

14 Climate control of biological UV exposure in polar and alpine aquatic ecosystems

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14.1 Introduction

The severe depletion of stratospheric ozone in Antarctica over the last two decades has generated much concern about the effects of rising UV-B radiation on marine and freshwater ecosystems (de Mora et al. 2000; Cockell and Blaustein 2001; Sommaruga 2001; Hessen 2002; Perin and Lean 2004) and has led to a broad range of research on UV optics, photobiology and photochemistry in the aquatic environment. The studies to date imply that certain ecosystem types may be especially prone to major changes in their spectral UV regime: clear lakes and oceans in the polar regions where ozone depletion is occurring and where UV wavelengths penetrate deeply into the water column (Vincent and Belzile 2003), and oligotrophic alpine waters which have little UV-screening protection because of their low concentrations of colored dissolved organic matter (CDOM; Morris et al. 1995; Williamson et al. 1996; Laurion et al. 2000; Markager and Vincent 2000). The biological communities in these ecosystems may also be more vulnerable to UV toxicity because of the inhibiting effects of cold temperatures on cellular repair of UV damage (Rae et al. 2000; Hoffman et al. 2003; MacFadyen et al. 2004).

The UV waveband is a highly reactive component of all environments exposed to the sun, and is subject to large fluctuations at multiple time-scales. It is increasingly apparent that climate may exert a strong control on these fluctuations, and that the amplitude of such effects can be much greater than those caused by moderate stratospheric ozone depletion. Major shifts in underwater UV are likely to accompany future climate change, with implications for many important photobiological and photochemical processes in the aquatic environment.

The aim of this chapter is to review the mechanisms, models and observations that link underwater UV exposure and climate change. We first describe a general model that has been applied with success and variously modified to address questions about how changes in the environment translate into UV exposure and responses. We then examine each of the terms in this model and their sensitivity to climate, and how they combine to result in climate control of biological UV exposure in the underwater environment. Finally, we illustrate by way of several case studies how paleo-ecological analysis can provide a valuable approach towards assessing the long-term role of climate in controlling biological UV exposure in alpine and polar aquatic ecosystems.

14.2 Model description

One approach towards assessing the effects of environmental change on spectral UV exposure is by way of the index 'weighted transparency', T^* , where the * indicates that the radiation at each wavelength is multiplied by its biological effectiveness. This index has been applied to cold lakes and oceans (Vincent et al. 1998; Pienitz and Vincent 2000; Gibson et al. 2000; Vincent and Belzile 2002) and has been modified and extended for more general use (Neale 2001; Lehmann et al. 2004). The parameter T^* allows the effects of stratospheric ozone depletion and changes in water column attenuation of UV to be assessed on a common, biologically relevant scale, and it is calculated by integrating the transparency of the water column to biologically weighted irradiance at each wavelength λ over the UV waveband 280-400 nm:

$$T^* = \int T^*(\lambda) d\lambda \quad (1)$$

For an ice-covered lake or ocean, $T^*(\lambda)$ may be partitioned as follows:

$$T^*(\lambda) = E_d(0^+) F (1-r) (1-f) (1/K_{dUV}) \varepsilon \quad (2)$$

where the parameters at each wavelength λ are:

$E_d(0^+)$ = the incident solar irradiance in relative energy units;

F = factor modifying that flux as a function of ozone depletion in the stratosphere;

r = the fraction of UV that is removed by surface reflection (albedo) from the snow, ice or water;

f = the fraction of UV that is removed by attenuation by overlying snow and ice;

K_{dUV} = the diffuse attenuation coefficient for downwelling UV irradiance in the water column;

ε = the biological weighting factor (BWF) which expresses the relative damage incurred by UV ($\varepsilon = 1.0$ at 300 nm). In the following sections we examine the implications of climate change for each of the terms in Eq. (2).

14.2.1 Incident UV irradiance ($E_d(0^+) F$)

Climate has the potential to substantially modify incident spectral irradiance through at least two mechanisms: changes in heat balance and transport processes in the stratosphere, and through changes in tropospheric cloud cover. The greenhouse energy-trapping effect in the troposphere is accompanied by less outgoing long-wave radiation into the lower stratosphere. In the longer term this results in stratospheric cooling, a strengthening of the polar vortex, and a prolongation of conditions that favor ozone loss (Staehelin et al. 2001). The Arctic stratosphere is thought to be on the brink of major ozone loss and would appear to be especially sensitive to a small amount of additional cooling (Dahlback 2002). There may also be larger scale transport effects. Greenhouse warming could lead to increased zonal flow in mid-latitudes causing the polar vortex to be more stable, again favoring ozone loss and a delay in the eventual recovery from CFC emissions (Shindell et al. 1998).

