Late Pleistocene record of elevated UV radiation in an Antarctic lake

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Abstract

Elevated ultraviolet irradiance (UVR, 280–400 nm) damages DNA and induces reorganisation within biological communities at the Earth’s surface. Southern high latitude aquatic ecosystems may be particularly susceptible because of low stratospheric ozone levels and extremely low contents of photoprotective dissolved organic matter (DOM). Surveys of shallow lakes and ponds in eastern Antarctica show that cyanobacteria survive elevated UVR exposure by increasing extra-cellular concentrations of photoprotective compounds, which are preserved in sediments together with photosynthetic pigments. Thus, reconstruction of long-term changes in biological UVR receipt, to provide a context for evaluating the long-term significance of recent changes in ozone column depth, is feasible in Antarctic settings. The sediment in Lake Reid (69° 8′ S, 76° 53′ E), Antarctica, spans the late-Pleistocene and contains UVR-absorbing pigments from benthic cyanobacteria. Here we show that mean exposure of these benthic cyanobacteria to UVR during the last glacial was more than three times higher than during the Holocene, likely due to short periods of photosynthetic activity coinciding with relatively high UVR fluxes, or due to increased UVR transmission to the Earth’s surface resulting from changes in external factors such as stratospheric ozone levels, cloud cover and surface albedo.

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1. Introduction

Elevated ultraviolet irradiance (UVR, 280–400 nm) damages DNA and induces reorganisation within biological communities at the Earth’s surface [1].
Fig. 1. Biological receipt of UVR in Lake Reid, East Antarctica. (a) Ratio of scytonemin to cyanobacterial carotenoids (TScyt:TCC) and cyanobacterial carotenoids to total chlorophyll (TCC:TChl), proxies for biological UVR (cf. [17]) and UVR+PAR receipt (cf. [18]). As lake water depth has previously been identified as the major environmental variable controlling the scytonemin concentration in Antarctic cyanobacteria its influence on the first ratio was excluded by a simple correction factor based on a non-linear regression equation between modern TScyt:TCC content and lake depth in 56 regional lakes. This equation (TScyt:TCC = 0.218 + exp(5.265 + (-3.095)*depth) was then used to correct the TScyt:TCC ratio in each layer of the core using diatom transfer function-based reconstructions of historical lake water depth [19]. Both the corrected and uncorrected data are shown. (b) Scytonemin concentration, and the ratio of scytonemin to chlorophyll. (c) Chronological data for the sediment core based on radiocarbon (14C, uncalibrated) dating of subfossil cyanobacterial mats and bulk organic material [12]. No reservoir correction was applied because 14C in the surface sediment is in near-equilibrium with modern atmospheric 14CO2 [8]. An exploratory thermoluminescence date at 85 to 86 cm yielded date ranges between 33,000 and 45,000 TL year BP broadly corroborating the radiocarbon date in this zone. Based on a fourth order polynomial curve fitted to the age depth data (excluding dates beyond radiocarbon detection limits) we estimate the age of the basal sediment by extrapolation to be within Marine Isotope Stage 5e.
Southern high latitude aquatic ecosystems may be particularly susceptible because of low stratospheric ozone levels [2] and extremely low contents of photoprotective dissolved organic matter (DOM). Antarctic ozone depletion is greatest during spring, when atmospheric concentrations decline by up to 40%. As a result of stratospheric ozone depletion fluxes of UVR-B (280–315 nm) have increased 6–14% since 1980, a trend expected to persist until at least 2050 [3]. Whereas UVR fluxes and their impacts are well documented for the instrumental period (post-1957) [1], little is known of their magnitude and variability on longer time scales. At Arctic and mid-latitude lakes, substantial (>3-fold) variations in UVR receipt over the past 10,000 years have been attributed mainly to changes in inputs of UVR-absorbing DOM from terrestrial plants and soils [4,5]. DOM sources are largely absent in the many regions of the Antarctic; hence changes in benthic UVR exposure are expected to be influenced only by variations in solar output, atmospheric transmission, ice cover and lake water transparency and depth. Surveys of shallow lakes and ponds in eastern Antarctica show that cyanobacteria survive elevated UVR exposure by increasing extracellular concentrations of photoprotective compounds such as scytonemin [6], which are preserved in sediments together with photosynthetic chlorophylls and carotenoids [7]. Thus, reconstruction of long-term changes in biological UVR receipt, to provide a context for evaluating the long-term significance of recent changes in ozone column depth, is feasible in Antarctic settings. The sediment in Lake Reid (69° 23’ S, 76° 53’ E), Antarctica, spans the late-Pleistocene [8] and contains UVR-absorbing pigments from benthic cyanobacteria.

