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The Ecological Significance of Solar UVR in the Polar Regions

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ABSTRACT. Spectral solar irradiance at the earth's surface will be briefly summarized as a function of latitude and season, both with and without a pronounced ozone hole. Representative data will show the spectral enhancement of UV-B radiation (280-320 nm) as a function of column ozone values expressed in Dobson Units (DU). The effects of solar ultraviolet radiation (UVR) on marine phytoplankton will be discussed primarily in Antarctic waters, but mention will also be made of similar studies in tropical and Arctic waters. Experiments in both polar regions included short-term incubations (4-12 hours) with inorganic radiocarbon and also long-term incubations (up to 17 days) where chlorophyll-*a* and total cellular organic carbon were determined daily in addition to floristic composition. The action spectrum for inhibition of photosynthesis by UVR shows that the shorter the wavelength of the radiation, the greater is the photoinhibitory effect. By using sharp cut-off filters, however, experimental results show that UV-A radiation (320-400 nm) generally accounts for considerably more inhibition of photosynthesis than does UV-B radiation. The magnitude of inhibition of integrated photosynthesis in the euphotic zone by enhanced UV-B radiation resulting from atmospheric ozone depletion is estimated to be approximately 4%, as compared to approximately 18% resulting from all UVR under normal ozone conditions. Although such a loss of photosynthate during the seasonal appearance of ozone depletion (mostly October-November) is not of great magnitude, the impact of enhanced UV-B radiation on the marine food web will be strongly dependent on the mechanism(s) responsible for the photoinhibitory effects. The ecological significance of enhanced UV-B radiation on the dynamics of the marine food web will be discussed in regard to (i) reversibility of the UVR-induced photoinhibition of photosynthesis, (ii) effects of physical mixing processes in the upper water column, (iii) adaptational responses which reduce sensitivity of cells to UVR, and (iv) differential species sensitivity to UVR.

Key Words: enhanced UV-B, photoinhibition, phytoplankton, primary production, solar ultraviolet radiation, UV-A

Introduction

Life on earth is partially protected from the short wavelengths of solar ultraviolet radiation (UVR) by many atmospheric constituents, of which oxygen (O_2) and ozone (O_3) are among the most important (Frederick *et al.* 1989). The absorption of UVR by ozone is very efficient in the region of the shorter UVR wavelengths, with the result that solar radiation, which extends to approximately 200 nm outside the atmosphere, is attenuated so that the shortest wavelengths which can be measured at the earth's surface are approximately 280 nm. The concentration of ozone, which is formed in the stratosphere by the action of solar UVR on oxygen, is also dependent upon temperature, oxygen, and trace chemical species (e.g., nitrogen oxides, hydroxyl radicals, and halogen atoms), with the result that the flux of UVR incident upon the earth varies considerably as a function of both latitude and season (WMO 1991; Madronich 1993). The total ozone column of the atmosphere is commonly expressed in

