cell-size effect.

Cultures of *Phaeodactylum tricornutum* showed an increase in cell size in response to UVB radiation (Behrenfeld et al. 1992). This is in keeping with evidence that UV exposure can arrest the cell division cycle in diatoms but might also indicate an adaptive response due to the greater protection conferred by UVR screening pigments in larger cells (Karentz et al. 1991). In a long-term experiment on periphyton colonization and growth in artificial stream channels, Bothwell et al. (1993) found that UVB induced a shift in the diatom assemblage toward larger-celled species. Contrasting

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with these observations, a study in Lac à l'Eau Claire (subarctic Québec) showed that photosynthesis by the larger cell fraction (>2 μm) had a twofold greater sensitivity to UVR than the <2-μm fraction and was inhibited more rapidly in the morning, as the sun reached its maximum height (Milot-Roy and Vincent 1994).

Our objective in the present study was to evaluate the hypothesis that cell size dominates over taxonomic differences in controlling the degree of UVR inhibition of primary production. We applied a photosynthetic assay to the phytoplankton communities within two contrasting subarctic lakes to determine whether there is a general relationship between cell size and UV sensitivity. These waters were especially appropriate for such experiments because their phytoplankton contain a broad spectrum of cell sizes, with taxonomic differences between size classes. Furthermore, there is increasing concern about UVR impacts on subarctic aquatic ecosystems because ozone depletion appears to be proceeding rapidly in this region (Kerr and McElroy 1993). These lakes contain chromophoric dissolved organic matter (CDOM) within a concentration range where small variations in CDOM give rise to large changes in underwater spectral UVR (Laurion et al. 1997); they may therefore be subject to seasonal variations in UVR penetration, as well as longer term effects caused by climate change (Vincent and Pienitz 1996).

Materials and methods

The study was conducted in the forest–tundra zone of subarctic Québec in August 1994 (five experiments; E1–E5) and 1995 (three experiments; E6–E8). The experiments in 1994 were performed in a large oligotrophic lake, Lac à l'Eau Claire (latitude 56°10′N; longitude 74°30′W; see Bergeron and Vincent [1997] for location of the lakes), with samples taken from the main western basin, from a small bay between the eastern and western basins (Pakatouk Bay) and from a small brown-water lagoon on an island in the western basin. The experiments in 1995 were performed in Lac Kayouk (latitude 55°17′N; longitude 77°46′W), a small coastal lake in the vicinity of Poste-de-la-Baleine. Bio-optical differences between sites and experiments are given below.

Profiles of solar radiation were obtained with a Biospherical PUV-500 radiometer that provided a measure of downwelling irradiance at 305, 320, 340, and 380 nm (full bandwidth at half maximum is 8–10 nm) and of downwelling photosynthetically available radiation (PAR; 400–700 nm). Fine structure temperature profiles were obtained with the same instrument. A coupled transmissometer (10-cm pathlength, Sea Tech) gave profiles of transmittance at 660 nm. Dissolved organic carbon (DOC) was measured in these samples by high temperature oxidation with a Shimadzu total organic carbon (TOC) analyzer model 5050 fitted with an ASI-5000 autosampler.

The impact of different UV radiation regimes on size-dependent photosynthesis was measured by incubating lakewater samples in Vicor quartz tubes (100 ml in duplicates) under UV-T Plexiglas (PAR + UVA + UVB), Mylar-D (PAR + UVA), and UF-3 Plexiglas (PAR). The spectral characteristics of the filters and the quartz tubes were verified with a Hewlett-Packard diode-array spectrophotometer (model HP-8452A). UV-T and UF-3 Plexiglas have cut-off wavelengths of 285 and 400 nm, respectively, and Mylar-D (supported by UV-T Plexiglas) has a cut-off wavelength of 340 nm. All three filters transmit approximately 90% of incident PAR. The quartz tubes were maintained horizontally at 15 cm under the water surface with an aluminum holder. The UF-3 treatment was considered to be the control treatment (no UVR) for estimating the percent inhibition caused by UVA or UVA + UVB and for statistical analyses.

