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Survey of mycosporine-like amino acid compounds in Antarctic marine organisms: potential protection from ultraviolet exposure*

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Date of final manuscript acceptance: September 28, 1990. Communicated by J. Grassle, New Brunswick

Abstract. To investigate the natural defenses of Antarctic marine organisms against exposure to ultraviolet (UV) radiation (280 to 320 nm), 57 species (1 fish, 48 invertebrates, and 8 algae) were collected during austral spring 1988 in the vicinity of Palmer Station (Anvers Island, Antarctic Peninsula) and were analyzed for the presence of mycosporine-like amino acids (MAAs), compounds that absorb UV radiation and may provide shielding from these biologically hazardous wavelengths. Nearly 90% of the 57 species examined contained MAAs, and eight specific MAA compounds were identified. Seven of these (palythine, porphyra-334, shinorine, mycosporine-glycine, palythene, asterina-330, and palythanol) have been observed previously in marine organisms from temperate and tropical latitudes. A new MAA, mycosporine-glycine:valine, was found in the Antarctic fish and in 38 of the invertebrate species examined. This study confirms widespread occurrence of MAAs in Antarctic marine organisms and suggests that these species have some degree of natural biochemical protection from UV exposure.

Introduction

During the past decade, springtime ozone depletion over the Antarctic and the Southern Ocean has resulted in unseasonably elevated levels of ultraviolet-B (UV-B) radiation (280 to 320 nm) reaching the earth's surface and has led to much speculation about the ecological impact of the Antarctic ozone hole (Karentz 1990, 1991, Voytek 1990). Although UV-B radiation is well recognized as a biological hazard (Harm 1980, Caldwell 1981, Calkins 1982), relatively little is known about the UV photobiology of Antarctic organisms or their ability to cope with increases in this environmental stress. Of primary interest is the identification of repair and protective mechanisms that may allow Antarctic species to survive and repro-

duce under the increased UV-B flux resulting from springtime ozone depletion (Lubin et al. 1989, Karentz and Lutze 1990).

In tropical and temperate marine organisms the synthesis or accumulation of UV-absorbing mycosporine-like amino acids (MAAs) has been recognized as a potential means of minimizing structural and physiological damage caused by UV exposure (Dunlap et al. 1988). Mycosporine is the generic name given to water-soluble, UV-absorbing fungal metabolites with a cyclohexenone chromophore conjugated with the nitrogen substituent of an amino acid or amino alcohol (Favre-Bonvin et al. 1976, Arpin and Bouillant 1981) (Fig. 1). Mycosporine-

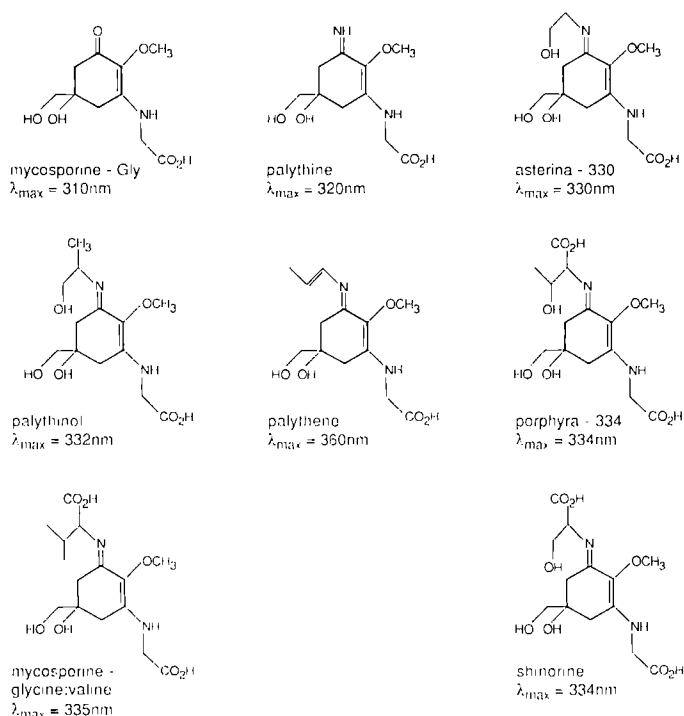


Fig. 1. Molecular structures and wavelengths of maximum absorbance ($\lambda_{\max}$) of eight MAAs identified in Antarctic species

* Contribution No. 502 from the Australian Institute of Marine Science

Phylum: class Species	Common name	Collection site	Habitat
Protozoa: Rhizopoda			
<i>Gromia oviformis</i> Dujardin	Rhizopod	Kristie Cove	Intertidal
Porifera:			
Sponge #1	Sponge	Hero Inlet	Subtidal
Sponge #3	Sponge	Kristie Cove	Intertidal
Sponge #5	Sponge	Kristie Cove	Intertidal
Sponge #6	Sponge	Kristie Cove	Intertidal
Coelenterata: Anthozoa			
Anemone #1	Sea anemone	Kristie Cove	Subtidal
Ctenophora: Tentaculata			
<i>Bolinopsis</i> n. sp.	Ctenophore	Hero Inlet	Plankton
<i>Callianira antarctica</i> Chun	Ctenophore	Kristie Cove	Plankton
Platyhelminthes: Turbellaria			
<i>Obrimoposthia wandeli</i> Hallez	Planarian	Kristie Cove	Intertidal
Planarian #2 ^a	Planarian	Kristie Cove	Intertidal
Nemertinea: Enopla			
<i>Amphiporus michaelsoni</i> Bürg	Ribbon worm	Kristie Cove	Intertidal
<i>Parborlasia corrugatus</i> McIntosh	Ribbon worm	Gamage Point	Subtidal
<i>P. fueguina</i> Serna de Esteban & Moretto	Ribbon worm	Kristie Cove	Intertidal
Annelida: Polychaeta			
<i>Aglaophanus ornatus</i> Hartman	Polychaete	Arthur Harbor	Subtidal
<i>Neanthes kerguelensis</i> McIntosh	Polychaete	Kristie Cove	Intertidal
<i>Terebella chlersi</i> Gravier	Polychaete	Hero Inlet	Subtidal
<i>Tomopteris carpenteri</i> Quatrefages	Polychaete	Hero Inlet	Intertidal
Polychaete #2	Polychaete	Kristie Cove	Intertidal
Annelida: Hirudinea			
<i>Trachelobdella australis</i> Blanchard	Leech	Kristie Cove	Intertidal
Mollusca: Gastropoda			
<i>Limacina helicina</i> Phipps ^b	Pteropod	Palmer Basin	Plankton
<i>Margarella antarctica</i> Lamy	Snail	Bonaparte Point	Intertidal
<i>Paludestrina antarctica</i> E. A. Smith	Snail	Kristie Cove	Intertidal
<i>Trophon</i> cf. <i>geversianus</i> Pallas	Snail	Kristie Cove	Intertidal
Nudibranch #1 ^c	Nudibranch	Kristie Cove	Subtidal
Mollusca: Polyplacophora			
<i>Tonicina zschau</i> Pfeffer	Chiton	Kristie Cove	Intertidal
Mollusca: Bivalvia			
<i>Cyamium</i> cf. <i>commune</i> Thiele	Clam	Kristie Cove	Intertidal
<i>Limulata</i> cf. <i>ovalis</i> Thiele	Clam	Kristie Cove	Intertidal
Arthropoda: Pycnogonida			
<i>Achelua spicata</i> Hodgson	Sea spider	Kristie Cove	Intertidal
Arthropoda: Crustacea			
<i>Calanus propinquus</i> Brady	Copepod	Palmer Basin	Plankton
<i>Cymodocella tubicauda</i> Pfeffer	Isopod	Kristie Cove	Intertidal
<i>Notasellus sarsi</i> Pfeffer	Isopod	Kristie Cove	Intertidal
<i>Euphausia superba</i> Dana	Krill	Palmer Basin	Plankton
<i>Halirages</i> sp.	Amphipod	Kristie Cove	Intertidal
<i>Bovallia</i> sp.	Amphipod	Bonaparte Point	Intertidal
<i>Pariphimedia</i> sp.	Amphipod	Bonaparte Point	Intertidal
<i>Jassa</i> sp.	Amphipod	Bonaparte Point	Intertidal
<i>Paraceradocus</i> sp.	Amphipod	Kristie Cove	Intertidal
<i>Pontogeneia</i> sp.	Amphipod	Arthur Harbor	Intertidal
<i>Orchomene</i> sp.	Amphipod	Palmer Basin	Plankton
Bryozoa: Gymnolaemata			
<i>Beania livingstonei</i> Hastings	Bryozoan	Kristie Cove	Intertidal
<i>Inversula nutrix</i> Jullien	Bryozoan	Cormorant Island	Intertidal
Echinodermata: Asteroidea			
<i>Granaster nutrix</i> Studer	Sea star	Kristie Cove	Intertidal
Echinodermata: Ophiuroidea			
<i>Amphioplus affinis</i> Studer	Brittle star	Kristie Cove	Intertidal

Table 1. Invertebrate and fish species collected near Palmer Station (Anvers Island, Antarctic Peninsula) for analysis of mycosporine amino acids

Phylum: class Species	Common name	Collection site	Habitat
Echinodermata: Holothuroidea			
<i>Cucumaria</i> cf. <i>georgiana</i> Lampert	Sea cucumber	Kristie Cove	Intertidal
<i>Ekmocucumis steineni</i> Ludwig	Sea cucumber	Kristie Cove	Intertidal
Chaetognatha			
Chaetognath #1	Chaetognath	Palmer Basin	Plankton
Chordata: Ascidiacea			
<i>Molgula enodis</i> Sluiter	Sea squirt	Kristie Cove	Intertidal
Chordata: Thaliacea			
<i>Salpa thompsoni</i> Foxton	Salp	Palmer Basin	Plankton
Chordata: Osteichthyes			
Icefish #1 (larvae)	Icefish	Palmer Basin	Plankton

Table 1 (continued)

^a Tentatively identified as *Plagiostomum* n. sp.
^b Complete identification: *L. helicina* ssp. *antarctica* f. *antarctica* Woodward
^c Tentatively identified as *Telarma antarctica* Odher

Division Species	Thallus type	Collection site	Habitat
Rhodophyta (red algae)			
<i>Curdia racovitzae</i> Hariot	Parenchymous	Kristie Cove	Intertidal
<i>Iridea chordata</i> (Turner) Bory	Parenchymous	Gamage Point	Intertidal
<i>Lithothamnion</i> cf. <i>antarcticum</i> (J. D. Hooker & Harvey) Foslie	Calcereous	Kristie Cove	Intertidal
<i>Palmaria decipiens</i> (Reinsch) Ricker	Parenchymous	Kristie Cove	Intertidal
<i>Phyllophora appendiculata</i> Skottsberg	Parenchymous	Gamage Point	Intertidal
Phaeophyta (brown algae)			
<i>Desmarestia menziesii</i> J. Agardh	Parenchymous	Kristie Cove	Subtidal
Chlorophyta (green algae)			
Green algal mat ^a	Filamentous	Gamage Point	Intertidal
Bacillariophyta (diatoms)			
Diatom mat ^b	Filamentous	Kristie Cove	Intertidal

Table 2. Algal species collected near Palmer Station (Anvers Island, Antarctic Peninsula) for analysis of mycosporine amino acids

^a *Ulothrix* cf. *australis* Gain, *Urospora* cf. *penicilliformis* (Roth) Areschoug
^b *Achnanthes* sp., *Licmophora* sp., *Navicula* sp.

like amino acids from marine organisms are imino-carbonyl derivatives of the mycosporine cyclohexenone chromophore. Over a dozen MAAs have been reported from marine algae and invertebrate species (Nakamura et al. 1982). These substances have strong absorption maxima in the range of 310 to 360 nm, which corresponds to biologically harmful wavelengths of UV. Because of the widespread occurrence of MAAs in marine organisms of temperate and tropical communities and the increase of springtime UV-B levels in the Antarctic, we have undertaken a survey of intertidal, subtidal and planktonic Antarctic organisms to determine whether polar species also contain MAA compounds with UV-absorbing properties.

Materials and methods

During late austral winter and spring (September to December) 1988, 1 species of fish, 48 species of invertebrates, and 8 species of algae were collected in the vicinity of Palmer Station (64°46'S, 64°03'W), a U.S. research facility located on Anvers Island along the western side of the Antarctic Peninsula (Tables 1 and 2). The majority of organisms (72%) were collected from rocky intertidal areas; the remaining species were from subtidal and planktonic habitats. Specific dates of collection can be obtained from the au-

thors. A number of invertebrates have been archived in various permanent collections. Information on voucher specimens and specific depositories for the invertebrate species is available from F. S. McEuen. Macroalgae were pressed and mounted as standard herbarium specimens, and algal mat communities were preserved in Lugol's solution (collections maintained by D. Karentz).

Invertebrates and fish were kept in filtered seawater for 1 to 3 d to allow them to void recently ingested material which may have contained UV-absorbing compounds. Organisms were frozen whole or after dissection. Lyophilized samples were ground with a mortar and pestle. Ground samples of 0.2 to 0.4 g were extracted in 3 ml of 80% methanol for 2 h. Extracts were centrifuged and supernatant was decanted. Pellets were re-extracted in fresh solvent twice more and all supernatants were pooled. Visible-UV absorption spectra (200 to 750 nm) of methanol extracts were recorded with a Hitachi model U-3200 scanning spectrophotometer. Subsamples of lyophilized material have been stored at -70°C (D. Karentz).

MAAs were separated and quantified by reverse-phase isocratic high-performance liquid chromatography (HPLC) (Nakamura et al. 1982, Dunlap and Chalker 1986). Samples were separated on a Brownlee RP-8 column (Spheri-5, 4.6 mm i.d. × 25 cm) that was protected by an RP-8 guard column (Spheri-5, 4.6 i.d. × 5 cm). To separate less polar MAAs, a 0.1% acetic acid and 25% methanol (v/v) solution was used as the mobile phase. For more polar, acidic molecules, samples were processed by "normal-phase" separation on the silica bed with 0.1% acetic acid and 75% methanol (Dunlap and Shick unpublished). Absorbances of MAAs were recorded at 280, 313, and 340 nm to indicate the wavelength range of maximum absorption.

Table 3 (continued)

Division Species	$\lambda_{\max}$	PI	PR	SH	MG	MV	PE	AS	PL	#	Σ
Chaetognatha											
Chaetognath #1	–	0	0	0	0	0	0	0	0	0	0
Chordarta											
<i>M. enodis</i>	327	104 *	32	89	30	34	8	2	0	7	298
<i>S. thompsoni</i>	328	0	0	0	0	0	0	0	0	0	0
Iceland #1	332	97	41	106	41	124 *	21	0	0	6	429
%		84	84	81	78	65	43	26	10	86	

Table 4. Wavelength of maximum absorbance ($\lambda_{\max}$) in UV-B range for methanol extract, concentrations ($\mu\text{g g}^{-1}$ dry wt) of individual MAAs (abbreviations as in Table 3), total number of MAAs (#), and total MAA concentration (Σ) ($\mu\text{g g}^{-1}$ dry wt), for each algal sample examined. Full genus names are given in Table 2

Division Species	$\lambda_{\max}$	PI	PR	SH	MG	MV	PE	AS	PL	#	Σ
Rhodophyta											
<i>C. racovitzae</i>	325	7177 *	0	1264	27	0	141	254	522	6	9385
<i>I. chordata</i>	325	885 *	0	582	5	0	110	72	229	6	1882
<i>L. cf. antarcticum</i>	335	0	138	291 *	0	0	0	0	0	2	429
<i>P. appendiculata</i>	333	14	0	1298 *	45	0	3	1	0	5	1361
<i>P. decipiens</i>	336	851 *	470	263	30	0	688	93	315	7	2709
Phacophyta											
<i>D. menziesii</i>	333	18 *	2	0	2	0	0	0	0	3	22
Chlorophyta											
Algal mat	329	115	40	125 *	0	0	0	15	0	4	295
Bacillariophyta											
Diatom mat	336	28	363 *	72	0	0	0	0	0	3	463

Species	PI	PR	SH	MG	MV	PE	AS	PL
<i>Ohrimoposthia wandeli</i>	99.1	98.9	98.4	99.5	98.8	0	0	0
<i>Parborlasia corrugatus</i>	98.3	97.5	98.6	99.7	100.0	0	0	0
<i>Limacina helicina</i>	99.1	98.8	98.8	99.2	99.0	100	0	0
<i>Cyamium cf. commune</i>	99.7	99.2	99.1	99.8	99.7	0	0	0
<i>Pontogeneia</i> sp.	99.0	98.7	98.5	99.1	99.9	100.0	100.0	100.0
<i>Inversula nutrix</i>	100.0	99.2	99.1	99.6	99.1	98.4	0	0
<i>Granaster nutrix</i>	99.1	98.8	98.6	99.1	100.0	0	100	0
<i>Curdia racovitzae</i>	95.9	0	92.7	99.4	0	92.3	97.3	98.0

Table 5. Extraction efficiencies (%) of each MAA (abbreviations as in Table 3) from representative species after three methanol extractions

MAAs were identified by co-chromatography and comparison of wavelength ratios with standards. These standards were prepared from extracts of organisms that have previously been characterized for MAA content: palythine, mycosporine-glycine, and palythanol from the zoanthid *Palythoa tuberculosa* (Takano et al. 1978a,b); porphyra-334 and shinorine from the red alga *Porphyra* sp. (Takano et al. 1979, Tsujino et al. 1980); and asterina-330 and palythene from the ocular lens tissue of the teleost *Plectropomus leopardus* (Dunlap et al. 1989). One UV-absorbing compound (mycosporine-glycine:valine) could not be identified in this way. Its chemical composition was determined by HPLC fractionation, alkaline hydrolysis, and identification of the hydrolyzed amino acids, glycine and valine, by standard chromatographic techniques (Gardner and Miller 1980).

