Transparency of Antarctic ice-covered lakes to solar UV radiation

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Abstract

Depth profiles of solar ultraviolet radiation (UVR), photosynthetically available radiation (PAR), and related variables were measured beneath the thick, permanent ice cover of four lakes in the McMurdo Dry Valleys (77°S, 162°E). These lakes span a range of phytoplankton concentrations (0.1–10 μg Chl *a* liter^{-1}) but receive little input of chromophoric dissolved organic matter (CDOM) from their barren, polar desert catchments. The diffuse attenuation coefficients for downwelling radiation (K_d) in the upper water column of the lakes were at or below those for clear natural waters elsewhere, with minimum values in Lake Vanda of 0.080 (305 nm), 0.055 (320 nm), 0.036 (340 nm), 0.023 (380 nm) and 0.034 (PAR) m^{-1}. The attenuation lengths ($1/K_d$) for these lakes and for a set of high latitude lakes in the northern hemisphere (tundra and boreal forest catchments) showed a close log–log relationship with dissolved organic carbon (DOC) concentrations ($r^2 \geq 0.90$; $n = 20$); dry valley lakes were at the high transparency end of this polar–subpolar continuum. Phytoplankton exposure to UVR relative to PAR is known to rise steeply with decreasing DOC in the concentration range 2–4 g m^{-3}; the addition of the dry valley lakes data shows the continuation of this upward, markedly nonlinear trend at lower DOC concentrations. Calculation of the biologically effective UVR dosage rate for the upper phytoplankton community of Lake Vanda indicated that sufficient UVR penetrates through the 3.5-m-thick lake ice to cause inhibition of algal growth. These results show that polar desert lakes are optical extremes in terms of their water-column transparency to UVR, and that their dilute, mostly autochthonous CDOM offers little protection against the ultraviolet-B radiation flux that is continuing to increase over the polar regions.

The impact of increasing solar ultraviolet-B radiation (UVB, 280–320 nm) on aquatic ecosystems has been of greatest concern in the southern polar region where the annual depletion of stratospheric ozone now extends from spring into late summer (Jones and Shanklin 1995). Although many studies have examined the penetration and potential effects of UVB in the Southern Ocean (Smith et al. 1992; McMinn et al. 1994; Prézelin et al. 1994), little is known about the nonmarine ecosystems of Antarctica in this regard. Lakes and streams are a prominent feature of desert landscapes around the margins of the Antarctic continent. These unique microbial ecosystems have a species-poor community structure that is limited by extreme isolation and the harsh continental environment (Vincent and James 1996). These communities must now contend with the additional stress of increasing short-wave ultraviolet radiation.

In many lakes in the temperate zone, the aquatic biota are protected from UVB (280–320 nm) and to a lesser extent UVA (320–400 nm) by the presence of chromophoric dissolved organic matter (CDOM). These materials (gelbstoff or gilvin) are composed of aromatic humic and fulvic acids brought in from vegetation and leaf litter in the surrounding catchment. Polar desert catchments tend to be largely devoid of plants, and the input of these allochthonous materials is greatly reduced relative to lower latitudes. Although dissolved organic carbon (DOC) concentrations in polar desert lake waters can be well above the limits of analytical detection, much of it is generated autochthonously by microbial processes within the lakes and streams (McKnight et al. 1991). Nuclear magnetic resonance analyses of this DOC in Antarctic lakes and ponds indicates that it differs from that found in temperate-latitude lakes by having a reduced ratio of aromatic to aliphatic organic residues (McKnight et al. 1994). These observations of low DOC in combination with low aromaticity imply that Antarctic lakes may be unusually transparent to solar ultraviolet radiation (UVR).

In the present study we examined the UV-attenuation characteristics of a series of four lakes located in the Mc-Murdo Dry Valleys region of Antarctica (77°S, 162°E). The lakes are permanently capped by thick (3.5–4.5 m) ice, although a peripheral moat region up to 100 m wide opens up around the ice cover each summer (1–3% of the surface area of the lakes; Spigel and Priscu 1998). They are fed by dilute meltwaters in ephemeral surface streams that flow from source glaciers to the lakes through barren catchments that contain only rare patches of cryptogams and no vascular plants. The streambeds, however, may contain rich microbial mats that have been previously identified as a significant source of DOC to the lakes (Downes et al. 1986; McKnight et al. 1991). The four lake waters chosen span the range of trophic states found within the region (details in Priscu 1995), from ultraoligotrophic Lake Vanda (Chl a of <0.1 mg m^{-3}) to the mesotrophic waters of Lake Fryxell (Chl a up to 10 mg m^{-3}).

Methods

Study sites and sampling—The four lakes are located in the southern region of Victoria Land where the recession of the Antarctic Ice Sheet has left deep valleys largely devoid of snow and glacier ice. Lakes Bonney, Hoare, and Fryxell are in the Taylor Valley, and Lake Vanda is in the adjacent Wright Valley. The perennial ice cover of each lake overlies a water column that remains unfrozen and highly stratified throughout the year, with strong vertical gradients in salinity and inverse temperature profiles (Vincent 1988; Spigel and Priscu 1998; and references therein).