Cloud cover and precipitation regimes are likely to change as a result of shifts in global climate, and these effects may be especially pronounced in the polar regions (Houghton et al. 2001). Increased open sea conditions will be accompanied by increased evaporation into the overlying air masses that at warmer temperatures can hold more moisture for subsequent cloud formation and precipitation. Global warming is also likely to accelerate the hydrological cycle at lower latitudes, resulting in increased atmospheric transport of water to the polar regions. At Spitsbergen, there has been a significant rise in precipitation from the 1960s to 1990s (Hanssen-Bauer and Forland 1998), however other sectors of the Arctic have shown little change or decreases (Vincent et al. 2001).

Cloud cover can have a strong effect not only on total incident UV radiation, but also on UV spectral composition. Gautier et al. (1994) found that incident UV-B irradiance in Antarctica was more closely correlated with cloud cover than stratospheric ozone. There was a positive correlation between the ratio of DNA-damage weighted UV-B irradiance to UV-A irradiance when the surface was covered by reflective snow and ice, and a negative correlation during open ocean conditions. These authors con-

cluded that cloud cover affects UV spectral ratios but that the effect is modulated by multiple back scattering between the surface and clouds. UV measurements over snow-covered ground have shown that incident erythemal (sunburn)-weighted UV on overcast days can be 80% higher than predicted from cloud attenuation because of these multiple reflections (Renaud et al. 2000).

14.2.2 Albedo effects (1-r)

Albedo, the ratio of upwelling (E_u) to downwelling (E_d) irradiance, is high in snow-covered alpine and polar environments and exerts a major control on the underwater UV radiation field. UV albedo for snow and white ice is generally > 80%, but decreases to 50-60% for bare melting ice and to as little as 30% for ponding meltwater over ice. The latter is a common feature over Arctic sea ice during late spring and summer (Perovich et al. 1998; Belzile et al. 2000), while in the drier Antarctic environment a scattering surface layer with high albedo can form during summer (Trodahl and Buckley 1990). Any climate change altering snow cover, duration of ice cover or the surface reflective properties of the ice, for example through meltwater ponds or rainwater over the ice surface, will drastically affect this albedo term and thus T^* . A snow-clearing experiment in Hudson Bay at the edge of the Arctic Ocean underscored the large albedo effect on UV transmittance through sea ice (details in Vincent and Belzile 2002). The removal of surface snow caused a 3 to 16 fold increase in the under-ice UV, thus a similar increase in T^* . Even a layer of snow only 2-cm thick reduced UV by a factor of 3, with slightly greater effects at the shorter wavelengths. Similarly, the removal of snow over a high Arctic ice-covered lake decreased albedo by 20% in the UV range and 13% in the PAR range (Belzile et al. 2001). Lake white ice, that is ice with a high air content, has a high albedo for PAR and UV, and lake ice whitening can occur with gradual warming over spring and summer (Howard-Williams et al. 1998).

14.2.3 Attenuation by snow and ice (1-f)

There are few published UV attenuation coefficients for snow and ice because of the difficulties of making measurements in these solid media. In early spring, about 1% of incident UV-B is transmitted through ~1.6 m of sea ice (Arctic: Perovich et al. 1998; Antarctic: Trodahl and Buckley 1990), however the development of ice algae can decrease UV transmittance by an order of magnitude (Perovich et al. 1998). Autochthonous

CDOM derived from ice algae has a significant impact on UV attenuation in sea ice, and the melting of the snow cover, ponding of the ice surface and flushing of the ice algae all tend to increase UV-B transmittance (Belzile et al. 2000). In Antarctica, a highly scattering sea-ice surface forms as the melt progresses, resulting in decreased UV-B transmission relative to early spring values (Trodahl and Buckley 1990). Freshwater ice is typically more transparent to UV irradiance than sea ice because of the absence of brine pockets and minimal ice-biota. Lake ice may even be more UV-transparent than the underlying lake water because of the exclusion of high molecular weight UV-absorbing CDOM during the freeze-up process (Belzile et al. 2002). Even Antarctic lake ice several meters thick can allow measurable transmission of UV to the waters beneath (Vincent et al. 1998), although if such ice contains high concentrations of light-scattering inclusions such as glacial sediments ('dirty ice') or bubbles ('white ice') the UV-transmittance is minimal. For example, the 5-m thick summer ice over Lake Hoare in the McMurdo Dry Valleys was highly scattering, and no UV radiation less than 310 nm was detected in the water column beneath the ice (Kepner et al. 2000).

The dynamics and timing of ice cover melting in spring have substantial effects on the UV exposure of biota in the underlying water column. In alpine lakes for example, UV irradiances at the top of the water column can be an order of magnitude higher after melt-out than under 1.8 m of snow and ice cover at similar solar zenith angles (Sommaruga 2001). Rautio and Korhola (2002) showed that the *Daphnia* population of a subarctic lake responded to ice cover break-up by immediate synthesis of UV-absorbing melanin pigment (Fig. 14.1). Towards fall, the melanin concentration decreased suggesting the pigmentation was a direct response to the increased UV exposure during the peak radiation period. Shorter ice cover duration and exposure to higher UV during the spring ozone depletion could potentially alter the aquatic communities in lakes and require them to invest more in such UV protection mechanisms. This melanin content of cladocera also offers potential to estimate ice cover regimes in the past by analysis of lake sediments, analogous to the cyanobacterial UV-pigment reconstructions that have been applied to date (see below).