Lakewater samples were collected at the subsurface and incubated for ~4 h around midday (from 11–12 h to 15–16 h) with ^{14}C-HCO_3^- at a final concentration of 160 nCi ml^{-1}. For the experiments in 1995, duplicate quartz tubes were also incubated in the dark to correct for passive uptake of ^{14}C; this correction was typically <10% of the total counts. After incubation, the quartz tubes were stored in the dark and cold for 1–3 h during transport and prior to filtration. Each tube sample was then separated into three aliquots to obtain the size fractions <2, 2–20, and >20 μm. For the experiments in 1994, one aliquot was directly filtered onto MFS (equivalent to GF/F) glass fiber filters (collecting total biomass), the second was prefiltered through 2-μm Nuclepore filters and then onto MFS filters (collecting cells <2 μm), and the other aliquot was prefiltered through 20-μm Nitex mesh and then onto MFS filters (collecting cells <20 μm); estimates for each size fraction were obtained by difference. For the experiments in 1995, the secondary MFS filtering step was replaced by direct counting of the Nuclepore and Nitex filters. We tested the quenching of each of these filters and obtained no differences. All filters were kept frozen until counting. They were subsequently placed in scintillation vials and fumed for approximately 20 h with 0.1 ml of 1 N HCl. Scintillation cocktail was added, and the samples were then counted in a Beckman LS 6500 scintillation counter. Each vial was run through two cycles to check that all chemiluminescence had dissipated. Lakewater samples for the measurement of dissolved inorganic carbon were preserved with mercuric chloride and subsequently analyzed with a Shimadzu TOC analyzer before and after acidification.

Samples for chlorophyll *a* (Chl *a*) analysis were fractionated as for the 1994 photosynthesis protocol with final filtration onto MFS glass-fiber filters. The pigments were then extracted in our field laboratory with boiling 90% (v/v) ethanol (Nusch 1980). The fluorescence of the extracts was measured with a Sequoia Turner model 450 fluorometer equipped with NB440 (blue excitation) and SC665 (red emission) filters and calibrated with a Chl *a* solution (Sigma Biochemical Co., Chl *a* from *Anacystis nidulans*) that had been analyzed by spectrophotometry. Pheopigments were corrected for by acidification. The standard error (SE) for triplicate Chl *a* analyses was 3–10% of the mean values.

Phytoplankton species composition at each study site was evaluated by inverted and epifluorescence microscopy. The samples were preserved with a solution of glutaraldehyde/paraformaldehyde (final concentration of 1%/0.1%). These were later examined under a Zeiss Axiovert 10 inverse epifluorescence microscope equipped with a Plan-Neofluor

Table 1. Characteristics of the near-surface waters at each site. Chl *a* = chlorophyll *a* for the total phytoplankton community, values in parentheses are SE (n = 3); K_d = vertical attenuation coefficient for downwelling irradiance. Profiling was on 6 August 1994 (western basin, Pakatouk Bay, lagoon) or 18 August 1995 (Lac Kayouk).

	Site			
Variable	Western basin	Pakatouk Bay	Lagoon	Lac Kayouk
DOC (mg liter^{-1})	2.3	2.9	15.9	5.6
Chl *a* (μg liter^{-1})	1.0 (0.1)	1.2	0.4	1.60 (0.05)
Temperature (°C)	8	10	10	15
Transmittance (%)	93	87	69	84
K_d (m^{-1})				
305 nm	2.7	6.3*	81*	18.8
320 nm	1.7	5.0	65*	13.5
340 nm	1.3	3.9	48*	11.1
380 nm	0.7	2.1	26*	6.3
PAR	0.19	0.47	2.4*	1.38

* Values calculated from the equations of Laurion et al. (1997).

100×/1.30 objective, and the species dominants were noted within each size class.

Results

DOC at the study sites varied from 2.3 to 15.9 mg liter^{-1}, giving a wide range of vertical attenuation coefficients for UVR and PAR (Table 1). Meteorological conditions also differed between experiments, giving rise to large differences in incident UVR (4.9–30.5 μW cm^{-2} nm^{-1} for UVR at 320 nm) and PAR (from 270 to 2,410 μmol photons m^{-2} s^{-1}). The spectral balance at the depth of incubation as measured by the ratio of radiation at 320 nm to full-waveband PAR varied between experiments and sites over the range 0.4–5.0 × 10^{-4} nm^{-1}. Experiments E1–E3 were performed in the western basin of Lac à l'Eau Claire (LEC; lowest DOC content) under variable cloud conditions. The fourth experiment was performed in the Pakatouk Bay (slightly higher DOC content) under scattered cloud conditions. The final experiment in 1994 was performed in the lagoon (E5) where DOC was highest, but under clear sky conditions. This latter site was too shallow for profiling and so the light penetration was estimated from the DOC measurements by the exponential $K_d(\lambda)$ model of Laurion et al. (1997) for subarctic lakes. Experiments in 1995 were conducted in Lac Kayouk, a shallow lake with moderate levels of DOC (Table 1), under clear sky conditions (E6) or scattered cloud (E7 and E8).

