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Review

Ecological considerations of Antarctic ozone depletion

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Abstract: Springtime ozone depletion over Antarctica has been observed for over a decade. Associated with ozone depletion is an increase in the levels of biologically harmful ultraviolet-B (UV-B) that reach the earth's surface, a situation that has prompted much controversy about the ecological effects of this atmospheric phenomenon on Antarctic ecosystems. A major hindrance to assessing the ecological impact is lack of appropriate data on Antarctic systems before the present ozone depletion cycle began. In addition, certain physical features of the Antarctic environment (clouds, snow and ice) and the UV-B photobiology (repair processes and protective strategies) of endemic species can alter the potential biological effects of this environmental stress in, as yet, undetermined ways. Increases in incident UV levels will most likely result in changes in the taxonomic structure of communities. The effects of these changes on net productivity and trophic dynamics cannot be accurately assessed without quantifying ambient doses of UV and characterizing the UV photobiology of individual species. Both the physical features of the springtime environment and the biological responses of endemic species must be considered in future research efforts to evaluate the biological consequences of the Antarctic ozone hole.

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Introduction

An annual pattern of ozone depletion over Antarctica has resulted in increased ultraviolet-B (UV-B) intensities each spring for the past decade and has led to much concern and discussion as to the effects of elevated UV-B levels on Antarctic ecology (Roberts 1989, Karentz 1990, Voytek 1990). The extent of ecosystem modification that has already taken place or that may be caused by future ozone depletion events is not known. There are certain physical features of the Antarctic environment (clouds, snow, ice, etc.) that may modify UV-B exposure, so that incident intensities and in-water transmission may not be accurately assessed from atmospheric models. In addition, little is known about the UV-B photobiology of endemic species. Organisms may have repair processes and protective mechanisms that can alter potential biological effects. These physical and biological factors must be taken into account if we are to accurately assess the effect of springtime ozone depletion on Antarctic ecosystems.

The Antarctic ozone hole

The ozone hole was first observed in the late 1970s and has become a predictable event in the springtime atmosphere over Antarctica (Farman *et al.* 1985, Solomon & Schoeberl 1988). Air pollutants and the physical properties of the springtime Antarctic atmosphere such as the polar vortex, unique characteristics of polar stratospheric cloud formations, cold temperatures, and other physical factors combine to produce the ozone depletion that creates the ozone hole (Hofmann 1989).

Depletion takes place within the polar vortex during September and October, and minimum levels can be sustained for several weeks. The depletion zone disappears when the polar vortex dissipates and ozone concentrations equilibrate with surrounding air masses. The extent of ozone depletion and the area of the depletion zone vary greatly from year to year. Decreases of over 50% in column ozone and up to 90% at specific altitudes have been measured (Hofmann *et al.* 1987). Before 1978, springtime ozone levels for the south polar regions averaged 300 Dobson units (DU) or higher. During 1987, the year of the lowest ozone values recorded over Antarctica, an ozone layer with minimum values of less than 125 DU covered nearly 50% of the continent, and the edges of the 250 DU zone reached the southern tip of South America, extending beyond the northern boundary of the Polar Front (Antarctic Convergence) (Fig. 1). Thus, the entire Southern Ocean was subjected to increased levels of incident UV-B radiation.

General aspects of UV-B photobiology

UV wavelengths are subdivided into four categories (Jagger 1985): vacuum UV (<200 nm), UV-C (far UV, 200–280 nm), UV-B (middle UV, 280–320 nm), and UV-A (near UV,

