

Influence of Ozone-Related Increases in Ultraviolet Radiation on Antarctic Marine Organisms¹

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SYNOPSIS. Every spring for the past two decades, depletion of stratospheric ozone has caused increases in ultraviolet B radiation (UVB, 280–320 nm) reaching Antarctic terrestrial and aquatic habitats. Research efforts to evaluate the impact of this phenomenon have focused on phytoplankton under the assumption that ecosystem effects will most likely originate through reductions in primary productivity; however, phytoplankton do not represent the only significant component in ecosystem response to elevated UVB. Antarctic bacterioplankton are adversely affected by UVB exposure; and invertebrates and fish, particularly early developmental stages that reside in the plankton, are sensitive to UVB. There is little information available on UV responses of larger Antarctic marine animals (*e.g.*, birds, seals and whales). Understanding the balance between direct biological damage and species-specific potentials for UV tolerance (protection and recovery) relative to trophic dynamics and biogeochemical cycling is a crucial factor in evaluating the overall impact of ozone depletion. After more than a decade of research, much information has been gathered about UV-photobiology in Antarctica; however, a definitive quantitative assessment of the effect of ozone depletion on the Antarctic ecosystem still eludes us. It is only obvious that ozone depletion has not had a catastrophic effect in the Antarctic region. The long-term consequences of possible subtle shifts in species composition and trophic interactions are still uncertain.

INTRODUCTION

Environmental concerns about ozone depletion arise from the fact that the ozone layer in Earth's atmosphere is an effective filter for the biologically harmful ultraviolet B radiation (UVB, 280–320 nm) present in sunlight. Even without ozone depletion, UVB penetrates into surface waters of the oceans and is a daily environmental hazard to many marine organisms. Therefore, increased ultraviolet radiation associated with recorded and predicted decreases in global stratospheric ozone is expected to have ecological consequences in marine communities. The most extensive destruction of ozone occurs over the Antarctic continent and the surrounding Southern Ocean. In this geographic region, over 50% depletion of column ozone has occurred each spring

(Sept–Dec) for the past two decades, causing increased amounts of UVB to reach Antarctic marine environments (Frederick *et al.*, 1998; Schoeberl *et al.*, 1996).

A major obstacle in assessing ecological UVB effects on the Antarctic marine ecosystem is that while ozone depletion has been occurring for over 20 yr, scientists did not accept the possibility of the Antarctic ozone “hole” until nearly a decade after the depletion cycles began (Solomon, 1990). Therefore, the first efforts to examine the biological effects of Antarctic ozone depletion did not commence until after 10 yr of repeated seasonal ozone depletion had already occurred. By this time any ozone-related changes in the marine environment would have been initiated and the ecosystem altered before biological investigations began. Species or individuals within populations that could not tolerate the immediate changes in UVB during the early rounds of ozone depletion would have been eliminated. The organisms present today are those

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that have survived two decades of increased springtime UVB.

Research conducted over the past decade has yielded a great deal of detailed information on biological responses to UVB exposure and there have been a number of prior reviews related to the effects of ozone depletion in Antarctica (Karentz, 1991, 1992; Marchant, 1997; Vernet and Smith, 1997; Weiler and Penhale, 1994; and others). However, there is still no satisfactory answer to the overriding question of "What is the effect of ozone depletion on the Antarctic ecosystem?". This paper builds on previous reviews and updates our understanding of how increased UVB radiation resulting from ozone depletion affects marine organisms in the Southern Ocean.

OZONE DEPLETION AND INCIDENT UV IN ANTARCTICA

Since the late 1970s, ozone concentrations over the Antarctic and surrounding Southern Ocean have exhibited a seasonal cycle of springtime minima exceeding 50% decline from "normal" ozone levels ("normal" \cong 300 Dobson units, DU) (Farman *et al.*, 1985; Newman, 1994; Schoeberl *et al.*, 1996). This annual phenomenon has been directly attributed to chlorofluorocarbons (CFCs) and other atmospheric anthropogenic pollutants that have been released into the atmosphere over the past 70 yr (Anderson *et al.*, 1991; Jones and Shanklin, 1995). Depletion of ozone over the Antarctic is caused by a combination of chemical and physical features of the springtime Antarctic atmosphere that favor ozone loss. These include 1) the presence of the polar vortex, an atmospheric circumpolar current that effectively isolates a large mass of air over the south polar region from adjacent air masses to the north; 2) extremely cold temperatures; 3) formation of polar stratospheric clouds that provide appropriate substrates for heterogeneous chemistry; and 4) after a long dark winter period, the presence of solar radiation that is required to catalyze ozone dissociation.