Substantial melting of seasonal snow and ice cover caused by rising temperatures has already been recorded in many parts of the world for example over cold lakes and rivers (Magnuson et al. 2000), arctic sea ice (Serreze et al. 2003) and lakes in the Antarctic Peninsula region (Quayle et al. 2002). Such changes are likely to have been accompanied by drastic shifts in underwater UV exposure. T^* calculations for an Arctic marine site

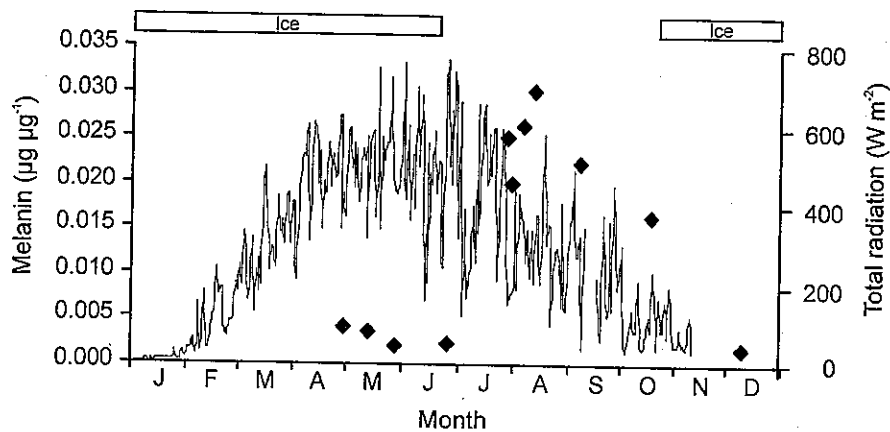


Fig. 14.1. Changes over time in the ground level total radiation and the *Daphnia umbra* melanin concentration in Lake Saanajärvi (69°05'N, 20°87'E; maximum depth = 24 m, altitude = 679 m a.s.l., DOC = 1.6 mg L⁻¹), showing the effects of increased underwater light intensity on pigment synthesis. The thickness of the ice exceeds 1 m in late spring. From Rautio and Korhola (2002)

showed that the removal of ice increased T^*_{PI} (T^* weighted for photosynthetic inhibition) by a factor of 12 and T^*_{DNA} by a factor of 22. The Arctic is likely to be more prone to this effect than the Antarctic in the immediate future. General circulation models (GCMs) predict that global warming will occur first and most intensely at high northern latitudes (Houghton et al. 2001) and there is evidence of accelerated impacts at some sites (Muel-ler et al. 2003). The north polar ice cap has experienced thinning and contraction over the last three decades and GCMs predict a complete loss of sea ice across the Arctic Ocean basin during summer by the end of this century (Vincent et al. 2001 and refs therein).

14.2.4 Water column transparency ($1/K_{dUV}$)

Colored dissolved organic matter (CDOM) is the primary attenuator of UV radiation in most aquatic environments. This still poorly defined mixture contains many substances, but the UV absorption is mostly due to aromatic polymers, notably humic and fulvic acids derived from terrestrial soils and vegetation. Alpine and polar lakes generally have very low concentrations of CDOM because of their sparse catchment vegetation, and the absorption coefficients for UV radiation per unit DOC may also be low because of the low relative importance of allochthonous versus aromatic, less UV-absorbing autochthonous carbon in these waters (Laurion et al. 2000). There is a non-linear relationship between UV-transparency and CDOM

concentration, and between UV spectral ratios such as UVB/UVA (Laurion et al. 1997), and many high latitude and alpine waters are in a range that is responsive to small changes in CDOM. However the large arctic rivers and the coastal waters that they discharge into contain much higher CDOM concentrations because they are fed by catchments that extend far to the south, below the treeline. Antarctica has no major rivers and no well-developed terrestrial vegetation, and as a consequence there are striking differences in the attenuation of UV radiation in coastal Antarctic versus Arctic waters (Fig. 14.2). The relative lack of CDOM in Antarctic waters means that these ecosystems may be more sensitive to other factors controlling biological UV exposure such as changes in depth, ice and snow cover and atmospheric properties.