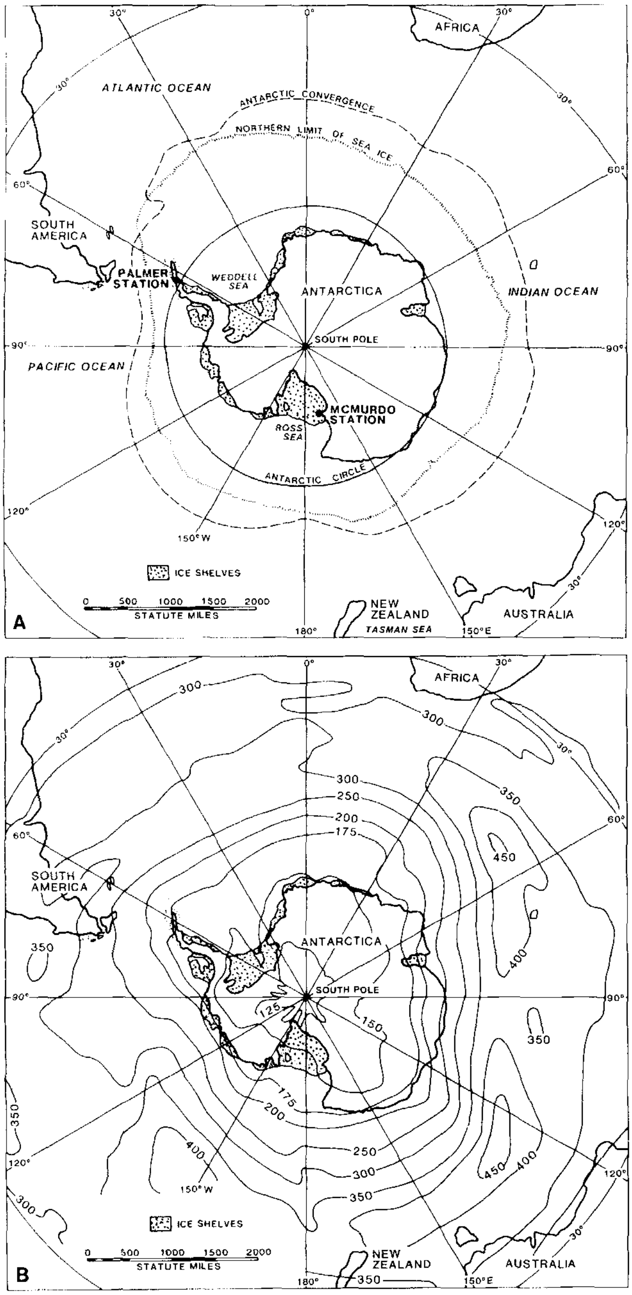

Fig. 1. (A) Map of Antarctica, the Southern Ocean, and surrounding continents. (B) Atmospheric ozone profiles over Antarctica from October 5, 1987 (modified from Krueger *et al.* 1989).

320–400 nm). Vacuum UV and UV-C are completely absorbed in the atmosphere and do not reach the earth's surface. UV-A is biologically both harmful and beneficial, but the transmission of these wavelengths through the atmosphere is not significantly affected by ozone concentrations. UV-B is a biological hazard, and UV-B wavelengths are differentially absorbed by stratospheric ozone (Dahlback *et al.* 1989). It has been calculated that with a 65% decrease (from 315 to 110 DU) in column ozone, radiation at 315 nm is increased 2.2-fold, whereas radiation at 305 nm is increased by 14-fold (Frederick & Snell 1988). The biological effects of UV-B are strongly wavelength dependent, even within a range of a few nanometers. For example, light at 295 nm has 1000 times the erythemal (sunburning) effect on human skin as light at 320 nm (Moseley 1988). Therefore, small changes in ozone concentration result in disproportionate changes in the biological harmfulness of incident UV-B radiation.

Direct mutagenic and lethal effects of UV-B exposure result from damage to DNA (Harm 1980). There are three known cellular repair mechanisms for UV-damaged DNA: photoreactivation, excision (dark) repair, and recombination repair (Cleaver & Kraemer 1989). In addition to genetic damage, other effects of UV exposure are related to absorption by RNA, proteins (enzymes, histones, hormones etc.), pigments and other biological molecules (Caldwell 1981). UV absorption can initiate changes in membrane structure and/or the chemical environment of cells, interfering with normal metabolic processes (respiration, photosynthesis, etc.) and resulting in decreased growth, impairment of reproduction, or death. The degree of UV sensitivity exhibited by an organism is related to the number and efficiency of its repair systems as well as the existence of avoidance strategies (behavior modification and physical protection from UV exposure). Dose rates and duration of exposure must also be considered in assessing biological damage and capabilities for repair.

Incident UV-B in Antarctica

Because of large solar zenith angles, light travels a longer path length through the atmosphere in polar regions than at other latitudes, resulting in less radiation reaching the earth's surface. The ozone layer is usually thicker at the poles than at equatorial latitudes, further reducing the intensity of incident UV-B wavelengths. Antarctic ozone depletion is initiated in early spring when the sun begins to rise above the horizon and day lengths south of the Antarctic Circle begin to increase from a winter minimum of 0 hours to the summer maximum of 24 hours.