During the past two decades the duration of the annual ozone depletion period has increased, minimum levels over the Antarctic have steadily declined and the areal ex-

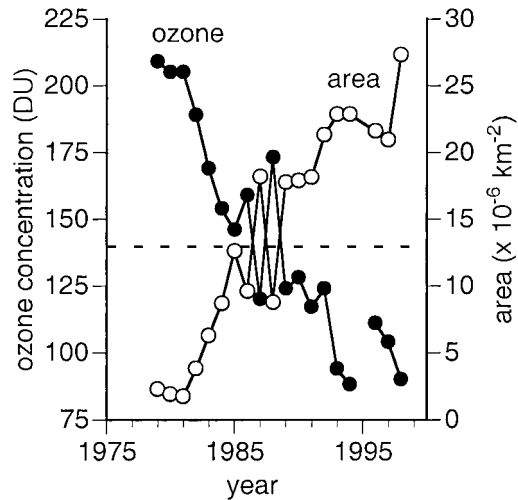
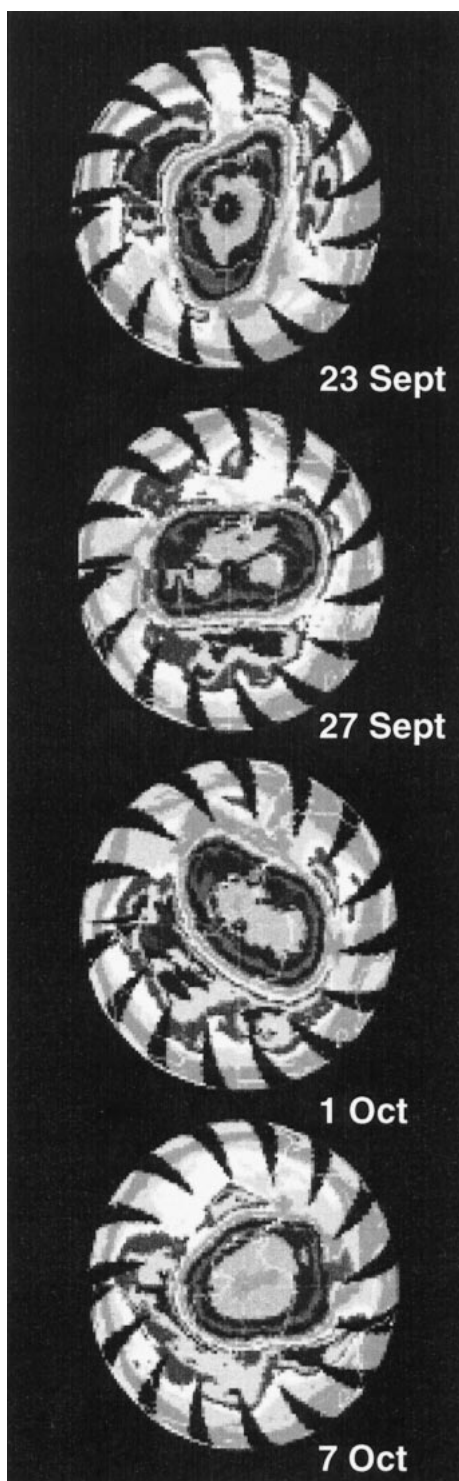


FIG. 1. Ozone trends over the Antarctic 1979–1998: annual minimum ozone concentrations from 60–90°S and mean area of ozone depletion (<220 DU) within the polar vortex from 7 Sept–13 Oct (no data for 1995). For reference, area of the Antarctic continent (13 million km²) is indicated by the broken horizontal line. Data are from the US National Aeronautics and Space Administration (NASA) (<http://jwocky.gsfc.nasa.gov>).

tent of the depletion within the polar vortex has expanded (Jones and Shanklin, 1995) (Fig. 1). Superimposed on these annual trends are short-term changes resulting from the rotation of the polar vortex (Fig. 2). Thus, coastal areas of the Antarctic continent and adjacent ocean waters under the margins of the vortex can be alternately exposed to high and low UVB levels within a period of several days (Fig. 3). The fluctuations in ozone concentrations and concomitant changes in incident UVB result in differences in the intensity of UVB in the water column and the depth of UVB penetration (Fig. 4). It is important to note that ozone depletion does not significantly affect UVA or higher solar wavelengths and UVA attenuation in water is lower than for UVB. Therefore, the incident and in water ratios of UVB to UVA vary with ozone levels and depth.

With widespread compliance to Montreal Protocol standards for the reduction of CFC usage and release, there is a positive prognosis for recovery from ozone depletion (Hofmann *et al.*, 1997; Madronich *et al.*,



1998; Montzka *et al.*, 1999). It is expected that within 40–60 yr, global ozone levels will return to “normal” and springtime ozone depletion over the Antarctic will no longer occur. While this is encouraging news, the impact of the past 20 yr of ozone depletion and of the predicted 4–6 decades of continued ozone losses on the Antarctic ecosystem is still uncertain.

UV PHOTOBIOLOGY OF ANTARCTIC ORGANISMS

Bacteria

While there have been a number of investigations of UV effects on freshwater Antarctic cyanobacteria (*e.g.*, Quesada *et al.*, 1995; Quesada and Vincent, 1997; Roos and Vincent, 1998; Vincent and Quesada, 1994), relatively little has been reported about the impact of ozone depletion on Antarctic marine heterotrophic bacteria. Early studies show that Antarctic bacterioplankton isolates do not possess UV-screening compounds that might protect cells, but they do have capability for recovery from UV-induced damage (Karentz, 1994). A primary cellular target for UVB is DNA. DNA absorbs UVB, altering the molecular structure and potentially impairing DNA function. There are several metabolic pathways that repair DNA damage and an organism can have various combinations of these repair mechanisms. Some Antarctic bacteria have photoreactivation, an enzymatic repair process that requires UVA or higher wavelength radiation (Karentz, 1994).