Climate change has the potential to exert a major influence on CDOM loading, with consequent impacts on underwater UV exposure. The mechanisms of effect include changes in catchment vegetation type and productivity, changes in precipitation and hydrology, and melting of permafrost soils and subsequent release of dissolved organic matter into the downstream receiving waters. For each of these processes, increasing atmospheric CO_2 and temperature are likely to result in increasing CDOM (e.g., Pastor et al. 2003; Freeman et al. 2004). This in turn will substantially release the biota from UV stress, although this positive effect may be

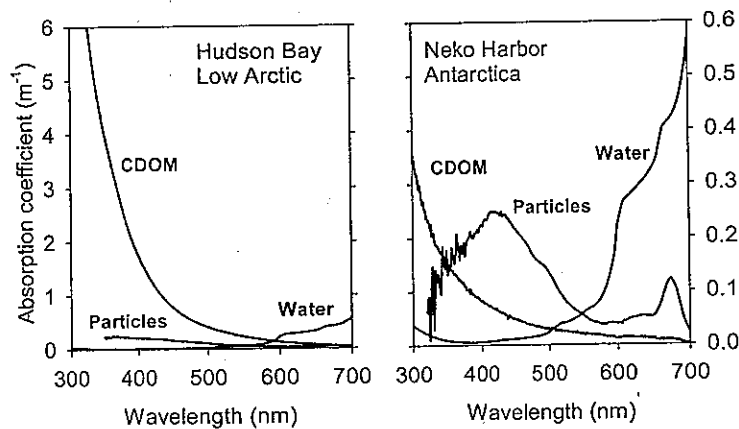


Fig. 14.2. CDOM influence in north versus south high latitude seas on underwater spectral radiation: Hudson Bay and Antarctica. Spectral absorption of water, particles and CDOM for Hudson Bay, 14 August 1999, and for Neko Harbor, Antarctic Peninsula, 3 January 2001.. Note the x10 difference in absorption scales (from Vincent and Belzile 2003).

offset by a reduced availability of PAR for photosynthesis (Arrigo and Brown 1996; Pienitz and Vincent 2000; Neale 2001; Lehmann et al. 2004).

There are steep spatial gradients in CDOM concentration across the Arctic Ocean. Coastal waters in some regions are strongly influenced by the CDOM inputs from large rivers. For example, the black waters of the Lena River have been observed up to 400 km offshore ($>5 \text{ mg L}^{-1}$ dissolved organic carbon at 4 m; Cauwet and Sidorov 1996) while in other regions, such as the North Water Polynya (NOW) between Greenland and Baffin Island, CDOM concentrations are extremely low and UV transparency is within the range reported for the Southern Ocean (Vincent and Belzile 2002). Major shifts in current patterns across the Arctic Ocean are likely to accompany any substantial change in climate. This in turn will lead to a redistribution of CDOM and large regional increases or decreases in underwater UV exposure. Large-scale shifts in the distribution of water masses have already been observed in the Arctic Ocean (Dickson 1999).

To evaluate the magnitude of spatial variability in north polar waters, T^* was calculated for an inshore water column at Hudson Bay (Canada) and for an offshore water column in the Arctic NOW polynya, both under ice-free conditions (Vincent and Belzile 2002). Moderate ozone depletion caused only a 5% increase in biological exposure weighted for UV-inhibition of photosynthesis (T^*_{PI}), whereas the difference in CDOM accounted for a 29-fold difference in underwater UV exposure between sites. For T^* weighted for DNA damage (T^*_{DNA}), moderate ozone depletion increased UV exposure by a factor of 2.3, but this was small relative to the 27-fold increase caused by differences in CDOM between sites.

In the lowest CDOM environments such as some alpine lakes (Laurion et al. 2000; Sommaruga 2001) and the Southern Ocean (Vincent and Belzile 2003), particles may also play a significant role in UV attenuation. Any climate-related effects that increase particle loading or the *in situ* growth of particles (bacteria and protists) therefore have the potential to affect underwater UV exposure. Some phytoplankton in alpine lakes contain UV-screening mycosporine-like amino acids (Sommaruga and Garcia-Pichel 1999), and stimulation of their growth by the nutrient enrichment accompanying even small rises in temperature (Sommaruga-Wögrath et al. 1997) would substantially reduce the UV transparency of the water column. Turbid glacial inputs are also known to decrease UV transparency, for example at Arctic Kongsfjord at Spitsbergen (Hanelt et al. 2001) and in the coastal Southern Ocean (Stambler et al. 1997). Climatic warming may therefore extend the magnitude and duration of these UV-attenuating effects through increased glacial melt.

14.2.5 Mixing and stratification (integral $1/K_{dUV}$)

Climate influences the depth, frequency and intensity of mixing of the surface layer of lakes and oceans, and this will directly affect UV exposure of planktonic organisms. Biota trapped at the surface during diurnal stratification will experience severe UV exposures, while deeper mixing communities will experience only intermittent, short-term UV stress. Studies on sub-arctic (Milot-Roy and Vincent 1994) and alpine lakes (Vincent et al. 1984) have shown the importance of diurnal thermoclines for UV- and PAR-dependent photoinhibition of algal photosynthesis. Diurnal stratification is likely to become more pronounced in a warmer climate, and may even select for more UV-tolerant genotypes. Deep mixing can eventually expose all of the water column plankton to surface UV, and if their rate of repair of the resultant damage is slower than the timescale of mixing then this deep circulation could potentially enhance the net water column UV damage (Neale et al. 1998b). Such effects may be especially pronounced in cold polar and alpine waters where repair is slowed by the ambient low temperatures (Rae et al. 2000). Most studies, however, show decreased UV-inhibition of total water column photosynthesis associated with deep mixing (Neale et al. 1998b; Barbieri et al. 2002). A modeling study by Huot et al. (2000) on bacterial DNA damage by UV, with repair by photo-reactivation and excision, showed that variations in mixed layer depth affected the net damage in the mixed layer (and to a much greater extent than changes in CDOM concentration), and that the speed of mixing affected the vertical distribution of damage. They noted that the latter effect could be significant if biological processes such as survival, productivity and viral lysis respond non-linearly to net DNA damage.

