

Transmission of ultraviolet radiation through the Antarctic annual sea ice and its biological effects on sea urchin embryos

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Abstract

Stratospheric ozone depletion over Antarctica is expected to continue for the next 50 years, with increases in ecologically damaging ultraviolet radiation (UVR: 290–400 nm), specifically the ultraviolet-B (UVB: 290–320 nm) portion of the spectrum. Most of coastal Antarctica is covered with 2–3 m of annual sea ice during the occurrence of the “ozone hole.” This physical barrier to UVR transmission has long been assumed to provide complete protection from the biologically damaging effects of UVR, especially for the planktonic developmental stages of the benthic invertebrate fauna. We found that short-wavelength UVB (down to 304 nm) is transmitted through the Austral spring annual ice of McMurdo Sound, and causes significant mortality and DNA damage in the embryos of the sea urchin *Stereochinus neumayeri*. Although mortality of sea urchin embryos has been reported for the open waters of the Antarctic, this is the first documentation of mortality and DNA damage for embryos under the annual sea ice. The degree of mortality and DNA damage was dependent on both year and depth, with higher mortality and DNA damage at 1 m depth below the ice compared to 3 m and 5 m. Greater DNA damage occurred in 2003 compared to 2002 despite the thicker annual ice (3.1 m vs. 2.5 m). Although the thickness of the annual ice was greater, the severity of the ozone hole, 230 Dobson units (DU) versus 320 DU, and the ratio of UVB to visible radiation was greater in 2003. Embryo and larval mortality from exposure to UVR under the annual ice should be considered as another abiotic factor potentially affecting the temporally episodic recruitment of invertebrates that occur in this benthic ecosystem.

In Antarctica the springtime depletion of stratospheric ozone (Hofmann et al. 1997; Solomon 1999) results in high irradiances of ultraviolet-B (290–320 nm) radiation (UVB) (Smith 1989, Madronich et al. 1998), and causes a decrease in primary productivity (Smith et al. 1992; Neale et al. 1998). The destruction of stratospheric ozone has been monitored since the early 1980s and the biological effects of ultraviolet radiation (290–400 nm UVR) have been quantified for several trophic levels down to a depth of 20 m in open water (Karentz 1994). The harmful effects of UVR on marine organisms include damage to proteins, lipids, and DNA with both sublethal and lethal results. Of particular concern is that stratospheric ozone depletion results in an increase in damaging UVB wavelengths without a proportional increase in longer ultraviolet-A (UVA: 320–400 nm) and blue wavelengths involved in photoreactivation and photorepair (Smith 1989). The most common type of damage caused directly by UVR is DNA damage in the form of photolesions such as cyclobutane pyrimidine dimers (CPDs) and 6–4 photoproducts. The proportion of these products formed on DNA

by UVR is ~75% for CPDs and 25% for 6–4 photoproducts. To repair these DNA lesions organisms have evolved the enzyme photolyase, a light-dependent enzyme that requires UVA and visible irradiances (350 nm to 450 nm) to be catalytic (Kim and Sancar 1993). The proportionally lower irradiances of UVA and blue wavelengths that occur during the “ozone hole” could potentially change the balance between damage and repair processes in favor of damage under these conditions.

Surface waters of near-shore coastal habitats contain the planktonic life-history phases of many species of fish, macrophytes, and benthic invertebrates. Several species of echinoderms are important broadcast spawning members of benthic communities in the Antarctic whose embryos and larvae are found in the water column (Pearse et al. 1991). These planktonic life-history stages are potentially more susceptible to the detrimental effects of UVR because they are transparent, actively dividing, and can be easily advected into the upper portions of the water column. During the Austral spring McMurdo Sound is covered with 2–3 m of annual sea ice, and it is generally accepted that the ice provides a physical barrier to UVB radiation reaching the underlying water column despite the fact that modeling studies have shown that UVB radiation can be transmitted through the annual ice (Trodahl and Buckley 1989, 1990; Perovich 1993), and UVB has been measured under 3.5 m of ice in Antarctic lakes (Vincent et al. 1998).