Another repair pathway in bacteria is the SOS response. The timing of induction of genes involved in the SOS response is an important factor in the level of UV-tolerance within Antarctic microbial populations (Helbling *et al.*, 1995). Initiation of the SOS response before UV exposure occurs

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FIG. 2. Rotational pattern of the polar vortex over a 14-day period during the 1997 ozone depletion cycle. Outer edge of ellipse represents 250 DU and inner isopleths indicate decreasing ozone concentrations (central area <100 DU). Images are from NASA (<http://jwocky.gsfc.nasa.gov>).

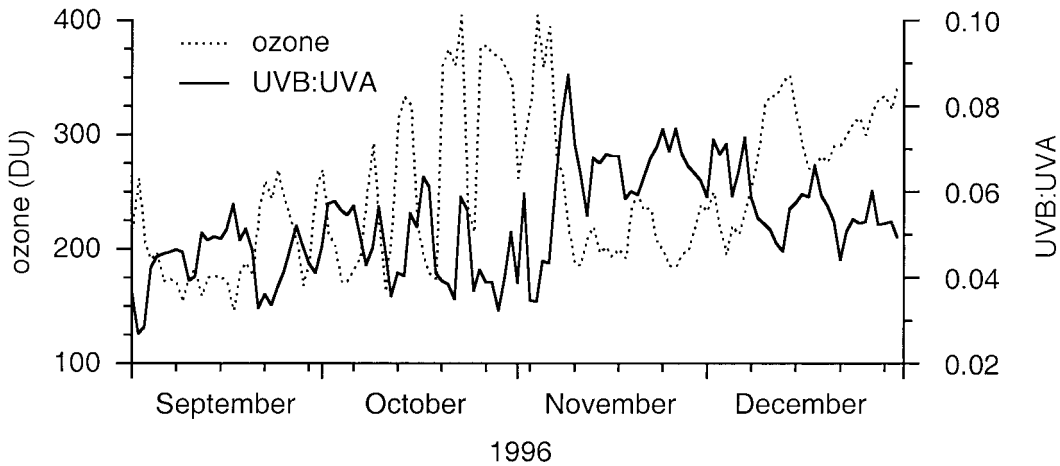


FIG. 3. Inverse relationship between column ozone and UVB over Palmer Station ($64^{\circ}46'S$, $64^{\circ}03'W$), Antarctic Peninsula during 1996. Ratio of UVB to UVA (UVB:UVA) is plotted to minimize effects of cloud cover that affect intensity but not spectral quality of incident UV wavelengths (Gautier *et al.*, 1994). Ozone data from R. McPeters, Head of NASA Ozone Processing Team; UV data from NSF Polar Programs UV Monitoring Network maintained by Biospherical Instruments, Inc., San Diego, CA.

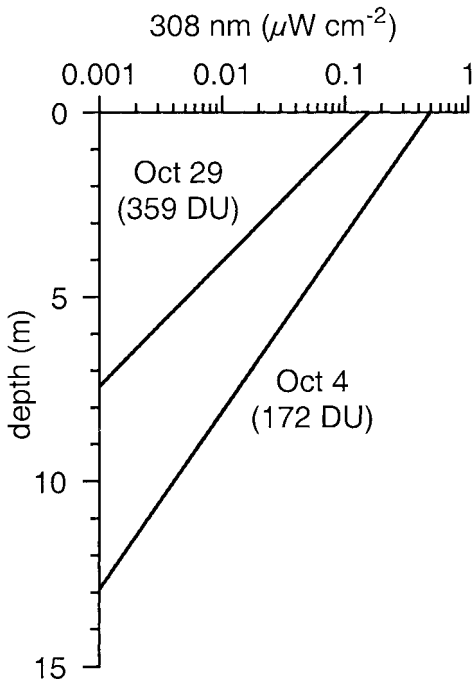


FIG. 4. Comparison of in water attenuation of UVB at 308 nm under two different ozone levels over Arthur Harbor, Palmer Station, Antarctic Peninsula in 1996. Data collected with a Biospherical PUV 500 spectroradiometer.

can significantly increase bacterial cell survival. Under natural daylight conditions, the SOS response in Antarctic microbial communities exhibits a diel cycle with activation of genes maximized during the early evening to support increased removal of DNA photoproducts during the relatively darker “night” period (Jeffrey *et al.*, 2000).