Any future shift in high latitude and alpine lakes from cold monomixis (continuous mixing during summer) to dimixis (stratification during summer) will also result in communities exposed to much greater UV as well as PAR. There is evidence from a Finnish subarctic lake (Korhola et al. 2002) of this type of thermal shift during the 20th century. This was accompanied by an apparent increase in productivity and the appearance of cladocerans in the zooplankton community. These Finnish lake results imply that the positive effects of increased PAR on ecosystem productivity were much greater than the negative effects of increased UV exposure.

The thermal effects of global climate change are also likely to be felt more strongly in clear lakes in general. In an analysis of interannual variations in climate and lake thermal regimes, Snucins and Gunn (2000) found that the volume of cold water was significantly reduced in clear lakes during warm summers, while colored lakes ($\text{DOC} > 4 \text{ mg L}^{-1}$) were less sensitive to the warming effects of climate change. They also suggested that

clear lakes will experience large thermal regime shifts in response to small variations in DOC loading.

The Arctic Ocean has a much shallower mixed layer than the open waters of the Southern Ocean because of the strong freshwater influence, and any change in precipitation and runoff into the Arctic Basin could modify mixed layer depth and thus UV exposure. Similarly, coastal Antarctic seas are often stratified by meltwater input (e.g., Antarctic Peninsula: Mitchell and Holm-Hansen 1991; Terra Nova Bay: Arrigo et al. 2000) and changes in glacial runoff and sea ice melt would affect mixing and UV. The loss of sea ice in a warmer polar climate would drastically increase surface UV exposure, but this would be at least partially offset by the wind-induced mixing of biota throughout a deepened surface layer.

14.2.6 Biological weighting factors (ϵ)

Biological weighting factors (BWF) express the quantitative relationship between biological damage and UV wavelength, and generally increase sharply with decreasing wavelength. The exact form of this relationship differs greatly among different types of biological effects as well as with duration of exposure, the pre-acclimation characteristics of the biological community, species composition and a variety of other factors that are currently subject to discussion and ongoing research. For example, the modeling study by Gibson et al. (2000) for the Arctic Ocean indicated the combined effect of ozone depletion and changes in CDOM in controlling the extent of DNA damage, and the much greater influence of CDOM in controlling the variations in UV-inhibition of photosynthesis. This was because the BWF for UV-photoinhibition is strongly influenced by UV-A as well as UV-B (both controlled by CDOM) whereas DNA-damage rises much more steeply with decreasing UV wavelength and UV-A.

Climate change is likely to result in species shifts, that in turn affect the capacity of the phytoplankton to acclimate. For example, Neale et al. (1998a) found that the UV-tolerance of phytoplankton in the Weddell-Scotia Confluence was highest in assemblages from shallow mixed layers, suggesting acclimation and-or selection for tolerant genotypes. Warmer temperatures in the present changing climate may allow increased efficiency of repair, and thereby shift the BWF curves of all species.

14.3 Paleo-ecological evidence of climate-UV effects

Paleolimnological or paleoceanographic reconstructions of past irradiance regimes ('paleo-optics', Pienitz and Vincent 2000) can substantially contribute to a better understanding of the magnitude, causes and consequences of temporal variability in UV radiation. Using microfossil remains (siliceous diatoms), photo-protective pigments (e.g., scytonemin) or bulk sedimentary characteristics (% organic matter) preserved in long sedimentary sequences (cores), such retrospective analyses permit reconstructions of past concentrations of UV-absorbing dissolved organic carbon compounds (DOC) that can be used to infer water column transparency, term ($1/K_{dUV}$) in Eq. (2), and other ecologically important optical properties such as UV/PAR ratios. The application of paleolimnological approaches to lakes at treeline show both that climatically-induced changes in the export of terrestrial (allochthonous) DOC to lakes are up to 100-fold more effective than modern stratospheric ozone depletion at altering biological exposure to UV (Pienitz and Vincent 2000), and that naturally occurring droughts can increase UV exposure in lakes by up to 10-fold (Yan et al. 1996). Analyses of fossil remains in arctic/boreal and alpine lakes suggest that historical variability in UV exposure has been high (e.g., Leavitt et al. 1997, 2003a,b; Pienitz and Vincent 2000; Saulnier-Talbot et al. 2003), and that lakes may have received twice as much UV prior to ca. 3000-4000 years ago than they do at present. Finally, when used in combination with long-term environmental monitoring (Schindler et al. 1996, 1997), historical reconstructions have proven valuable at identifying the importance of UV relative to other stressors in regulating lake structure and function. Thus, although further research is required to validate fossil interpretations, paleoecological analyses of lake sedimentary records can provide valuable insights into the history of UV exposure and its potential impacts on aquatic ecosystems.