To assess the biological effects of UVR under the annual sea ice we used embryos from the sea urchin *Stereochinus neumayeri*, a numerically dominant member of the Antarctic

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Table 1. Comparison of column ozone, sea ice thickness, and maximum integrated values of typical PAR, UVR, UVA, and UVB, and UVB:PAR ratios measured during the 5-d experiments at Cape Armitage in 2002 and 2003.

	2002			2003		
	Surface	Ice	Deep	Surface	Ice	Deep
Ozone (DU)	320			230		
Ice thickness	2.5 m			3.1 m		
UVR ($W m^{-2}$)	23.24	0.2250	0.1192	25.78	0.1593	0.1433
UVB ($W m^{-2}$)	0.75	0.0022	0.0007	1.40	0.0028	0.0009
UVA ($W m^{-2}$)	22.49	0.2238	0.1185	24.38	0.1563	0.1424
PAR ($W m^{-2}$)	189	2.17	1.087	213	1.74	1.087
UVB:PAR	0.00397	0.00101	0.00064	0.0066	0.00161	0.00083
NSF UVB*	0.92			1.45		

* National Science Foundation UV Monitoring Network (McMurdo Station). Integrated between 290 and 320 nm ($W m^{-2}$).

benthic community. This sea urchin has a circumpolar distribution and plays an important role in the trophic biology of the benthos (Arntz et al. 1994; Brey et al. 1995). In laboratory experiments early embryos of *S. neumayeri* are sensitive to UVB radiation, and 100% of embryos at depths of 0.5 and 1.5 m and >95% of embryos at 5 m exhibit abnormal development in the open waters of McMurdo Sound during the late Austral spring (Lesser and Lamare unpubl. data). Similarly, embryos of *S. neumayeri* from the open waters of the Antarctic peninsula also exhibit significant effects of UVR on development (Karentz and Bosch 2001), but only 25% of embryos exhibited abnormal development in full sunlight at 5 m. One possible explanation for these differences is that the attenuation coefficients for UVR in the coastal waters of the Antarctic peninsula (Stambler et al. 1997) are generally much higher than those observed for McMurdo Sound (Lesser and Lamare unpubl. data). Here we present the results of field experiments showing that UVR can be transmitted through the annual sea ice in the Antarctic and that the low irradiances of UVR measured have significant biological effects on developing embryos of the sea urchin *S. neumayeri*.

Methods

Measurements of ultraviolet radiation—In the Austral spring of 2002 and 2003 the spectral irradiance of both UVR and photosynthetically active radiation (PAR), reaching the snow-covered (3–6 cm) ice around Cape Armitage (77°51.62'S, 166°40.63'E) in McMurdo Sound as well as under the ice and on the seafloor (6.7 m depth with respect to the ice/water interface), was measured. Additionally, measurements of snow and ice albedo were taken simultaneously with the underwater spectra. The snow ranged in depth from 3–6 cm and irregularly covered the surface of the ice. Measurements of reflected solar irradiance was made with a spectroradiometer mounted on a tripod with the sensor facing the ice approximately 2 m from the ice. All spectral irradiance measurements of ultraviolet radiation were made simultaneously with scanning spectroradiometers (LiCor 1800UW) beginning on the same day in both 2002 and 2003 (27 October). The spectroradiometers were programmed to scan three times every hour (total scan time approximately

45 s) at 2-nm intervals from 300–700 nm and the hourly mean reported in units of $W m^{-2} nm^{-1}$. The instruments use a cosine-corrected sensor, a single monochromator, and a filter wheel to reduce stray light by isolating and measuring different portions of the spectrum, and are calibrated using National Institute of Standards and Technology traceable standards. The instrument sensor has a 50% detection range of ± 2 nm on either side of the wavelength being measured, and minimum excitation energies on the order of $10^{-8} W cm^{-2} nm^{-1}$. The temperature dependence of the detector varies from -0.1% to 0.5% over the spectral range of measurements. Comparisons of this instrument to other commercial instruments and model results have shown that all measured and modeled irradiances agreed within their respective errors (Kirk et al. 1994). The Li-1800UW measurements also agree very well with data collected by the National Science Foundation UVR Monitoring Program (Table 1, <http://www.biospherical.com/NSF/default.asp>). All spectral data were scrutinized for signals approaching the noise level of the instrument's photodiode. In all cases where low signal-to-noise was observed at a particular wavelength, all data from that wavelength and all shorter wavelengths were eliminated from the data set. Bulk spectral attenuation coefficients ($K_d m^{-1}$) for the snow, ice, and water column, representing the effect of all layers from the top of the snow to the bottom of the water, in both the visible and UVR portions of the spectrum, were calculated as described by Kirk (1994).