In Antarctic bacterial communities, UVA (320–400 nm) exposure can contribute to a greater proportion of UV-induced death than UVB wavelengths (Helbling *et al.*, 1995; Marguet *et al.*, 1994). Similar observations are reported from temperate bacteria (Sommaruga *et al.*, 1997) and Antarctic phytoplankton (see below). UVA is not attenuated by ozone, does not cause significant DNA damage by direct absorption and can facilitate DNA repair through photoreactivation. However, both UVB and UVA are involved in a variety of photochemical reactions in seawater and in intracellular fluids that result in the production of reactive species (*e.g.*, peroxide and hydroxyl radicals) that cause oxidative damage to organic molecules (including DNA). Although UVB wavelengths are more harmful on a per photon basis, UVA wavelengths comprise a much greater proportion of the UV radiation present in the solar spectrum;

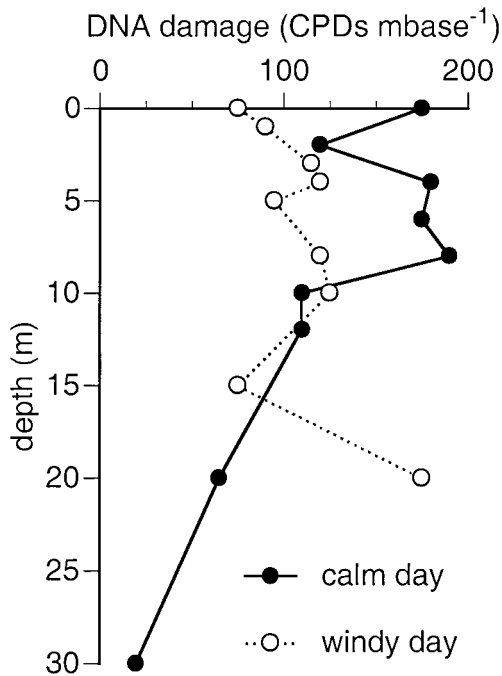


FIG. 5. Differences in the depth distribution of UVB-induced DNA damage (cyclobutane dimers per megabase) in the Gerlache Strait (64°30'S, 62°20'W), Antarctic Peninsula relative to water column stability (minimal mixing on calm day, increased water column turnover on windy day). Data from Jeffrey *et al.* (1997). (Modified with author's permission.)

therefore, under ambient sunlight, UVA elicits a stronger biological response.

Two important aspects of the cumulative impact of UV are the intensity and the duration of exposure. For planktonic organisms, vertical mixing of the water column is a key issue in regulating these two factors. On calm days with little wind, UV-induced DNA damage in Antarctic bacterioplankton is greatest at the surface (0–10 m) and then decreases sharply with depth in the stabilized water column (Fig. 5) (Jeffrey *et al.*, 1997). On moderately windy days, turnover of the water column promotes lower damage accumulation and more uniform damage levels with depth. It is presumed that as cells are moved more quickly out of shallow waters with higher UV irradiances, the balance of damage and repair shifts in favor of repair processes and cells experience a more expedient recovery. The issue of vertical mixing is also crucial

for the evaluation of UV effects on eukaryotic planktonic organisms (see below).

Phytoplankton

Research on UVB effects on phytoplankton has been the predominant area of study relative to the biological impact of ozone depletion in Antarctica. The focus on phytoplankton is predicated on the assumption that declines in primary productivity caused by increases in UVB stress will readily translate into ecosystem disruption by reducing trophic energy transfer. The structure of the Antarctic pelagic food web and the location and activity of various predators and consumers is dictated by seasonal changes in phytoplankton abundance and distribution (Ainley *et al.*, 1991; Barnes and Clarke, 1995; Clarke, 1988; Ross *et al.*, 2000). Moreover, small single-celled organisms with short generation times (<several days) and little control over positioning in the water column would be more exposed and more vulnerable to UVB than larger multicellular organisms with protective surface layers and longer generation times (months to years).

The initial studies of UV effects on Antarctic primary production were undertaken in 1987, ten years after the Antarctic ozone depletion cycle had begun (El-Sayed and Stephens, 1992; El-Sayed *et al.*, 1990; Stephens, 1989). This work was followed by a series of field studies that measured productivity of phytoplankton under ambient ozone depletion (Helbling *et al.*, 1992; Holm-Hansen *et al.*, 1993; Smith *et al.*, 1992; Vernet *et al.*, 1994; and others). These investigations quantified ¹⁴C incorporation in whole water samples incubated at various depths under full sunlight and with selective filters to partition the solar spectrum by removing UVB or UVB plus UVA. Biological weighting functions that describe the spectral response of phytoplankton photosynthesis have also been established for Antarctic phytoplankton under ambient and artificial UV radiation (Boucher and Prézelin, 1996a, b; Neale *et al.*, 1994, 1998a).

In general, the quantitative results of various studies are quite similar. Full sunlight conditions that include both UVA and UVB

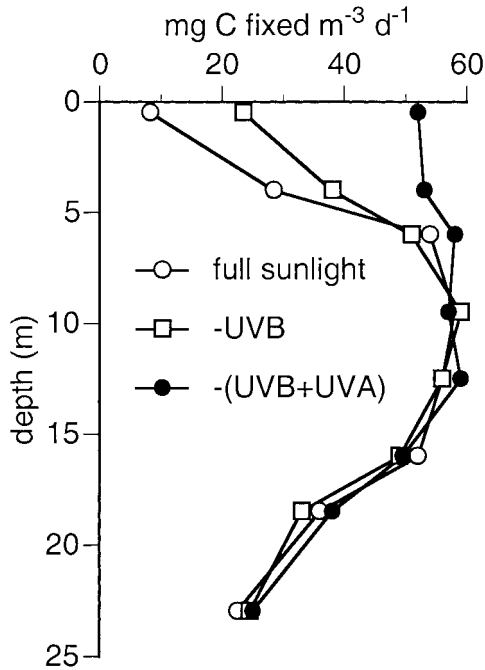


FIG. 6. UV inhibition of primary productivity in Arthur Harbor, Antarctic Peninsula ($64^{\circ}46'S$, $64^{\circ}03'W$). Incubations were made under full sunlight, with UVB removed ($-UVB$) and with both UVB and UVA removed [$-(UVB+UVA)$] (Holm-Hansen *et al.* 1997). Reprinted with permission from Cambridge University Press.