Extraction efficiencies for 80% methanol were determined for representative species of each type of organism collected (Chalker and Dunlap 1982, Dunlap and Chalker 1986). Total content of specific MAAs in each sample was calculated from HPLC peak

areas with calibration factors determined by analysis of standards and corrected by the extraction coefficient. Final concentrations are presented as micrograms of MAA per gram dry weight of tissue.

Results

Extracts from the majority of species examined had absorbance peaks in the range of 315 to 335 nm (Tables 3 and 4, Fig. 2). All extraction efficiencies for invertebrate species were > 98% after three extractions (Table 5). Extraction efficiencies for algal tissues were slightly lower for some MAAs. Eight MAAs were identified (Figs. 1, 3). Seven of these compounds are known from previous work on tropical and temperate marine organisms: palythine (Takano et al. 1978a), porphyra-334 (Takano et al. 1979), shinorine (Tsujino et al. 1980), mycosporine-

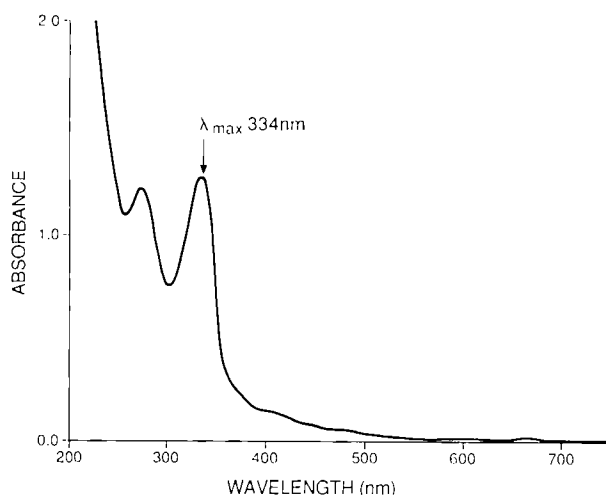


Fig. 2. *Pontogeneia* sp. Example of a spectrophotometric scan of a methanol extract (1:1 dilution), with peak absorption at 334 nm

glycine (Ito and Hirata 1977), palythene (Takano et al. 1978b), asterina-330 (Nakamura et al. 1981), and palythanol (Takano et al. 1978b). An eighth MAA, which has not been reported in organisms from other latitudes, was found in 29 of the 48 Antarctic invertebrate species studied. A UV-absorption maximum at 335 nm indicated that the chromophore is an N-substituted iminomycosporine amino acid (Nakamura et al. 1982). Analysis of the alkaline hydrolysis products identified this compound as mycosporine-glycine:valine (Fig. 1).

Of the species examined, 86% of the invertebrates and all of the algae contained at least one MAA. Only two crustacean species, *Euphausia superba* and *Pontogeneia* sp., contained detectable amounts of all eight MAAs. Of the invertebrates, 76% had mycosporine-glycine, shinorine, porphyra-334, and palythine; 65% contained these four plus mycosporine-glycine:valine. Palythene (43%), asterina-330 (26%), and palythanol (10%) were less common. Mycosporine-glycine:valine was not found in algal extracts, but the other seven MAAs were found in various combinations.

Seven invertebrate species had no detectable levels of MAAs. Only two ctenophore species were collected and neither contained MAAs, although the methanol extract of *Callianira antarctica* had a distinct absorbance peak at 330 nm. MAAs were also absent from the body walls of the two holothuroid species examined. However, the methanol extract of one of these species, *Cucumaria* cf. *georgiana*, had an absorbance peak of 330 nm, and analysis of ovarian tubule tissue from *Ekmocucumis steineni* showed traces of porphyra-334, shinorine, mycosporine-glycine, and mycosporine-glycine:valine. No MAAs were found in the rhizopod, the salp, or the chaetognath analyzed; however, the methanol extract of the salp had an absorbance peak at 328 nm.

Egg capsules of the whelk *Trophon* cf. *geversianus* were also devoid of MAAs, but five MAAs were identified from adults. The body of the snail *Margarella antarctica* contained porphyra-334, shinorine, palythine, and asterina-330, but the shell and egg ribbons contained

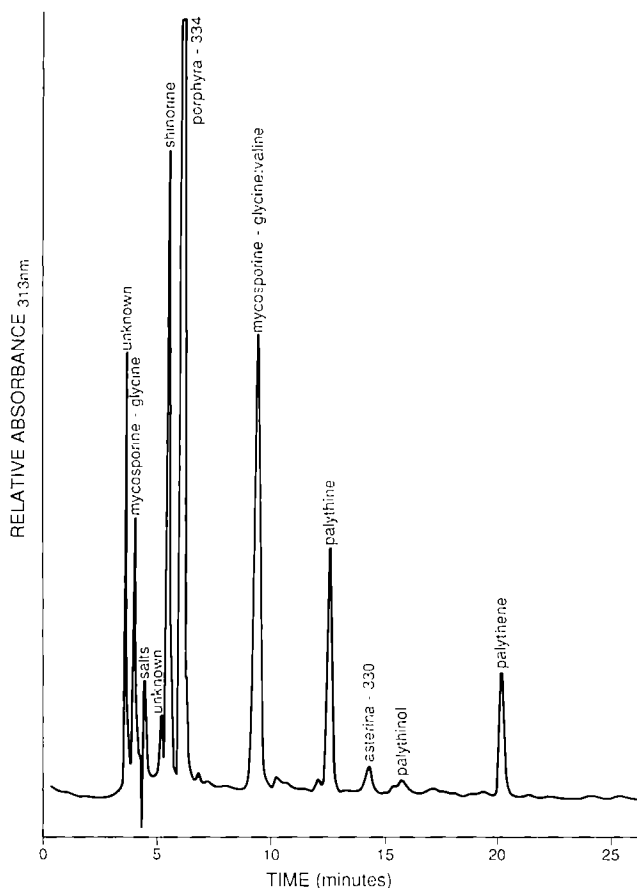


Fig. 3. *Pontogeneia* sp. Isocratic reverse-phase separation of MAAs from an invertebrate on an RP-8 column with a mobile phase of 25% methanol and 0.1% acetic acid

only trace amounts of palythine. Externally brooded embryos of the ribbon worm *Amphiporus michaelsoni* contained the same complement of MAAs as the adult sample.

The highest concentration of a specific MAA was $7177 \mu\text{g palythine g}^{-1}$ dry wt of the red alga *Curdia racovitzae*. The highest concentration found in an invertebrate was $941 \mu\text{g mycosporine-glycine g}^{-1}$ dry wt of the pteropod *Limacina helicina*. Most of the invertebrates contained several hundred micrograms of total MAAs per gram dry weight (Table 3). Total amounts of MAAs were considerably higher in the non-calcareous red algae than in any other group examined, ranging from 1361 to $9385 \mu\text{g g}^{-1}$ dry wt (Table 4).

Relative concentrations of individual MAAs within organisms varied among species for both invertebrates and algae, regardless of taxonomic affinities (Fig. 4). The Nemertinea were the only phylogenetic group that showed any consistency in the relative amounts of MAAs found. Shinorine was the predominant MAA in 35% of the species analyzed; palythine was predominant in 22%, mycosporine-glycine in 12%, porphyra-334 in 10%, and mycosporine-glycine:valine in 6% of the taxa analyzed. Asterina-330, palythanol, and palythene were never the most abundant MAA within a species and rarely accounted for more than 10% of the total MAA complement.

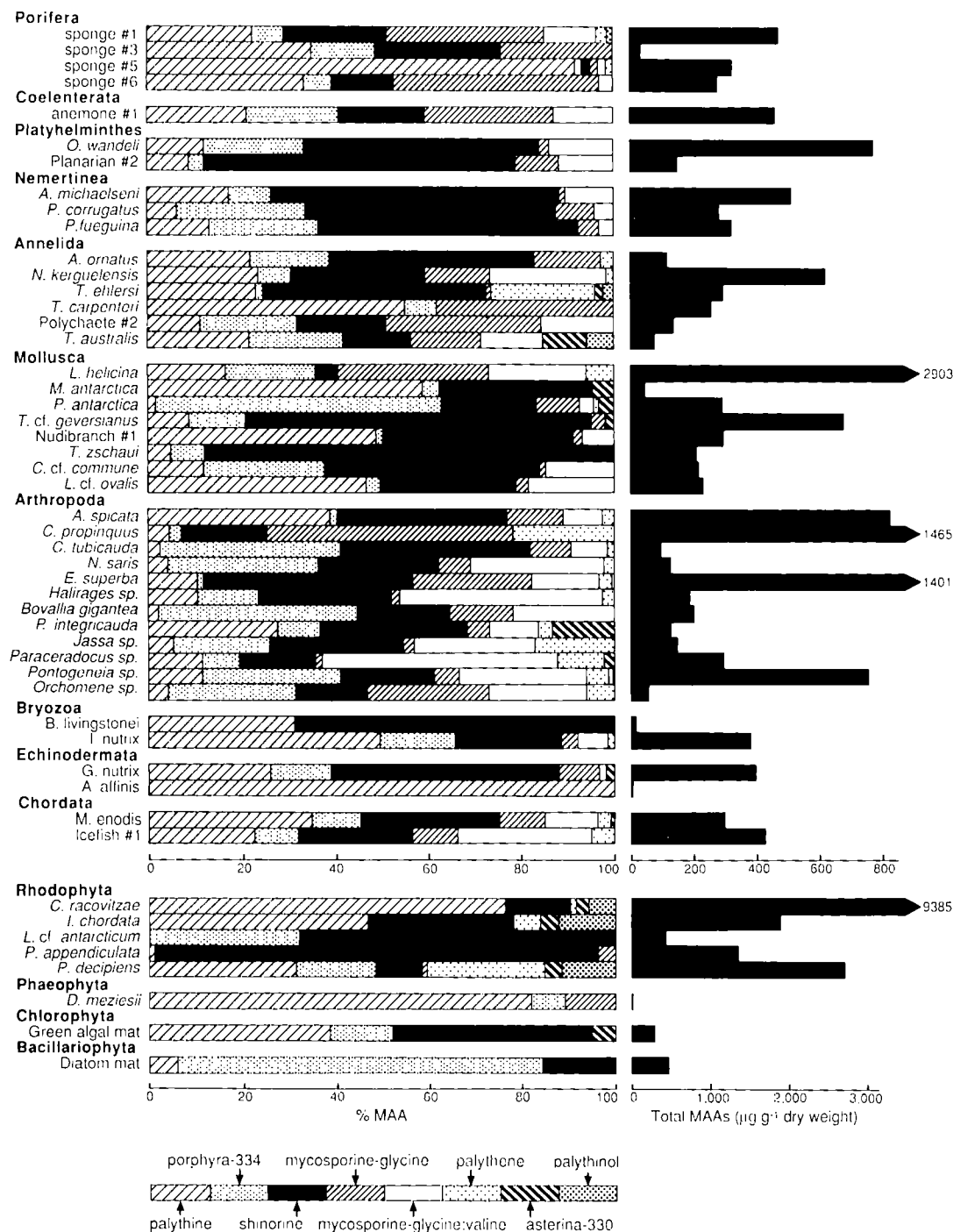


Fig. 4. Amounts of individual MAAs relative to total MAA content within each invertebrate and chordate species (top) and within each algal species (bottom)

Discussion

MAAs have previously been isolated from a variety of fungi and marine organisms (Arpin and Bouillant 1981, Nakamura et al. 1982) but have not been reported in terrestrial plants. Several unidentified UV-absorbing compounds have been extracted from 35 Antarctic lichen species, representing 85% of the lichen taxa surveyed, but UV-absorbing properties were not evident in Antarctic mosses (four species examined) (Karentz and Dunlap un-

published). In marine organisms, identical MAAs have been found in diverse species from temperate and tropical latitudes (Yoshida and Sivalingham 1970, Sivalingham et al. 1976, Ito and Hirata 1977, Takano et al. 1978a, b, 1979, Chioccare et al. 1980, Tsujino et al. 1980, Nakamura et al. 1981, 1982, Dunlap and Chalker 1986, Dunlap et al. 1989), and there has been one previous report of MAAs in the Antarctic krill *Euphausia superba* (Nakamura et al. 1982). The results of the current survey indicate that MAAs are common in marine species from the

Antarctic, and widespread occurrence of MAAs at all latitudes suggests a conservative trait in the evolution of organisms. This is not unrealistic if one considers that during the origins of life on earth there was no ozone layer and incident UV-B intensities were much higher than they are today (Fischer 1965, Cloud 1968, Margulis 1981). The evolution of photosynthesis resulted in the introduction of oxygen and, consequently, UV-filtering ozone to the earth's atmosphere. Therefore, protection from UV exposure would have been an important phenotypic feature in the early evolution of eukaryotic organisms and in the subsequent processes of speciation and natural selection (Harm 1980, Yentsch and Yentsch 1982). This genetic information for biochemical defense against UV exposure has subsequently been retained in fungi and marine organisms. Other groups that must cope with more constant and direct UV irradiation, such as terrestrial plants, have developed more elaborate protective mechanisms, including morphological adaptations (e.g. leaf shape and orientation), pigments (e.g. anthocyanins, carotenoids), and other UV-protecting compounds (e.g. furanocoumarins, flavanols) (Caldwell 1981, Zangerl and Berenbaum 1987, Tevini and Teramura 1989).

The evolutionary implications of MAA distribution in organisms have not been addressed. In marine species MAAs have been reported from algae, invertebrates and fish, but phylogenetic trends in the occurrence of MAAs have not been observed (Chioccare et al. 1980, Plack et al. 1981, Dunlap et al. 1989). Lack of correlation has been distinctly noted among tropical fish species (Dunlap et al. 1989) and is also apparent in the Antarctic data set presented in the present study. The absence of MAAs in certain taxonomic groups was most obvious; e.g. it was characteristic of the few ctenophore and holothuroid species examined in this study.

Methanol extracts of several organisms (ctenophore, salp, and holothuroid species) gave evidence of UV-absorbing properties by spectral analysis, but individual compounds responsible for the UV-absorbing chromophore were not detected by the chromatographic techniques used in this study. The majority of species analyzed in this study contained four or more MAAs. The cumulative effect of having several MAAs with different absorption maxima between 310 and 360 nm is that UV-filtering capability is broadened, thus increasing protection across a larger range of wavelengths. Only broad generalizations can be made about the diversity of MAAs found in several of the phylogenetic groups studied. All of the nemertean species collected contained an identical complement of MAAs in similar proportions. All of the Arthropoda, Porifera, and Platyhelminthes examined had mycosporine-glycine, shinorine, porphyra-334, and palythine, but quantities and relative distributions varied greatly. With few exceptions, these four MAAs tended to co-occur in the invertebrates and were always present with mycosporine-glycine:valine.

In the algae, UV-absorbing compounds have been observed most commonly in the Rhodophyta (red algae) (Sivalingham et al. 1974a, b, Tsujino et al. 1980, and others), and they have been reported from a few species of

Cyanophyta (blue-green algae) (Shibata 1969, Sivalingham et al. 1974b, Haxo et al. 1987) and Pyrrophyta (dinoflagellates) (Balch and Haxo 1984, Carreto et al. 1989, 1990a, b, Vernet et al. 1989). Extracts from Chlorophyta (green algae) and Phaeophyta (brown algae) do not have strong absorption in the UV wavelengths (B. Chalker, pers. comm.). In the present study, species from these groups and from the Bacillariophyta (diatoms) had fewer MAAs, with much lower concentrations, than did the Rhodophyta.

Biologically harmful UV wavelengths can penetrate to at least 20 m in the ocean (Jerlov 1950, 1976, Smith and Baker 1979, Karentz and Lutze 1990), and even a short residence time in surface waters or in intertidal areas could result in detrimental exposure. The invertebrate species with the highest MAA concentrations were from surface plankton samples: *Limacina helicina* (2903 $\mu\text{g g}^{-1}$), *Calanus propinquus* (1465 $\mu\text{g g}^{-1}$), and *Euphausia superba* (1401 $\mu\text{g g}^{-1}$). These species, which are most likely to have received the highest doses of UV, had almost twice the concentrations of MAAs as the other organisms examined. Within our data set, correlations based on habitat are inconsistent, as not all planktonic species exhibited high MAA concentrations. Density of biological organisms, concentration of dissolved and suspended materials, weather conditions, sea surface state and presence of an ice layer affect the penetration of UV within Antarctic marine environments (Karentz 1990, 1991). Hydrographic factors that control vertical mixing will subsequently affect the residence time of planktonic organisms in the upper layers of the water column. Without knowledge of the exposure history of collected specimens, it is not possible to evaluate the effect of habitat on MAA content within the present data set.

Limited information is available on the biosynthesis and metabolic functions of MAAs. MAAs are obviously synthesized by algae, but we do not know if UV protection is their primary function or is instead a secondary role. There is no evidence yet that MAAs are synthesized de novo by animals. It is assumed that they are ingested in plant material and accumulate in the animal tissues. The majority of invertebrate species analyzed in this study were from intertidal habitats. Mycosporine-glycine:valine was not present in any of the intertidal algae examined; however, this MAA was very common at higher trophic levels. Without more complete experimental data, it is not possible to determine whether animals synthesize these compounds de novo or accumulate and structurally modify them after ingestion.

The Antarctic ozone hole is a recent annual event in the springtime austral atmosphere. From 1 August to 30 November 1988, ozone concentrations over Palmer Station and vicinity fluctuated between 198 Dobson units (DU) (14 October) and 396 DU (18 November) (Krueger et al. 1989). The potential biological hazard of incident UV-B in Antarctic during this period was more than 50% greater at the lowest ozone concentrations relative to UV-B filtered through a normal (> 300 DU) ozone column (Karentz and Lutze 1990). During spring, day lengths increased from a few hours to nearly 24 hours, establishing a defined gradient of increasing radiation

exposure. Our data represent MAA concentrations from organisms sampled during the period of changing UV regimes. The degree of variability in the actual concentration of MAAs within a species (related to age, physiological state, collection site, etc.), and whether seasonal changes in UV exposure regulate synthesis or trophic accumulation, are not known. Differences in MAA concentrations have been related to habitat depth in both corals (Dunlap et al. 1986) and algae (Sivalingham et al. 1974a). Laboratory studies of the dinoflagellate *Alexandrium excavatum* have demonstrated that MAA synthesis is stimulated by UV-A light (320 to 400 nm) (Carreto et al. 1990a). These observations suggest that an increase in MAA content is a physiological adaptation to UV exposure.