Atmospheric ozone levels of 150 Dobson units (TOMS Satellite data 1996–2002), among the lowest values on Earth, have been recorded over Lake Reid. Owing to extremely low turbidity and low concentrations of DOM, lakes in this region have very transparent waters (e.g. $K_d$PAR 0.18 m$^{-1}$, $K_d$UV,λ 0.26 m$^{-1}$, $K_d$UV-B 0.29 m$^{-1}$) [9]. Benthic cyanobacteria dominate the biota, forming extant mat layers up to 38 cm thick [10], and produce the UVR-screening pigment scytonemin [12]. Scytonemin occurs in vivo in Antarctic microbial mats in oxidized (yellow-green) and reduced (red) forms, both of which are effective photo-protectants biochemically [6] and under laboratory conditions [11]. Although scytonemin and carotenoids absorb both PAR and UVR, scytonemin ($\lambda_{\text{max}}$ 252 and 386 nm) was preferentially induced in laboratory experiments involving stepwise increases in UVR exposure, whereas it was not detected in cultures grown without UVR [11]. A radiocarbon (AMS $^{14}$C) and thermoluminescence-derived chronology for a core from the deepest point of Lake Reid (4 m) shows that sediments above 45 cm depth are of Holocene age [8] and those between 45 and 102 cm are of last glacial age (Fig. 1c). Sediments between 102 and 116 cm are older than 41,800 $^{14}$C years before present but could not be dated accurately using existing technologies. Age-depth modelling, fossil diatom species composition, inferred water depth, and comparison with nearby lakes indicate that these sediments most likely date from the last interglacial, Marine Isotope Stage 5e (MIS 5e) [12].

2. Methods

Pigments were extracted from fresh sediments using standard procedures [13,14] and were isolated and quantified using a Kromasystem 2000 high performance liquid chromatograph equipped with a Kontron pump, autosampler, photodiode-array detector, and Waters Spherisorb ODS2 column. Each compound or derivative was calibrated by reference to authentic compounds following SCOR protocols [15]. Pigment concentrations are expressed as ng g$^{-1}$ total organic C (TOC), the metric that most accurately captures past variations in algal abundance and community composition [16,17]. Biological receipt of UVR was estimated from the sum of UVR-absorbing scytonemin and related pigments expressed as a ratio with total cyanobacterial carotenoids (TScyt:TCC). This, and other similar indices, are linearly related to the depth of UVR penetration [17] and record variations in the average exposure of photosynthetically-active cyanobacteria to UVR, independent of population size [4,17]. Estimates of cyanobacterial receipt of PAR+UVR were derived using an index based on the ratio of cyanobacterial carotenoids: total chlorophyll (TCC:TChl), similar to a method used for diatoms [18]. Finally, to approximate the proportion of metabolic effort cells expended on photo-protection versus photosynthetic...
production, scytonemins were expressed as a ratio with total chlorophylls (TScyt:TChl).

3. Results and discussion

Sedimentary pigment abundances allow quantitative reconstruction of past UVR receipt from an abundance ratio of total scytonemin to total sedimentary carotenoids [5,10] (TScyt:TCC, see Methods). The UVR receipt, based on this biological proxy (TScyt:TCC), was ca. 3.4 times higher during the last glacial (mean ratio 2.4±1.1 SD) than in the Holocene and MIS 5e interglacials (0.7±0.25 SD, and 0.7±0.3 SD, respectively, Fig. 1a) and mean ratios of total scytonemin to total chlorophyll (TScyt:TChl) were 4.9 times greater, suggesting that, during growth periods, the metabolic effort of benthic cyanobacteria was geared towards photo-protection rather than photosynthesis (Fig 1b). Increases in both ratios result from elevated concentrations of UVR-screening pigments (Fig 1b) rather than decreasing levels of photosynthetic pigments (Fig 2d). The increase in cyanobacterial receipt of photosynthetically active radiation (PAR)+UVR was less marked: changes in the TCC:TChl ratio (see Methods) being ca. 0.25 times that of the UVR proxy (Fig 1a). Thus, the incident radiation was elevated in both UVR and PAR with the proportion of UVR being higher during the glacial period.