Multivariate analysis of modern diatom assemblages preserved in surface lake sediments has been used to develop statistical models (transfer functions) based on the relationships between the present-day species composition and environmental conditions (e.g., Pienitz and Smol 1993; Fallu and Pienitz 1999; Fallu et al. 2005). Application of these models to fossil diatom assemblages in long sedimentary sequences (cores) allows quantitative reconstructions of past lake conditions over 100s to 1000s of years, including DOC content, water colour and optical regime (e.g., Pienitz and Vincent 2000; Dixit et al. 2001; Ponader et al. 2002; Saulnier-Talbot et al. 2003; Fallu et al. 2004). Further details on the calibration data set approach and standard procedures involved in the development of dia-

tom-based inference models for DOC and other variables are given in Pienitz and Smol (1993) and Fallu and Pienitz (1999).

14.3.1 Lakes at the subarctic treeline

To address the potential impact of long-term climate change relative to that of ozone depletion, Pienitz and Vincent (2000) combined paleolimnological analyses with bio-optical models based on present-day conditions in lakes of northern Canada. This new paleo-optical approach allowed them to estimate past underwater light conditions from DOC concentrations that

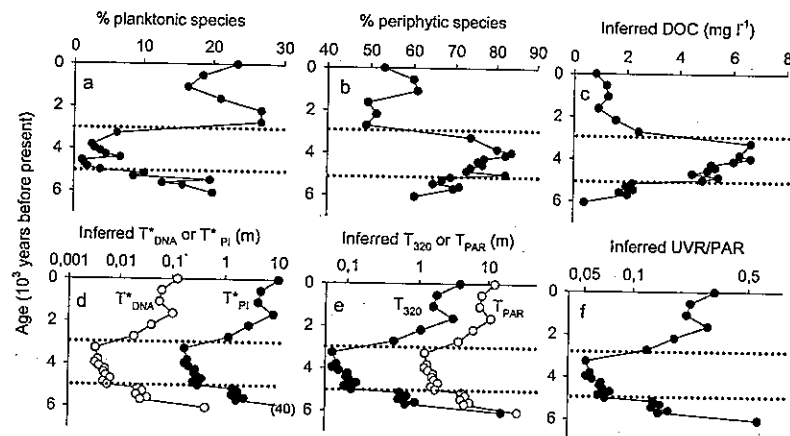


Fig. 14.3. Changes in fossil diatom community structure and inferred optical conditions in Queen's Lake, Northwest Territories (Canada). Diatom data are expressed as a percentage of the total number of valves in each sample associated with planktonic or benthic taxa. Diatom species data were used to infer DOC concentration (mg DOC L^{-1}), biologically weighted UV exposure (T^*_{PI} or T^*_{DNA}) and underwater spectral balance (water column transparency for 320 nm UVR [T_{320}], PAR [T_{PAR}], and the ratio between the two [UVR/PAR]) over the last 6000 years. The dotted lines delimit the period of mid-Holocene maximum forest cover. This analysis demonstrates that biotic exposure to UVR varies substantially due to changes in catchment vegetation and DOC supply, and that during the mid-Holocene climatic warm period, UVR exposure declined by two orders of magnitude. Climatic cooling beginning at ca. 3000 yr BP reduced DOC inputs by reducing soil development and DOC supply, and led to increases in UVR penetration that were up to 4000-fold more significant than those expected to arise from a moderate (30%) ozone depletion. From Pienitz and Vincent (2000)

were inferred from fossil diatom assemblages preserved in Holocene sedimentary deposits from a lake near the northern treeline (Queen's Lake; lat. 64°07'N, long. 110°34'W) in the central Northwest Territories, Canada (Fig. 14.3). Analysis of fossil pollen records indicates that regional vegetation cover was sparse and tundra-like following deglaciation ca. 8000 yr BP and persisted until trees colonized the catchment ca. 5000 years ago (MacDonald et al. 1993).

Diatom community structure and inferred DOC levels showed three distinct and abrupt changes during the history of Queen's Lake. Both diatom biomass and inferred DOC concentrations were low ($< 2 \text{ mg DOC L}^{-1}$) during the initial lake phase, with particularly few fossils recovered from sediments dating prior to 5000 yr BP. This initial period of lake existence was followed by major and rapid shifts in fossil species composition and inferred chemical conditions ca. 5000 yr BP, with increased ratios of periphytic:planktonic taxa to $>70\%$ of the total diatom assemblage.