Through the use of radiative transfer models with inputs of ozone concentration, solar output, surface albedo, and other physical factors, it has been estimated that springtime levels of incident UV-B under the ozone hole are comparable to Antarctic midsummer intensities that are filtered through a normal ozone column (Frederick & Snell 1988). Actual measurements of incident UV irradiances in Antarctica were not made until early in 1988, when the U.S. National Science Foundation installed UV spectroradiometers at South Pole (90° S), McMurdo (77° 51'S 166° 40'E), and Palmer (64° 46'S 64° 03'W) stations. Incident UV-B irradiances can now be quantified and wavelength ratios calculated (Lubin *et al.* 1989a, b).

Day-to-day variations in UV-B irradiances are related to changes in weather (clouds) that reduce the total amount of solar radiation that reaches the earth's surface. During spring 1988, there was considerable fluctuation of daily irradiances of UV-B wavelengths (Fig. 2A); however, elevated values were evident during October and November, coinciding with the period of maximum ozone depletion (Fig. 3). Ozone depletion over the Antarctic was not as severe in 1988 as in 1987; however, the distinct temporal pattern of changes in ozone concentration was evident. Ozone gradually increased from mid-October through November. These data represent the repetitive seasonal pattern that has occurred since the late 1970s. Under constant ozone values of 300 DU or higher, UV-B irradiances would have increased monotonically with time, correlating closely to daily decreases in solar zenith angle.

When the ratio of high energy UV-B (298–303 nm) to longer wavelengths (342–347 nm) from the UV-A region are plotted against time, the temporal shift in wavelength distributions is more clearly apparent (Fig. 2B). These data reflect the spectral absorption characteristics of ozone. As ozone concentration increases, the ratio of UV-B to longer wavelengths decreases. This aspect of ozone depletion is critical in terms of an increased biological hazard, as the wavelength complement of incident UV shifts towards the shorter, more biologically harmful wavelengths.

There are no data available to compare ground-level UV intensities from previous decades with present-day irradiances. However, the new data set is providing valuable information for development of atmospheric models that will permit a more precise estimate of historical UV fluxes based on the existing long-term data sets of ozone concentrations and weather observations.

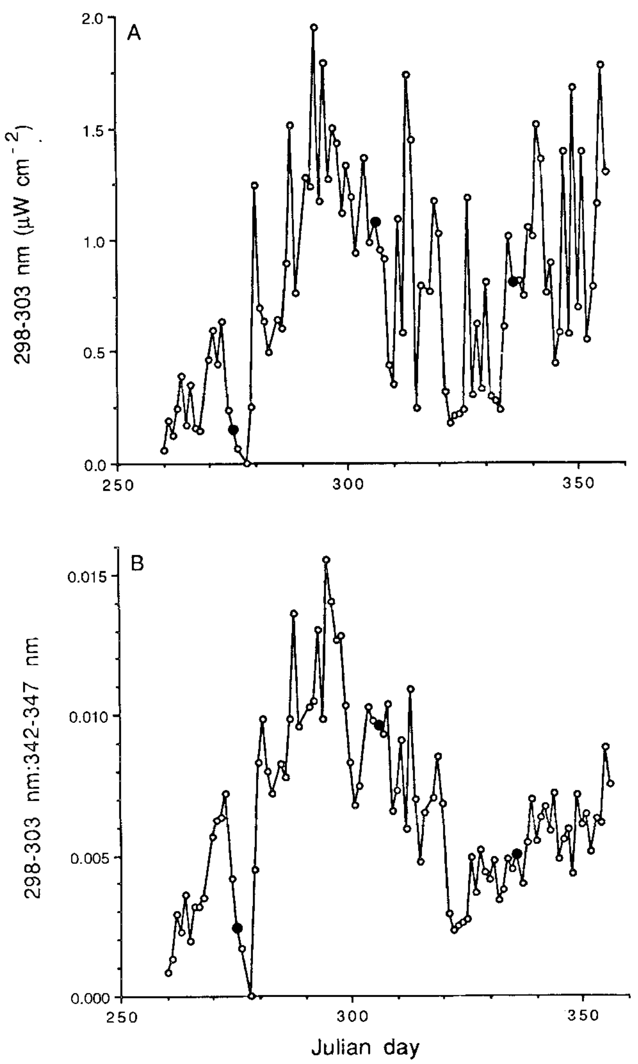

Fig. 2. a) Integrated noon UV-B irradiances (298–303 nm) at Palmer Station, Anvers Island, Antarctic Peninsula, during spring 1988. Data were obtained from the U.S. National Science Foundation UV Monitoring Program. Filled symbols indicate 1 October, 1 November and 1 December.

b) Ratios of UV-B (298–303 nm) to UV-A (342–347 nm) wavelength bands for noon data collected at Palmer Station during spring 1988.