Several lines of evidence suggest that changes in inferred UVR receipt were not caused either by variations in preservation conditions or by within-lake controls of UVR exposure (ice cover, lake depth and transparency, or species turnover linked to salinity and temperature). Pigment degradation in lakes is strongly regulated by oxygen levels (hence redox potential) in the waters or sediments [14]. The stratigraphic profile of inferred UVR receipt in Lake Reid sediments shows no correspondence with bacteriochlorophyll a, a specific marker of anoxygenic photoautotrophs [7], indicating lack of a direct association with preservation conditions. The ratio of oxidised:reduced forms of scytonemin, a sensitive indicator of the cellular redox environment, did not vary in concert with changes in UVR receipt (Fig. 2a) suggesting stable redox conditions at the cellular level. Furthermore, the close correspondence between diatom frustule biovolume and carotenoids attributed to the diatom component of the primary producer community (Fig. 2b) implies a relatively constant preservation environment. Reconstructions of lake depth using diatom-based transfer functions [19] indicate that it did not vary in concert with the UVR proxy in the past (Fig. 2c). Similarly, adjustment of UVR indices for past changes in lake depth using modern relationships between sedimentary scytonemin content and lake depth (Figs. 1a and 2c) did not alter the historical profiles of UVR receipt significantly. Salinity effects on community composition can also be discounted because of the absence of a relationship between diatom-inferred salinity (Fig. 2c) and the profile for UVR receipt. Furthermore, studies of 56 regional lakes show no systematic species turnover in the salinity range experienced in Lake Reid during the late Pleistocene [10]. Temperature effects on species composition are also unlikely in the deep, ice covered parts of the lake: low temperatures persist throughout the year in the deeper parts of similar lake systems [20]. The relatively constant ratio of eukaryotic algal pigments to cyanobacterial pigments (Fig. 2c) also argues against major species changes among the dominant primary producers, though scytonemin-rich cyanobacterial morphotypes [21] would be expected to be favoured during periods of high UVR receipt. The paucity of UVR-absorbing DOM in this and other regional lakes and ponds indicates that changes in the transparency of the water column are unlikely to have controlled the spectral irradiance in Lake Reid in the past. Finally, changes in ice cover cannot explain the increased UVR receipt. Ice has a higher UV attenuation coefficient than water [22], and lake ice is assumed to have been thicker and more persistent during glacial periods. Thus, decreases in both UVR+PAR receipt would be expected if increased ice cover was the major control, with UVR being depleted to a greater extent [22].

The only remaining within-lake controls that could have caused increased concentrations of UVR-absorbing pigments during the last glacial period are the timing of periods of photosynthetic activity, changing snow cover on the lake ice, and behavioural adaptations to low light intensity. It is possible that the benthic cyanobacteria experienced higher mean ratios of UVR:PAR as a result of shorter growth seasons during the glacial relative to
Fig. 2. Within-lake controls on biological receipt of UVR at Lake Reid, East Antarctica. (a) Ratios of oxidised to reduced forms of scytonemin in the Lake Reid sediment core. The presence of reduced scytonemin is an indicator of local oxygen conditions within the cyanophyta [7]. (b) Direct comparison of the biovolume of sedimented diatom frustules with carotenoids (fucoxanthin, diatoxanthin, diadinoxanthin) attributed to the diatom component of the primary producer community in this lake (log scales). (c) Historical lake depth and salinity reconstructions based on diatom transfer functions with jack-knifed $r^2$ of 0.76 and 0.83 and root mean squared errors of prediction of 0.22 and 0.32, respectively [19]. (d) Total sedimentary concentrations of chlorophylls and carotenoids (not corrected to the sediment accumulation rate). (e) Ratios of algal and diatom carotenoids (fucoxanthin, diatoxanthin, diadinoxanthin, lutein, β-carotene) to cyanobacterial carotenoids (myoxanthin, zeaxanthin, canthaxanthin, echinenone).
those of the interglacials if these coincided with periods of high UVR flux. Ice core evidence [23] suggests that the snow accumulation rate on the interior Antarctic plateau declined during the last glacial. Although no data exist for the coast, a reduction in snow cover on the lake ice (consistent with cooler conditions and increased glacial sea ice coverage [24]) could have increased UVR and PAR transmission provided it offset the greater duration and thickness of lake ice cover that we assume during the glacial. Some cyanobacteria may also have experienced increased exposure to UVR by colonizing the underside of lake ice, a behavioural adaptation to low light intensity [9,10].