The static incubation protocol adopted in our UVR experiments would not be appropriate for deeply mixing water columns but simulated the effect of diurnal thermoclines in retaining phytoplankton in the near-surface waters for prolonged periods (hours). Near-surface thermoclines are a feature of LEC (Milot-Roy and Vincent 1994; Bergeron and Vincent 1997) and of Lac Kayouk (Scully and Vincent 1997). At Lac Kayouk for example, a near-surface thermocline typically formed during calm afternoons at ~0.8 m, giving a shallow surface mixed layer where the average irradiance was 61% of surface PAR and 9% of surface UVB

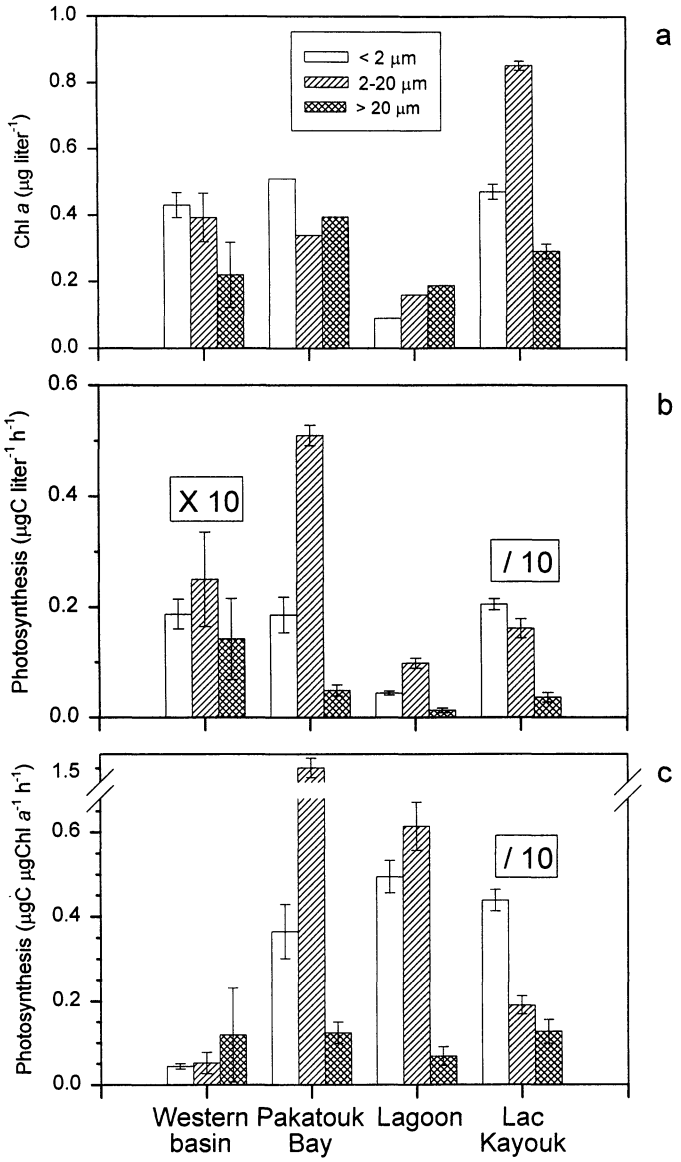

Fig. 1. Size distribution of Chl *a* (a), photosynthesis under PAR + UVR (b), and photosynthesis per unit biomass (c) at the four sampling sites. Error bars represent ± 1 SE (n = 6 for western basin and lac Kayouk, n = 2 for Pakatouk Bay and the lagoon).

(320 nm). The water samples incubated in our quartz tube assay (at 0.15 m) were exposed to a comparable average irradiance of 81% of surface PAR and 13% of surface UVB. At the clearer LEC sites, near-surface stratification was also often found in the top few meters of the water column but with more complex multiple thermoclines, reflecting the wind and thermal history of the lake over the preceding days.