Antarctic life forms

There is little terrestrial life in Antarctica (Laws 1984, Bonner & Walton 1985). Yeast and bacterial species are found in all habitats, whilst the distribution of mosses and lichens is more limited; endolithic bacteria, fungi, algae, and lichens have been found even in the extremely harsh environment of the interior Dry Valleys (Weller *et al.* 1987). Unicellular algae are the basis for communities in and on the snow, creating patches of pink, yellow, or green and supporting a variety of associated bacteria and microfauna. Visible terrestrial life in Antarctica is mostly concentrated on the Antarctic Peninsula, an area that has a relatively warmer, maritime climate compared with the rest of the continent. Lichens and mosses flourish, and two species of vascular plants can be found on in a few areas of the Peninsula and its related maritime islands (Longton 1985). Hidden within these plant communities are a variety of primary and secondary consumers that include protozoans and small invertebrates (Clarke 1985).

There are no terrestrial vertebrate animals native to Antarctica; those found on land come from the sea. Aside from the largely coastal vegetation and the breeding visits of birds and seals, Antarctic biology also has an important aquatic component. Freshwater and saline lakes on the continent support a variety of organisms and go through seasonal freezing and thawing cycles; however, most Antarctic species are marine.

There are four major marine community types in Antarctica: intertidal, benthic (bottom), epontic (ice), and pelagic (water column). The marine organisms that make up these communities are similar to inhabitants of marine systems at other latitudes, although there is a high degree of endemism of Antarctic species (White 1984). The epontic community is a unique association of microalgae, bacteria, protozoans,

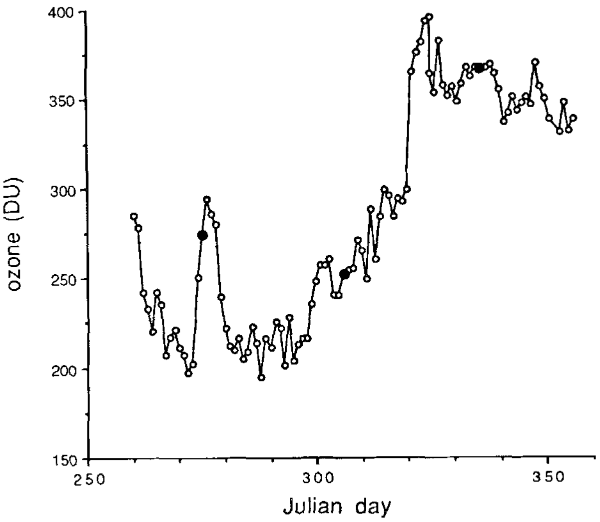

Fig. 3. Stratospheric ozone concentrations over Palmer Station during spring 1988. Data were obtained from Krueger *et al.* (1989) and Krueger (pers. comm.). Filled symbols indicate 1 October, 1 November and 1 December.

and invertebrates that inhabit the interstitial brine-filled spaces between crystals of sea ice. In the spring, ice communities can form extensive patches of high productivity in areas where there is little biomass or productivity in the water column.

Environmental factors that affect UV exposure in Antarctica

Clouds

Cloud estimates in Antarctica are difficult to make and data are unusually subjective in comparison to other parts of the world. Nevertheless a clear general problem is obvious. During much of the year, skies over much of Antarctica and its surrounding seas are overcast (Schwertdfeger 1970) but there are both seasonal and geographical differences. The mean percentage cover in early spring varies from 39 to 50% on the plateau, and 67% in coastal East Antarctica to 83% in coastal West Antarctica. In general the circumpolar band of maximum cloud is north of the belt of lowest pressure at sea level and south of the belt of strongest westerly winds. Coastal areas have the highest cloud cover, as for instance at Palmer Station where the average number of cloudy days per month at Palmer Station during August, September and October 1987 was 21, and an additional 8 days per month were partly cloudy (U.S. National Science Foundation 1987). These weather conditions are typical for springtime skies. This extensive cloud cover serves to mitigate the impact of UV stress on Antarctic communities which are mostly coastal, by reducing radiation intensity but has little effect on spectral quality (Frederick & Snell 1988, Lubin *et al.* 1989a, b).