Regardless of whether the UV protective properties of MAAs are a primary or secondary function, or whether MAAs are synthesized or bioaccumulated, the existence of these compounds within a cell may shield internal components and organelles from the full impact of incident UV radiation. The presence of this natural UV filter system within such a high percentage of species studied implies that Antarctic organisms have some degree of biochemical protection from physiologically harmful UV-B wavelengths during the springtime ozone depletion event known as the ozone hole.

Acknowledgements. We thank Antarctic Services, Inc., staff at Palmer Station for logistical assistance; R. M. Ross and her field group for collections of Palmer Basin samples; R. L. Moe for identification of algal species; E. M. Burreson, A. Child, O. Coleman, D. J. Eernisse, D. Fautin, C. Gust, J. Harasewych, G. Hendler, T. L. Hopkins, R. Larson, C. and F. Monniot, J. L. Norenburg, D. L. Pawson, G. A. Schultz, P. Scott, R. Sluys, K. Stuck, O. S. Tendal, S. van der Spoel, L. Watling, and J. Winston for assistance with invertebrate taxonomy; B. E. Chalker and J. E. Cleaver for helpful discussions; D. Barnes, E. Drew, and two anonymous reviewers for comments on the manuscript; M. McKenney for editing the manuscript; and S. Clarke and M. Eden for drafting figures. This research was supported by U.S. National Science Foundation grant DPP 87-12533 to D. Karentz and J. E. Cleaver; Office of Health and Environmental Research U. S. Dept. of Energy contract DE-AC03-76-SF01012 to the Laboratory of Radiobiology and Environmental Health, U.C.S.F.; and a Visiting Investigator award from the Australian Institute of Marine Science to D. Karentz.

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Evaluation of biologically harmful ultraviolet radiation in Antarctica with a biological dosimeter designed for aquatic environments

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Abstract

A biological dosimeter has been developed for use in aquatic environments. This method is based on the sensitivity of a DNA repair-deficient strain of *Escherichia coli* (CSR06) to ultraviolet (UV) radiation. The dosimeter permits evaluation of the penetration of biologically active UV radiation within a water column, reflecting the potential effect of exposure over selected time intervals. With the use of various filters, the biological dosimeter can discriminate between the effects of UV-B (280–320 nm) and UV-A (320–400 nm) or other selected portions of the solar UV spectrum. During springtime ozone depletion over the Antarctic in 1988, a general relationship was observed between stratospheric ozone concentration and the contribution of incident solar UV-B radiation to lethality of dosimeter cells. The use of dosimeters within the water column indicated that significant amounts of UV-B can be transmitted to a depth of 10 m and biological effects of UV could be detected to 20 and 30 m. Biological dosimeters may provide a means of standardizing in-water UV measurements across all types of aquatic habitats and at any geographical location.

The intensity and spectral distribution of radiation at the earth's surface are dependent on factors such as solar output, weather, and spectral absorbance of atmospheric gases and particles (both naturally occurring

and as pollutants). Ozone differentially absorbs UV-B (280–320 nm) wavelengths, and the spectral quality of incident UV-B radiation is directly correlated with ozone concentrations in the stratosphere. Global changes in incident UV radiation have been predicted as increased concentrations of pollutants in the atmosphere continue to destroy ozone (Cutchis 1974; Rowland 1989). The Antarctic "ozone hole" is a unique ozone depletion phenomenon that accentuates the potential effects of this ecological problem.

UV-B radiation is biologically harmful (WHO 1979; NRC 1984). UV-B wavelengths are strongly absorbed by DNA and proteins, causing structural changes in these molecules that can interfere with vital cel-

Acknowledgments

We thank A. Sancar and G. B. Sancar for the gift of the CSR06 cell line, H. Steier and M. Harrington for help in design and construction of sampling frames, D. Lubin and C. R. Booth for assistance with acquisition of light data, G. Mitchell for use of Schott glass filters, J. E. Cleaver for discussion, R. G. Zepp and two anonymous reviewers for comments, and M. L. McKenney for editing the manuscript.

This research was supported by National Science Foundation grant DPP 87-12533 to D. Karentz and J. E. Cleaver and by the Office of Health and Environmental Research, U.S. DOE contract DE-AC03-76-SF01012.

lular processes of growth and reproduction (Harm 1980). Exposure to UV-B also results in various observable responses, such as the erythema (sunburning), tanning, and carcinogenesis of human skin. Within the 40-nm range of UV-B wavelengths, there is a distinct gradient of biological effect, with shorter, higher energy wavelengths causing greater damage at equivalent intensities. For example, light at 295 nm has 1,000 times the erythematous effect on human skin as light at 320 nm (Moseley 1988). Changes in the spectral distribution of radiation emitted from a light source (solar or artificial) will alter the biological response. Integrated irradiance values do not provide information on the intensity of specific wavelengths within the integrated range. Any measurement of UV radiation that is to be applied to biological systems must take into account the wavelength-dependent effects described above (Calkins and Blakefield 1986).

At present, there is no standard methodology for quantifying the subsurface transmission of UV radiation in aquatic environments. Direct, in-water measurements of UV radiation are difficult to make. Most estimates of in-water UV intensities and spectral distributions have been derived from models based on solar output, atmospheric ozone concentration, hydrographic parameters, and latitude (Zaneveld 1975; Baker and Smith 1982). Actinometry (Zepp and Cline 1977; Wood 1987; Karentz unpubl.) and waterproofed, broad-band UV photodetectors for radiometric measurements (Smith and Calkins 1976; Karentz unpubl.) have been used by only a few researchers. These measurements have an inherent bias because actinometric solutions and photodetectors do not have 100% response across the UV-B wavelength range, but usually follow a normal distribution function.

An in-water UV spectroradiometer has been designed and used in natural waters (Smith and Baker 1979, 1981, 1982; Smith et al. 1980). Data obtained have been analyzed in conjunction with various biological weighting functions and hydrographic parameters to model the penetration of UV radiation through the water column. At present, because of the expertise and cost

required in design, construction, and use of this instrument, there is only one in existence. Therefore, it is not a generally available approach to monitoring UV radiation in aquatic systems. Even with direct data from this instrument, weighting functions need to be applied to estimate biological doses resulting from wavelength-dependent effects.

For any organism, changes in the molecular structure of DNA are primary biological consequences of UV exposure, and the DNA damage spectrum shows distinct wavelength dependency (Setlow 1974; Peak and Peak 1982). Pyrimidine residues in the DNA molecule are involved in the formation of most DNA-UV photoproducts. They include dimers, adducts, and DNA-protein cross-links (Harm 1980). At least three major cellular mechanisms interact with UV-damaged DNA to restore the original genetic code: photoreactivation, excision repair, and recombinational repair (Cleaver and Kraemer 1989). Photoreactivation is a single-enzyme system activated by visible light that corrects one class of cyclobutane pyrimidine dimer in DNA. Excision repair is a system that corrects a range of DNA damage by removal and replacement. Recombinational repair is a complex process in which damaged DNA is reconstructed through DNA replication and strand exchange. DNA repair mechanisms work most efficiently at low levels of damage. There is a level at which the number of DNA lesions will be lethal, preventing the cell from maintaining its metabolism at the minimal rate necessary for growth and reproduction. Therefore, quantification of cell survival can be used to evaluate biologically active UV radiation in a natural environment (Harm 1969, 1980; Rupert 1982).

In this report, we describe a biological dosimeter for monitoring the transmission of biologically active UV radiation in aquatic environments. The dosimeter was used in Antarctica to evaluate the biological effects of incident and in-water UV radiation during the development and dissipation of the ozone hole in spring 1988. The dosimeter is based on the UV sensitivity of a DNA repair-deficient strain of bacteria that cannot correct changes in DNA molecular

structure caused by UV radiation. When these cells are exposed to UV light, DNA photoproducts accumulate, and cell death occurs at relatively low numbers of such products within the genome. Quantification of survival after exposure to ambient light at selected depths can be used as a dosimetric method to evaluate UV transmission in aquatic environments.

Methods

Origin and genotype of dosimeter—The organism selected for the dosimeter was *Escherichia coli* strain CSR06. This cell line contains the following mutations of the wild-type strain (K-12) from which it was derived (Sancar and Rupert 1978): *F⁻*, *thr-1*, *leuB6*, *proA2*, *phr-1*, *hisG4*, *argE3*, *thi-1*, *uvrA6*, *ara-14*, *lacY1*, *galK2*, *xyl-5*, *mtl-1*, *rpsL31(strep^R)*, *tsx-33*, λ^- , and *supE44*. Most of these mutations are related to nutritional requirements (Bachmann 1983), and two are relevant to its use as a UV dosimeter. The cells are deficient in the DNA repair mechanisms of photoreactivation (*phr-1*) and excision repair (*uvrA6*). These genetic defects prevent the excision of pyrimidine dimers from DNA, making cells more sensitive to UV exposure than the wild-type. Cells can be made maximally sensitive by including a recombinational repair mutation *rec⁻*, but cells that are *uvr⁻ rec⁻* are killed by 1–2 photoproducts per genome (Lewin 1974) with 0.1% survival of a population after 30 s of exposure to sunlight (Harm 1979). This degree of sensitivity makes these cells too difficult to handle under both field and laboratory conditions. The *uvr⁻ rec⁺* genotype can survive up to 50 photoproducts per cell, corresponding to 1 per 80,000 base pairs of DNA.

The CSR06 cell line is resistant to the antibiotic streptomycin [*rpsL31(strep^R)*], and the addition of streptomycin to the medium reduces the possibility of contamination by wild-type bacteria that are streptomycin sensitive.

Dosimetric procedure—Samples (0.1 ml) from an overnight culture of CSR06 grown at 37°C in Luria-Bertani (LB) nutrient medium containing 50 $\mu\text{g ml}^{-1}$ streptomycin (Maniatis et al. 1982) were diluted in 10 ml of fresh LB (1:100 dilution). Cell suspen-

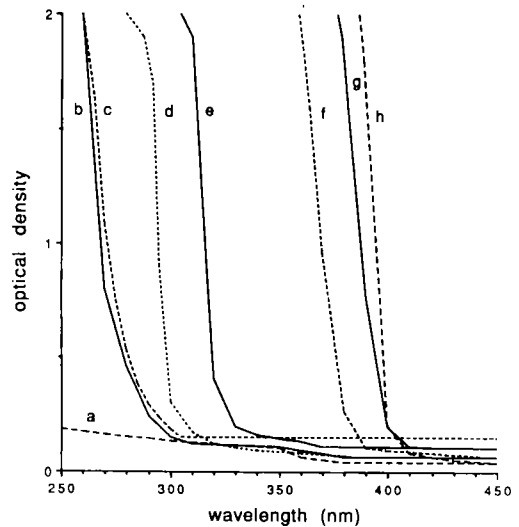


Fig. 1. UV-absorption spectra of various materials that can be used to partition the solar UV spectrum (thicknesses range from 0.4 to 3.2 mm): a—polyethylene (Whirlpak bag); b—acrylic (Plexiglas UVT); c—cellulose acetate (Catalina Plastic and Coating Corp.); d—polyvinyl chloride (Koroklear); e—polyester (Mylar); f—acrylic (Plexiglas 55); g—polycarbonate (Lexan); h—acrylic (Polycast UF3, similar to Plexiglas UVF).

sions for UV exposure were made up in LB containing 20% glycerol by adding 1–2 μl of the 1:100 diluted culture for each milliliter of the required total volume. The final cell concentration was $1\text{--}3 \times 10^4$ cells ml^{-1} . Two milliliters of this cell suspension were heat sealed (without air bubbles) in the middle of a 6-oz (177.4 ml) Whirlpak bag to form a 35- × 65-mm packet. Whirlpak bags are made of polyethylene, are sterile, and are transparent to UV-B wavelengths (Fig. 1 a). The packaged cell suspensions were placed under the desired exposure conditions for a specific interval. After exposure, cell suspensions were transferred to sterile tubes, and 10 μl from each treatment was spread onto a 10-cm Petri plate containing 25–30 ml of LB agar with 50 $\mu\text{g ml}^{-1}$ streptomycin. Plates were inverted and incubated at 37°C. Eighteen to 24 h after plating, colonies were large enough to count, and numbers per plate were recorded. Control plates were set up from unexposed samples, which were packaged and handled in the same manner and at the same temperature as exposed cell suspensions. Calculations of the percentage of survival of cells after each

treatment were made relative to the unexposed controls. If culturing equipment is not available at the field site, samples can be refrigerated at 4°C for several days or frozen at -20°C, or preferably -70°C, for several months and plated at a later date.

Data presented here are from triplicate plate counts. In our hands, and with the dilutions indicated above, 10 μ l of the unexposed LB-glycerol cell suspension results in 100–500 colonies per plate. This number is reasonable to count by hand and sets a lower limit of sensitivity between 0.2 and 1% survival.

Effects of temperature on dosimetric results—As described below, the work presented here was conducted in Antarctica at ambient water temperatures of -2° to 1°C. When not in the water, cell suspensions were kept refrigerated until plating. Under these conditions cells do not divide. To determine the effect of warmer water temperatures, packaged cell suspensions were incubated 4 h in the dark at 0°, 10°, 20°, and 30°C. Four replicate samples were plated for each temperature.

Dose response of CSR06—CSR06 cells were exposed to 0, 10, 50, 100, 500, or 1,000 J m⁻² of UV-B at a rate of 12.5 J m⁻² s⁻¹ (1,250 μ W cm⁻²). The light source was a bank of 5 UV fluorescent lamps (BLE-8TB02, Spectronics Corp.). The intensity of wavelengths emitted approximated a normal distribution from 275 to 350 nm with an accentuated emission peak at 313 nm. The lower limit of wavelength emission was due to the spectral properties of the phosphor and a sharp cutoff filter was used to remove wavelengths above 320 nm. UV intensity was measured with a Spectronics DM-300N radiometer, a broadband photodetector designed for quantifying UV-B radiation from artificial lamp systems.

Response of CSR06 to sunlight—Fieldwork was conducted at Palmer Station (64°46'S, 64°03'W), a U.S. research facility at Arthur Harbor, Anvers Island, along the Antarctic Peninsula. Times are recorded as Greenwich mean time (GMT). Local apparent noon at Palmer Station occurs at 1600 GMT. The time-course of survival during daylight was monitored on 4 and 13 October 1988. Cell suspensions were exposed

to total ambient sunlight for 12 intervals of 1 h each from 1100 to 2300 GMT.

To determine the spectral response of CSR06 cells to various portions of the solar UV spectrum, we exposed cell suspensions to incident sunlight and sunlight filtered through various UV-absorbing materials. Exposures were made at sea level on 10 dates from late September through November 1988. Incubations were started at 1530 GMT and samples were collected at 1-, 2-, and 3-h intervals. Mylar polyester film (Fig. 1 e) was used to remove UV-B wavelengths below 316 nm, and Plexiglas 55 acrylic plastic (Fig. 1 f) was used to remove wavelengths below 360 nm. These two materials selectively screen out major portions of the UV-B and UV-A wavelengths present in solar radiation. Additional filtering materials can be used to further partition the solar UV spectrum (Fig. 1) or neutral-density screening can be used to modify the rate of the biological response by reducing radiation intensity.

A similar experiment was conducted on 2 December 1988. Cell suspensions were exposed from 1500 to 1600 GMT under Schott glass filters with wavelength cutoffs of 290, 305, 320, and 365 nm.