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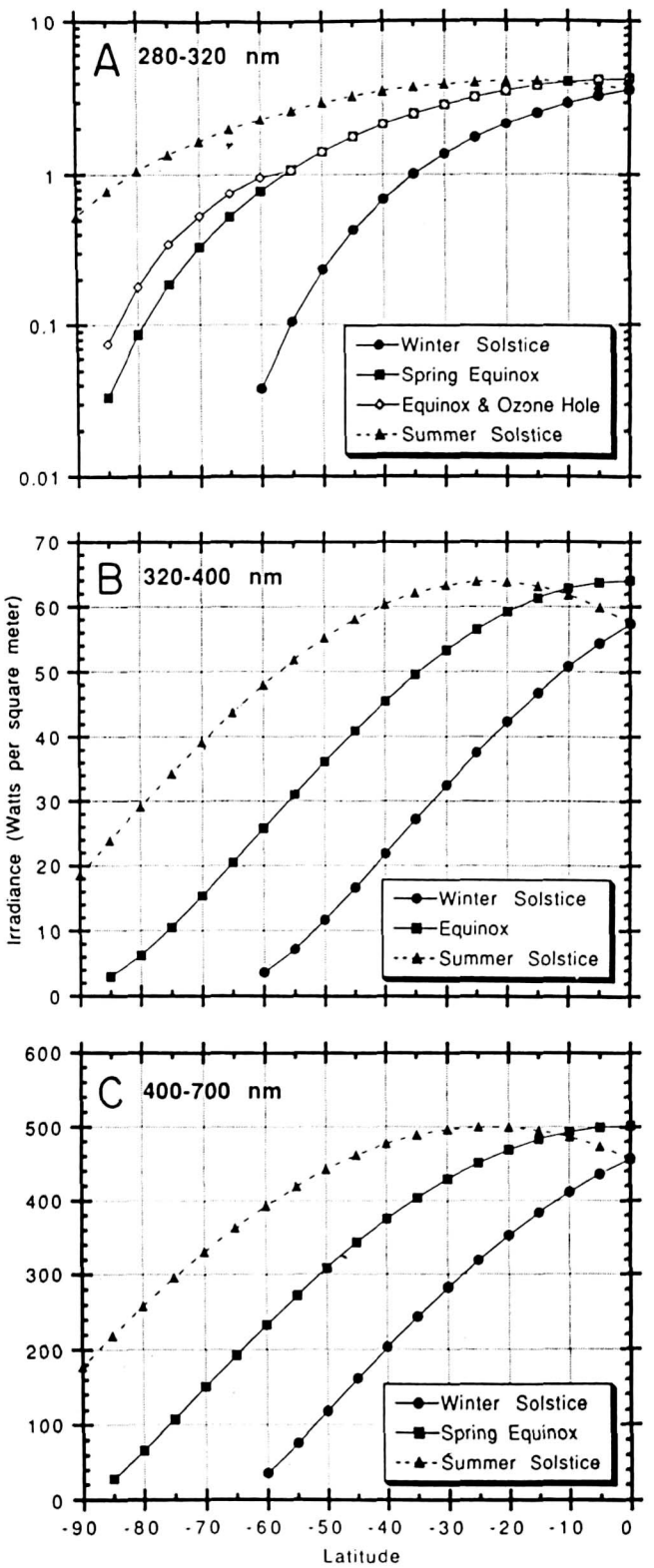

Fig. 1. Results of atmospheric radiative transfer calculations showing local noon solar irradiance incident upon the earth as a function of latitude and season in the southern hemisphere, in addition to increased UV-B radiation at vernal equinox under the severe Antarctic ozone depletion of 1987. Note the change in ordinate scales for the integrated values for the three spectral regions. A, UV-B radiation; B, UV-A radiation; C, Photosynthetically Available Radiation. Data from Holm-Hansen *et al.* (1993b).

Dobson Units (DU), where one DU equals 2.69 x 1020 molecules of O_3 per m^2 (Madronich 1993). The highest concentrations of ozone (300 to >400 DU) are generally found over the polar regions during winter, with the lowest concentrations (<280 DU) being at low latitudes in the tropics. This distribution of ozone, coupled with the change of solar elevation angle with latitude, results in very high incident solar UVR at low latitudes, and decreasing UVR irradiance toward the polar regions (see Fig. 1).

Sporadic events such as volcanic eruptions which inject material into the world's atmosphere may lower incident UVR upon the earth's surface by specific destruction of ozone as well as by general scattering and absorption of both UVR and visible radiation. In contrast to such sporadic events, the depletion of ozone in the stratosphere in the altitude ranges from approximately 15 to 50 km over Antarctica (referred to as the 'ozone hole') during late winter to mid-spring is a predictable and seasonal event. The first evidence of such an ozone hole over Antarctica was obtained by British scientists at Halley Bay in the late 1950s, but the severity and significance of the depletion was not generally recognized until the 1980s (WMO 1994). The inception and increasing severity of the ozone hole more or less parallels the industrial production and release of chlorofluorocarbons (CFCs) and of certain bromine compounds, which are believed to play a major role in the seasonal catalytic destruction of stratospheric ozone over Antarctica. Although CFCs and bromine compounds are distributed worldwide, a pronounced seasonal ozone hole is found only over Antarctica due to the unique atmospheric conditions (i.e., low temperatures and the presence of polar stratospheric clouds in the polar vortex) that exist at high latitudes in the southern hemisphere.

The resulting increase in incident UVR is of biological significance as the shorter the wavelength of the radiation, the greater is the energy per photon, and this spectral region of the UVR overlaps the absorption spectrum of many cellular macromolecules, including the genetic material deoxyribonu-

cleic acid (DNA). The following sections briefly summarize some of the more important aspects concerning the potential impact of enhanced UVR on the marine food web.