Snow

During spring when ozone levels are at their lowest, terrestrial communities are buried under several centimetres to several metres of snow. Although white light is transmitted through snow layers and can support a low level of photosynthesis (Curl *et al.* 1972), UV wavelengths are rapidly attenuated and snow provides UV protection. Snow surfaces have very high albedos, and as water content and density of snow increase, the absorption of radiation decreases, so that age and wetness of snow can significantly influence reflectance and transmission of solar radiation (Curl *et al.* 1972, Blumthaler & Ambach 1988). Without snow cover, the snow algae, moss, and lichen communities have direct solar exposure and are subjected to the highest UV doses.

Ice

The Southern Ocean accounts for 10% of the world's ocean area (Heywood & Whitaker 1984). Eighteen percent of the Southern Ocean is permanently covered by floating glacial ice sheets, and an additional 55% can be covered by sea ice at the end of winter (Heywood & Whitaker 1984, Foster 1984) (Fig. 1A). The presence of an ice layer is an important factor in mediating the effect of UV-B on Antarctic marine ecosystems.

Under 1–2 m of ice the euphotic (visible light) zone can extend to at least 3 m (Palmisano *et al.* 1986). Few measurements of UV intensity and spectral distributions have been made under ice, but transmission of visible light through sea ice has been measured (Weller 1969, Buckley & Trodahl 1987a, b, Trodahl *et al.* 1987). Scattering and absorption of light by sea ice is a function of albedo, salinity, and the vertical heterogeneous structure (grain size, density, and water content) of the ice layer. The spectral distribution and intensity of light reaching the water column is further modified by ice communities. Mathematical modeling of UV light transmission through sea ice suggests that the physical characteristics of new ice during early spring enhance the transmission of UV wavelengths by about 20% compared with older ice, which is more turbid (Trodahl & Buckley 1989). This calculation is based on an ice layer without snow cover. Considering the high albedo of snow surfaces, sea ice with snow probably provides a substantial filter for UV-B wavelengths. Indirect evidence for UV protection by an ice layer can be inferred from observations made by Palmisano *et al.* (1986), who studied the photosynthetic physiology of *Phaeocystis pouchetii*, a common Antarctic phytoplankton bloom species, as populations were transported from open water to under the annual ice shelf. While under the ice, *Phaeocystis* was more efficient in using lower light levels for photosynthesis without increasing cellular chlorophyll content. This response may be due to reduced exposure to harmful UV wavelengths that were filtered by the surface ice layer.

The formation of sea ice around the continent is irregular and varies greatly from year to year. Also, the circumpolar ice pack is not continuous. Fractures of various sizes occur, ranging from leads of 1–10 km in width to polynyas (ice-free areas) that can encompass hundreds of thousands of square kilometers (Gordon & Comiso 1988). Polynyas are considered to play a major role in the transfer of heat energy between the ocean and the atmosphere, affecting both global temperatures and mixing processes in the Southern Ocean. The formation of polynyas results in exposure of large areas of the ocean surface to direct solar radiation.

Initiation of spring phytoplankton blooms has been associated with certain hydrographic characteristics of open water areas adjacent to ice edges (Smith & Nelson 1985, Sakshaug 1989). Sea ice organisms may be seeding the water column to produce the spring bloom; alternatively, the bloom may be initiated by the low concentration of cells that have wintered under the ice. Regardless of the mechanism, extensive patches of phytoplankton are found in early spring in the open waters of the marginal ice zone, polynyas, tidal cracks, and other gaps within the ice pack. The localization of this concentrated food source can attract herbivores and their predators, bringing a wide variety of organisms into open water areas and exposing them to higher UV levels.

Coastal polynyas can extend up to 100 km from the coast (Gordon & Comiso 1988). These polynyas expose intertidal areas where the fast ice pulls away from the shoreline. Daily tidal changes and winds can cause a scouring of intertidal habitats as ice moves back and forth across intertidal surfaces. Therefore, in the early spring, as organisms begin to colonize the resulting bare areas of the intertidal zone, they are fully exposed to maximum UV levels, especially at low tide. During the period of the ozone hole, elevated UV doses may disrupt the established temporal patterns of intertidal species succession and population development. Once a macroalgal community develops, many organisms benefit from the protection provided by this canopy layer, but the initial effects of direct exposure may be critical.