Use of the dosimeter for water-column measurements—To determine the vertical profile of biologically active UV-B within the water column, we attached packets of cell suspensions by plastic cable ties to frames made of polyvinyl chloride tubing (Fig. 2A), and the frames were connected to each other by fixed lengths of line. A weight was used to stabilize the line in the water as it descended from a surface buoy. When deployed, cell suspensions were parallel to the water surface and received directly transmitted light as well as reflected and scattered radiation. The frames remained at fixed depths (0, 1, 5, 10, 20, or 30 m) during the incubation (Fig. 2B). To discriminate between lethality caused by UV-B vs. longer wavelengths of sunlight, we incubated cell suspensions at each depth with or without Mylar. During deployment and retrieval, cell suspensions were protected from exposure to extraneous sunlight by transport and storage in light-proof plastic bags. The dosimeter was used routinely in Arthur Har-

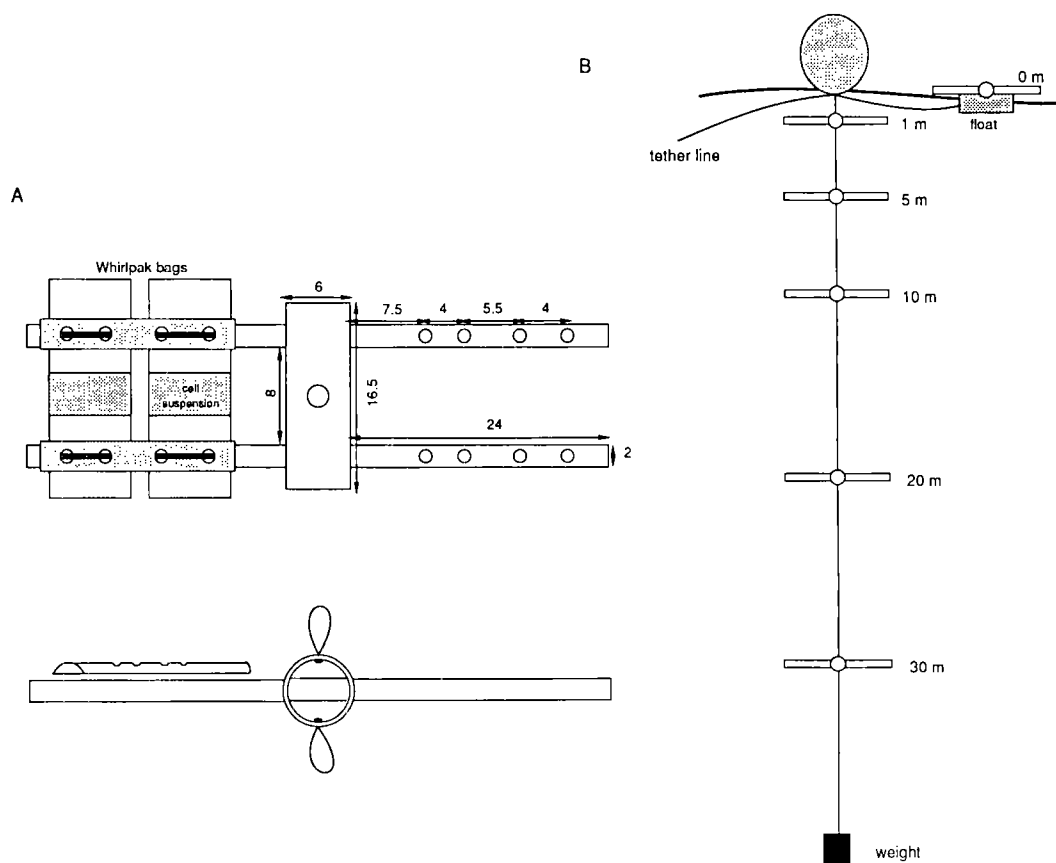


Fig. 2. A. Sample frame made of PVC pipe to which cell suspensions are attached for incubation at depth (dimensions in cm). Two lengths of 2-cm-o.d. pipe are inserted through a 6-cm central support. Segments of 2-cm pipe are cut in half lengthwise and used as clamps to hold bag edges flat. Plastic cable ties (37 cm) are woven through holes in the frame and easily pierce the double layer of polyethylene bag. B. Sampling array deployed for monitoring to 30 m. Frames are clipped together with fixed lengths of line for easy deployment and retrieval.

bor during the 1988 Antarctic spring. Complete results of seasonal studies will be reported elsewhere. Data from two different days are presented here. These incubations were made on 6 October 1988 for 3 h (1600–1900 GMT) and on 11 November 1988 for 8 h (1300–2100 GMT).

Results

Where zero survival values are not critical for data interpretation, semilogarithmic plots are presented, and occurrence of zero values is noted. In some instances it was considered more important to include the zero values in the figure than to use log transformation.

There was 4% or less difference in survival among cells incubated at four tem-

peratures (Table 1). With vigorous agitation of medium, optimal growth of *E. coli* occurs at 37°C. Cell suspensions for dosimetry are in a 20% glycerol solution and sealed in airtight polyethylene bags. Without constant aeration, cell growth is inhibited at temperatures up to at least 30°C. Therefore, this

Table 1. Mean number of cells per dish, standard error (SE) for four replicates, and percent survival relative to 0°C for *Escherichia coli* CSR06 cells incubated at four temperatures under standard conditions used for dosimetric measurements.

°C	Mean	SE	% survival
0	496	10	100
10	481	7	97
20	480	3	97
30	477	6	96

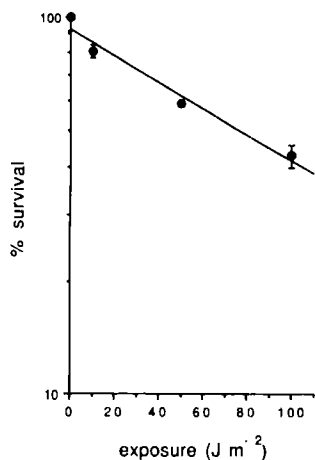


Fig. 3. Survival of *Escherichia coli* CSR06 cells exposed to fluorescent UV-B lamps (cell survival at an exposure of 500 J m^{-2} was 0).

method can be used in most aquatic habitats without temperature effects. As a standard precaution, dark controls should be incubated at the same temperature at which samples are exposed.

The survival curve for *E. coli* CSR06 demonstrates a linear dose response of this cell line to artificial UV-B exposure (Fig. 3). Regression analysis of these data gives a correlation coefficient of 0.97. At exposures of 500 J m^{-2} and higher, no survival was detected (lower limit of sensitivity for this experiment was 0.5% survival). The UV fluorescent lamp system used does not simulate natural sunlight. This experiment was designed to demonstrate the dose response of CSR06 cells to a UV-B light source that has a constant flux and fixed spectral output. Neither of these properties remains constant during natural sunlight exposures.

On 4 and 13 October 1-h sunlight exposures made at local apparent noon resulted in lower survival of CSR06 cells than exposures of 1 h in early morning or late afternoon. There were significant differences between dates. From 1600 to 1700 GMT, 40% of cells survived on 4 October and 7% survived on 13 October. When survival data for each hourly interval from both dates are plotted against integrated irradiance values from the UV-B region of the solar spectrum, a generally linear response of CSR06 cells to the gradient of solar radiation exposure

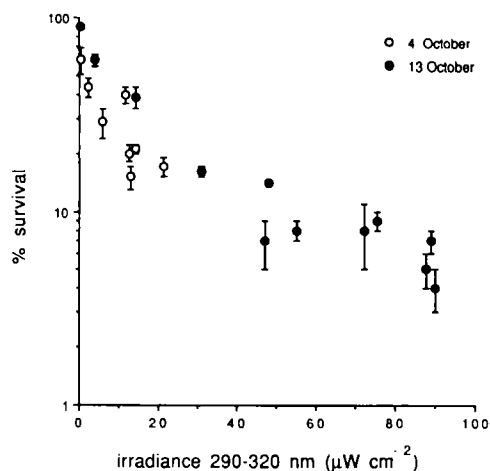


Fig. 4. Survival of *Escherichia coli* CSR06 cells after 1-h exposures to total ambient sunlight on 4 and 13 October 1988. Irradiance values are instantaneous measurements taken at the start of each exposure period.

is evident (Fig. 4). Incident light data were obtained from the U.S. National Science Foundation UV-monitoring program. Data are collected by a scanning spectroradiometer. Measurements are made once hourly during daylight. The spectroradiometer scans from 290 to 700 nm in ~ 20 min. Changes in weather, cloud cover, and solar zenith angle occur during the scanning period and add indeterminable bias to the data set. Irradiance values presented here represent the sum of instantaneous measurements made at 0.5-nm increments from 290 to 320 nm during the initial portion of the hour of incubation. Light values were not integrated over time. (Not all survival values obtained for 4 October are presented because corresponding light values are not available.)

Clustering of 4 October survival data on one side of the plot is due to the much lower maximum in incident light intensity measured on that day than on 13 October. The highest intensity of integrated UV-B irradiation measured on 4 October was $21.2 \mu\text{W cm}^{-2}$ (1700 GMT); on 13 October the maximum was $90.1 \mu\text{W cm}^{-2}$ (1700 GMT). Hourly changes in radiation intensity follow a distinct diurnal pattern (Fig. 5A). However, irradiance levels increase differentially across wavelengths with decreasing solar zenith angle (Fig. 5B). On 13 October there

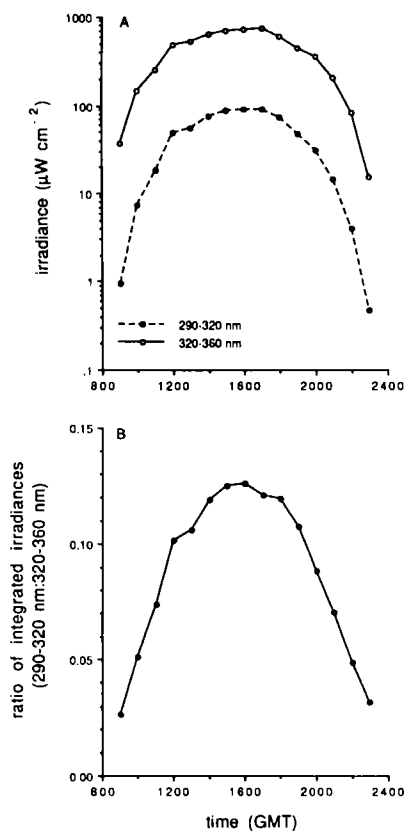


Fig. 5. A. Integrated hourly irradiance for 290–320- and 320–360-nm wavelength regions on 13 October 1988 at Palmer Station. B. Hourly ratios of integrated irradiance.

was a 10% change in the ratio of UV-B to higher wavelengths from sunrise to noon.

Cloud cover was lighter on 13 October than it was on 4 October (when it also snowed during the middle of the day), and vertically integrated atmospheric ozone concentration was 25% lower. If we compare incident light data collected on these two dates at times of day with similar solar zenith angles, so that light was passing through approximately equivalent cross-sectional areas of the atmosphere, 13 October (1400 GMT) was 1.7 times as bright as 4 October (1600 GMT) for the visible portion of the solar spectrum, but differences in UV-B wavelengths were much greater (Table 2). In the 5-nm interval around 300 nm, sunlight intensity was 750 times higher.

CSR06 exhibits a differential response to selected portions of the solar UV spectrum (Figs. 6 and 7). As progressively larger segments of the solar UV spectrum were removed from the light field, survival of CSR06 increased. Removal of wavelengths below 305 nm increased survival at least 100% on 2 December (Fig. 7). Filtering out wavelengths below 320 doubled the number of surviving cells.

A comparison of cell survival made on the 10 different dates for only 1 h of solar exposure (1530–1630 GMT) indicates a range of responses in both level of killing

Table 2. Atmospheric data and integrated values for incident irradiances ($\mu\text{W cm}^{-2}$) of 5-nm wavelength intervals in the UV-B region and visible range (400–625 nm) of the solar spectrum measured at Palmer Station on 4 October 1988 at 1600 GMT and on 13 October 1988 at 1400 GMT. Ratio of UV-B to higher wavelengths in the UV-A region on each date and the magnitude of difference (Mag) between irradiance values of the two dates is also indicated.

	4 Oct	13 Oct	Mag
Ozone concn*	280 DU	214 DU	
Sky conditions	snowing	partly cloudy	
Solar zenith angle†	60.09°	60.29°	
Wavelength interval†			
290 nm	0.00006	0.00060	10.0
295 nm	0.00037	0.03477	94.0
300 nm	0.00081	0.61647	752.2
305 nm	0.07294	4.76791	65.4
310 nm	1.34029	16.04590	11.9
315 nm	6.21313	32.09697	4.9
320 nm	15.08970	47.32005	3.0
400–625 nm	4,586.359	7,679.115	1.7
290–320 nm : 320–360 nm	0.037	0.122	

* Data from Krueger et al. 1989.

† Data from NSF UV-monitoring program.

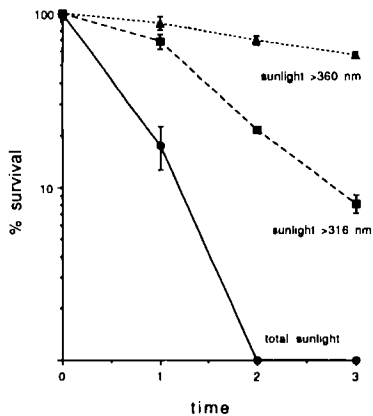


Fig. 6. Survival curves of *Escherichia coli* CSR06 cells exposed to full sunlight (> 290 nm), sunlight > 316 nm, and sunlight > 360 nm. (Points on X-axis represent observed survival of 0.) These data are representative of the general spectral response observed in 10 repetitions of this experiment made during spring 1988.

by total sunlight and enhancement of survival by removal of UV-B wavelengths lower than 316 nm (Fig. 8A). Cell survival after 1 h of exposure to noon solar radiation varied from 0 (6 October) to 64% (10 November). Enhancement of survival by removal of UV-B wavelengths ranged from 1 (30 November) to 51% (26 September). Daily stratospheric ozone concentrations over Palmer Station during spring 1988 were obtained from the 1988 Antarctic Ozone Nimbus-7 TOMS Atlas (Krueger et al. 1989).

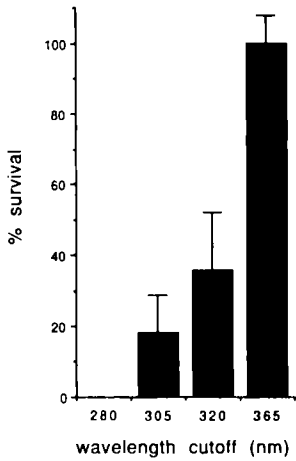


Fig. 7. Survival of *Escherichia coli* CSR06 cells after 1-h exposures under Schott glass sharp-cut filters on 2 December 1988.

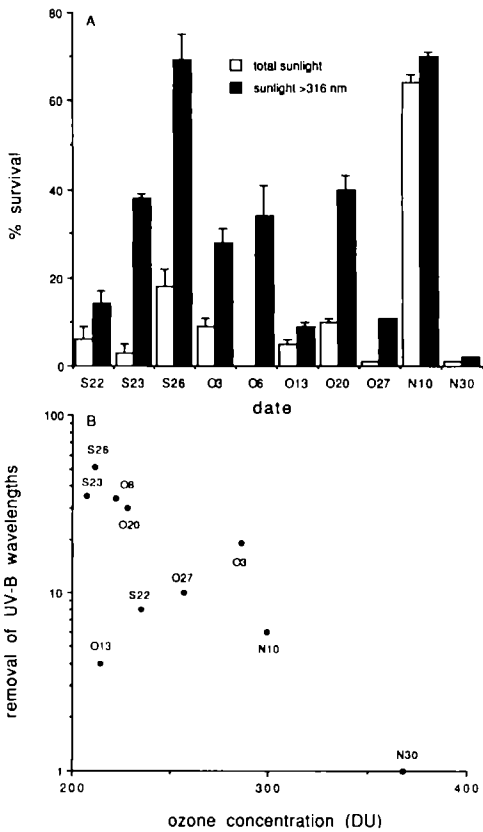


Fig. 8. A. Survival of *Escherichia coli* CSR06 cells on indicated dates in September, October, and November 1988 after 1 h of exposure to full sunlight and sunlight > 316 nm. (Survival on 6 October in full sunlight was 0.) B. Comparison of percent enhancement of survival by removal of UV-B wavelengths to stratospheric ozone concentration over Palmer Station on indicated dates.

When differences in survival between total solar exposure and sunlight without UV-B are plotted against ozone values, a generally linear relationship is evident (Fig. 8B). As ozone increases, enhancement of survival decreases.

Dosimeters incubated at various depths in the water column of Arthur Harbor showed decreases in cell survival to 20 m on 6 October 1988 and to 10 m on 11 November 1988 (Fig. 9). Up to 25% enhancement of survival by shielding from UV-B occurred on 6 October at 10 m after 3 h of exposure. No enhancement was observed at 10 m or below on 11 November after 8 h of exposure. Incident light levels were com-

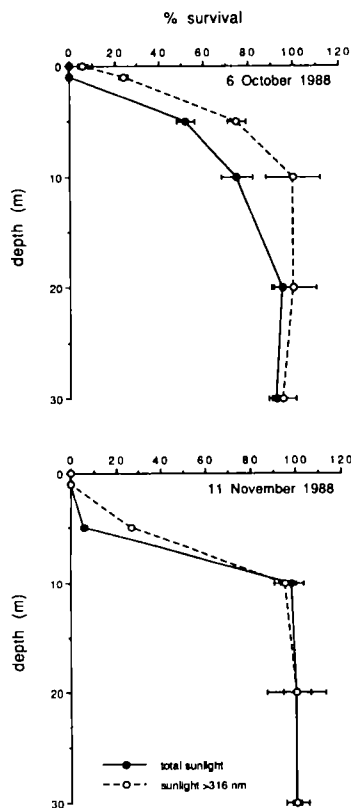


Fig. 9. Survival of *Escherichia coli* CSR06 cells from the surface to 30 m after total sunlight exposure and exposure to sunlight >316 nm in Arthur Harbor on 6 October and 11 November 1988.

parable on these two dates (Fig. 10). At 1600 GMT solar zenith angle was 59.2° on 6 October and 47.1° on 11 November, and ozone levels were 222 and 296 Dobson units (DU), respectively.

Discussion

In UV-photobiological studies, responses to a gradient of radiation exposure are characterized by survival curves. In the simplest form, a survival curve represents a logarithmic function,

$$\log(S/S_0) = -cF \quad (1)$$

where S_0 is the original number of cells irradiated, S is the number of survivors after irradiation, c a constant quantifying the sensitivity of the organism, and F the UV fluence (energy received per unit area) (Harm 1980). The large majority of survival curves published are based on laboratory expo-

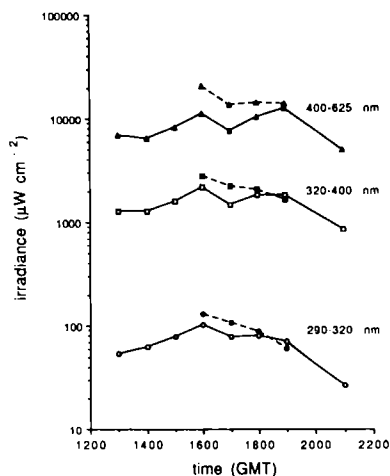


Fig. 10. Integrated irradiance for 290–320, 320–400, and 400–625 nm on 6 October (dashed lines) and 11 November (solid lines) during incubation periods for dosimeter results presented in Fig. 9.

sure to a fixed light source so that flux (fluence rate) and spectral quality are constant. In this situation, cellular responses will follow a logarithmic curve that will be modified by the repair capabilities of the organism. Closest fit to Eq. 1 will occur in cases where there is little or no repair of UV-induced damage.