A 10-cm-diameter sampling hole was drilled through the ice by auger at the deepest site of each lake and was then melted out to a diameter of 30 cm. The hole was protected with an opaque cover until the time of sampling. Water samples from beneath the ice were obtained with Van Dorn or Niskin sampling bottles. All measurements were conducted during the midsummer period from late November 1995 to mid-January 1996.

Water column profiling—The four lakes were profiled with PNF-300 and PUV-500 underwater radiometers (Biospherical Instr.). The PNF-300 recorded depth, quantum scalar photosynthetically active radiation (PAR, 400–700 nm), upwelling radiance centered at 683 nm (solar-induced fluorescence, Lu683), and temperature fine-structure (10-cm depth intervals). The PUV-500 instrument provided a measure of cosine-corrected downwelling UVR at 305, 320, 340, and 380 nm (full bandwidth at half-maximum of 8–10 nm) and of downwelling, cosine-corrected PAR. A SeaTech beam transmissometer was connected to the PUV profiler and gave the percentage of transmission of a collimated beam of 660-nm light across a 10-cm cell (transmittance). The instrument also recorded depth and temperature.

The profilers were slowly lowered through the water column of each lake while measurements (8–12 per meter) were recorded on a portable computer. At all four lake sites the holes were covered during profiling to prevent the direct transfer of solar radiation from the atmosphere to the water column; all measured values were therefore of the diffuse downwelling radiation field after transmission through the thick ice. For the Taylor Valley measurements, the holes were covered with opaque canvas during profiling. Because of the persistent winds in the Wright Valley, the hole in the ice at Lake Vanda was covered by a tent (basal area of 4 m^2) to protect the computer at the surface of the ice from freezing temperatures. The PUV radiation data were corrected for dark current by subtracting the minimum asymptotic value at the bottom of the profile or, if a constant minimum was not achieved at the lowermost depths (e.g. the long-wave UVR and PAR measurements in Lake Vanda), the dark correction was obtained by fitting the radiometer with a light-tight Neoprene cap. Values for the 305-nm channel were corrected according to Kirk et al. (1994). The diffuse attenuation coefficients (K_d) were determined from linear regressions of natural logarithm radiation against depth using data points within the log-linear portion of the curve for the upper water column, or for the lower euphotic zone, in the 1-m depth stratum immediately above the deep Lu683 peak. Shading of the profiler caused by the opaque covers over the holes in the ice was generally negligible because of the large solar zenith angle at this latitude and the scattering effect of the thick ice cover. However, inspection of the depth curves for Lake Vanda indicated some shading effect of the tent on radiation fluxes within the ice and in the upper 3–4 m of the water column (changing K_d with depth). For the depth range of 8–20 m, the plots were log-linear, indicating that the shading effect was restricted to shallower depths. The upper water-column K_d values for Vanda were therefore calculated for the depth stratum of 10–20 m to ensure that any shading influence was eliminated.

CDOM measurements—The CDOM characteristics at each site were determined by measurements of DOC concentration [DOC] and CDOM fluorescence (F_{CDOM}). For these analyses the lake water was filtered through Sartorius 0.22-μm membrane filters immediately after collection and then stored in Nalgene bottles in the cold (4°C) and dark until analysis. DOC was measured in these samples by UV oxidation using a Dohrman model DC 180 low-level TOC analyzer.

CDOM fluorescence was measured in a Shimadzu RF 5000U spectrofluorometer by emission scans from 360 to 600 nm with the excitation beam set to 348 nm and a slit width of 5 nm on both sides. For these measurements the fluorescence signal at 450 nm (peak height) was normalized to the Raman signal area to give F_{CDOM} in Raman units (nm^{-1}) as described in Determann et al. (1994). All samples were measured in acid-clean, fused silica cuvettes (Suprasil I), which were triple-rinsed with the sample prior to measurement.