The period of forest advance corresponded to a major increase in algal production, recorded as the sediment mass-specific concentration of diatom valves, as well as a three-fold increase in inferred DOC levels. Based on fossil pollen analyses, Pienitz and Vincent (2000) argued that changes in lake chemistry and production resulted from climatic warming that stimulated treeline advance and increased forest density for about 2000 years. Finally, diatom-based reconstructions indicated that DOC concentrations declined $>85\%$ after 3000 yr BP, concomitant with the onset of Neoglacial climatic cooling and a southward retreat of treeline (MacDonald et al. 1993).

The large and rapid changes in DOC imply that Queen's Lake experienced major shifts in the underwater optical environment over the last 6000 years as a consequence of climate-induced variation in forest development (Pienitz et al. 1999). Consistent with this hypothesis, application of T^* calculations for UV-inhibition of photosynthesis and UV-damage of DNA showed that the inferred DOC shifts were equivalent to a two order-of-magnitude decrease in exposure to biologically-effective UV during the mid-Holocene vegetation maximum between ca. 5000 and 3000 yr BP. In contrast, the most recent 3000 years were characterised by a >50 -fold increase in levels of damaging UV. Overall, changes in DOC concentrations arising from climatic variability increased exposure to photosynthetically damaging UV to an order-of-magnitude greater extent than a moderate (30%) decline in stratospheric ozone levels. Pienitz and Vincent (2000) noted, however, that the large photoinhibiting effect of UV irradiance after treeline retreat would be at least partially offset by the major increase in PAR for photosynthesis under these conditions of much reduced CDOM.

More recently, Lehmann et al. (2004) have modified and refined the biologically weighted transparency model by extending it out into the PAR waveband and by including separate terms for light-dependent photosynthesis and light-dependent inhibition of photosynthesis. This approach allows a quantitative estimate of water column photosynthesis ($[P]$) under different UV regimes via the relationship:

$$[P] = a (T_{PUR})^b I (T_{PIR})^c \quad (3)$$

where T_{PUR} is transparency weighted for photosynthetically utilisable radiation calculated over the waveband 400-700 nm; T_{PIR} is transparency weighted for photosynthesis-inhibiting radiation over the full waveband 280 to 700 nm; and a , b and c are statistically fitted constants. Lehmann et al. (2004) applied this model to the Queen's Lake paleolimnological data set and their results confirmed that decreasing CDOM concentrations during the retreat of the treeline would result in a significant increase in UV-inhibition of photosynthesis. However, this effect (as % reduction in $[P]$) was a factor of ten less than the T^* calculations predicted, in particular because the increasing water clarity also allowed greater exposure to PAR. This in turn resulted in more total water column photosynthesis that substantially offset the negative effects of increased biological UV exposure. These results have important implications for climate impact studies because they draw attention to the full spectral consequences of changing light regimes, and the need to examine the net effects of both positive and negative responses to environmental change.

14.3.2 Climate change effects on UV exposure in Rocky Mountain lakes

Climatic control of past UV exposure has also been identified as a key factor regulating lake production and algal community composition in lakes at the alpine treeline. Using fossil pigments and organic matter preserved in lake sediments, Leavitt et al. (2003b) quantified past UV exposure in the 12,000 year history of subalpine Crowfoot Lake, located near the alpine treeline in the Rocky Mountains (Alberta, Canada). Their study revealed highest concentrations of UV-absorbing algal pigments and declining algal biomass during periods of early lake existence following deglaciation as well as during the last ca. 4,000 years, when external DOM inputs are believed to have been lowest and UV exposure highest. Based on fossil pigment and bulk organic matter-derived estimates of irradiance penetration, they calculated that algal abundance was reduced 10 to 25-fold during these periods of high UV exposure. However, at all other times in the

lake's history (ca. 10,050-4,000 yr BP), photoprotective pigments associated with high UV were absent from sediments and the total algal abundance was high.

14.3.3 Past UV exposure in Antarctica

The lakes at high latitudes are especially suitable for UV studies as they have limited or no terrestrial sources of UV-absorbing DOM within their catchments (Vincent and Pienitz 1996). Therefore changes in UV would be expected to arise solely from changes in solar production, atmospheric transmission, ice and snow cover or lake depth. Using a similar pigment approach as above, Leavitt et al. (2003a) showed that shallow lakes in Antarctica have been exposed to variable levels of UV of the Holocene, and higher levels in the preceding interglacial (Hodgson et al. 2005). Their analyses of lake sediments indicated that photo-protective pigments (scytonemin and its derivatives) were relatively more abundant in sediments older than 4000 years. The reconstruction further indicated that receipt of UV irradiance by benthic cyanobacteria in antarctic lakes has varied by at least 400% during the past 13 000 years. At present, photoprotective pigments, including scytonemin, are common in algal communities in antarctic lakes that are shallow (< 4-6 m depth) and transparent, and their abundance has been shown to increase as a function of algal exposure to UV (Hodgson et al. 2005).