Incident and in-water solar radiation does not necessarily have a constant flux or fixed distribution of wavelengths, which is the primary reason why this dosimeter system was developed. A measure of 100 $\mu\text{W cm}^{-2}$ of UV-B does not indicate the contribution from each wavelength, and various spectral distributions could yield this irradiance. Because of the wavelength dependency of biological responses, equal values of total irradiance obtained from integration across wavelength ranges can have different biological consequences. For this reason, it is very difficult to assess the biological relevance of measured radiation. The linear response of CSR06 cells to a UV-B lamp source verifies that survival data accurately quantify relative doses of UV received. Under natural sunlight, differences in survival of dosimeter cells will indicate differences in the biological harmfulness of incident radiation during exposure.

Variations in UV intensity and spectral quality occur during the course of a day as

the sun moves across the sky. As solar zenith angle decreases, light passes through a thinner layer of ozone, more UV-B reaches the earth's surface, and the ratio of UV-B to higher wavelengths increases. Clouds can affect the intensity of incident light without altering its spectral distribution in the UV-B wavelengths (Lubin et al. 1989); therefore, changes in weather will alter atmospheric transmission of radiation, and incident intensities can vary on a time scale of minutes or less. Results presented here were solar exposures made over periods of one or more hours. During these incubations both intensity of irradiance and spectral quality varied on an indeterminable time scale. The scanning spectroradiometer did not monitor short-term changes (<20 min) in the incident light field, but the biological consequences are integrated in the response of the dosimeter cells.

The biological dosimeter can discriminate between lethality caused by specific wavelength ranges of the solar UV spectrum. Non-UV-B radiation also causes detrimental biological effects. Mortality was caused by wavelengths >316 nm, and to a small extent by exposure to wavelengths >360 nm. In recent tests conducted in San Francisco with sunlight filtered through Polycast UF3 (Fig. 1 h), we established that this residual lethality is due to UV wavelengths between 360 and 400 nm and not to wavelengths of the visible spectrum. Harm (1978) has established that the survival of *E. coli* cells after exposure to solar radiation of wavelengths >360 nm is partially dependent on DNA repair. Therefore, these longer wavelengths also produce DNA lesions, even though it takes several orders of magnitude increase in fluence to cause the same level of damage as from shorter UV-B wavelengths. In addition to DNA damage, non-UV-B wavelengths interfere with other cellular processes. This dosimeter will reflect all of the lethal biological hazards of the radiation field to which it is exposed.

Cells irradiated by unfiltered sunlight for 1 h at noon on 10 dates during the Antarctic spring showed a range of survival responses. Each of these data points reflects the biological effect of the total irradiance and spec-

tral quality of solar radiation during each exposure period. These results can be interpreted as a relative measure of the biological harmfulness of the radiation received by each sample. Sunlight reaching the earth's surface at noon on 6 October caused greater biological damage than light received at noon on 10 November. By filtering out wavelengths <316 nm, the contribution of this portion of the solar spectrum to lethality was observed.

Differences between dates are related to the spectral composition of the incident light and the corresponding fluence of each wavelength. Because of the dramatic changes that occur in the stratospheric ozone concentration over Antarctica during spring, it has been possible to establish a generally linear relationship between the percent enhancement of survival by removing UV-B and the daily ozone concentration. As ozone levels increased, the fluence of UV-B wavelengths decreased, altering the ratio of UV-B to longer wavelengths. Consequently, we observed a corresponding decrease in the contribution of UV-B wavelengths to cell death.

The survival of cells at six depths reflects the vertical profile of UV light transmitted, reflected, and scattered from the surface to 30 m. Differences in survival between samples incubated with and without Mylar indicate mortality caused by the transmission of UV-B wavelengths within the water column. At 0- and 1-m depths, little or no difference between total sunlight and UV-B-filtered exposures was evident. These observations are related to radiation effects of wavelengths >316 nm that have caused significant lethality, obscuring UV-B effects. Increased sensitivity under higher UV exposures can be achieved by reducing exposure times.

Prolonged incubations were used in the present study to assess UV-B effects at greater depths receiving low levels of light. On 6 October 25% of cells were killed after exposure to unfiltered sunlight reaching 10 m. When cell suspensions were shielded with Mylar, removing wavelengths below 316 nm, no cells died. Therefore, biologically harmful wavelengths of UV-B were present at 10 m in the water column during the 3-

h incubation. On 11 November, with lower zenith angles and more than twice the exposure time, no effects of UV-B were observed at 10 m. Hourly intensities of UV-B and UV-A were fairly similar, and the sea surface received much higher UV irradiance during the 8-h exposure on 11 November than during the 3-h exposure on 6 October.

Differences in survival on these two dates represent differences in the transmission (penetration and scattering) of UV-B within the water column. On 6 October mean chlorophyll concentration from 0 to 30 m was $0.5 \mu\text{g liter}^{-1}$, whereas the spring bloom reached its peak during the week of 11 November ($24.5 \mu\text{g liter}^{-1}$). The reduced depth of detection of UV-B on 11 November, even with a longer exposure time, is at least in part related to changes in the spectral absorbance characteristics of the water column caused by development of the phytoplankton bloom.

The dosimeter system described here provides a means of evaluating biologically active wavelengths within aquatic environments and of comparing exposure levels between selected wavelength ranges, depths, times (daily and seasonal), and geographic locations. This biological dosimeter has several advantages over radiometric instruments.

First, all depths can be monitored simultaneously. Owing to logistical requirements and cost, in-water UV radiometers are not usually equipped with multiple photodetectors, and different depths cannot be monitored simultaneously. Furthermore, the light field can change appreciably within the time it takes to scan a range of wavelengths, to switch sensors, or to move to another depth within the water column. With the biological dosimeter system, an array of samples can be deployed at any number of selected depths and exposed under various filters during the same time period.

Second, results of the dosimeter reflect total exposure over a selected time interval. Some radiometers used with in-water UV photodetectors have continuous monitoring capability, but the logistics of setting out the photosensor and maintaining a fixed position can be difficult. With radiometric data,

exposure levels over a given interval are usually interpolated from instantaneous measurements. Under clear-sky conditions this interpolation can be made relative to changes in solar zenith angle and stratospheric ozone concentration. Because weather conditions greatly affect the intensity of incident UV, estimates from instantaneous data must be carefully corrected.

The biological dosimeter registers total exposure at each depth, regardless of changes in weather, providing an accurate record of UV dose over a designated period. Therefore, cellular responses of the dosimeter can reflect a higher degree of accuracy relative to the biological effect of solar exposure than is possible to obtain from a conventional radiometric data set. In addition, low levels of UV at a given depth may not be detectable by electronic instruments that are recording an instantaneous signal. Prolonged exposure of the dosimeter permits high sensitivity in UV detection. In shallow waters or high light intensities, 100% mortality can occur very rapidly, and lethal effects of non-UV-B radiation may be significant. Careful selection of filters and exposure times should be made in these cases.

Third, results indicate direct biological effects. Radiometric results must be analyzed relative to selected biological weighting functions to account for the wavelength-dependent action of light on living cells. The DNA damage spectrum is most commonly used for this type of analysis, but plant response and erythral functions can also be applied. The use of a DNA repair-deficient organism to monitor UV exposure levels eliminates the necessity of a weighting function.

There is very little (if any) information published on the rates of DNA damage and repair in aquatic organisms under natural light conditions. Owing to several characteristics, the *E. coli* dosimeter provides direct data on the upper limit of the biologically active UV dose received by aquatic organisms. *Escherichia coli* CSR06 cells accumulate DNA damage because of the absence of photoreactivation and excision repair systems and reflect damage that can be incurred by any organism in the monitored aquatic environment. In repair-proficient

organisms, photoproduct induction and repair occur simultaneously. Instantaneous measurements of biological responses or photoproduct concentrations thus do not provide valid data on exposure. *Escherichia coli* cells are at the small end of the size range for aquatic cells. Larger cell or body size provides an advantage by internal protection of organelles or organs. The longer the path length through which the UV radiation must pass, the greater the absorption of UV, reducing the exposure of nuclei and thus protecting the DNA from UV damage. Because of the small size of *E. coli* cells, the dosimeter records a maximal level of exposure of genetic material.

Escherichia coli cells are nonpigmented. Many species of aquatic organisms are pigmented, contain UV-absorbing compounds, or may have a cell wall or other external covering that acts as a filter for UV radiation. The dosimeter therefore registers a higher absorbed dose than would most likely be sustained by natural organisms in the environment. Dosimeter data can, however, provide a valid basis on which to evaluate the UV photobiology of species relative to their natural environment. When used in conjunction with radiometric instruments, the biological dosimeter can provide data required for calculation of biological weighting functions needed to assess the biological relevance of in-water UV measurements.

Fourth, the method involves relatively low cost and minimal logistical support. The dosimeter requires the use of standard bacteriological culture facilities. Major expendable items are incubation bags, Petri dishes, and nutrient medium. Field deployment and retrieval can be managed from a dock or a small boat and do not require ship support, although the system has been used easily at sea. There is very little chance of malfunction (no electronic components or moving parts). We routinely sampled at six depths from 0 to 30 m, but the number of samples and maximal depth can be selected for each individual study. When properly tethered or anchored, the sample array can be left unattended. Once samples are collected, colonies can be plated and data processed within 24 h, or, if necessary, exposed sam-

ples can be stored for culturing at a more convenient time.

Fifth, the biological dosimeter can be used as a standardized measure for UV transmission within aquatic habitats. The dosimeter is designed to assess biological effects of UV that are quantifiable relative to cell survival. This system can be used in any field situation and may also be useful in conjunction with laboratory experiments. During exposure periods the dosimeter response is independent of temperature. Because dark controls are run with each set of exposures, no calibration is involved in the interpretation of results, as is routinely required of radiometric detectors.

The response of the dosimeter varies with the spectral quality and intensity of UV light. Observed results are an integrated response that quantifies the potential biological harmfulness of ambient sunlight. The use of various filters permits evaluation of the potential effects of specific wavelength intervals. Survival data can be compared among varying incubation times and locations to quantify the relative biological impact of ambient UV levels. Although the development of this dosimeter was prompted by observations of the Antarctic ozone hole and associated increases of UV-B in the Antarctic marine ecosystem, ozone depletion is a global problem. There has been an increased interest in determining the effects of UV-B in natural environments at all latitudes, and standard methods of monitoring UV-B in aquatic habitats need to be established. The dosimeter registers lethal doses of UV relative to a repair-deficient organism, providing a direct measurement of UV exposure within the water column. We propose that biological dosimeters can provide a means of standardizing in-water UV measurements across all types of aquatic environments and geographical locations, either in conjunction with radiometric data or in situations where radiometric techniques are not available.

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Submitted: 17 July 1989

Accepted: 10 January 1990

Revised: 26 January 1990

Report on studies related to the ecological implications of ozone depletion on the antarctic environment

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Annual springtime ozone depletion over Antarctica has resulted in an increase in the intensity and spectral distribution of solar ultraviolet-B (UV-B) radiation reaching the Earth's surface (Frederick and Snell 1988). UV-B is known to have many harmful biological effects (Harm 1980). This range of wavelengths (280–320 nanometers) is absorbed by DNA and proteins, causing conformational changes in molecular structure that interfere with the normal functioning of these molecules in cell metabolism. The antarctic ozone hole has been in existence for over a decade, and ecological changes that could be caused by increased UV-B have already been initiated. Long-term effects have yet to be identified, but the consequences of increased UV-B levels in the antarctic marine environment are a primary concern.

The project described here examined several aspects of ultraviolet radiation related to the photobiology of antarctic organisms. Field studies and collections were made in the vicinity of Palmer Station (64°46'S 64°03'W) at Arthur Harbor, Anvers Island, on the Antarctic Peninsula.

Quantification of UV-B in the aquatic environment. Biological dosimetry, actinometry, and radiometry were used to study the vertical transmission of UV-B within the water column of Arthur Harbor from September to December 1988. This period coincided with the opening and closing of the 1988 ozone hole (October to November). The biological dosimeter used a DNA repair-deficient bacterial cell line to measure relative levels of biologically active UV-B within the water column. Actinometry is based on the UV photolysis of specific compounds. Parantiroanisole was used as an actinometer (Dulin and Mill 1982) in conjunction with the biological dosimeter. Instantaneous measurements of UV-B were made with a waterproofed broadband UV-B photodetector. An example of results obtained with these three methods is presented in figure 1.

Atmospheric factors such as the angle of the Sun, ozone concentration, and cloud cover affect the spectral distribution and intensity of UV-B that reaches the Earth's surface. Hydrographic factors such as dissolved matter, particulates, and phytoplankton concentration affect the transmission of UV wavelengths through the water column. Chlorophyll concentrations and total DNA content of the waters of Arthur Harbor were determined during this study. Complete analyses of light and hydrographic data are under way.

DNA repair in antarctic organisms. Eight species of planktonic diatoms isolated from Arthur Harbor and maintained in culture were studied to characterize DNA repair mechanisms and the effects of UV-B exposure on population development (figure 2). Preserved samples from additional experiments conducted during the 1988 season are being analyzed to determine specific molecular characteristics of DNA damage and repair in antarctic phytoplankton species.

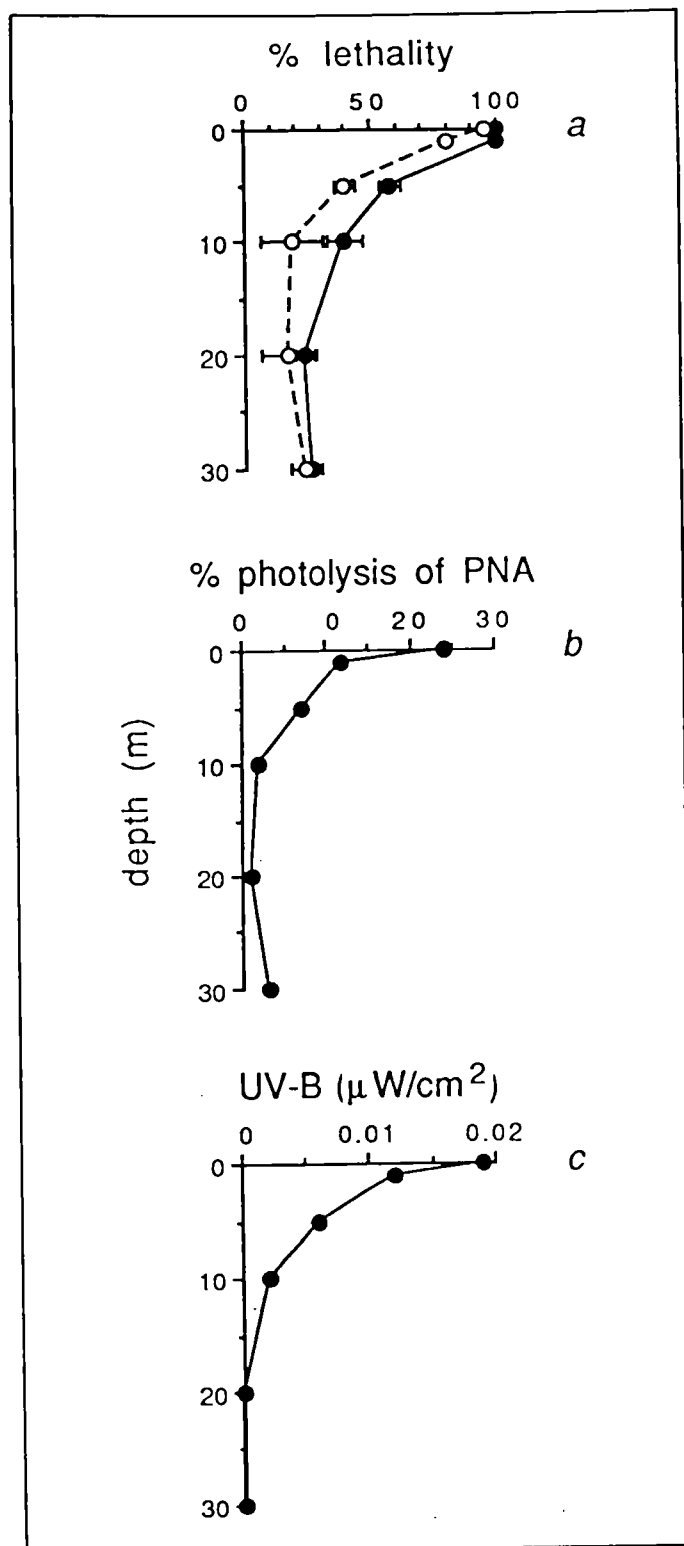


Figure 1. Measurements of in-water ultraviolet-B (UV-B). A. Biological dosimetry: Lethal effects of ambient in-water UV radiation exposure to a bioassay organism. Filled circles denote full-light incubations; open circles denote samples exposed to ambient light from which UV-B wavelengths were filtered out; and bars denote mean $\pm$ SE. Cells were exposed at the indicated depths for 3 hours on 6 October 1988. B. Actinometry: Photolysis of parantiroanisole (PNA) caused by UV-B exposure within the water column. Incubation conditions were the same as for A. C. Radiometry: Instantaneous UV-B measurements made with a broadband photodetector at local noon. (m denotes meter. μ W/cm² denotes microwatts per square centimeter.)