Results and Discussion

Vertical structure—At the time of sampling the lakes were covered by 3.5–4.6 m of ice. Each lake had a peripheral band of thin ice (<25 cm thick) in December, melting out to become a narrow moat of open water in January. The distinctive thermal properties of each of the four lakes is illustrated by the PNF-300 measurements of temperature
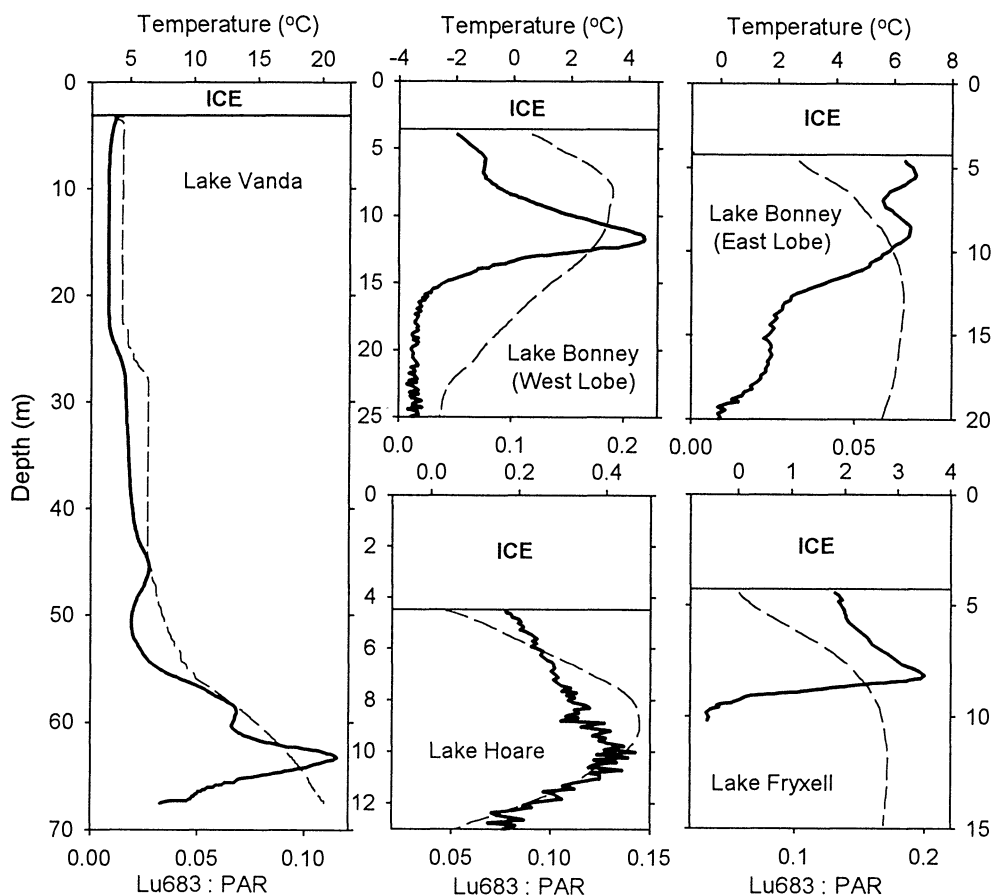
Fig. 1. Depth distribution of temperature (– – –) and solar-induced fluorescence (Lu683 normalized to PAR; ———) in the McMurdo Dry Valleys lakes, summer 1995–1996. Measurements were at 1145 h on 10 January 1996 (Lake Vanda), 0545 h on 9 December 1995 (west lobe of Lake Bonney), 1420 h on 10 December 1995 (east lobe of Lake Bonney), 0100 h on 13 December 1995 (Lake Hoare), and 1930 h on 7 November 1995 (Lake Fryxell).

fine-structure (Fig. 1). Consistent with earlier profiles from these lakes (*see above*), temperatures rose with depth through the entire (Vanda) or upper water column (Bonney, Hoare, Fryxell); these inverse thermal gradients were accompanied by strong vertical gradients in dissolved salt content as indicated by the large difference in conductivities between the top and bottom of the water columns—from <0.1 S m^{-1} (at 15°C) in the surface waters of all lakes to 1.1 (Hoare), 8.8 (Fryxell), 105 (Vanda), 126 (Bonney west lobe), and 148 S m^{-1} (Bonney east lobe) at the bottom (details in Spigel and Priscu 1998).

The solar fluorescence profiles (Lu683) normalized to quantum scalar PAR (both obtained by PNF-300) were in keeping with previous reports that the lakes differ considerably in phytoplankton biomass and vertical distribution (Fig. 1). The upper water-column values followed the sequence Vanda < Bonney < Hoare < Fryxell. In the east lobe of Lake Bonney a fluorescence peak occurred near the ice, with a second deeper maximum in the vicinity of the oxycline. At the other lake sites Lu683 values were relatively low near the ice and rose to a maximum in or near the oxycline. Deep phytoplankton maxima are consistent with previous records of Chl *a*, in vivo fluorescence, and photo-

synthesis from these lakes (Vincent 1988; Lizotte and Priscu 1994).

PAR attenuation—There were marked differences between the four lakes in their transparency to PAR. The penetration through the ice varied from ~10% (Vanda) to ~1% (Fryxell) of downwelling solar PAR. The diffuse attenuation coefficients for PAR in the upper water column (K_{dPAR}, Table 1) similarly rose by about one order of magnitude over the sequence Vanda (clearest), Bonney, Hoare, and Fryxell (most turbid). Logarithmic plots of PAR irradiance (E_{PAR}) as a function of depth were linear in the low-conductivity melt-waters of the upper water column and could be approximated by a single K_{dPAR} value for each lake. However the log $E_{PAR}(z)$ function became markedly nonlinear at greater depths, particularly in the bottom waters of the lakes (Fig. 2). This nonlinearity corresponded with large increases in the beam transmittance values (Table 1) and was likely the result of increased concentrations of particulate light-absorbing materials as well as CDOM. There was no statistically significant correlation between upper water column K_{dPAR} and either DOC ($r = 0.94$; $n = 4$; $P = 0.06$) or F_{CDOM} ($r = 0.86$; $n = 4$; $P = 0.14$).