The three Chl *a* fractions, <2 μm (picoplankton), 2–20 μm (nanoplankton), and >20 μm (microplankton), were well represented at each site (Fig. 1a). The picoplankton fraction of Chl *a* was slightly higher at the western basin and Pakatouk Bay stations, whereas in Lac Kayouk, the nanoplanktonic cells assumed greatest importance. Microscopic

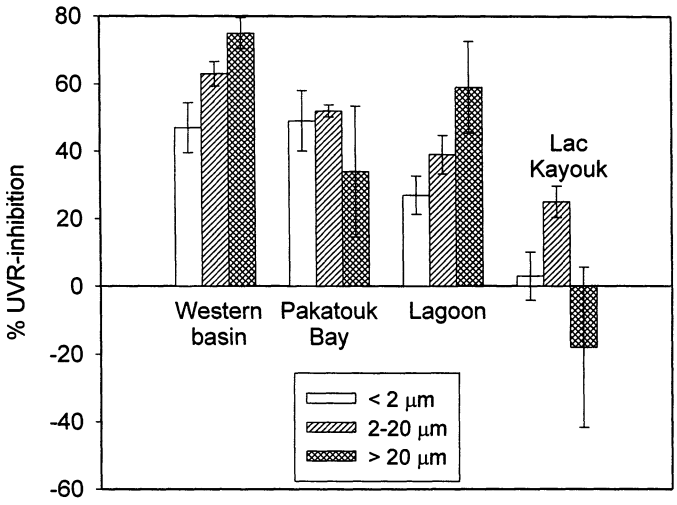

Fig. 2. The percent inhibition of photosynthesis by total UV radiation for each size fraction at the four sampling sites. Error bars represent ± 1 SE (n = 6 for western basin and lac Kayouk, n = 2 for Pakatouk Bay and the lagoon).

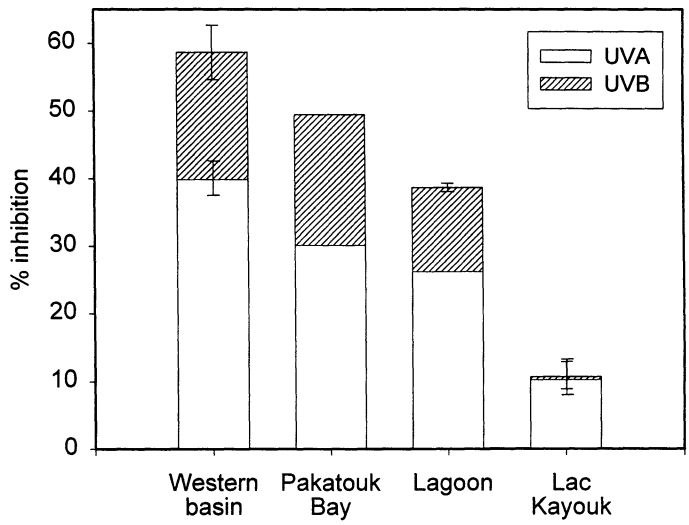

Fig. 3. Comparison between UVA and UVB inhibition of the total community photosynthesis for each sampling site. Error bars represent ± 1 SE (n = 6 for western basin and lac Kayouk, n = 2 for Pakatouk Bay and the lagoon).

analysis of the LEC phytoplankton (western basin and Pakatouk Bay) showed that the picophytoplankton community was exclusively dominated by phycoerythrin-rich picocyanobacteria. The nanoplankton contained a diverse assemblage of species including phytoflagellates (particularly *Ochromonas, Dinobryon,* and *Trachelomonas* sp.) and diatoms (mainly *Cyclotella* sp). Unidentified flagellates smaller than 10 μm comprised up to 20% of the total nano- plus microplankton cell count. The concentration of cells (~2–80 μm) was 700 ml^{-1} in the western basin and 1,100 ml^{-1} in Pakatouk Bay. Some cyanobacteria were also present as filaments or colonies >20 μm (*Dactylococcopsis, Microcystis, Anabaena,* and *Oscillatoria* sp.), thus contributing to the microplankton. The lagoon contained picocyanobacteria, small eukaryotes (2–5 μm), and colonial cyanobacteria. For Lac Kayouk experiments, the nano- plus microplankton cell concentration averaged 2,900 ml^{-1} (SE 400 ml^{-1}), comprising chrysophytes, diatoms, and colonial cyanobacteria, with an abundant picophytoplankton dominated by picocyanobacteria.