UVR in Geologic Time

The question is often asked if life on earth has not been exposed to ozone holes prior to the conditions now existing in the Antarctic. In order to answer this it is necessary to look at the composition of the earth's atmosphere in geologic time. When life originated on earth (thought to be about 2.5 billion years ago), it is believed that the atmosphere did not contain either oxygen or ozone, and hence UVR incident upon the earth would have extended down close to 200 nm. With the evolution of oxygen-evolving photosynthetic mechanisms (thought to have occurred in aquatic environments about 0.5 billion years ago), oxygen and ozone would slowly accumulate in the atmosphere and concomitantly the UVR incident upon the earth would decrease. Early life on earth would thus have been exposed to much greater fluence of short wavelength UVR than at the present time, even under the most extreme ozone hole in the Antarctic. During this long period since the advent of green plant photosynthesis, it can be expected that both plants and animals would have evolved mechanisms to utilize the energy in UVR for specific reactions and also to evolve adaptive mechanisms to minimize or repair any cellular damage by UVR. Examples of utilization of UVR wavelengths in specific metabolic reactions are (i) the utilization of UV-A (320 to 400 nm) radiation to produce the reducing power required for photosynthetic assimilation of CO_2 (Neori *et al.* 1988), (ii) UV-A induced photorepair of structural damage to DNA resulting from UV-B (280-320 nm) radiation (Mitchell and Karentz 1993), and (iii) the UV-B-activated synthesis of vitamin D in skin tissue of vertebrates (Webb 1993). It is generally recognized, however, that most organisms at present do experience 'UVR stress' and hence any additional UVR (as the enhanced UV-B radiation under the ozone hole) can result in cellular damage. In the sections below only the deleterious effects of solar UVR on aquatic microorganisms will be discussed.

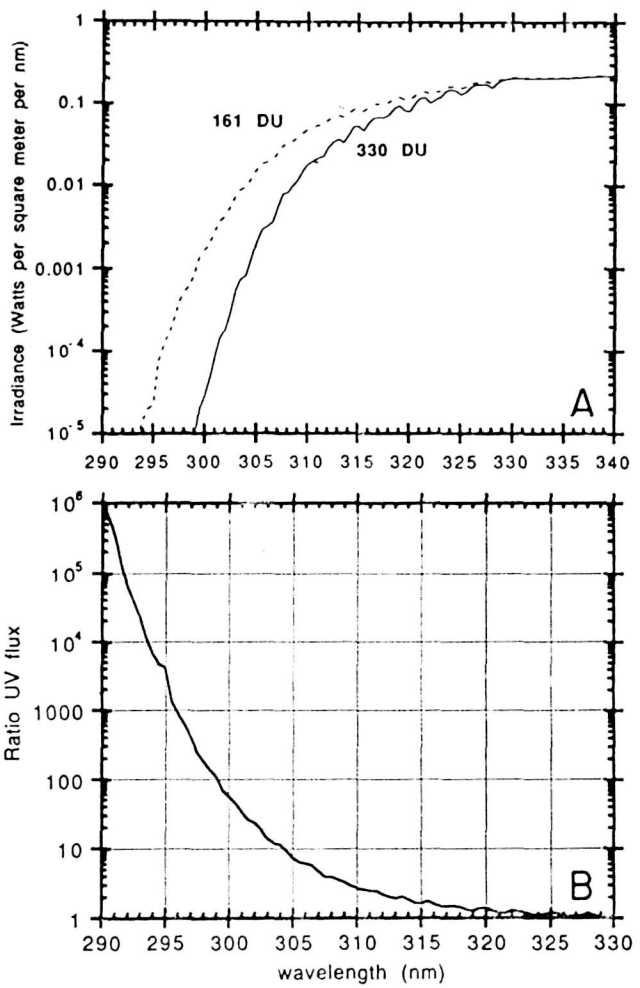

Fig. 2. Spectral UVR irradiance at local noon at McMurdo Station (77° 51' S) in the Antarctic as influenced by ozone concentrations in the atmosphere. A, Solid line: spectral UV-B radiation measured on October 20, 1988, with a 'normal' ozone concentration of 330 Dobson Units (DU); Dashed line: spectral UV-B radiation measured under the ozone hole (161 DU) on October 20, 1989, showing enhanced flux of shorter wavelengths. Data from the two days have been normalized at 340 nm. Note that ordinate values are on a log scale. B, Ratio of spectral UV-B radiation for the two days shown above (values under the ozone hole divided by values under normal ozone concentrations). Data from C. R. Booth.