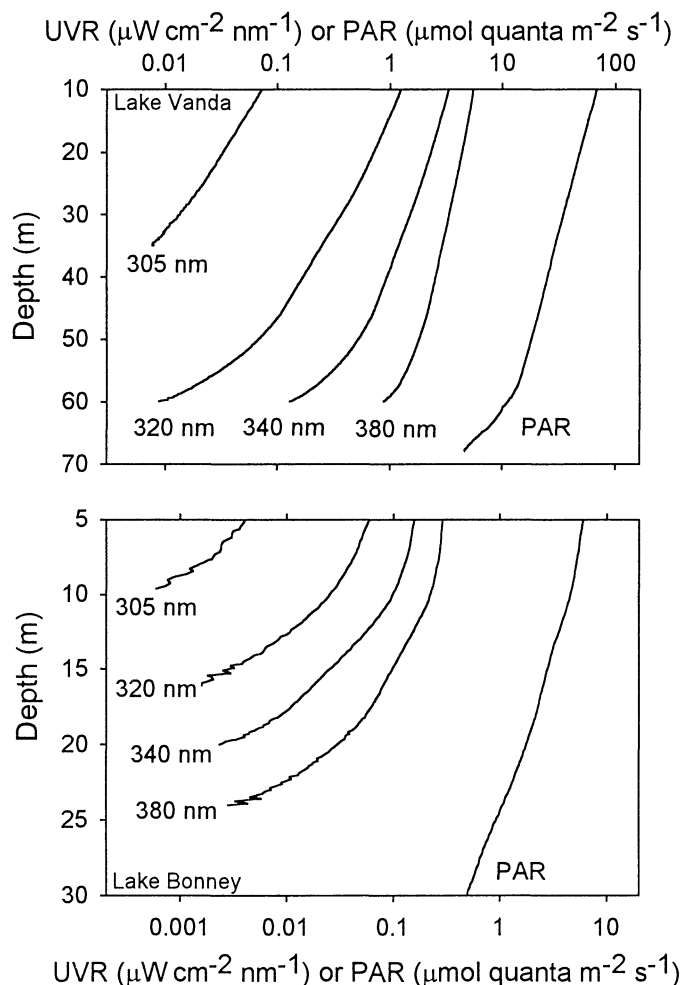UVR (μW cm^{-2} nm^{-1}) or PAR (μmol quanta m^{-2} s^{-1})

Fig. 2. Log distribution of UVR and PAR with depth for the two clearest McMurdo Dry Valleys lakes, Lake Vanda and Lake Bonney (east lobe). Profiling times and conditions are given in Table 1.

Table 1. Optical and chromophoric dissolved organic matter (CDOM) characteristics of the McMurdo Dry Valleys lakes during summer 1995–1995. Upper indicates upper water column, average values for the depth strata (in meters): 10–20 (Vanda), 5–7.5 (Bonney east lobe), 6–8 (Hoare), 6–7.5 (Fryxell). Lower indicates lower euphotic zone, average values for the depth strata (in meters): 64–65 (Vanda), 9–10 (Bonney east lobe), 11–12 (Hoare), 8–9 (Fryxell). UVR data are for the upper water column only (same depth range as for upper K_{PAR}). CDOM values are for water sampled 1–2 m below the ice. Measurements were at 1130 h on 10 January 1996 at Lake Vanda (clear skies), 1215 h on 14 December 1995 at Lake Bonney (high clouds), 1230 h on 15 December 1995 at Lake Hoare (overcast), and 0930 h on 14 December 1995 at Lake Fryxell (high scattered clouds).

	Lake Vanda	Lake Bonney	Lake Hoare	Lake Fryxell
K_{dPAR} (m^{-1})				
Upper	0.034	0.053	0.197	0.214
Lower	0.148	0.066	0.175	0.605
Transmittance (%)				
Upper	94.1	86.1	89.0	85.2
Lower	69.1	82.7	89.2	74.4
K_{dUVR} (m^{-1})				
K_{d380}	0.023	0.054	0.391	1.005
K_{d340}	0.036	0.060	0.480	1.365
K_{d320}	0.055	0.124	0.705	1.295
K_{d305}	0.080	0.305	—*	—*
CDOM				
DOC (mg liter^{-1})	0.30	0.67	1.3	2.0
F_{CDOM} (nm^{-1})	0.0037	0.0115	0.0189	0.0411

* Insufficient UVR penetration to calculate K_d.