Photosynthetic rates for the total community exposed to full-waveband PAR + UVR ranged from 0.02 to 0.8 μg C liter^{-1} h^{-1} for LEC experiments, with biomass-specific values of 0.02–0.6 μg C μg Chl a^{-1} h^{-1}, reflecting different light conditions at the time of incubation and/or light histories for these lake communities. Photosynthesis was higher for the Lac Kayouk phytoplankton, ranging from 3.3 to 4.9 μg C liter^{-1} h^{-1} (2–3 μg C μg Chl a^{-1} h^{-1}). The nanoplankton fraction provided the largest contribution to photosynthesis at LEC while the picoplankton fraction dominated photosynthesis at Lac Kayouk (Fig. 1b), reflecting species and/or physiological differences between the assemblages. Photosynthesis per unit biomass (Fig. 1c) was maximal in the nanoplankton or microplankton fractions at LEC but in the picoplankton fraction in Lac Kayouk.

A split–split plot ANOVA was performed on the percent inhibition of photosynthesis caused by UVA and UVA + UVB. Effects of experiment, treatment, and cell size were tested. The LEC experiments (E1–E5) were pooled but treated separately from the pooled data set for the Lac Kayouk experiments (E6–E8). The ANOVA for LEC sites showed that there were no significant differences between sites, but the averaged UVR inhibition (calculated from photosynthesis values of total biomass) in the more transparent western basin tended to be higher than at the other sites (58% compared to 44%). The ANOVA for the pooled LEC data showed no overall significant differences between cell sizes (P = 0.08, df = 2; F = 2.9). However, there was some evidence of a trend that was in direct opposition to the hypothesis of increasing UV sensitivity with decreasing cell size. The mean inhibition caused by UVA plus UVB was 43% for picoplankton, 54% for nanoplankton, and 61% for microplankton. Similarly, the UVA inhibition was 21% (picoplankton), 31% (nanoplankton), and 49% (microplankton). Thus, the smallest cells were the least sensitive to UV exposure, and the largest cells the most sensitive, in both UVR treatments (Fig. 2). In Lac Kayouk, there were significant differences between pico- or nanoplankton and microplankton, but in contrast to LEC, microplankton was less sensitive and even stimulated by UVR (on average by +18%). The average sensitivity of the nanoplankton fraction (UVR inhibition of 25%) was higher than that for the picoplanktonic fraction (4%), but the difference was not significant.

For the LEC sites, the two UVR treatments (UVA + UVB and UVA) had significant effects on photosynthesis and were significantly different from each other (df = 1; F = 13.4; P = 0.0012; Fig. 3). The treatment exposing the cells to the full UVR spectrum gave more photoinhibition (average of 52%) than the treatment with UVA alone (average of 32%). Consequently, UVB inhibition lowered photosynthesis by an additional 20%. There was no significant difference between treatments for the phytoplankton community of Lac Kayouk,

indicating that UVA almost completely dominated the UVR effects at this site.

Discussion

As found in previous limnological studies in the subarctic, phytoplankton in the <2-μm fraction were a major component of total community biomass (42% of total Chl *a*) and productivity (one third of total primary production under natural sunlight) at all sites in both lakes (Fig. 1). The potentially high sensitivity of small cells to UVR is therefore of considerable ecological interest for aquatic ecosystems in this region. Contrary to the size-dependency hypothesis, however, our experiments consistently showed that the smallest celled phytoplankton are relatively resistant to UVR. In both UVR treatments the picoplankton fraction for LEC experiments was either least inhibited or showed no significantly greater inhibition than was observed in larger-sized fractions (Fig. 2), despite their disadvantage of a high surface-to-volume ratio for screening protection.