Field experiments with freshly fertilized embryos—Reproductively mature *S. neumayeri* were collected from Cape Armitage and induced to spawn by intracoelomic injection of $0.5 mol L^{-1}$ KCl; the gametes were collected and diluted in filtered ($0.2 \mu m$) seawater prior to fertilization of eggs. Freshly fertilized embryos (FFE) were reared at a density of 5–10 individuals ml^{-1} in gently stirred 2–4-L culture vessels placed in sea tables of flowing seawater ($-1.8^\circ C$). In situ experiments with FFE were conducted under the annual ice at Cape Armitage. A 15-m line with appropriate anchors and flotation devices was suspended under the ice. At 1, 3, and 5 m below the ice a single polyvinyl chloride rack, approximately 31×62 cm, with Vexar netting was attached for the deployment of the larval containers and filters. Each rack

at each depth contained WhirlPak bags ($n = 3$ for each treatment at each depth) containing FFE for a total of nine bags per rack. The bags held a volume of approximately 125 ml and the density of embryos in these bags was 3–5 individuals ml^{-1} . The three treatment groups were created using long-band pass filter Plexiglas that divides the UVR spectrum while keeping visible radiation the same; the UVR treatment (both UVB and UVA) consisted of UVR transparent Plexiglas [UVT, 50% transmission cutoff at 285 nm], the UVA only treatment consisted of UVR transparent Plexiglas and Mylar-D [UVA, 50% transmission cutoff at ~ 320 nm], and the controls (no UVR) consisted of UVR opaque Plexiglas [UVO, 50% transmission cutoff at ~ 395 nm]. Both experimental and control groups were deployed for 5 d, which is the time required for *S. neumayeri* to develop from one stage to another (e.g., from blastula to gastrula; Bosch et al. 1987) at -1.8°C . We have also tested the WhirlPak bags for possible toxicity (negative) on sea urchin embryos. After deployment the surviving embryos were enumerated microscopically, photographed, and stored (-80°C) for the analysis of DNA damage. The irradiance of UVR under the treatments was calculated from the ambient UVR at that depth and the spectral properties of the filters (Table 1).

Quantification of DNA damage—CPDs were measured using a monoclonal antibody (TDM-2) in an enzyme-linked immunoabsorbent assay-based system (Mori et al. 1991). Genomic DNA was isolated using commercially available kits (Qiagen), and 100 ng of DNA from each sample was used in the assay. The DNA was denatured at 100°C for 10 min, followed by rapid cooling in ice (4°C) for 10 min. The single-stranded DNA was then adhered to flat-bottomed 96-well microtiter plates with 0.3% protamine sulfate in phosphate-buffered saline (PBS, pH 7.5). Blocking buffer (100 μl of 1% bovine serum albumin in PBS) was placed in each well for 1.5 h, then emptied and rinsed. The primary antibody (100 μl of TDM-2), at a dilution of 1:1,000, was placed in each well and incubated at 37°C for 1.5 h. After rinsing, 100 μl of a goat anti-mouse IgG secondary antibody (1:3,000 dilution), conjugated with horseradish peroxidase, was placed in each well and incubated at room temperature for 2.0 h. The wells were rinsed and the final color development was carried out with Sigma Fast reagents (Sigma) and read using a plate reader (Bio-Rad) at 490 nm after 30 min and the addition of 50 μl of $2 \text{ mol L}^{-1} \text{H}_2\text{SO}_4$ to stabilize the final color development. All rinse steps consisted of three rinses with 0.05% Tween-20 in PBS.