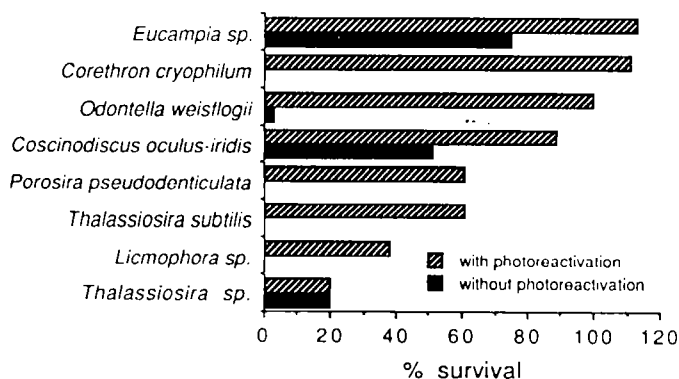


Figure 2. Survival of cultured diatom cells after irradiation by 1,000 joules per square meter of UV-B light (peak emission 313 nanometers) and 8 days of growth under light conditions that supported or prevented photoreactivated repair of DNA.

Identification of UV-B-absorbing compounds. During the spring of 1988, eight macroalgal species, 34 lichens, seven mosses, and 114 invertebrates were screened for the presence of UV-B absorbing compounds. Eighty-five percent of these samples showed distinct absorbance peaks in the UV-B wavelength range (figure 3). These samples are being analyzed by high-pressure liquid chromatography to identify specific compounds and relate their structure to those of UV-B-absorbing compounds that have been found in tropical and temperate species (Dunlap and Chalker 1986). This work is being completed in collaboration with Walter Dunlap of the Australian Institute of Marine Science.

Conclusions. Results from this project have demonstrated that biologically significant fluxes of UV-B radiation occur down to 10 meters and can reach to 30 meters in antarctic coastal waters during the ozone hole. Photoreactivation may be the predominant pathway for DNA repair in antarctic diatoms and observed differences in cell division rates support previous conclusions that the major effect (if any) of increased UV-B in the antarctic in the antarctic environment may be changes in the taxonomic structure of plankton communities. It also appears that many antarctic species are able to synthesize compounds that act as natural "sunscreens," providing protection from UV-B exposure.

I would like to thank field party members M.C. Land and F.S. McEuen for their assistance; and the Palmer staff from

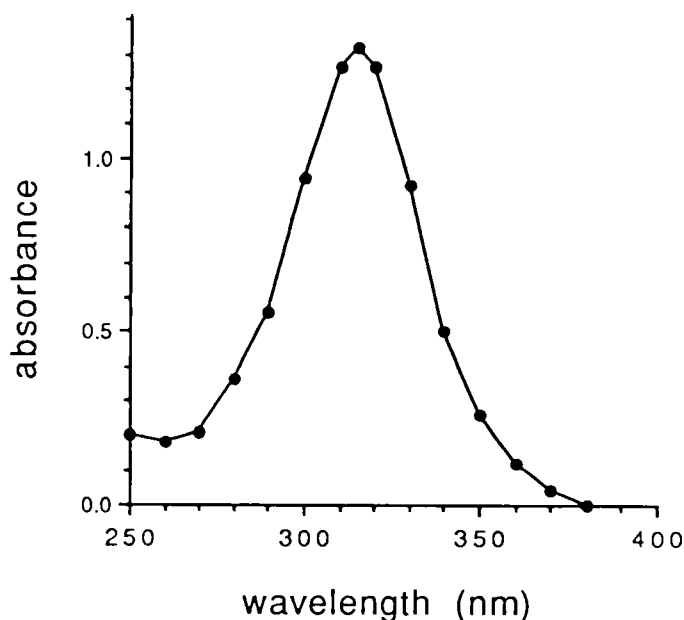


Figure 3. Example of a spectrophotometric scan of a cell extract (1:100 dilution) that has UV-absorbing properties. These data are from a red algal species (*Curdiea racovitzae*). (nm denotes nanometer.)

ITT/Antarctic Services, Inc., for their excellent support. This project was sponsored by National Science Foundation grant DPP 87-12533 to D. Karentz and J.E. Cleaver and by the Office of Health and Environmental Research, U.S. Department of Energy, contract DE-AC03-76-SF01012.

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Delayed density-dependence

SIR — Population ecologists have frequently failed to detect significant density-dependence, the pivotal prediction of the theory of population dynamics, in natural populations of animals. Various statistical techniques for demonstrating density-dependence have been described and tested (for example see refs 1, 2), but many difficulties still remain^{3,4}.

closely for moths, but we found less delayed density-dependence than expected by chance for aphids (the model is not very appropriate for aphids with several overlapping generations per year).

We are not suggesting that the delayed density-dependence demonstrated by Turchin is not real or important, but we do suggest that the high incidence detected by him is due to the selection of forest pest species with a tendency towards outbreak dynamics. More generally, the kind of data

Our results strongly suggest that delayed density-dependence is rare in these insects and, by implication, in most insect populations. Although delayed density-dependence is uncommon in British moths and aphids, we do find non-delayed density-dependence to be common (manuscript in preparation).

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DELAYED DENSITY-DEPENDENCE IN INSECT POPULATIONS

Taxon	Number of species	series	Significance level	Observed fraction	χ^2	P
Moths	357	4,306	0.05	0.045	1.13	0.287
			0.01	0.014	2.84	0.092
			0.05	0.022	15.62	<0.001
Aphids	92	1,405	0.01	0.004	3.22	0.073

Lengths of the time-series are from 10 to 24 years.

Turchin has pointed out⁵ that most current techniques are unsuitable for detecting delayed density-dependence. Therefore, if population regulation with time lags is common, the overall level of density-dependence may be underestimated.

Turchin demonstrated this problem with an analysis of 14 sets of time-series data on forest insects, eight of which showed clear evidence of delayed density-dependence. We have analysed a large set of time-series data on annual abundances of moths and aphids using the light-and suction-trap networks of the Rothamsted insect survey⁶ (our full analysis will be published elsewhere). We have looked at the occurrence of delayed density-dependence using Turchin's method⁵, and present our results in the table.

We counted the fractions of time-series that showed significant delayed density-dependence at 5 and 1% levels. (By chance, one would expect that 5 and 1% of the time-series would show a delayed effect at these levels.) The observed fractions of significant delayed effects match the expected values

typically analysed by population ecologists are biased towards the most abundant and outbreak species, which means that the current population-dynamic conclusions based on these data should be viewed with caution⁴. Our data consist of 'ordinary' insect populations, without any bias with respect to their abundance or dynamics.

DNA damage in the Antarctic

SIR — The Antarctic ozone hole represents a cycle of annual springtime depletion of stratospheric ozone over the continent and surrounding ocean areas, with consequent increases in levels of ultraviolet-B radiation (UV-B, 280–320 nm)¹. The ecological impact of this increased radiation is of particular concern for Antarctic marine communities, which depend on the productivity of phytoplankton at the base of short food chains. There has been much speculation about ecological effects based on *a priori* assumptions about unique photobiological properties of Antarctic organisms. A common misconception is that because these organisms inhabit an area of relatively low ambient ultraviolet intensity, Antarctic species may be more sensitive to UV-B exposure than their temperate or tropical counterparts². But Antarctic species are derived from temperate and tropical stocks and should therefore retain a capacity for biochemical protection from ultraviolet exposure³ and for repair of radiation-induced damage.

During 1987 and 1988 we carried out one of the first on-site evaluations of ultraviolet exposure and photobiological responses of nine phytoplankton species at Anvers Island in the Antarctic⁴. We discovered that biologically effective UV-B can be detected as deep as 20 m during springtime ozone depletion⁵ and noted that the morphology of the cells influenced the amount of initial DNA damage⁴. The nine diatom species, which spanned nearly three orders of magnitude in

cell volume with considerable variation in surface area: volume ratios, exhibited a nearly 100-fold range in the total number of photoproducts induced. All species investigated showed evidence of both photoreactivation and excision repair at ambient Antarctic temperatures, but with considerable species variation. *Chaetoceros neglectus*, for example, removed 31% of cyclobutane dimers in 6 h but did not repair any (6–4) photoproducts; *Corethron cryophilum* repaired 46% of the dimers induced and 94% of the (6–4) photoproducts⁴.

The ozone hole has existed for more than ten years. Obvious catastrophic events have not been noted. Our results indicate that Antarctic phytoplankton have diverse capacities for sustaining and repairing UV-induced damage to DNA and as a group are not defenceless against this environmental stress. Cumulative biological effects of the ozone hole are apparently subtle alterations in species interactions, and it may take longer than a decade for these perturbations to have an observable effect. The UV photobiology of individual species needs to be a key focus in future research efforts.

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Scientific Correspondence

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If new results are being described, priority is generally given to communications that do not describe work in which the author is involved. Authors of contributions of this nature should explain in a covering letter why theirs has a particular claim on *Nature's* space. Contributions may be sent to referees and, in the case of matters arising from material published in *Nature*, are sent to the author of that article for comment. A more detailed guide to authors is available from Washington or London. □

OREGON RESEARCH AND DEVELOPMENT CORPORATION



April 8, 1991

Senator Al Gore
United States Senate
Washington, DC 20510-4202

file

*file - make a
definition - US*

Dear Senator Gore:

Thank you for your letter dated March 13, 1991. I appreciate your taking time enough to write.

I wanted to point out to you at this time that I am experiencing the deforestation problem locally. I own an estimated 130 acres of forest land which is private. All around me everyone has sold there forest lands (within 5 minutes of the city I might add) to private loggers. In turn these loggers are cutting the logs and shipping them overseas.

According to the U.S. Department of Interior, logs are being exported to Japan and other countries from private and State lands. My office in Tokyo is presently reporting logs being stored in and around Tokyo. It is my understanding as well that they are sinking the logs in Tokyo Bay for preservation.

Please be aware that we must have some type of a law that protects private lands. Fir bearing trees are being cut considerably, however, very little oak is being cut. The scrub oak in Oregon grows quite rapidly and will grow around and overcome the new fir trees. Of course, keep in mind that at this time 92% of the old growth and 45% of the new growth have been cut. The figures presently out there are not correct. The research out there is very false.

Also, keep in mind that the weather is changing rapidly and drought situations are occurring throughout the world. This is caused by the massive amounts of forest destructions on private and public lands. Deforestation is also effecting our water shed and fish (salmon) population.

Laws must provide protection for both the private lands and the public lands. Just because individuals own property does not mean that they can butcher it.

Sincerely,

OREGON RESEARCH AND DEVELOPMENT CORPORATION

William a Curtright
William Curtright
President/C.E.O.



United States Department of the Interior

BUREAU OF LAND MANAGEMENT
WASHINGTON, D.C. 20240



MAR 29 1991

IN REPLY REFER TO:

5000 (230)

Mr. William Curtright
Chief Executive Officer
Oregon Research and Development Corp.
1895 16th Street, SE
Salem, Oregon 97302

Dear Mr. Curtright:

Thank you for your letter of March 11, 1991, to Secretary of the Interior Manuel Lujan, Jr., concerning deforestation of the old growth. The Secretary has asked the Bureau of Land Management (BLM) to respond to your letter.

It is true that many logs are being exported to Japan and other countries, but the logs are being exported from private and State lands. It is unlawful to export any unprocessed timber originating from Federal lands. The Forest Conservation and Shortage Relief Act of 1990 was enacted on August 20, 1990, and prohibits export of unprocessed timber originating from Federal lands (export of unprocessed timber from Federal lands has been banned since 1974 by a provision in annual appropriations bills). This Act also prohibits substitution of unprocessed timber originating from Federal lands for unprocessed timber originating from private lands that was exported. The Act also prohibits export of unprocessed timber originating from State lands, except for 25 percent of the annual sales volume from State lands in Washington. The Act also defines "unprocessed timber" by specifying the types of product that are considered as processed. This Act when fully implemented should decrease the amount of unprocessed timber that is exported.

We are not aware of any significant problems with reforestation due to companies going bankrupt. To the contrary, data published in the RPA Assessment of the Forest and Rangeland Situation in the United States, 1989 show that softwood timber inventory and growth on forest industry lands have been increasing since 1952. The timber industry in the Pacific Northwest is doing a very good job of planting trees to replace those harvested.

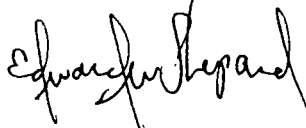
It is not practical to stop logging, as you suggest, because there is a great demand for wood and paper products in this country and any decrease in domestic production would have to be replaced by imports from other countries or replaced by substitute materials that are nonrenewable, less energy efficient, and much more environmentally harmful. Increased imports of wood products would likely be from nations that do not manage their forests as well as we do in this Country; therefore, the world environment would be damaged more.

There are steps being taken at this time to improve the conditions of our forests and the environment, for example, President Bush's "America the Beautiful" initiative and the American Forestry Association's "Global ReLeaf" program. Protection of the environment is a major concern of the Administration and the industry is also concerned.

If you have any further questions on this matter, please let us know.

Sincerely,

ACTING

A handwritten signature in dark ink, appearing to read "Edward J. Shepard". The signature is fluid and cursive, with the first name "Edward" being more prominent.

Chief Division of Forestry

Review

Ecological considerations of Antarctic ozone depletion

DENEB KARENTZ

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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.

Received 5 March 1990, accepted 9 August 1990

Key words: Antarctic, ecology, ozone, ultraviolet

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,

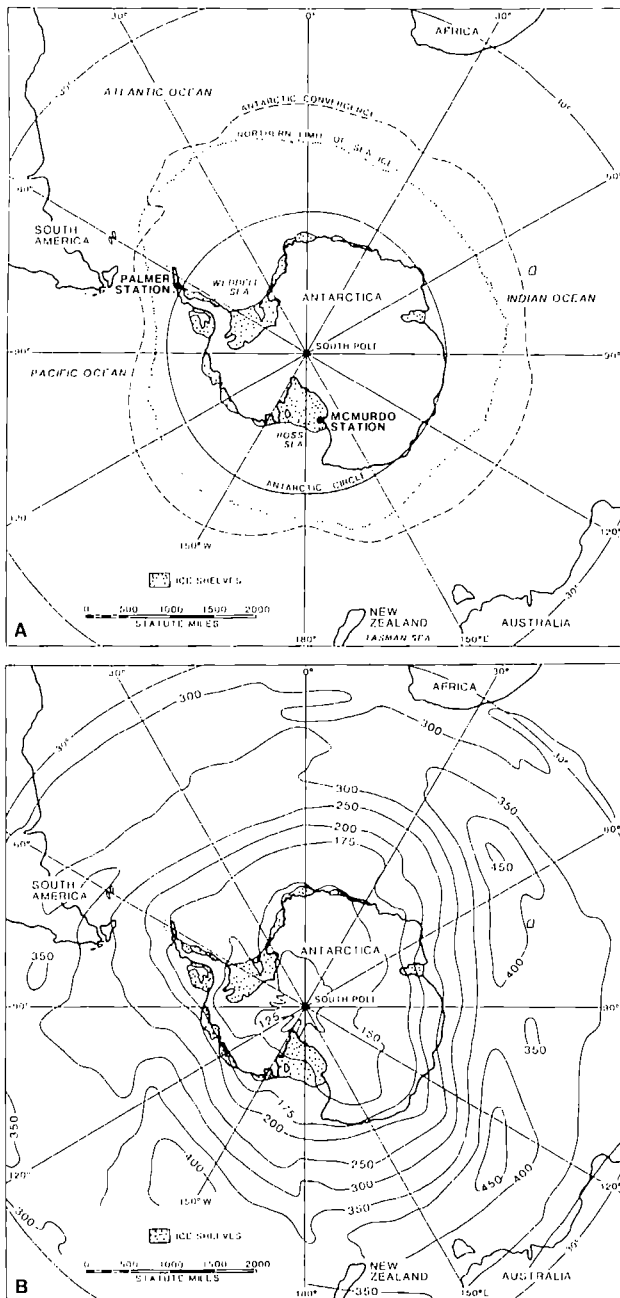


Fig. 1. (A) Map of Antarctica, the Southern Ocean, and surrounding continents. (B) Atmospheric ozone profiles over Antarctica from October 5, 1987 (modified from Krueger *et al.* 1989).

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 erythral (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.

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

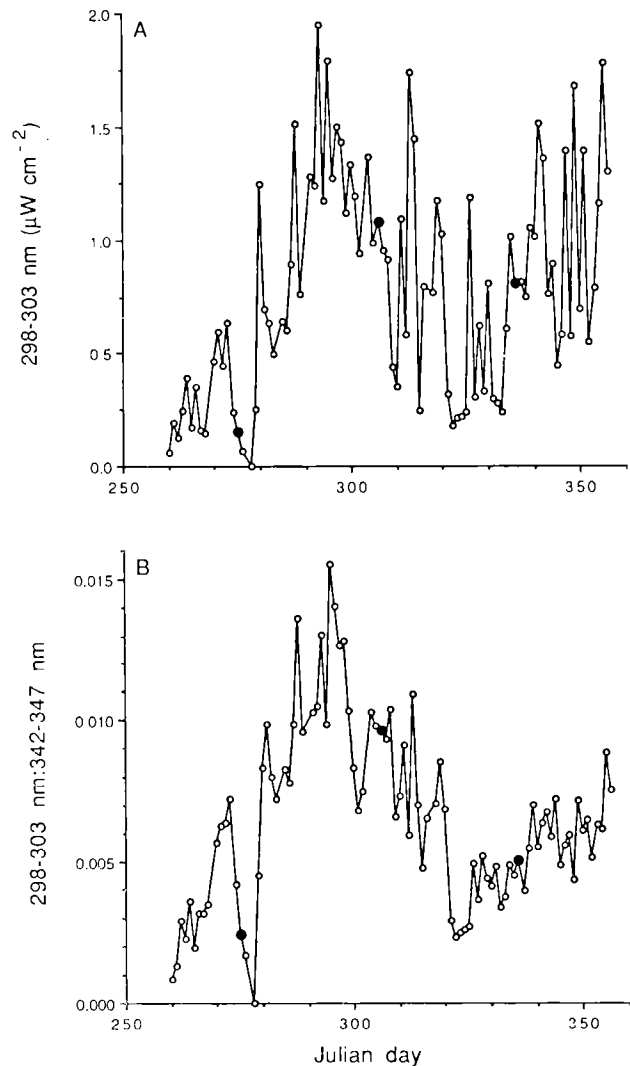


Fig. 2. a) Integrated noon UV-B irradiances (298–303 nm) at Palmer Station, Anvers Island, Antarctic Peninsula, during spring 1988. Data were obtained from the U.S. National Science Foundation UV Monitoring Program. Filled symbols indicate 1 October, 1 November and 1 December.