The picophytoplankton in subarctic lakes is mostly composed of *Synechococcus*-like cyanobacteria (Bergeron and Vincent 1997; this study). This group of picoplankton also dominates in the clear tropical oceans where the cells must be capable of tolerating high UVR fluxes that are characteristic of low latitudes. Cyanobacteria in general are known to have a variety of effective defenses against UV-induced damage including multiple copies of their genome, protective pigments and enzymes against reactive oxygen species, and various repair mechanisms for UV-damaged DNA and photosystems (Quesada and Vincent 1997). Our results imply that genetic differences between taxa in these UVR tolerance mechanisms are much greater than differences attributable to any cell-size relationship. Even closely related species of cyanobacteria can show large differences in UVR tolerance that are not related to their respective UVR-screening capabilities (Quesada and Vincent 1997). Of the numerous studies that have addressed the impact of ozone depletion and the consequent increase in UVB on phytoplankton, many have found large interspecific differences in UV tolerance (e.g., Jokiel and York 1984; Wängberg et al. 1996; Xiong et al. 1996). Cell size would appear to be only one factor contributing to these differences, and many other cellular properties such as morphology (shape, setae, colonies), placement of organelles, DNA base content and sequence (Karentz et al. 1991), antioxidants and repair capabilities, may play an equal or greater role.

The microplankton fraction (>20 μm) showed a qualitatively different response to UVR in the two lakes, with strong inhibition in LEC but no effect or even UV stimulation of activity in Lac Kayouk (Fig. 2). The large variance in this size fraction is most likely caused by the presence of clumps. The different responses may reflect differences in species composition: in Lac Kayouk, the microplankton fraction was largely composed of aggregated cyanobacteria (*Merismopedia* sp., *Chroococcus* sp.) and chlorophytes (*Oocystis* sp.) often surrounded by mucus, whereas in LEC, the microplankton was predominantly as filaments (*Anabaena* sp., *Oscillatoria* sp.). Individual cells of these latter species may be subject to less protection by internal shading, although differences in other cellular properties as listed above may also have contributed to the disparate UV responses by microplankton in the two lakes.

Ambient solar radiation conditions are likely to have contributed to some of the observed differences between experiments. Total UVR inhibition of photosynthesis (calculated from photosynthesis values of total biomass) was not correlated with UVR ($P = 0.16$) nor with PAR ($P = 0.36$), but it was weakly correlated with the UVR/PAR ratio at the depth of incubation ($n = 5$; $r = +0.84$; $P = 0.07$), suggesting the influence of underwater spectral balance (but not absolute irradiances). This weak correlative relationship is consistent with field and laboratory studies that have shown the importance of spectral balance in controlling UV effects (Prézelin et al. 1994; Quesada and Vincent 1997).

The ambient light conditions prior to incubation are also likely to have had an influence on the sensitivity of the phytoplankton to UVR exposure (Helbling et al. 1992). UV inhibition in Lac Kayouk was consistently low despite the relatively high ambient UVR during the incubation. The phytoplankton in this shallow lake would have experienced on average a brighter light regime than the more deeply mixed LEC communities, and because ice out occurs in Lac Kayouk several weeks earlier than in LEC, this coastal lake population would have also benefited from a longer period of bright PAR plus UVR acclimation.

In the fixed-depth incubation assays conducted here the UV effects were strong but were dominated by UVA, with on average <30% of the total UVR response attributable to UVB (Fig. 3). This is consistent with previous assays (e.g., Milot-Roy and Vincent 1994) and underscores the need to understand better the background effects of natural UVA + UVB in order to predict the potential responses to stratospheric ozone depletion and climatic change. Our assays were incubated in the near-surface waters, simulating the effect of solar UVR and PAR on phytoplankton trapped in diurnal thermoclines. There is a sharp decline in the UVB/UVA and UVB/PAR ratios with depth, and therefore at greater depths in the euphotic zone the photoinhibition of photosynthesis is likely to be exclusively determined by UVA and PAR.

There appears to be increasing acceptance in the literature that cell size is a primary determinant of UVR sensitivity (e.g., Häder et al. 1995). Our results, and those from other studies (Jokiel and York 1984; Helbling et al. 1992; Peletier et al. 1996; Wängberg et al. 1996) are not consistent with this view. The large differences in UV sensitivity between taxa can be associated with protection mechanisms other than UVR-screening pigments, and these are less likely to be inversely related to cell size. Small, highly active cells may even be more efficient at mitigating UVR effects than some larger cells because of their faster biosynthetic rates (Peters 1983), resulting in more rapid repair of damaged cellular components. Our study shows that despite their large optical cross section per unit biomass, picocyanobacteria, which are a major component of lakes in the north and south polar regions (Vincent and Pienitz 1997), are relatively resistant to UVR and may therefore be less vulnerable to the

effects of rising UVB radiation over these regions than other phytoplankton groups.

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