Water column

The transmission of UV within the ocean has not been well documented even though evidence of UV transmission to a depth of at least 20 m was reported forty years ago (Jerlov 1950). Since that time few actual measurements of in-water UV intensities have been made (Smith & Calkins 1976, Smith and Baker 1979, Smith *et al.* 1980); most estimates of UV penetration have been calculated through the use of mathematical models that require inputs of incident radiation and various hydrographic parameters (Zaneveld 1975, Smith & Tyler 1976). Although a number of studies have pointed out the biological effects of UV on marine organisms (Calkins 1982), UV radiation has only recently been considered a significant environmental stress in biological oceanographic studies. The classic example of this oversight is the standard methodology used for estimates of *in situ* photosynthetic carbon production. These measurements have traditionally been carried out in bottles made from borosilicate, a form of glass that screens out UV-B and thereby provides an overestimate of productivity. Up to a 65% decrease in production was observed when phytoplankton were incubated in UV-transparent vessels instead of UV-B-filtering glass (Lorenzen 1979, Maske 1984).

A major reason for the lack of in-water UV-B measurements is that standardized instruments are not generally available, and the wavelength dependency of biological responses requires that data on spectral quality be collected within the water column (Kullenberg 1982, Smith 1989). Broadband photodetectors do not provide adequate information for complete biological assessment. During the spring of 1988, the transmission of biologically active UV-B wavelengths was routinely monitored in coastal Antarctic waters by means of a dosimeter system based on a UV-sensitive bacterial cell line (Karentz & Lutze 1990). The results from this work indicated that during the springtime period of ozone depletion, biologically active wavelengths of UV-B consistently penetrated to depths of 10 m. On some sample dates, biologically harmful wavelengths of UV-B were detected to 20 m.

The initial limitation to the penetration of light in the Southern Ocean, especially at wavelengths greater than 310 nm, is the large solar zenith angle that results in an equally large angle of incidence, increasing reflectance and minimizing the amount of light entering the water column. Atmospheric and sea surface conditions affect the intensity and spectral composition of the incident light, and many hydrographic factors affect penetration through the water column. These include the spectral characteristics of dissolved substances, the concentration of particulate matter, and the density and composition of the plankton. During the period of the ozone hole, Antarctic waters are extremely transparent owing to low concentrations of cells, particulates and dissolved substances; therefore, UV penetration is maximized.

Two U.S. expeditions to the Antarctic have measured carbon uptake of phytoplankton to assess the effect of UV-B on photosynthesis and primary production in the Southern Ocean. In one set of experiments, natural phytoplankton populations were held in large outdoor tanks under UV-B light regimes of ambient UV, enhanced UV or no UV (El-Sayed *et al.* 1990a, b). Results indicated that ambient and enhanced UV levels decreased carbon uptake relative to treatments that did not include solar UV radiation. Changes in pigment concentrations resulting from the various UV exposures were also investigated; it was found that the phytoplankton do respond to UV stress by shifting pigment content of cells (Bidigare 1989). A second study of natural phytoplankton populations incubated at specific depths within the water column under ambient light with or without filtration of UV-B showed that UV-B inhibited photosynthetic production most significantly in the upper few meters of the water column; no effects were detected below 20 m (U.S. National Science Foundation 1989).

Mixing is an important factor to be considered in determining the UV dose received by an individual organism within the water column (Kullenberg 1982, Bidigare 1989). Except for a few buoyant organisms and floating eggs and larvae that remain at the surface, most pelagic organisms do not remain at fixed depths but are carried up and down through the water column by various physical processes. Shallow mixing layers are established within 30–50 km of the ice edge as melt water stratifies and stabilizes the water column. This phenomenon facilitates the development of the ice edge phytoplankton bloom (Sakshaug 1989, Smith & Nelson 1985). The depth of the mixed layer affects the availability of light for photosynthesis as well as the duration and intensity of UV exposure. Estimated times for mixing from the surface to the bottom of a 10-m surface layer can range from 30 minutes to several hundred hours (Denman & Gargett 1983). Furthermore, many zooplankton species undergo an active vertical migration in and out of the euphotic zone on a diurnal basis. Therefore, UV exposure cannot be determined by single-depth assessments of UV influence, and residence time within the range of the UV photic zone must be taken into account. The mixing aspect may greatly modify the effect of UV; certainly, reduced and intermittent exposure times are less harmful than constant irradiation. Transport to lower depths during daylight hours allows time for repair without additional accumulation of photoproducts, thus minimizing instantaneous levels of damage.