wavelengths support lower rates of primary productivity than partitioned radiation regimes (Fig. 6). Both UVA and UVB cause inhibition of photosynthesis and in the majority of observations, UVA is responsible for a greater proportion of the decrease in carbon fixation than UVB (for the same reasons as discussed above for bacteria) (see also Boucher and Prézélin, 1996a; Davidson and Marchant, 1994). From studies with static depth incubations, the calculated impact of ozone-related changes in UVB on reducing primary productivity has been estimated at 3–15%. When vertical mixing is considered as a means of ameliorating UVB effects by reducing the duration of exposure and allowing time for recovery from UV stress, ozone-dependent reductions in primary productivity are estimated at <1–9% (Arrigo, 1994; Boucher and Prézélin, 1996b; Neale *et al.*, 1998b).

Observations of short-term (daily) re-

sponses and temporal adaptation to UV exposure in natural Antarctic phytoplankton communities suggest that cells respond rapidly to UV and can quickly adjust physiological parameters for greater UV tolerance (Figueroa *et al.*, 1997; Karentz and Spero, 1995). Species-specific differences in UV sensitivity have been documented and indicate that differential responses occur within the phytoplankton (Davidson *et al.*, 1996; Helbling *et al.*, 1994; Karentz *et al.*, 1991a; Villafañe *et al.*, 1995). The ecological implications of shifts in the taxonomic and size structure of phytoplankton communities may be a significant impact of ozone depletion and require further study and evaluation.

UV can influence a number of other physiological processes in Antarctic phytoplankton including inhibition of dimethyl sulphonium propionate (DMSP) production (Hefu and Kirst, 1997), decreasing rates of uptake of inorganic nitrogen (Döhler, 1997; Döhler *et al.*, 1995), initiating shifts in the size of specific amino acid pools and increasing the concentration of saturated fatty acids (Goes *et al.*, 1997). Changes in nitrogen metabolism can be accompanied by variations in pigments, with UVB causing photo-destruction of chlorophylls (Döhler, 1998a). Phytoplankton can also synthesize heat shock proteins to further ameliorate UV stress (Döhler *et al.*, 1995).

Some Antarctic phytoplankton species contain UV-absorbing compounds, mainly the common mycosporine-like amino acids (MAAs) shinorine and porphyra-334 (Table 1) (Bidigare *et al.*, 1996; Helbling *et al.*, 1996; Lesser *et al.*, 1996; Marchant *et al.*, 1991; Riegger and Robinson, 1997). MAAs are believed to have a photoprotective function with concentrations regulated by solar exposure. However, the induction response in Antarctic phytoplankton is not consistent relative to wavelength nor does the concentration of UV-absorbing compounds always correlate with UV tolerance (Davidson *et al.*, 1994; Helbling *et al.*, 1996; Riegger and Robinson, 1997).

Sea ice microalgae

During early spring the Antarctic continent is surrounded by sea ice that provides

TABLE 1. Occurrence (+) of MAAs in Antarctic phyla and divisions.*

phylum/division	SH	M2	PI	PR	MG	PL	AS	PE	MV	#	Σ	%
Phototrophs												
Bacillariophyta ^{a,b,c,d,e}	+	+	+	+				+	+	0–5	27	81
Rhodophyta ^{a,f}	+		+	+	+	+	+	+		2–7	7	100
Phaeophyta ^a			+	+	+					3	1	100
Heterotrophs												
Protozoa ^a										0	1	0
Porifera ^{a,f}	+		+	+	+	+		+	+	1–7	18	100
Cnidaria ^{a,f}	+		+	+	+			+	+	1–5	3	100
Ctenophora ^a	+		+	+	+		+		+	0	2	0
Platyhelminthes ^a	+		+	+	+				+	5	2	100
Nemertinea ^a	+		+	+	+				+	5	3	100
Annelida ^a	+		+	+	+	+	+	+	+	4–7	6	100
Bryozoa ^{a,f}	+		+	+						1–6	3	100
Arthropoda ^{a,f}	+		+	+	+	+	+	+	+	1–7	15	100
Echinodermata ^{a,f}	+		+	+	+		+		+	0–6	12	58
Mollusca ^{a,f}	+		+	+	+	+	+	+	+	1–7	13	100
Chaetognatha ^a	+		+	+	+			+	+	0	1	0
Chordata ^{a,f}	+		+	+	+		+	+	+	0–7	7	86

SH = shinorine, M2 = mycosporine-2-glycine, PI = palythine, PR = porphyra-334, MG = mycosporine-glycine, PL = palythanol, AS = asterina-330, PE = palythene, MV = mycosporine-glycine:valine

* Also indicated are number of MAAs found in individual species (#), total number of species analyzed (Σ) and percent of species within each group that contained any MAAs (%).