Magnitude of Enhanced UV-B Radiation

The most important effect of ozone depletion in the stratosphere is to increase the fluence of UV-B radiation (Fig. 2A). The shorter the wavelength of the

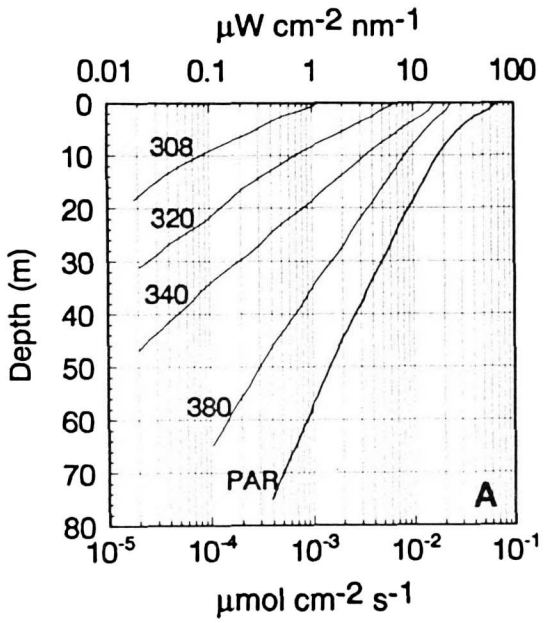

Fig. 3. Attenuation of UVR and PAR (close to local noon) in the upper water column at 61° S in January of 1992 at a station close to Elephant Island, Antarctica. Values for four UV wavelengths (use upper scale) and for PAR (lower scale) were recorded using a profiling UV-radiometer (model PUV-500, Biospherical Instruments Inc.).

enhanced radiation, the greater is the increased fluence at that wavelength relative to the fluence under normal ozone conditions (Fig. 2B). The biological impact of this enhanced short-wavelength UV-B radiation is, however, mitigated by the very low fluences at wavelengths below 310 nm (note the exponential ordinate in Fig. 2A) and the fact that these short wavelengths are rapidly attenuated in the water column as compared to the attenuation of UV-A radiation or PAR (Fig. 3). Figure 1A shows the extent to which the 1987 ozone hole in the Antarctic increased the irradiance of integrated UV-B radiation. It is seen that the elevated fluences were still lower than the fluence of UV-B at the time of the summer solstice. In recent years, however, the ozone hole has been larger and with greater depletion in the stratosphere, with the result that the UV-B fluences in September-October at Palmer Station (64° S) may come close to the late December values >2.0 Watts m^{-2}. It should be noted that the data in Fig. 1 and the high UV-B fluences reported at Palmer Station represent clear-sky days. Heavy cloud cover (which acts basically like a neutral density filter and attenuates both UVR and visible radiation) is very common in the Antarctic, however, with the result that clouds largely mask any effect of low ozone levels on incident UV-B fluences (Frederick 1997). It should also be noted that ozone also has some absorption in the visible region of the spectrum; low ozone concentrations will thus result in slightly higher levels of incident photosynthetically available radiation (PAR, 400-700 nm), which may be advantageous to plankton living in low-light environments, such as in or below sea ice (Arrigo 1994).

Action Spectrum for UVR-Induced Cell Injury

An action spectrum (also referred to as biological weighting functions) specifies the amount of damage incurred by any specific cell process (e.g., photosynthetic rate, DNA damage, etc.) as a function of the energy of the incident radiation at any wavelength (Coohill 1997). An action spectrum will thus be specific to the measured metabolic process for the organism being studied and for the conditions prevailing during the observation period. The most common action spectrum used by biological oceanographers shows the spectral impact per unit incident energy on the rate of photosynthesis as measured by CO_2 incorporation. Although there is considerable variation in these published action spectra (e.g., see Lubin *et al.* 1992; Neale *et al.* 1994; Helbling *et al.* 1992), they all show that the maximal photoinhibition per unit incident energy is at the shortest wavelength (<300 nm), with the response decreasing in an exponential fashion with increasing wavelength. These action spectra are quite similar to action spectra describing the effect of UVR on a variety of other metabolic processes in both aquatic and terrestrial plants.