UVR attenuation—UVA and UVB radiation were measurable to depths well beneath the ice in all four of the Dry Valley lakes. The diffuse attenuation coefficients for UVR (K_{dUVR}) in the upper water column varied 20- to 50-fold between lakes (Table 1), with the same sequence of transparency as for PAR (Vanda > Bonney ≫ Hoare > Fryxell). In Lake Vanda, the clearest lakewater, short-wave UVB (305 nm) was recorded to at least 30m, and long-wave UVA (380 nm) to 60 m (Fig. 2). Our lowest recorded K_d was 0.023 m^{-1} for 380-nm UVR in the upper water column of Lake Vanda, a value well below the K_d for PAR over the same depth range (Table 1). This is consistent with measurements in clear ocean waters showing that K_d values for wavelengths over much of the PAR region (specifically 500–700 nm) are greater than for 380 nm (Smith and Baker 1981).

The log $E_{UVR}(z)$ plots were more curvilinear than the equivalent profiles for PAR, with a marked increase in K_{dUVR} at depth (Fig. 2). There was a significant relationship between the attenuation of each UVR waveband in the upper water column and CDOM; for example, K_{d340} values for the

four lakes correlated positively with DOC ($r = 0.96$; $n = 4$; $P = 0.04$) and F_{CDOM} ($r = 0.98$; $n = 4$; $P = 0.02$) but not with transmittance ($r = -0.59$; $n = 4$; $P = 0.41$). We do not have corresponding CDOM data for the lower portion of the water columns, but DOC is known to rise to high values (>10 mg C liter^{-1}) in the saline bottom waters of all of these lakes (McKnight et al. 1991; Matsumoto 1993). An alternative explanation for the abrupt increase in K_{dUVR} toward the bottom of the lakes is that our correction values for the dark current were in error; this seems unlikely given that the effect was observed at irradiances at least two orders of magnitude above the dark current offset for the long wavelength UVR (380 nm).

The diffuse attenuation coefficients for UVR as well as PAR in the McMurdo Dry Valleys lakes are at the lowermost end of the range for oligotrophic lakes and oceans; the Vanda and Bonney data, for example, are slightly lower than the alpine lakes profiles with a similar PUV instrument by Morris et al. (1995). Lower values of K_{dPAR}, however, have been obtained for another Antarctic desert lake, Lake Untersee in the Schirmacher Oasis of East Antarctica, where Kaup (1995) reported a minimum value of 0.022 m^{-1} for the top 35 m of the lake. The K_{dUVR} values for the surface waters of Vanda are 14–43% lower than the diffuse attenuation coefficients for the "clearest ocean waters" as tabulated by Smith and Baker (1981). In part this may reflect the wider
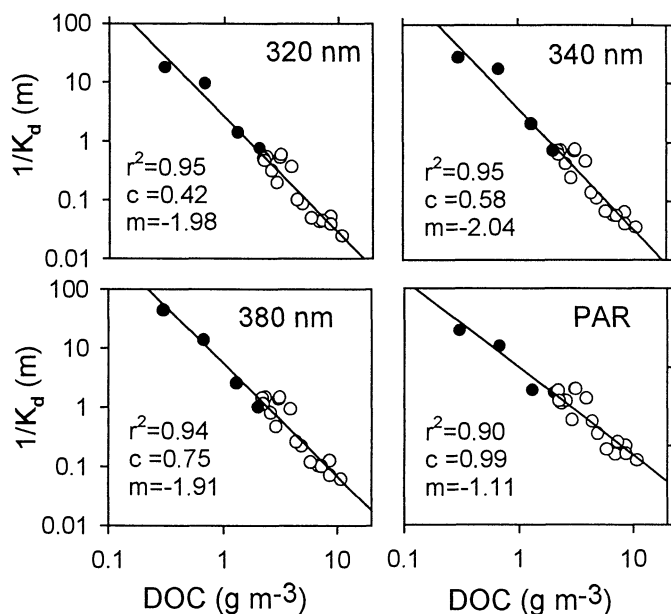
Fig. 3.   UVR and PAR transparency ($1/K_d$) vs. DOC concentration for the four dry valley lakes (●) and northern high latitude lakes (○, data from Laurion et al. 1997). The log–log regression lines and coefficients are for all data in each waveband (c, intercept; m, gradient). The transparency scale for PAR is from 0.1 to 100 m.
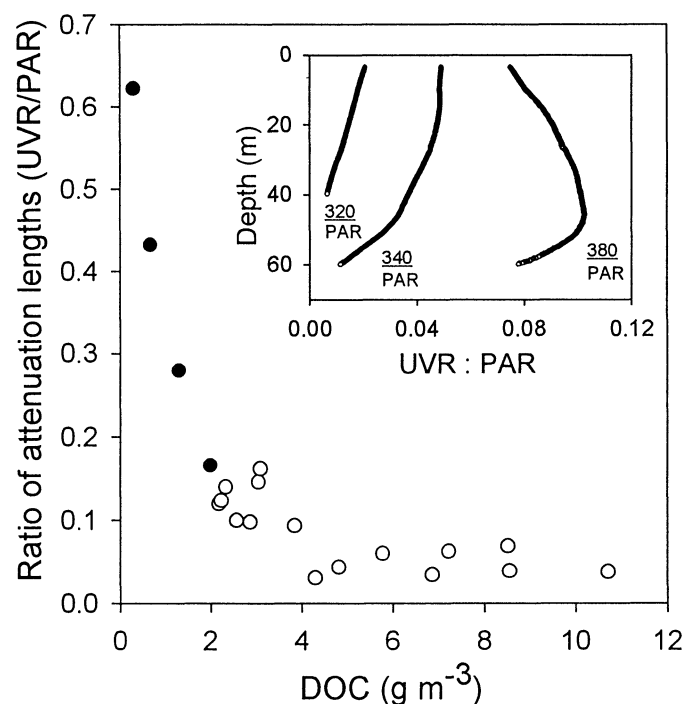