^a Karentz *et al.*, 1991b; ^b Bidigare *et al.*, 1996; ^c Helbling *et al.*, 1996; ^d Lesser *et al.*, 1996; ^e Riegger and

a habitat for a variety of microscopic organisms. The ice and the resident community effectively filter both UV and higher wavelengths used for photosynthesis, greatly attenuating the amount of sunlight in the water column. Low light levels result in low phytoplankton densities and low water column productivity; therefore, primary production by the ice algal community provides a significant contribution to the Antarctic food web during spring. Under a “normal” ozone column 1–5% of incident UV radiation penetrates through the sea ice. With ozone depletion there is an increase in incident UVB, but not higher wavelengths, and consequently UV transmission through the ice increases to 10% (Ryan and Beaglehole, 1994). Under higher UV exposures, ice algal production is estimated to decrease by 5% (Ryan and Beaglehole, 1994); however, UVB may have stronger effects on standing crop (up to 40% decline) and species successional patterns that depend on the amount of snow cover and initial species composition (McMinn *et al.*, 1999). Detailed studies of photosynthetic responses of the ice community to UVB emphasize

the need for more extensive research on UV effects in the sea ice biota (Prézélin *et al.*, 1998; Schofield *et al.*, 1995).

Macroalgae

There are few studies relating to the UV-photobiology of Antarctic macroalgae. These organisms contain UV-absorbing MAAs with Rhodophyta having higher concentrations (400–9,000 $\mu\text{g MAAs g}^{-1}$ dry weight) than the Phaeophyta and Chlorophyta species examined (20–200 $\mu\text{g MAAs g}^{-1}$ dry weight) (Table 1) (Karentz *et al.*, 1991b). This phylogenetic pattern is typical for these groups at other latitudes.

The photosynthetic pigments of Antarctic macroalgae have a rapid response to UV exposure and UVB and UVA stress elicit differential responses. *Leptosomia simplex* (Rhodophyta) responds to artificial UV exposure with declines in chlorophyll pigments; but increases in carotenoids, molecules that have photoprotective anti-oxidant functions (Döhler, 1998b). A comparative study of UV inhibition of photosystem II in nine species of Antarctic macroalgae shows that significant species-specific differences

exist, and Chlorophyta and Phaeophyta are more tolerant of UV exposure than the Rhodophyta (Bischof *et al.*, 1998). The authors conclude that increases in UV resulting from ozone depletion might be a factor in establishing the vertical zonation of Antarctic macrophytes.

Zooplankton

Observations in temperate freshwater communities have underscored the importance of understanding the direct effects of UV on consumer populations (Bothwell *et al.*, 1994), but little research has been conducted on the UV-photobiology of Antarctic zooplankton. A limited amount of information is available for *Euphausia superba* (krill). *E. superba* contains all seven MAAs that have been identified from Antarctic organisms (Karentz *et al.*, 1991b), suggesting at least a minimum capacity for UV shading of vital cellular targets.

Euphausia superba DNA has a very low (32%) guanine-cytosine base composition (Jarman *et al.*, 1999). Since UV-induced DNA damage is predominantly comprised of adducts formed between adjacent thymine residues (*e.g.*, cyclobutane dimers and pyrimidine-pyrimidone 6–4 photoproducts), the high adenine-thymine complement may predispose krill to higher concentrations of DNA damage than occur in other organisms. Malloy *et al.* (1997) have observed relatively high levels of DNA repair in *E. superba* under laboratory conditions; however, ambient levels of DNA damage are not known.

Examination of historical data on krill abundance, westerly wind fluctuations and ozone levels over a 20-yr period (1977–1997) provides the first connection between ozone depletion and variability in krill populations along the Antarctic Peninsula (Naganobu *et al.*, 1999). Correlations are evident between *E. superba* abundance and ozone levels and the areal extent of ozone depletion. Krill recruitment is not closely correlated to ozone levels, but appears to be affected by sea level pressure (fluctuations in westerly winds). The large annual variability in the estimates of krill abundance and the two-year period required for sexual maturity contribute to the complexity of

evaluating the biological impact of large scale environmental variables.

Studies from other latitudes provide evidence of higher sensitivity to UVB in early developmental stages of marine invertebrates than in adults (*e.g.*, Damkaer *et al.*, 1981; Giese, 1939). Similar observations have been reported for fish larvae (Hunter *et al.*, 1981; Vetter *et al.*, 1999). The accelerated developmental activity and minimal morphological complexity of embryos and larvae make them more vulnerable than adult animals. UV exposure during early stages of development can cause developmental delays and/or lethality that will affect recruitment to adult populations.