It should be noted that much of the work with UVR in laboratory experiments have utilized lamps which emit UV-C radiation (<280 nm; usually centered close to 254 nm). As no measurable fluence of solar UV-C penetrates the atmosphere to reach the earth's surface, effects of UV-C will not be discussed

in the sections below.

Deleterious Effects of UVR on Organisms

In order to cause cellular damage, the energy in a photon of radiation must first be absorbed by some cellular component or molecule which is referred to as the *chromophore*. The chromophore may be an important cell constituent that may suffer direct damage from the absorbed energy, in which case it is also referred to as a *target* molecule (e.g., DNA; dimers may be formed upon absorption of UV-B radiation). The energy absorbed by a chromophore may also be used to produce energetic oxygen species (e.g., free radicals) which can in turn damage target molecules via *photodynamic* reactions. The oxidative stress thus experienced by cells may be expressed by adverse affects on many cellular components and metabolic pathways. Chromophores may also dissipate the absorbed energy as heat loss or coupled chemical reactions, in which case there may be no deleterious cellular effects.

The deleterious impact of UVR on microbial cells can be demonstrated for a great many cell components (e.g., nucleic acids, photosynthetic pigments, proteins, cell membranes), physiological pathways (e.g., photosynthesis, respiration, nitrogen fixation, nitrogen metabolism, ATP synthesis), and cell functions such as motility and phototactic movements (Häder 1997). For general reference to these studies, see books by Young *et al.* (1993), Tevini (1993) and Weiler & Penhale (1994). Only two of these cellular processes (photosynthesis and DNA function) will be briefly discussed below.

Effects of UVR on primary production

As photosynthetic reduction of CO_2 provides the food-base for all higher trophic levels, many studies have been restricted to describing the impact of UVR on short-term rates of photosynthesis by conventional radiocarbon techniques. Some studies have utilized artificial illumination in an attempt to mimic solar radiation under high and low ozone conditions, but it must be recognized that the exact

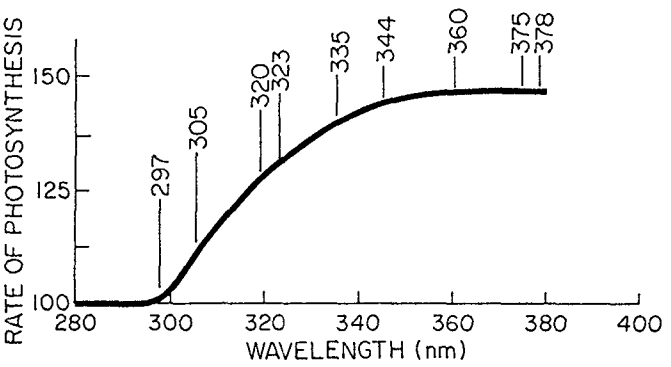

Fig. 4. Magnitude of inhibition of photosynthesis of Antarctic phytoplankton by solar UVR that has been selectively 'cut off' by use of glass or plastic filters. The numbers above the line indicate the spectral cut off of the various filters used in the experiments. The rate of photosynthesis in the quartz control vessels was set at 100%. The bold line, which has been generalized from all our data, represents the increase in photosynthetic rate relative to that in the quartz vessels.

spectral irradiance of sunlight cannot be duplicated, especially at various depths in the water column, and hence use of lamps introduces a degree of uncertainty in regard to extrapolating results to natural conditions in the water column.

If one uses sharp cut-off filters to eliminate spectral regions incident upon natural phytoplankton assemblages, it is possible to relate the magnitude of inhibition of photosynthesis to the wavelengths of UVR incident upon the phytoplankton cells (Fig. 4). From these data it is seen that UV-A radiation accounts for approximately 50% of the total inhibition by UVR, and that the shorter UV-B wavelengths (<305 nm) account for only a small proportion of the total inhibition. In spite of the fact that these short wavelengths are the most damaging per unit incident energy, the reason that they do not result in greater inhibition of photosynthesis is that the fluence of these short wavelengths is very low (see Fig. 2).