The transmission of UV radiation through the water column catalyses a variety of photochemical reactions that can significantly alter water chemistry. Chief among these is the generation of peroxides and free radicals. Laboratory studies in mammalian cell systems have shown that UV irradiation of liquid medium near cells reduces the rate of DNA synthesis and that this effect can be reversed by the protective action of catalase (Dendy *et al.* 1967). Research into UV effects on aquatic organisms has focused on direct exposure; the effects of UV-related changes in water chemistry have been overlooked and need to be investigated (Mill *et al.* 1990).

Biological factors that mitigate UV stress in Antarctic organisms

Sea birds, penguins, and seals receive the full impact of UV exposure when on land, and time spent out of the water is usually related to breeding habits. Nests are built on the ground among rocks, and nesting birds have full exposure to solar UV. Eggs are protected by the body of the incubating parent and a UV-opaque shell. For birds and seals, feathers and fur should provide adequate protection of the skin from UV exposure, but eyes and noses may be affected. UV thresholds for corneal damage in Antarctic birds (penguins and skuas) are higher than those of domesticated fowl (chickens and ducks) and this has been attributed to adaptation for prevention of snow blindness (Hemmingsen & Douglas 1970). Little information is available for speculation on the effects of increased UV levels. There is evidence of UV-induced carcinomas in agricultural livestock that have been translocated from temperate to tropical areas where they receive higher daily doses of UV (Daniels & Johnson 1987); however, extrapolation to Antarctic mammals and the ozone hole phenomenon is tenuous.

Algal, invertebrate, and other vertebrate marine species also have various degrees of protection provided by outer cell layers, exoskeletons, skin, and scales. These protective features are species-specific. Under equivalent UV exposures, actual biological doses received will depend on the differential UV screening properties of external layers. A recent survey of Antarctic invertebrates and algae (Karentz *et al.* 1990) has shown that these organisms contain UV-absorbing mycosporine amino acids (MAAs) similar to those of tropical and temperate marine species (Dunlap *et al.* 1989). UV-absorbing substances have also been observed in Antarctic marine phytoplankton (Mitchell *et al.* 1989, 1990, Vernet *et al.* 1989). These compounds may act as natural sunscreens, protecting internal organs and/or organelles from excessive doses of UV. There is some indication that the concentration of MAAs in corals and algae is related to UV exposure history since decreased concentrations have been measured in organisms collected at lower depths (Sivalingham *et al.* 1976, Dunlap *et al.* 1986). A similar trend has been recorded for Antarctic phytoplankton (Vernet *et al.* 1989). Biochemical protection from UV exposure appears to be a common strategy, but relatively little work has been completed on the ecological aspects of UV-blocking compounds.

Preliminary work on the responses of Antarctic bacteria and phytoplankton species to UV exposure suggests that photoreactivation is a primary means of repairing UV-induced damage to the DNA and ensuring survival of these organisms (Karentz 1988, 1989, Karentz *et al.* 1990). In Antarctic marine diatoms, a wide range of UV sensitivity occurs between species and laboratory studies have shown that there is nearly a 100-fold variation in the amount of DNA damage induced by UV exposure. No information is available on photoproduct induction and repair under ambient UV levels in natural systems. A major obstacle to this line of research is appropriate methodology. Most laboratory experiments on UV photobiology are not suitable for transfer into the field. New approaches and modifications of current methods are required to address this problem properly.

Antarctic communities have high species diversity comparable to other geographic areas, and species are widely distributed (Clarke 1985, Weller *et al.* 1987). Marine animals are large and abundant; they have long life-spans with slow growth and maturation (White 1984). Antarctic species are derived from temperate stock populations; it is estimated that marine biota of the Southern Ocean have evolved over 50 million years. During this time they have responded to the gradual cooling of ocean waters and have developed adaptations to ensure survival under low temperature stress (Clarke 1985). Many Antarctic marine fauna are brooders and do not have pelagic larval stages like many of their temperate and tropical counterparts. This particular evolutionary adaptation to the cold polar environment also offers considerable protection to eggs and embryos from excessive UV exposure. Because polar species have evolved from organisms originally inhabiting lower latitudes, genetic information required for repair and protective mechanisms related to UV exposure may have been retained within their genomes.