Many of the most common benthic macroinvertebrate species in the Antarctic reproduce with a planktonic stage during the austral spring when the greatest deterioration of ozone occurs (Bosch *et al.*, 1987; Pearse *et al.*, 1991). These include the sea star *Odontaster validus*, the sea urchin *Sterechinus neumayeri* and the ribbon worm *Parborlasia corrugatus*; all of which produce eggs <0.2 mm diameter and have planktotrophic larval development (Bosch *et al.*, 1987; Pearse *et al.*, 1991; Stanwell-Smith and Peck, 1998). Embryos and larvae of some of these species (*e.g.*, *Sterechinus*) contain MAAs. MAAs provide a protective sun screening function for urchin embryos in temperate species (Adams and Shick, 1996) and similar observations have been made for *Sterechinus neumayeri* (DK/IB, unpublished data). However, MAA concentrations are not sufficient to prevent excessive damage to embryos that inhabit shallow surface waters (<5–10 m) (Fig. 7).

The early development of the Antarctic sea urchin *Sterechinus neumayeri* has proved to be a reliable model for the study of UV effects on early invertebrate development. *In situ* measurements of DNA damage, abnormality in development and lethality show that incident UVB is detrimental to development without ozone depletion, and that increased exposure under ozone-depleted conditions exacerbates responses (Fig. 7). UV effects on embryos are generally not observed at incubation depths below 5 m, suggesting that only individuals drifting very near the surface for prolonged

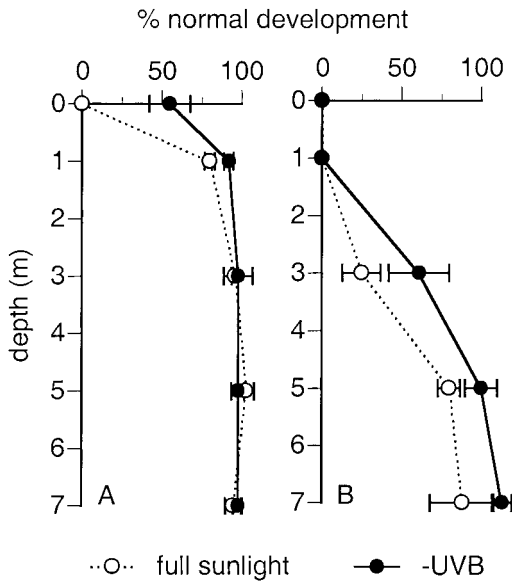


FIG. 7. Representative data on development of Antarctic sea urchin (*Sterechinus neumayeri*) embryos under A) high (mean = 339 ± 58 DU) and B) low (mean = 200 ± 13 DU) column ozone. Incubations were initiated with zygotes. Cultures were incubated for 5 days with four replicates under three light treatments (full sunlight, minus UVB and dark) at each depth. The percentage of embryos exhibiting normal and abnormal (e.g., irregular cleavage, morphological aberrations, death) development were determined by microscopy. Data corrected for dark treatments.

periods of time would be adversely affected by UV exposure. Embryos and larvae of *Sterechinus* and other benthic invertebrates have been found in surface waters (Bosch *et al.*, 1987; Stanwell-Smith *et al.*, 1999); however, because residence times and mixing rates are not known, it is not possible to assess the vulnerability of these species to ozone-related changes in UV.

The effects of ultraviolet light on the embryos and larvae of the sea star *Psilaster charcoti* have also been studied. This species represents a second major type of invertebrate developmental strategy with the production of large (0.7 mm diameter) yolk-laden eggs and free-swimming non-feeding larvae (Pearse *et al.*, 1991). Although MAAs are lacking in *P. charcoti*, the relatively large size and high amounts of carotenoids in eggs and embryos might be expected to provide effective protection against UVB exposure. However, when zy-

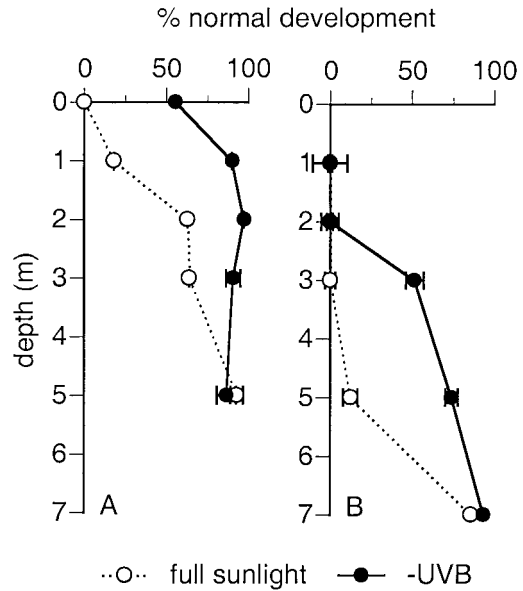


FIG. 8. Development of Antarctic sea star (*Psilaster charcoti*) embryos under A) high (mean = 312 ± 71 DU) and B) low (mean = 184 ± 9 DU) ozone column. Details as in Figure 7.

gotes and early cleavage embryos are incubated *in situ*, both UVB and UVA cause considerable damage to embryonic development under "normal" and depleted ozone columns (Fig. 8). The degree of damage and the maximum depth of the UVB effect are comparable to those observed in *S. neumayeri*; but the implications of these results are quite different. Eggs released by *P. charcoti* float upwards at rates of 1.5–2.0 m/hr *in situ*, a velocity that would allow them to move from depths occupied by adults to depths at which they are vulnerable to UV damage in less than 1 day or before the third embryonic cleavage is completed.