Fig. 4.   Ratio of UVR (at 320 nm) to PAR attenuation lengths as a function of DOC for the McMurdo Dry Valleys lakes (●) and northern high latitude lakes (○). Insert: UVR : PAR ratios as a function of depth in Lake Vanda.

bandpass of our instrument relative to that used by Smith and Baker, but it also implies that Lake Vanda is a global extreme in UVR transparency. Unlike the ocean, Vanda and other dry valley lakes receive minimal inputs of CDOM from terrigenous sources; they are also isolated from direct wind-induced turbulence, with stable conditions that would favor the rapid sedimentation of particles. Polar desert lakes, particularly Lake Vanda, would seem an ideal optical environment for refining the upper-bound estimates of absorption and scattering by pure water via the approach pioneered by Smith and Baker (1981).

Attenuation lengths—The correlations between K_{dUVR} and CDOM imply that dissolved organic compounds are the main UV-attenuating components in the surface waters of the dry valley lakes. Previous studies on lakes elsewhere over a higher [DOC] range have shown that K_{dUVR} can be described as a power function of [DOC] (Scully and Lean 1994; Morris et al. 1995). If K_{dUVR} equals $[DOC]^m$, it follows that $\log(1/K_d)$ equals $-m \log[DOC]$, where $1/K_{dUVR}$ is the attenuation length, a direct measure of UVR transparency. We examined this relationship by plotting log attenuation length vs. log[DOC] for the UVR and also PAR data from the dry valley lakes, and superimposed the values determined by Laurion et al. (1997) for high-latitude lakes in the northern hemisphere. These latter measurements were obtained with the same PUV-500 profiler across the boreal forest–tundra transition in northern Canada, and extended the analysis to a higher range of [DOC] values than found in the McMurdo Dry Valleys lakes. In each UVR waveband, the data from all lakes fell along a close-fitting regression line that explained 94–95% of the variance in log $1/K_d$ (Fig.

3). This relationship was also significant for PAR, with a slightly lower goodness-of-fit (90%). These log–log regressions are remarkably tight given the heterogeneous sources of CDOM across this spectrum of lakes and catchment types. In part this may reflect our sampling bias toward oligotrophic lakes in which water and CDOM control the underwater light field. In waters with a higher concentration of seston (e.g. nutrient-rich lakes in the coastal and maritime regions of Antarctica), the scattering by biotic and abiotic particulates likely plays a greater role and would result in transparency values below the regression lines obtained here. The close fit of our data to a power function is consistent with previous studies (Scully and Lean 1994; Morris et al. 1995) and implies that there is an increasing proportion of aromatic residues in the DOC pool with increasing [DOC].

Waveband ratios—Several studies have noted the importance of waveband ratios, in particular UVR : PAR (Smith et al. 1992; Vincent and Roy 1993; Prézelin et al. 1994) and UVB : UVA (Quesada et al. 1995; Quesada and Vincent 1997), in controlling the balance between photochemical damage and repair in biological systems. In the dry valley lakes these ratios varied down the water column to a greater extent than in typical lakes and oceans because of the marked changes in [DOC] with depth. The most striking pattern was in Lake Vanda where E_{380} : E_{PAR} initially increased with depth to a maximum at 45 m, and thereafter decreased (Fig. 4, insert). This pattern results from the greater attenuation of longer wavelengths in the PAR range relative to long UVR wavelengths in the upper water column,

and the increased absorption of UVR toward the bottom of the lake, associated with elevated [DOC]. The ratios of E_{320}: E_{PAR} and E_{340}: E_{PAR} both showed a continuous decrease with depth throughout the water column.