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.

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,

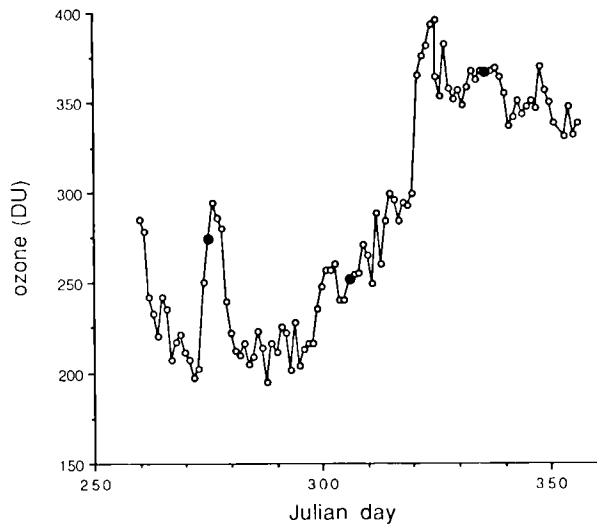


Fig. 3. Stratospheric ozone concentrations over Palmer Station during spring 1988. Data were obtained from Krueger *et al.* (1989) and Krueger (pers. comm.). Filled symbols indicate 1 October, 1 November and 1 December.

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 (Schwerdtfeger 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 paleoecological 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.

Acknowledgments

I would like to thank Drs. J.E. Cleaver, R.B. Painter and T.J. Smayda for helpful discussion and M.L. McKenney for editorial comments on this manuscript. Figure 1 was compiled and drafted by the Cartographic Services Laboratory, University of Wisconsin-Milwaukee. This work was supported by U.S. National Science Foundation Grant DPP 87-125333 and by the Office of Health and Environmental Research, U.S. Department of Energy, contract DE-AC03-76SF01012.

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Dr. Polly ~~Palmer~~ [

357-7894

Palmer, McMurdo, So. Pole & in Argentina

— monitoring instruments for 3 yrs

1) Bahia didn't interfere

John Frederick - U. Chicago

Summer values of UV @ Palmer

was didn't increase but duration did.

Cloud effects

biological consequences -- effect on phytoplankton

— in the field

→ different species were sensitive

→ some species have UV blocking cpds in them

→ DNA damage & repair

→ nutrient uptake

for 5 researchers

Ray Smith U. ^{CA} Santa Barbara

* oil spill effects → biggest impact will be on birds

come back in 4 yrs.

UV blocking cpds on corals (invertebrates)

Clear removal of a

believe it is the algae that produce the color.

oil spill was
at Palmer; did
to cancel some of
the products

* Antarctic data set is best in world

macroalgae & phytoplankton - also found in fish eyes -
don't know yet

governs

affects their DNA, photosynthesis

interferes w/ reproduction

now working on phytoplankton & other marine org.
on 1 yr - a bit

UV physics & optical biological
effects

People to talk to:

① John Cullen 902-494-3557 ^{Halifax} Canada

photosynthesis props of phytoplankton cultures

* iron seeding *

* get a summary sent from Mtg on this

left msg 4/11/91

② John Frederick UCh ^{University of Colorado, Chemistry & Climate} 312 702 3237

physics of UV

③ Osmond Holm-Hansen Scripps 619 534 2339

primary productivity of phytoplankton ^{UV} ~~NO~~ UV _{low UV}

④ Deneb Karentz UCSF 415-476-2333

DNA damage & repair
UV blocking caps

⑤ Ray Smith ^{invited to do science article on results} UCSB Santa Barbara 805-893-4709

UV penumbra in ocean

physiologists modelling

UV in water column

* talk abt
new NASA
data

out of
country til
April 16

Aug, Sep '90
on cruise
in Ant.
thru the UV
front. met
of org. when
chief
scientist

Danab Karenta

Antarctic ozone hole

phytoplankton species -- U wide range of response
certainly will be an impact on their growth & repro.

Lab studies -- indoor species from Ant. -- wide
range of response

Some -- no effect

why?

- ① UV-blocking cpd natl biochemicals
- ② cellular mechanisms that can repair damage

what will the new species do??

We don't have a baseline to know

agricultural crop -- not much genetic variability --

will get wiped out.

other plants are sensitive

larger the cell, further
away the nucleus is.

~~smaller~~ larger the cell -- the more resistant it is
→ this could be a problem 'cause

other things in food chain maybe can't
digest the large cell.

problem trying to monitor the UV → cloud cover

UV does pass thru clouds → clouds cut down

Roy Smith - monitored

if not an
essential
protein
not the
protein

damage -- can get nicks; dmg. in bonds between adjacent base
morphological dmg. need to be in perfect order

major problem here at this time -- knowing what

* UV-B ~~does~~ not used for photosynthesis. -- visible is.
UV A damages but need.

harmful all around

* not linear -- $\downarrow$ ~~UV-B~~ ^{more} bigger than linear

50% $\downarrow$ ozone $\rightarrow$ 150% $\uparrow$ in sunburning effects

UV levels in Antarctica

Delayed density-dependence

SIR — Population ecologists have frequently failed to detect significant density-dependence, the pivotal prediction of the theory of population dynamics, in natural populations of animals. Various statistical techniques for demonstrating density-dependence have been described and tested (for example see refs 1, 2), but many difficulties still remain^{3,4}.

closely for moths, but we found less delayed density-dependence than expected by chance for aphids (the model is not very appropriate for aphids with several overlapping generations per year).

We are not suggesting that the delayed density-dependence demonstrated by Turchin is not real or important, but we do suggest that the high incidence detected by him is due to the selection of forest pest species with a tendency towards outbreak dynamics. More generally, the kind of data

Our results strongly suggest that delayed density-dependence is rare in these insects and, by implication, in most insect populations. Although delayed density-dependence is uncommon in British moths and aphids, we do find non-delayed density-dependence to be common (manuscript in preparation).

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DELAYED DENSITY-DEPENDENCE IN INSECT POPULATIONS

Taxon	Number of species	Number of series	Significance level	Observed fraction	χ^2	P
Moths	357	4,306	0.05	0.045	1.13	0.287
			0.01	0.014	2.84	0.092
Aphids	92	1,405	0.05	0.022	15.62	<0.001
			0.01	0.004	3.22	0.073

Lengths of the time-series are from 10 to 24 years.

Turchin has pointed out⁵ that most current techniques are unsuitable for detecting delayed density-dependence. Therefore, if population regulation with time lags is common, the overall level of density-dependence may be underestimated.

Turchin demonstrated this problem with an analysis of 14 sets of time-series data on forest insects, eight of which showed clear evidence of delayed density-dependence. We have analysed a large set of time-series data on annual abundances of moths and aphids using the light-and suction-trap networks of the Rothamsted insect survey⁶ (our full analysis will be published elsewhere). We have looked at the occurrence of delayed density-dependence using Turchin's method⁵, and present our results in the table.

We counted the fractions of time-series that showed significant delayed density-dependence at 5 and 1% levels. (By chance, one would expect that 5 and 1% of the time-series would show a delayed effect at these levels.) The observed fractions of significant delayed effects match the expected values

typically analysed by population ecologists are biased towards the most abundant and outbreak species, which means that the current population-dynamic conclusions based on these data should be viewed with caution⁴. Our data consist of 'ordinary' insect populations, without any bias with respect to their abundance or dynamics.

DNA damage in the Antarctic

SIR — The Antarctic ozone hole represents a cycle of annual springtime depletion of stratospheric ozone over the continent and surrounding ocean areas, with consequent increases in levels of ultraviolet-B radiation (UV-B, 280–320 nm)¹. The ecological impact of this increased radiation is of particular concern for Antarctic marine communities, which depend on the productivity of phytoplankton at the base of short food chains. There has been much speculation about ecological effects based on *a priori* assumptions about unique photobiological properties of Antarctic organisms. A common misconception is that because these organisms inhabit an area of relatively low ambient ultraviolet intensity, Antarctic species may be more sensitive to UV-B exposure than their temperate or tropical counterparts². But Antarctic species are derived from temperate and tropical stocks and should therefore retain a capacity for biochemical protection from ultraviolet exposure³ and for repair of radiation-induced damage.

During 1987 and 1988 we carried out one of the first on-site evaluations of ultraviolet exposure and photobiological responses of nine phytoplankton species at Anvers Island in the Antarctic⁴. We discovered that biologically effective UV-B can be detected as deep as 20 m during springtime ozone depletion⁵ and noted that the morphology of the cells influenced the amount of initial DNA damage⁴. The nine diatom species, which spanned nearly three orders of magnitude in

cell volume with considerable variation in surface area: volume ratios, exhibited a nearly 100-fold range in the total number of photoproducts induced. All species investigated showed evidence of both photoreactivation and excision repair at ambient Antarctic temperatures, but with considerable species variation. *Chaetoceros neglectus*, for example, removed 31% of cyclobutane dimers in 6 h but did not repair any (6–4) photoproducts; *Corethron cryophilum* repaired 46% of the dimers induced and 94% of the (6–4) photoproducts⁴.

The ozone hole has existed for more than ten years. Obvious catastrophic events have not been noted. Our results indicate that Antarctic phytoplankton have diverse capacities for sustaining and repairing UV-induced damage to DNA and as a group are not defenceless against this environmental stress. Cumulative biological effects of the ozone hole are apparently subtle alterations in species interactions, and it may take longer than a decade for these perturbations to have an observable effect. The UV photobiology of individual species needs to be a key focus in future research efforts.

SENEB KARENTZ
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NATIONAL SCIENCE FOUNDATION

News

Jeffrey Norris
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FOR RELEASE: IMMEDIATE
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PLANKTON AT BASE OF ANTARCTIC FOOD CHAIN VARY NEARLY 100-FOLD IN SUSCEPTIBILITY TO ULTRAVIOLET-LIGHT-INDUCED DNA DAMAGE

Global loss of protective ozone in the stratosphere allows more ultraviolet radiation to reach Earth, and has raised concerns about increased human risk for skin cancer and immune-system suppression. But scientists are also worried about life forms, including the plants and animals that make up the highly productive marine-based food chain of Antarctica, where seasonal ozone depletion is greatest.

In all life forms, the genetic material, DNA, can be damaged by ultraviolet radiation, but organisms differ in the amount of damage they receive and in their abilities to repair this damage.

Ecosystem-wide effects of UV radiation in Antarctica may not be predictable any time soon. Nonetheless, laboratory studies at the National Science Foundation-managed U.S. Palmer Station on the Antarctic Peninsula reveal nearly one-hundred-fold differences in the amount of genetic damage sustained when various phytoplankton species are exposed to certain wavelengths of UV light.

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-2-

Phytoplankton, one-celled plants at the base of the antarctic marine food chain, manufacture organic material that sustains virtually all other organisms in the ecosystem.

"Some phytoplankton are very sensitive, and some aren't," said Deneb Karentz, research associate at the University of California, San Francisco, who performed the work with colleague David L. Mitchell, a post-doctoral fellow.

To do their laboratory experiments, Karentz and Mitchell collected diatoms, phytoplankton with glass shells made from silica. The diatoms they used were among the most abundant phytoplankton in antarctica waters in September, 1988, when the seasonal ozone hole was forming.

Karentz and Mitchell exposed nine species of diatoms under intense UV light to look for chemical changes in the small building-block molecules of DNA, called nucleotide bases. For this experiment, the researchers used middle-wavelength UV light, UV-B, which is most strongly absorbed by ozone.

To form the basic structure of DNA, nucleotide bases are linked end-to-end in a long strand. Each nucleotide base also pairs off with a complementary nucleotide base on another strand, giving rise to the double-stranded, helical DNA macro-molecule. This DNA structure encodes the genes that guide cell growth and metabolism. Unrepaired damage to nucleotide base pairs within genes can foul up the finely-tuned regulation and production of cellular proteins, harming or even killing an organism.

Using radioactive tracers to locate defects, the scientists found that the diatom species Coscinodiscus oculus-iridis incurred mutations to its DNA chains about once every 170,000 nucleotide base pairs when exposed to UV-B radiation, whereas another species, Nitzschia kerguelensis, was damaged on average about once every 1,800 base pairs.

In the laboratory, Karentz and Mitchell found that some species were better able to persevere after UV exposure. "Consistent with the diverse molecular response to UV light, we also found that the ability of phytoplankton to survive the effects of UV-B light was extremely variable," Mitchell and Karentz wrote in a report to be published later in the Antarctic Journal of the United States.

Karentz told NSF, "The results show it's important to look at individual species, because there is the potential for shifts in overall species composition within the ecosystem."

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It is possible that the timing and intensity of the ozone hole and the associated increase in penetration by UV-B radiation may reduce populations of some phytoplankton species, Karentz said, allowing other species more resistant to UV-B damage to opportunistically expand their niches.

If this happened, the incidence of secondary, domino-like effects on the health of animal populations higher up the food chain--krill, fish, penguins and whales, for example -- might depend on how choosy krill and other phytoplankton--eating animals are about the species they graze upon.

To combat DNA damage, phytoplankton, like higher plants and animals, including humans, possess DNA repair mechanisms. By this measure, too, the diatom species examined by Karentz and Mitchell exhibited distinct responses. "The capacity of individual diatoms to excise damage ranged from negligible to near complete removal within six hours," Karentz and Mitchell reported.

Though UV radiation is damaging to organisms, longer wavelength UV-A light also is required by phytoplankton for one type of DNA repair, called photoreactivation. This mechanism appeared to play an important role in the varied rates of DNA repair achieved by the diatoms, Karentz said.

Because phytoplankton also require visible light to drive photosynthesis and to mend damage to their photosynthetic systems, many biologists believe that it is important to consider the amounts of all three of these wavelength bands of electromagnetic radiation when examining biological impacts of the ozone hole. The ozone hole does not affect penetration by UV-A or visible wavelengths.

"There is a growing recognition that we should not just consider direct damage due to increased UV-B radiation," according to John J. Cullen, who also studies UV effects on phytoplankton as a research scientist with Bigelow Laboratory for Ocean Sciences in West Boothbay Harbor, Maine. "In examining the ozone hole's effect on biological processes, we should also look at the ratio of UV-B to visible light and UV-A, and the combined effects of all three," Cullen told NSF.

Besides having the ability to repair DNA, many antarctic organisms produce their own UV sunscreens, as do their temperate and tropical water counterparts, Karentz said. Working with Walter C. Dunlap of the Australian Institute of Marine Science, Karentz found that 86 percent of 57 species studied produced from one to seven previously known UV-absorbing compounds. These species included icefish larvae, algae and invertebrates such as krill. Karentz and Dunlap also discovered a new UV-absorbing

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compound, which they detected in 60 percent of invertebrates analyzed, including krill. These findings will also be published in the Antarctic Journal and in the journal Marine Biology.

Palmer Station studies of ozone depletion and UV irradiance by John E. Frederick, professor of atmospheric sciences at the University of Chicago, and Dan Lubin, a post doctoral fellow at Scripps Institution of Oceanography, University of California, San Diego, indicate that UV-B radiation during the October, 1988 ozone hole was about the same as during the summer solstice, while UV-B incidence during the more severe October, 1989 ozone hole exceeded levels of 1989 solstice. The researchers also found that ozone concentrations and UV-B irradiance at Palmer could change greatly over a period of hours as the ozone shifted position.

The average daily UV-B radiation dose to Palmer, which, at 64 degrees 46 minutes south latitude, is far enough north for researchers to experience sunrise and sunset every day of the year, is about 200 times greater at noontime during the height of summer compared to noontime during the winter, Frederick said. UV-A radiation at Palmer is about 20 to 25 times greater in summer compared to winter, he added.

The laboratory experiments of Karentz and Mitchell were not intended to mimic natural lighting conditions in the water column, but Karentz said the findings should reflect the relative sensitivities of species to increased penetrance of UV-B radiation due to the ozone hole.

According to Greta Fryxell, professor of oceanography at Texas A & M University, who studies marine phytoplankton associated with antarctic ice and the open ocean, "Laboratory and field work together make the most sense. There are many variables in the field; lab work can tell you what to focus on. The lab work on these species gives a good indication of what to look for."

This fall, Karentz will participate in field experiments off the Antarctic Peninsula on an expedition of the NSF research ship, Polar Duke, to be led by Raymond C. Smith, professor of geography at the University of California, Santa Barbara. The experiments are designed to determine the impact of the ozone hole on the antarctic marine ecosystem.

Smith will use a new underwater spectrophotometer of his own design to obtain the first useful data on UV levels from antarctic waters. Karentz recently developed a portable biosensor that uses DNA damage to a bacterium as a proxy for UV incidence. The bacterium is a mutant Escherichia coli strain

-more-

lacking DNA repair mechanisms. Karentz hopes to calibrate her biosensor using Smith's measurements, which would allow the biosensor to be used to estimate UV levels in situations where no underwater spectrophotometer is available.

Researchers taking part in the expedition will make measurements of visible and UV light at many depths, and they will study how water circulates and transports plankton. The scientists will examine photosynthesis, biomass, pigment production and DNA damage for a variety of species.

October stratospheric ozone levels over Antarctica have been on a declining trend for at least 10 years, the period for which available ozone data has been analyzed. "We're looking at an ecosystem that already may have been affected by the hole," Smith said.