Several other groups of Antarctic organisms have floating eggs that could potentially be exposed to maximum UV fluences during the most crucial stages of early development (Bosch, 1989; Malloy *et al.*, 1997; Pearse *et al.*, 1991). DNA damage and repair have been examined in Antarctic ichthyoplankton (eggs and larvae), including the floating eggs of *Chaenocephalus aceratus* (icefish) (Malloy *et al.*, 1997). DNA damage levels in icefish eggs collected from surface waters were significantly cor-

related to total daily incident UVB irradiance and DNA repair rates were correspondingly high. Here again, limited data preclude any substantial evaluation of UV effects on these organisms.

Benthic invertebrates

Coastal areas of the Antarctic have an abundant and diverse benthic faunal component. During spring, sea ice effectively scours most inter- and subtidal areas leaving behind very few organisms with the notable exception of the limpet *Nacella concinna*. During springtime ozone depletion, the majority of benthic organisms resides in relatively deep water and is well protected from UV exposure by both the sea ice and the overlying water column. Research on UV defenses of these organisms indicates that the majority (~90%) contain UV-absorbing MAAs (Table 1) (Karentz *et al.*, 1991b; McClintock and Karentz, 1997). As found at other latitudes, there is a distinct partitioning of MAAs in different tissues with highest concentrations localized in ovaries and eggs (Karentz, 1994; Karentz *et al.*, 1997). Digestive tissues can also contain appreciable amounts of MAAs, but body walls have low concentrations and sperm have little or non-detectable amounts of MAAs. It is generally accepted that MAAs are bioaccumulated.

MAA concentrations in benthic Antarctic species do not appear to be correlated to ambient UV levels relative to seasonal changes in day length or ozone levels (Karentz *et al.*, 1997). However, along the Antarctic Peninsula there is a consistent vertical gradient of MAA concentration from the intertidal to depths of 30 m. In contrast, there is generally a lower level of MAAs in benthic organisms collected in McMurdo Sound where depths of habitation are deeper and food supply is more likely to be of detrital origin rather than live algal material (McClintock and Karentz, 1997). Other aspects of the UV-photobiology of Antarctic benthic invertebrates have not yet been investigated.

Vertebrates

Aside from a few studies that included fish (mostly larval stages) (Karentz *et al.*,

1991b; Malloy *et al.*, 1997; McClintock and Karentz, 1997), no direct investigations of ozone depletion effects on higher animals have been undertaken. Fish, birds, seals and whales are physically well protected from UV-induced damage by scales, feathers, fur and thick skin layers. The only study relating to the UV-photobiology of Antarctic organisms prior to the inception of ozone depletion examined sensitivity of UV-induced corneal damage in the eyes of Antarctic birds as compared to birds from temperate latitudes (Hemmingsen and Douglas, 1970). Polar birds have higher UV thresholds for damage attributed to their existing adaptation to the higher albedo of snow and ice that creates a high UV environment.

If there is an impact of ozone depletion on larger marine organisms, it is expected to occur through potential limitation of food sources. Evaluation of the UV effects on birds and mammals is confounded by the fact that there are many environmental variables that can be implicated in regulating the size and fitness of a population. The multi-year life histories of these organisms also make it especially difficult to establish cause and effect; therefore, the impact of a single environmental variable is not readily apparent. Consideration of the synergist effects of environmental factors is necessary and this requires careful and consistent long term monitoring on a time scale of decades (*e.g.*, Trivelpiece and Fraser, 1996).

CONCLUSIONS

When the existence of Antarctic ozone depletion was finally accepted, dire predictions were made about the fate of the Antarctic ecosystem (Buckley and Trodahl, 1990; El-Sayed *et al.*, 1990). Based on the extremely limited information available at the time, these were reasonable assumptions. Today, with the benefit of a larger database on population and community responses to UV, the effect of ozone depletion in the Antarctic does not seem quite so drastic; yet much more complex (Arrigo, 1994; Holm-Hansen *et al.*, 1997; Vernet and Smith, 1997 and others). The focus on phytoplankton has clearly established that primary productivity declines by just a few percent under ozone depletion and that this

amount of loss is perhaps insignificant relative to the magnitude of seasonal and annual variability that occurs in the Southern Ocean (Smith *et al.*, 1992). However, this does not imply that ozone depletion may not be a substantial stress to the Antarctic ecosystem.

One of the major conclusions of the 1998 UNEP Assessment of Environmental Effects of Ozone Depletion emphasizes that UV effects on the complex interactions within an ecosystem cannot be reduced to monitoring primary productivity (Häder *et al.*, 1998). Modification of the structure of communities is a more likely response and one that has far-reaching implications. These kinds of changes are also much more difficult to quantify and evaluate, and this presents a great challenge.

Antarctica is the only place on Earth where such large predictable ozone losses occur, and as such it provides a unique location for ozone-related research. Results of studies conducted in the Antarctic have provided invaluable information on the UV-photobiology of organisms and processes that have counterparts at other latitudes. While these data have helped to reduce some of the uncertainty about the risks of ozone depletion, they have also emphasized the importance of more detailed understanding of UV effects in aquatic systems and have stimulated many new avenues of research.

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