A comparative index of the UVR versus PAR transparency of natural waters is given by the ratio of attenuation lengths for E_{320} and E_{PAR}. In optically homogeneous water columns this index multiplied by surface E_{320}: E_{PAR} is numerically equivalent to the ratio of water column integrals for the two wavebands, and is a relative measure of UVR versus PAR exposure. The ratio has been shown to rise steeply with decreasing [DOC] in the concentration range 2–4 mg liter^{-1} (Laurion et al. 1997). The addition of the dry valley lakes data to the subarctic lake data set shows the continuation of this upward, markedly nonlinear trend at much lower DOC concentrations, with Lake Vanda providing an extreme upper value (Fig. 4).

Biological effects—Although the UVR transparency of McMurdo Dry Valley lake waters is high in absolute terms and is also high relative to PAR, the exposure of biota to UVR is greatly reduced by the overlying ice-cover. UVR-attenuation by the ice-cover alone could not be accurately assessed in the present study; such measurements would require the placement of under-ice sensors by divers or via a remotely operated positioning system, as well as careful attention to the effects of surface shading and melt holes. Our results, however, allow an initial estimate of under-ice UVR by back-extrapolating the upper log-linear part of the $E_{UVR}(z)$ curve to the lower ice surface, and by interpolating between the midpoints of the individual waveband channels on the PUV-500.

For the plankton community at 4.5 m in Lake Vanda (1 m below the clearest lake ice) we calculate a radiation flux of 14.5 μW UVB (280–320 nm) cm^{-2} and 405 μW UVA (320–400 nm) cm^{-2}. Using a biological weighting function derived from Cullen et al. (1992), this equates to a biologically equivalent dosage rate (BEDR) across the full UVR spectrum of 18.1 μW cm^{-2}. Recent studies on Antarctic cyanobacteria at low temperature (Quesada and Vincent 1997) indicate that a BEDR of this magnitude, if supplied continuously over 5 d, would reduce growth rates by 28–53%. Our measurements for Lake Vanda were near midday and are therefore not representative of the full diurnal cycle. However, most of the daily photosynthesis is likely to take place during 0900–1500 h, and the BEDR is sufficiently high to expect some biological effect. Photophysiological studies from Lake Bonney indicate that the sub-ice phytoplankton are highly adapted to the perennial shade regime (Neale and Priscu 1995) and are unusually sensitive to photoinhibition by UVR (Neale et al. 1994).

Higher UVR dosage rates may be experienced by dry valley lake phytoplankton earlier in the season when the surface of the ice is less ablated and has a much lower albedo; for example, in Lake Vanda, transmission through the ice declines from 21% of surface downwelling PAR in September to 13% in December (Howard-Williams et al. 1998). The spring period of higher transmission would also coincide with the period of increased UVB associated with stratospheric ozone depletion, although such effects would be re-

duced by the larger zenith angle at that time. Most of the phytoplankton community in these lakes, however, is located well beneath the ice (Fig. 1) and is protected from the incident UVA and UVB by the overlying water column. The biological effects of UVR will be most severe for the plankton and benthos in the moat region that is covered by thin ice early in the season, and then contains open water during December–January each year. Benthic microbial mats are a feature of this moat region, and their bright red and orange pigmentation attracted the attention of early explorers walking over the lake ice (Taylor 1916). These cyanobacteria-dominated communities contain a surface layer that is rich in carotenoids, one of several defenses against high incident UVR (Vincent and Roy 1993).

The McMurdo Dry Valleys lakes have been previously identified as global "end-members" in terms of many of their physical (Spigel and Priscu 1998), geochemical (Matsumoto 1993; Lyons et al. 1998), and biological properties (Neale and Priscu 1995; Vincent and James 1997). Our results show that these lakes must also be considered global extremes in terms of their transparency to solar UV radiation. Deep UVR penetration is likely to be a general feature of polar and alpine environments where catchment vegetation is sparsely developed. The extreme UVR transparency found in this study is probably characteristic of lakes in other polar desert regions such as the Canadian High Arctic and other ice-free areas around the margins of Antarctica. Such regions also coincide with the latitudes of highest stratospheric ozone depletion and increasing UVR.

References

Cullen, J. J., P. J. Neale, and M. P. Lesser. 1992. Biological weighting function for the inhibition of phytoplankton photosynthesis by ultraviolet radiation. Science **258**: 646–650.

Determann, S., R. Reuter, P. Wagner, and R. Willkomn. 1994. Fluorescent matter in the eastern Atlantic Ocean. 1. Method of measurement and near-surface distribution. Deep-Sea Res. **41**: 659–675.

Downes, M. T., C. Howard-Williams, and W. F. Vincent. 1986. Sources of organic nitrogen, phosphorus and carbon in Antarctic streams. Hydrobiologia **134**: 215–225.

Howard-Williams, C., A.-M. Schwarz, I. Hawes, and J. C. Priscu. 1998. Optical properties of the McMurdo Dry Valley lakes. Antarctic Res. Ser. **72**: 189–203.