-end-

(8/17/90)

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The Cousteau Society

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Telefax Transmittal

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DATE: April 12

TO: Katy McGinty (Senator Gore)

RECIPIENTS FAX: 202-224-~~8850~~ 0580

RECIPIENTS PHONE:

FROM: Rick Schwabacher (703-892-8842)

TOTAL PAGES (Including Transmittal page):

6

COMMENTS:

Katy, Maybe this will help...

Professor S. Z. El-Sayed (Marine Biologist)
Department of Oceanography
Texas A+M University
409-845-2134

Call
anytime
after
10 on
m.w.

Also - NSF held a workshop on
Ultraviolet Radiation + Biological Research in Antarctica
on June 7-8, 1988. Jack Talmadge (357-7766)

OR ANYONE IN THE Polar Affairs divisions should be
able to get you copies of the Papers.

C. Susan Weiler in the Polar Program organized the Workshop

FYE - Press info sheet

Conf w/ Al
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he talked to
McCormick →
phosphorus



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- 22 & methyl chloroform } transport
inhibited cause are attracted by
OH. } into stratosphere

OH in stratosphere
ozone depletion. ? = how OH generated
photolysis of H₂O?

UV-β ↑ OH - in trop. (∴ O₃ ↓ &
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production
of OH in
trop.)

trop ↑ → lifted up
hadley circ.

West. Pacific 6°C.

United States Senate

WASHINGTON, DC 20510-4202

Date: April 17, 1991

To: Katie McGinty

From: Hayes Peyton

Paula dipurno with cousteau re: ozone in the ocean and Ultra violote
Light contact Dr Thomas cohill (president of the american society of
photo biology at western Ky U 502-745-4052 or 0111

502-782-9329 (home) she suggests she starts with Him

INTERVIEW

Barbara Prézelin:

Taking On the Challenges

Dr. Barbara Prézelin is professor of biology at the University of California, Santa Barbara (UCSB). Last fall she was co-chief scientist on "Icecolors '90," a research expedition to Antarctica funded by the National Science Foundation. Its purpose was to study the effect of the ozone hole on the growth of ocean plants—the phytoplankton that form the base of the ocean food chain. The Icecolors team gathered groundbreaking measurements of the ozone hole's effects. These measurements will form an important data base for use by other scientists. A highly respected biological oceanographer, Prézelin has participated in many ocean research cruises and has authored many papers on ocean productivity. Editor Mary Batten interviewed Dr. Prézelin in her office at UCSB.

What is meant by ocean productivity?

Primary production is the measure of the rate at which ocean plants grow.

What role do ocean plants play in the food chain?

They're the base of the ocean food chain. In the open ocean they are free-floating; therefore, they're called phytoplankton. They're mostly small, single cells that live in just the upper reaches of the ocean where the light penetrates. They're productive only in the sunlight region, which is a very small lens at the top of the ocean. Their ability to grow successfully in that sunlit lens determines how much new organic carbon, or foodstuffs, are available for grazers that live throughout the entire ocean.

What is the depth of the light lens?

It varies. Near shore, in very turbid waters, it could be just a couple of meters (6.5 ft.) thick. In the clearest open-ocean waters, it could be 150 meters (493 ft.) at the most.



Biological oceanographer Dr. Barbara Prézelin is in the forefront of scientists using a new research technology called bio-optics. By examining the colors of the wavelengths of light coming into the ocean, it is possible to determine the rate at which ocean plants grow.

Compared to the 3,750-plus meters (12,303 ft.), which is the mean depth of the ocean, it's very thin, but it's the most biologically dynamic area. It's the activity in that thin, sunlit lens between the depths of the sea and the atmosphere that supports much of the biological activity in the ocean.

How does the process work?

Basically, carbon dioxide (CO₂) from the atmosphere comes into equilibrium with the water. Then, the plants take up this gas and convert it—with the aid of sunlight—into an organic form that can be simply consumed. This is the process of photosynthesis. The rate at which this carbon is fixed, as we call it, is often directly proportional to the amount of oxygen that phytoplankton put out.

How do you measure the productivity of ocean plants?

You can measure it in two simple ways. First, you can measure the rate at which carbon dioxide (CO₂) goes into a phytoplankton cell and becomes fixed or you can measure the rate at which oxygen comes off. We're also working on a new way of measuring production by determining the relationship between the amount of light that goes into the water column, the amount of light that is absorbed by the phytoplankton to be used in photosynthesis, and how efficiently that light is used to form organic carbon. This is

what we call a bio-optical model; and we already have a few that are quite successful in limited regions of the ocean where they've been tested. Our goal is to have bio-optical models to predict carbon production throughout the ocean. Second, because this is an optical technique, we can use all kinds of optical sensors, whether they're on satellites or moorings, to get much greater coverage than we can obtain by taking a one-bucket sample out of the ocean. With bio-optics we can look over large areas of the ocean and see how much light is going in, estimate how much is being used to drive photosynthesis, and how much carbon would be fixed at different locations. Then we'd have a beautiful aerial map of production, which could change day to day.

Is this what inspired the name of your previous project called "Watercolors"?

Yes. My colleague Ray Smith from UCSB's Center for Remote Sensing and I have a longstanding collaboration on field expeditions. The purpose of all of our expeditions has been to better understand how water optics—the colors of wavelengths of light coming into the ocean—effect phytoplankton growth and, in turn, to be able to predict the effect of phytoplankton growth on the ocean color, which can be routinely "seen" by remote sensing from moored optical instruments or a variety of aerial flyovers, including satellites. Our initial work off California was so encouraging that we received funding again from the National Science Foundation to apply the same approach to Antarctic phytoplankton. Thus, our "Watercolors '88" became our "Icecolors '90" expedition to Antarctica.

What was the goal of this project?

We wanted to look for the effect of increased ultraviolet (UV) light—due to a loss of ozone—on the water-column dynamics of production, without being misled by the natural variability in the ecosystems. Our experience in "Watercolors '88" and "Fronts '85," another earlier study, was very important because both of those projects were carried out in highly variable regions of the ocean where you have water boundaries between a warm-water mass and a cold-water mass; and we would look at how you could predict the variability across that region. But the ozone area is really an atmospheric front. There is a very sharp boundary marking the inside of a hole, in which the ozone has been severely depleted, and the outside of a hole, where it has not been depleted. Since this hole is not a stable feature of the Antarctic, but rotates and wobbles, we could approach it the same way we had approached a water front. Basically this involved staying at a single location, letting the ozone hole move around us and then following the variability, taking measurements inside and outside the hole, and comparing the differences. It's the difference that gives you the real sense of how much effect the diminished ozone has.

What was the status of the hole when you were in Antarctica last fall?

The surprising thing was that last year the ozone hole formed earlier, was deeper than ever reported before, and lasted longer. This enabled us to see several cycles of the

ozone hole oscillating over us. We could repeat our experiments two to three times on both sides of the hole so that we could have some sense of replication of our observations. We weren't taking single observations and running with them.

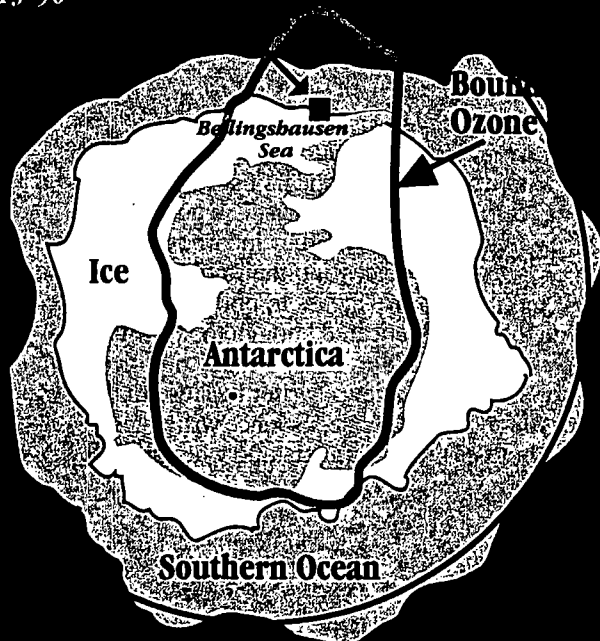
What were some of the first-time-ever types of measurements?

An instrument called LUVSS, which stands for Light and Ultraviolet Submersible Spectroradiometer, allowed us for the very first time to clearly measure how much ozone-dependent UV light is actually getting into a water column at any given time. This optical instrument measures all the colors of light coming into the ocean, which can be divided into three spectral regions. The visible region (colors we see with our eyes) is called photosynthetically available radiation (PAR), as this light is used by plants to drive photosynthesis. Ultraviolet (UV) light is of higher energy than PAR and is capable of disrupting biological activities inside living cells. UV-B radiation is part of ultraviolet light, and it is this light which strikes the Earth in increasing amounts when the ozone thins. UV-A radiation, also part of ultraviolet light, has an energy between UV-B and PAR and is not affected by the thinning ozone. Depending upon the organism, UV-A light that strikes cells may be absorbed by natural sunscreens, used for photosynthesis, and also do biological damage. Before our fieldwork was done, we didn't know the balance of light colors that the phytoplankton were seeing on a moment-to-moment, day-to-day basis. This work is very important for characterizing underwater light fields, and the information can be used to assure that laboratory studies are done in the realm of environmental reality.

The LUVSS instrument, which is a one-of-a-kind optical instrument designed and built by Ray Smith's group, was attached to an ROV (remotely operated vehicle) with a video camera and deployed at sea with a tether. We were thrilled to see instantaneous readouts of all of the underwater light-field data as the ROV was brought to depth and then allowed to rise to the surface. We could take light measurements for several kinds of water that you encounter in the Antarctic ocean in the spring: clear, open water; water covered with many kinds of patchy ice; and right up under the ice, where often a lot of phytoplankton are concentrated. So Ray Smith's group will now be able to get the precise color exposure rates for different kinds of Antarctic marine environments.

The other new instrument was an on-site mooring system that we call MATWINGS in honor of my technician Allen Matlick, who designed it. At a given depth, you can deploy three wings, which are incubation containers with phytoplankton samples from that same depth. You can see how fast they grow, what kind of pigment changes occur and what kind of damage takes place. The difference between the three wings is that one wing will let in all the UV-A, UV-B, and photosynthetic light; another will let in only UV-A and photosynthetic light; and the third will let through only photosynthetic light. So we can use that data and plot, as a function of exposure, how much inhibition of plant growth we actually observed on site.

Icecolors
Oct-13-90



During the "Icecolors '90" expedition to Antarctica (September-November, 1990), the scientists and crew of the research vessel Polar Duke repeatedly crossed the marginal ice zone of the Bellingshausen Sea. The multidisciplinary team measured the effect of the ozone hole on ultraviolet penetration into the Southern Ocean and its impact on the growth of springtime phytoplankton.

We'd have a much larger impact on global warming by controlling the beginnings of the problem rather than trying to find a garbage pile to dump it in at the end where the consequences are unknown. Nature has an incredible healing capacity, but in the case of global warming, unlike many other environmental threats, the rate of change is so fast that it is an imminent threat. Therefore, we have to proceed as if the worst-case scenario exists because the rate of change could be so quick that it could get beyond us.

Can you relate your data on reduced productivity to the argument for stopping the production of chlorofluorocarbons (CFCs)?

At this point it is a verifiable fact that when the ozone hole opens over the Antarctic, there is a stress on phytoplankton vitality which results in a reduction of productivity. It's in our best interests to reduce the output of chemicals that reduce the ozone, but I am also very aware that Third World countries may pay a higher price than we do; and I have trouble with how you make that all happen fairly.

You're now well established in your field, but did you encounter difficulties along the route? And do those difficulties still confront women who go into science?

The nature of the difficulties has changed, and the opportunities are better than they've ever been, but they're certainly not on an equal par with those available to men. It's not a sex-blind business, and until it is, women will always face special limitations that they'll have to learn to deal with in addition to all the other job skills that go into this business. In my particular case, I always did very well in my classes; so on a competition scale, I could always hold my own. Where I felt limited was in the eyes of the beholder. The expectations of me were limited. The considerations to include me were generally afterthoughts, if they even occurred as afterthoughts. The initial kinds of job offers that came my way were definitely a scale below those offered my male colleagues; and to my disappointment, many of the professors whom I admired felt that those lower-scale offers were really wonderful for me—to take a teaching position, for example, because I could have my children in the summer. I don't think I would have entered this business if I weren't naturally comfortable in the company of men and enjoyed things such as technology and science and pragmatism and making things happen. Those are

What effect does the increased UV-B, due to the thinning of the ozone hole, have on ocean productivity in Antarctica?

Comparing results from inside the hole to outside the hole, there is definitely a negative impact on the production rates of the phytoplankton inside the hole. I'm a little cautious right now about saying how much, but even a small-percentage impact is significant when you take into account that similar areas surround the entire Antarctic. It's harder to extrapolate from that what the food-chain consequences will be because a lot of the food-chain dynamics aren't clearly sorted out for the Antarctic. Our major job was to get a data base that's objective and unrefutable and, therefore, useful for trying to make a policy decision.

How can the study of these very tiny plants—the phytoplankton in Antarctica—help us to gain a better understanding of global warming?

Phytoplankton are considered one of the primary sinks for atmospheric carbon, in part because they turn it over so fast. In fact, cities that want to reduce their carbon load are advised to set out rapidly growing plants that can be clipped frequently and renourished. In that sense, phytoplankton play a really important role, but it's difficult to put a number on it. I don't think the solution to global warming is to increase the carbon sink of production in the ocean. It's clearly been shown that increasing global warming—while increasing the inorganic carbon potentially available to phytoplankton—will not enhance a rate of production sufficiently to do away with more than a very small part of the problem, naturally or artificially. Instead of looking at the ocean as a potential future sink of more and more carbon, we're better off trying to do what we can to curb the sources, reduce the emissions and conserve on that level.

things I've always enjoyed, so I was comfortable; but the clear feeling that people are not comfortable with you—particularly if you maintain your femininity—was bothersome. I couldn't see sacrificing my femininity, and I never have.

Before I left for Antarctica, my daughter Christine drew a picture of our ship, the *Polar Duke*. At the bottom, in big bold letters, it says, "MY MOM." I felt very proud to put this picture on the door of my cabin. I felt proud because that was my daughter's view of me, and it seemed rare that a daughter can have this view of her mother. I also felt very comfortable with my own position as a leader and a decision-maker, while at the same time being a woman in the minority in a field that's usually dominated by men. I felt very comfortable displaying this picture, which is very feminine and very personal. I was also highly rewarded by crew, colleagues and students who just loved the picture. And it cheered me on lots of days. So it was sort of my emblem, and I will always treasure it.

What advice would you give young women who want to go into the sciences?

The best preparation is an enthusiasm for the subject because that's what keeps you going through thick or thin. On top of that, you need a willingness to put in very long hours and to know that success will require you to be in the upper reaches of your class, not the mid-reaches. You also need to persevere, to study, to help each other, and to try to become sex-blind as quickly as possible. It's much more rewarding to become sex-blind in your work so you're not contributing further to sex barriers. Women also need to be willing to speak up clearly when something is not working well for them.

You've been an educator for 15 years. How would you assess the state of science education at the college level?

It's certainly getting better, in part because of the heavy emphasis on the science program and the quality of entering students, at least in the environmental sciences. The average knowledge about the environment and breakthroughs in science and medicine strike me as far more sophisticated than when I was that age. People seek out scientific information. The media has a lot to do with it because the media personalizes science. It shows people how science relates to them and how it could impact their health and well-being. If we raised our expectations of science knowledge publicly and in schools, the students would be able to meet them. We need to increase our expectations of what people should know, rather than compromising it in order to meet an average interest level.

How does the instantaneousness of communication impact you as a scientist?

With the ability to keep society as a whole up-to-date on a day-to-day or hourly basis, there is pressure to give an opinion before you've had the time to process the data. You're aware of the urgency, and you're aware of your responsibility, but you risk making a terrible mistake if you

don't get the time to consider the information. Everything would be better if we were allowed time for consideration before we had to give conclusions—whether it's science or politics. We're going to pay a price for giving conclusions without fully considering a subject.

What does the public need to understand about the scientific process with respect to communication of conclusions?

They should be very skeptical of sweeping generalizations that come out in the media. The public should have a wait-and-see attitude before they incorporate any findings into their personal choices and their political action, particularly if the findings are meant to politically motivate. Most of the public is sophisticated enough to know that the pursuit of scientific fact takes time. I really put the burden of responsibility on the science writer because that individual has a tremendous influence. Science writers need to know enough about science to understand when they have a complete story or when they just have a fancy headline.

What do you try to achieve with the teams that you take on expedition?

The kinship that we feel with each other is a key ingredient in our success because it keeps us working together, keeps us consistent. During "Icecolors '90," my goal was to help the group become interdependent in a good way, to constantly raise the challenges and the responsibilities of everybody. When the cruise came to a close, I tried to make some notation to myself as to how successful I thought it was. Clearly it was technically successful—in terms of taking complex, state-of-the-art equipment into a challenging environment and making it all work at once, which was one of the big demands. There was the personal satisfaction in doing what many said couldn't be done, and doing it well with a group of people who were great going in and were even better coming out.

My feeling for my own students, as well as for many of the other people I got to know on the expedition, is a sense of pride in being on the same team with them. I will always be very proud of my students because I feel that they've all shown that they have the capabilities to be really fine explorer scientists. What I noticed in them that I admire personally, is that they not only reaped benefits and advantages from being a team, but that they recognized it and have made personal choices as to how they would set up their own research programs where talented, interdependent people, working together cooperatively—rather than competitively—can do excellent science and enjoy it and have a lot of personal growth at the same time. Science can be so good in all aspects, and that is not necessarily the history of science; but it could be the future and we would all benefit if it were. I enjoy going to sea, both for the science and for the sense of growth. The beauty of Antarctica made me feel very overwhelmed and very joyful. It was as if I had been blind and was given the gift of sight for the first time. I like to be challenged and to see what I can do; and there's nothing like success to make you want to try again. 