14.3.4 Deglaciation responses in a coastal subarctic lake, Hudson Bay

Saulnier-Talbot et al. (2003) used a diatom-based paleo-optical approach to estimate past depths of UV penetration in coastal Lake Kachishayoot (northwestern Québec, Canada; lat. 55°20.0' N, long. 77°37.4'W; 102 m a.s.l.) following its isolation from the marine waters due to glacio-isostatic rebound of Hudson Bay lowlands. Prior comparisons of optical environments in coastal systems have revealed that shifts from marine to freshwater conditions are accompanied by increased DOC, changes in C-specific UV attenuation and declines in UV penetration (Conde et al. 2000). Consistent with these modern observations, Saulnier-Talbot et al's (2003) multi-proxy investigation revealed abrupt increases in diatom-inferred DOC concentrations and water color that coincided with the retreat of postglacial marine waters and the arrival of spruce trees within the landscape and catchment of the study site. Their investigation also revealed large changes in the underwater irradiance environment over the course of

the postglacial period, from extremely high UV exposure following the initial formation of the lake and its isolation from the sea, to an order-of-magnitude lower exposure associated with the development of spruce forests in the catchment. Furthermore, the use of additional macrofossil markers revealed that UV penetration remained low even following forest retreat due to the development of alternate DOC sources in the catchment such as *Sphagnum* wetlands.

14.3.5 UV-exposure in lakes during glacial retreat at Glacier Bay, Alaska

A final paleo-ecological example is based on a set of modern day ecosystems, but environments that span a gradient of different ages and degrees of maturity in successional development. Major variations in CDOM and in underwater UV radiation have been observed in the chronosequence of lakes associated with the retreat of ice over the last 12,000 years in the Glacier Bay area, Alaska. Lakes near the glacier face and up to a few decades old have high pH and low DOC. With the gradual development of alder, coniferous forest and peatlands, the lakes have become more acidic, more dilute and have accumulated DOC associated with the slow but continuous accretion of soil organic matter. This soil development has been accompanied by a shift in hydrology from groundwater flow to increased near-surface runoff resulting in increased flow through the peat and weathered soil horizons, increasing the efficiency of transfer of organic matter from soil to water (Engstrom et al. 2000). Measurements of UV penetration in some of these lakes showed that 1% of surface UV at 320 nm was correlated with DOC content, and ranged from 0.6 m in a 90-year old coloured lake to more than 14 m in a 10-year old clear lake. These disparate optical conditions also corresponded with major differences in zooplankton community structure, and transplant experiments confirmed that UV exposure had a strong effect on zooplankton survival, but to an extent that varied according to species (Williamson et al. 2001). These results provide strong evidence that climate effects on vegetation and hydrology are likely to have a major influence on underwater UV exposure and associated impacts.

14.4 Conclusions

There are many mechanisms linking UV exposure to climate in the aquatic environment. Some are caused by climate-induced changes in the strato-

sphere, while many are associated with temperature-related effects on the main UV-attenuating components of natural waters, notably changes in snow and ice cover, and in CDOM associated with shifts in terrestrial vegetation. There are also a variety of hydrological effects of climate with major implications for underwater UV such as changes in snow and rainfall (with runoff, vegetation and albedo effects), evaporation and cloud cover, pathways of runoff and degree of interaction between the soil and water. Finally, there are more subtle effects such as changes in wind-induced mixing and climate-induced shifts in species composition towards more or less UV-tolerant species. Many of these effects are likely to be especially pronounced in arctic, antarctic and alpine aquatic ecosystems where there is a precarious balance between freezing and melting throughout summer, and in which CDOM concentrations are often in a range where small changes have a large effect on UV transparency. As shown with the many examples and models summarized here, several of these climate change mechanisms can have much greater impacts on biological UV exposure than the recently observed human-induced changes in stratospheric ozone. The paleo-ecological examples provide several lines of evidence for the overriding control exerted by external catchment processes, in turn mediated by climate, on the underwater optical conditions in lakes. All arctic investigations to date converge on the conclusion that biotic exposure to UV should have been greatest early in lake history immediately after deglaciation or retreat of postglacial seas, prior to the development of terrestrial sources of UV-absorbing DOM. Because past episodes of UV exposure appear to have been greater than those arising from many modern processes, these analyses offer insights (potentially at annual resolution) into the unique impacts of UV on ecosystem processes, including those occurring immediately after lake formation when DOM inputs are lowest. In the Antarctic, the near absence of UV-absorbing CDOM means that the absorption and transmission characteristics of ice, snow and the atmosphere are likely to be more important. Finally, to what extent will the future warming of polar and alpine regions result in UV-mediated changes in biological and biogeochemical processes in the aquatic environment? Higher temperatures will mean longer open water conditions (more UV) but also more vegetation and CDOM input. The mobilisation of DOC within alpine and northern permafrost soils has the potential to cause a massive influx of CDOM, and substantial increases in UV-shading. However, the beneficial effects of these changes may be offset by the concomitant decrease in availability of light in the visible range for photosynthetic production. The future assessment of climate impacts in polar and alpine regions will require close attention to the net result of these opposing effects.

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