Jones, A. E., and J. D. Shanklin. 1995. Continued decline of total ozone over Halley, Antarctica, since 1985. Nature **376**: 409–411.

Kaup, E. 1995. Solar radiation in water bodies, p. 286–290. *In* P. Bormann and D. Fritsche [eds.], The Schirmacher Oasis, Queen Maude Land, East Antarctica, and its surroundings. Justus Perthes Verlag.

Kirk, J. T. O., and others. 1994. Measurements of UV-B radiation in two freshwater lakes: An instrument intercomparison. Arch. Hydrobiol. Beih. Ergebn. Limnol. **43**: 71–99.

Laurion, I., W. F. Vincent, and D. R. S. Lean. 1997. Underwater ultraviolet radiation: Development of spectral models for northern high latitude lakes. Photochem. Photobiol. **65**: 107–114.

Lizotte, M. P., and J. C. Priscu. 1994. Natural fluorescence and quantum yields in vertically stationary phytoplankton from perennially ice-covered lakes. Limnol. Oceanogr. **39**: 1399–1410.

LYONS, W. B., AND OTHERS. 1998. Geochemical linkages among glaciers, streams and lakes within the Taylor Valley, Antarctica. Antarctic Res. Ser. **72:** 77–92.

MATSUMOTO, G. I. 1993. Geochemical features of the McMurdo Dry Valleys lakes. Antarctic Res. Ser. **59:** 95–118.

MCKNIGHT, D. M., G. R. AIKEN, AND R. L. SMITH. 1991. Aquatic fulvic acids in microbially based ecosystems: Results from two desert lakes in Antarctica. Limnol. Oceanogr. **36:** 998–1006.

———, E. D. ANDREWS, S. A. SPAULDING, AND G. R. AIKEN. 1994. Aquatic fulvic acids in algal-rich Antarctic ponds. Limnol. Oceanogr. **39:** 1972–1979.

McMINN, A., H. Heijnis, and D. Hodgson. 1994. Minimal effects of UVB radiation on Antarctic diatoms over the past 20 years. Nature **370:** 547–549.

MORRIS, D. P., AND OTHERS. 1995. The attenuation of solar UV in lakes and the role of dissolved organic carbon. Limnol. Oceanogr. **40:** 1381–1391.

NEALE, P. J., M. P. LESSER, AND J. J. CULLEN. 1994. Effects of ultraviolet radiation on the photosynthesis of phytoplankton in the vicinity of McMurdo Station (78°S). Antarctic Res. Ser. **62:** 125–142.

———, AND J. C. PRISCU. 1995. The photosynthetic apparatus of phytoplankton from a perennially ice-covered Antarctic lake: Acclimation to an extreme shade environment. Plant Cell. Physiol. **36:** 253–263.

PRISCU, J. C. 1995. Phytoplankton nutrient deficiency in lakes of the McMurdo dry valleys, Antarctica. Freshwater Biol. **34:** 215–227.

PRÉZELIN, B. B., N. P. BOUCHER, AND R. C. SMITH. 1994. Marine primary production under the influence of the Antarctic ozone hole: Icecolors '90. Antarctic Res. Ser. **62:** 159–186.

QUESADA, A., MOUGET, J.-L., AND W. F. VINCENT. 1995. Growth of Antarctic cyanobacteria under ultraviolet radiation: UVA counteracts UVB inhibition. J. Phycol. **31:** 242–248.

———, AND W. F. VINCENT. 1997. Strategies of adaptation by Antarctic cyanobacteria to ultraviolet radiation. Eur. J. Phycol. **32:** 335–342.

SCULLY, N., AND D. R. S. LEAN. 1994. The attenuation of ultraviolet radiation in temperate lakes. Arch. Hydrobiol. Beih. Ergebn. Limnol. **43:** 135–144.

SMITH, R. C., AND K. S. BAKER. 1981. Optical properties of the clearest natural waters (200–800 nm). Appl. Optics **20:** 177–184.

SMITH, R. C., AND OTHERS. 1992. Ozone depletion: Ultraviolet radiation and phytoplankton biology in Antarctic waters. Science **255:** 952–959.

SPIGEL, R. H., AND J. C. PRISCU. 1998. Physical limnology of the McMurdo Dry Valley lakes. Antarctic Res. Ser. **72:** 153–187.

TAYLOR, G. 1916. With Scott: The silver lining. Dodd Mead & Co.

VINCENT, W. F. 1988. Microbial ecosystems of Antarctica. Cambridge Univ. Press.

———, AND M. R. JAMES. 1996. Biodiversity in extreme aquatic environments: Lakes, ponds and streams of the Ross Sea sector, Antarctica. Biodiv. Conserv. **5:** 1451–1471.

———, AND S. ROY. 1993. Solar ultraviolet-B radiation and aquatic primary production: Damage, protection and recovery. Environ. Rev. **1:** 1–12.