The data in Fig. 4 are indicative of expected photoinhibition by UVR close to the surface of the water column. For ecological purposes, it is necessary to determine the impact of such UVR on the integrated primary production in the entire euphotic zone, which is generally close to 90 m in Antarctic waters. Figure 5, which is based on many *in situ* experiments in Antarctic waters, shows that no inhibition

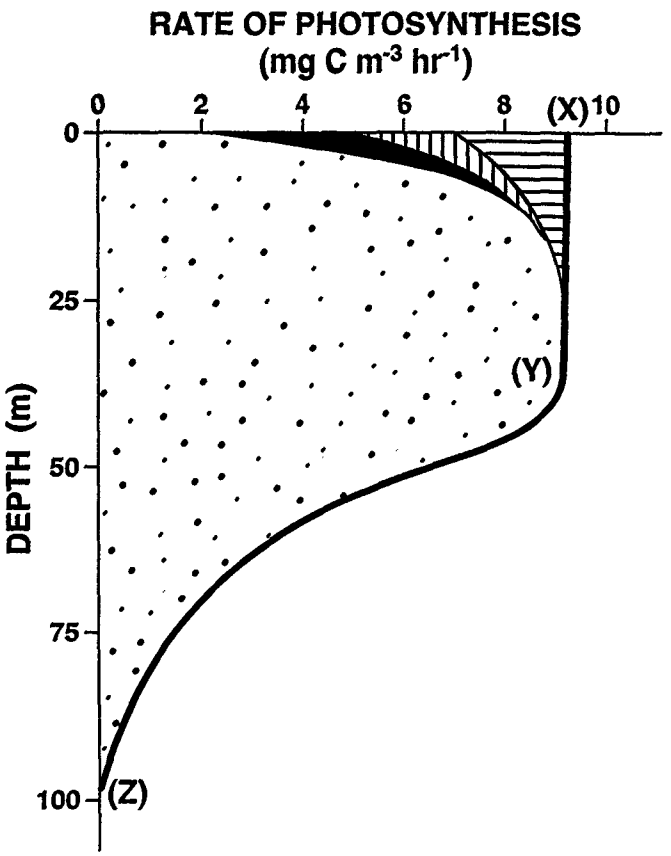

Fig. 5. Diagram to illustrate the inhibitory effect of UV-A (horizontal lines) and UV-B (vertical lines) radiation on rates of primary production under normal ozone conditions, and the impact of enhanced UV-B radiation (black area) under a well developed ozone hole in the Antarctic. The dotted area represents the integrated primary production not affected by UVR. In the depth range from (X) to (Y) photosynthesis is light saturated; from (Y) to (Z) photosynthetic rates are light limited.

by UVR can be detected below approximately 25 m, and that total inhibition by UV-B radiation (even under low ozone conditions) does not exceed the inhibition caused by UV-A radiation. Similar observations have been made by Smith *et al.* (1992). As net photosynthesis can be measured down to approximately 90 m, the total inhibition by UVR on integrated primary production has been estimated to be approximately 18% under normal ozone conditions of 350 DU. Under a well developed ozone hole of 150 DU, the additional loss due to enhanced UV-B radiation as been estimated to be approximately 3.8% of integrated primary production (Holm-Hansen *et al.* 1993a). The impact of UVR on Arctic phytoplankton at 70° N (Helbling *et al.* 1996) is quite similar to that described above for Antarctic phytoplankton.

The percent losses of primary production quoted above pertain to clear-sky days in areas experiencing the seasonal ozone depletion in October-November. As the ozone hole is mostly over land and sea-ice areas and only during two months each year, the loss of primary production due to the ozone hole will be much less than the above figure of 3.8%. Assuming a worst-case scenario, the loss of primary production in waters south of the Antarctic Polar Front has been estimated to be <0.20% (Holm-Hansen *et al.* 1993a).