Possible external influences on UVR receipt during the glacial include changes in transmission to the Earth’s surface through variations in cloud cover, atmospheric turbidity and stratospheric ozone column depth. From contemporary climate observations, the extensive ice-shelves [25] and sea-ice [26] of the last glacial can be assumed to have led to reduced cloud cover, atmospheric turbidity and precipitation over Antarctica [27], enhancing transmission of UVR through the atmosphere [28]. The extensive glacial ice cover may also have increased surface albedo [24] and consequent back scattering of UVR from the lower atmosphere. The latter can amplify diffuse down-welling irradiance by as much as 10% [28] and is of particular importance at high latitudes where snow and ice cover (albedo between 75–100% [24]) persist through the summer [28].

Solar UVR output is assumed to vary by less than 1% during a typical solar cycle [29,30], hence long term changes cannot be tested or predicted by global climate models (see Appendix A). During the late Pleistocene, the steep thermal gradients between low and high latitudes probably intensified or stabilized the circumpolar vortex isolating the Antarctic stratosphere, a key physical factor in polar ozone depletion in spring [24]. More persistent vortices, combined with enhanced stratospheric cooling, could have reduced stratospheric temperatures below the −80 °C threshold for formation of polar stratospheric clouds, which are essential for rapid depletion of ozone during spring [31]. Given that modern-day differences in Arctic and Antarctic ozone levels are attributed to the relative strengths and durations of their respective polar vortices, it seems likely that deepening the vortex would induce some degree of change, albeit limited in the absence of anthropogenic CFCs.

Based on modern datasets (viz. regression model in Fig. 1 caption) the 3.4 times increase in UVR-absorbing pigments during the last glacial equates to a reduction in lake depth by a factor of >2. This implies that biological receipt of damaging irradiance during periods when the cyanobacteria were photosynthetically active was greater during the last glacial period than at any time since the start of the Holocene. Furthermore, the range in exposure was substantially greater than at any time during the modern instrumental record and the Holocene era (Fig. 1a). The combination of factors that resulted in elevated biological receipt of UVR (and PAR) in this Antarctic, clear-water lake during the last glacial is not known precisely. Nevertheless, by eliminating within-lake controls, we deduce that long-term variation in UVR exposure resulted from changes in the timing and/or duration of photosynthetic activity, behavioural adaptations to low light intensity, or changes in UVR transmission to the Earth’s surface.

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Appendix A

Future global climate modelling may identify or eliminate potential mechanisms for increased UVR receipt during the last glacial. Preliminary extrapolations from the current generation of general circulation models (GCMs) suggests that lower CO2 concentrations during the last glacial period could have reduced ozone concentrations because of warm-
ing in the upper stratosphere and enhanced ozone depletion [32]. For example, GCM runs from IPCC scenario A2 [3] predict that increased atmospheric CO$_2$ over the next 50 years (369 ppmv in 2000 to 532 ppmv in 2050) will cool the upper stratosphere ~6 K and alter gas-phase reactions for ozone such that average O$_3$ concentrations will increase ca. 3% [32]. By extrapolation, with atmospheric CO$_2$ reduced to about 200 ppmv during the last glacial maximum (IPCC 2001 summary, p. 40 [33]) stratospheric warming would be expected and may have resulted in depleted O$_3$ levels through a similar mechanism. However, the current consensus amongst modellers appears to be that there are wide variations in the predictions of how ozone responds to changed atmospheric CO$_2$ (as cited in the WMO report [3]), so reverse extrapolations of low CO$_2$ to low ozone in a glacial period remain difficult to constrain in the current generation of models. An additional, and substantial problem is that cloud feedbacks are not yet included in climate models [34] and this is important when trying to estimate UV flux at the Earth’s surface, particularly in Antarctica where cloud cover is known to have changed in response to regional ice extent [27].

References