In contrast to the marine ecosystem, ice and snow have receded from coastal terrestrial areas of Antarctica only in the last 12,000 years. This is a short time on an evolutionary scale, and we can presume that terrestrial organisms have retained UV defenses found in the more northerly organisms from which they were derived. Weller *et al.* (1987) have summarized the general aspects of biological adaptation in Antarctic species relative to evolution from earlier environments.

Conclusions

A major consideration (that generally goes unmentioned) in evaluating the ecological impact of springtime ozone depletion is that the ozone hole has now been in existence for over a decade. Any biological and subsequent ecological effects that can result have already been initiated. This is especially true for organisms with short generation times such as the bacterioplankton and phytoplankton, in which population response to environmental stress can occur on the order of hours to a few days. Springtime phytoplankton communities in the Southern Ocean follow classic species successional patterns found in other ocean areas. Dominance is continually shifting between species, and the taxonomic structure of the plankton community undergoes major changes during the course of bloom initiation, maintenance and decline. The ozone hole has added an environmental stress that has most certainly already modified existing successional sequences.

Analyzing the genetic and ecological effects that increased UV exposure may have had on Antarctic organisms is hindered by the lack of UV photobiological research conducted before the development of the ozone hole. An intensive literature search may be warranted to determine possible trends or differences between data sets from the 1980s and those from previous years, but variations in locations of research, annual patterns of species succession, and methods used by different researchers greatly complicate a study of this type (Heywood & Whitaker 1984). What is really needed is a molecular indicator of UV exposure history that could be used on paleological samples collected in ice and sediment cores. Even here, resolution may be a significant problem, as we are dealing only with a ten year old perturbation rather than changes spanning geologic time.

An exciting new development here has been the work by Markham *et al.* (1990) on historical levels of flavonoids in mosses. Levels of flavonoids in dried moss samples (*Bryum argenteum*) from the Ross Sea area, collected between 1957 and 1989, were compared with stratospheric ozone concentrations over South Pole. Flavonoid concentrations increased as ozone levels decreased. Since flavonoid synthesis is directly related to UV-B exposure, this approach might allow extant herbarium material to provide more comprehensive coverage of ozone depletion patterns over all of Antarctica. Indeed, Markham and his co-workers have identified a mid-1960's anomaly with unexpectedly high levels of flavonoids which corresponds to a short-term fall in ozone concentration over South Pole.

It must also be emphasized that the springtime increase in UV over Antarctica is a relative temporal shift, not an increase in the maximum UV irradiance that has ever reached the surface. Therefore, the biological consequences of increased UV-B in Antarctica do not rest entirely upon the ability of organisms to cope with UV exposure, but on their ability to cope with summer levels of UV occurring during spring. With the occurrence of the ozone hole, the seasonal gradient of increasing UV levels no longer exists; the full summer complement of UV can be experienced during the initial period of illumination that occurs right after winter darkness. This is an important consideration because, although there is a large body of literature on the effects of UV on organisms, extremely little is known about the adaptive responses of marine organisms in the field. Nor do we know how much damage is sustained and how much can be repaired under Antarctic conditions of ozone depletion, short day lengths, and freezing ambient water temperatures. The effect of shifted ratios of UV-B to higher wavelengths on the balance of biological damage to photoreactivation repair is also not known. These aspects of UV photobiology need to be studied in field populations. We have very little information about the range of possible UV protective and repair mechanisms that can occur in nature or about the possible adaptive responses of marine populations to UV stress. And we know the least about Antarctic organisms.

A large degree of interspecies variation in the efficiency of DNA repair, dose responses, and occurrence of UV-absorbing substances has been observed in the responses and protective mechanisms of the few Antarctic species studied. Interspecies differences in the ability to cope with UV are perhaps the most crucial factor in assessing the ecological implications of ozone depletion at any latitude. Increased UV-B will cause shifts in the taxonomic structure of communities that may be accompanied by changes in the availability and nutritional value of primary food sources, ultimately altering the transfer of energy between trophic levels (Worrest *et al.* 1978). We do not have sufficient information to model any such scenarios. At this time it is as likely that UV-sensitive species will be replaced by more resistant taxa that have comparable food value and are as easily captured and eaten, as that shifts caused by UV stress will result in inedible replacement species or a significant decline in productivity. To evaluate the ecological implications of continued springtime UV-B stress on species associations and trophic interactions, research efforts need to focus on the quantification of UV exposure as modified by the Antarctic environment and on the UV photobiology of individual species. Direct investigation of UV-B effects on terrestrial, freshwater and marine ecosystems and species is a feature of current US, UK and Swedish programmes.

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