Damage to DNA

Many studies with Antarctic phytoplankton have demonstrated structural damage to DNA (formation of DNA dimers) resulting from incident UVR radiation (Mitchell and Karentz 1993). The ecological significance of such damage determined in short-term experiments is, however, difficult to assess as all plant and animal cells have many mechanisms to repair such damage to DNA (Karentz 1994). Some of these enzymatic repair mechanisms are light-activated, whereas others can occur in darkness. Although most field studies have emphasized the importance of enhanced UV-B radiation in regard to formation of DNA dimers, it should be noted that photodynamic processes initiated by UV-A radiation (i.e., DNA is the target molecule, but is not the chromophore initially absorbing the radiation) can also cause functional DNA damage in some organisms (Setlow *et al.* 1993).

Reversibility of UVR-Induced Damage

Most studies referred to above have used short-term incubations (<one day), so that it is difficult to predict the impact of UVR on long-term growth and reproduction of phytoplankton. The question of whether or not UVR-damage is reversible is of great significance in regard to long-term impacts on rates of primary production. As phytoplankton circulate within the upper mixed layer (UML; generally around 40-50 m in Antarctic waters) of the water

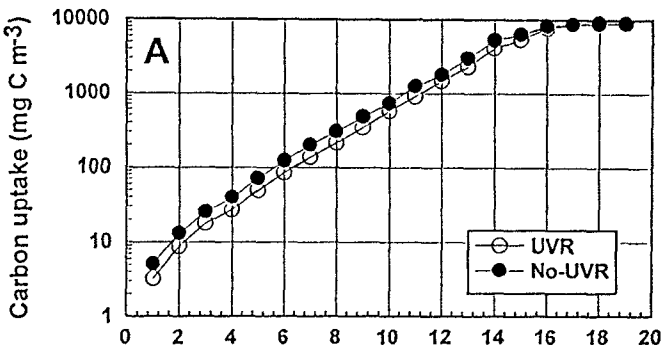

Fig. 6. Rates of CO_2 incorporation in cultures of natural Antarctic phytoplankton assemblages when exposed to just visible radiation (solid circles) and when exposed to visible radiation + UVR (empty circles). From Villafañe *et al.* (1995).

column, if UVR near the surface resulted in permanent cellular damage or loss of viability, the impact of UVR would be pronounced throughout the entire UML. If, however, the cell damage is quickly reversible, then the impact of UVR would be evident only in the upper portion of the UML as illustrated in Fig. 5. Preliminary experiments in the Antarctic have indicated that the inhibition of photosynthesis by UVR is reversible, and also that phytoplankton have adaptive mechanisms which can minimize the extent of UVR-induced damage under conditions of prolonged exposure to UVR (Fig. 6). Data in this figure show that UVR inhibits CO_2 incorporation by approximately 50% at the end of the first day, but that the rates of photosynthesis (with or without UVR) are about the same during the next two weeks.

Cellular Mechanisms to Minimize Damage by UVR

The many ways in which phytoplankton can minimize damage by UVR include (i) synthesis of UV-screening compounds which dissipate the absorbed energy without damage to cell constituents (Dunlap *et al.* 1986), (ii) synthesis of enzymes to repair DNA damage (Karentz 1994), (iii) movement and orientation of organelles within cells, (iv) phototactic movements of organisms away from the light source (Häder and Häder 1989), and (v) synthesis of enzymes or compounds to remove energetic oxygen species (Lesser and Stochaj 1990). The significance of these 'UVR defense mechanisms' to the dynamics of the microbial food web in polar waters is not well understood. In regard to the extent to which phytoplankton can adapt to high fluence of UVR, it is of interest to note that phytoplankton in tropical waters, which are exposed to higher fluences of UVR than ever encountered in polar waters, do not seem to be inhibited by direct solar radiation (Helbling *et al.* 1992).

Major Problems which Require Further Study

As can be seen from the above sections, our understanding of the impact of solar UVR on marine ecosystems in the polar regions is limited to short-term studies, the results of which are difficult to extrapolate to long-term functioning of the food web. Problems that require further studies include (i) the basic mechanism(s) which result in inhibition of photosynthesis, (ii) the degree to which any UVR-induced damage is reversible under normal environmental conditions, (iii) the extent to which cells can adapt (i.e., acclimate) to increasing fluences of UVR so as to minimize UVR-induced damage, (iv) the impact of differential species sensitivity on the size spectrum and chemical composition of the natural phytoplankton assemblages, and (v) the effect on the dynamics of the food web resulting from differential sensitivity to UVR of phytoplankton as compared to grazing heterotrophic organisms.

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