Data analysis—Both survivorship and CPD concentration were statistically analyzed using a two-way analysis of variance (ANOVA), with treatment and depth as fixed factors at a significance level of 5%. No unequal variances were detected using the F_{\max} test, and individual treatment differences were assessed using the Student–Neuman–Keuls (SNK) multiple comparison test. Ratios and percentages were arcsine or log transformed for analysis and back transformed for presentation.

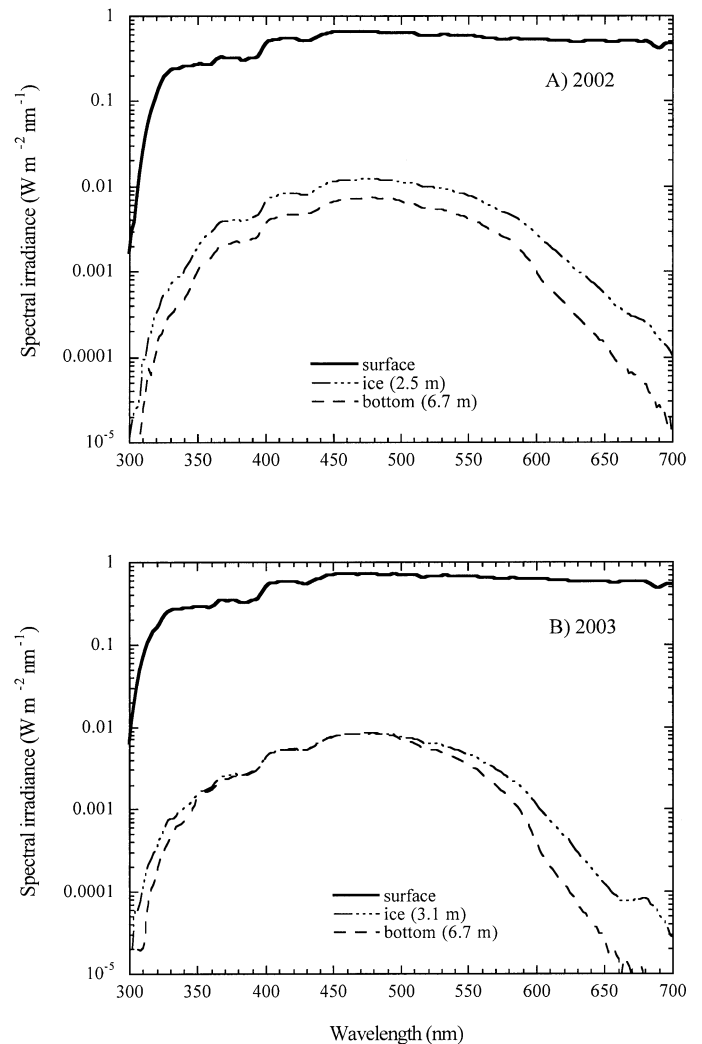


Fig. 1. Maximum spectral irradiance measurements made for Cape Armitage in (A) 2002 for surface, under ice, and seafloor (6.7 m); (B) 2003.

Results

Transmission of UVR through the annual sea ice—In 2002 the ozone hole rapidly diminished and the mean ozone concentration during the 2002 experiment was 320 Dobson units (DU), whereas in 2003 it was 230 DU, including 3 of 5 experimental days below 200 DU. Both UVA and UVB radiation were transmitted through the annual ice in 2002 and 2003 (Fig. 1A,B; Table 1). Bulk attenuation coefficients (K_d) of both the ice and water column were similar but lower in 2003 throughout the entire UVR spectrum (Fig. 2A), as were the surface albedo measurements, which are lower (55–75%) in the UVR portion of the spectrum compared to the PAR portion (75–80%) of the spectrum (Fig. 2B). The majority of the attenuation of both UVR and PAR is due to the overlying annual ice and snow with a minor water column component. Measurements of the inherent optical properties of the water column show that absorption (a), backscattering (b_b), and beam attenuation (c) coefficients are extremely low and dominated by the water component (Lesser unpubl.

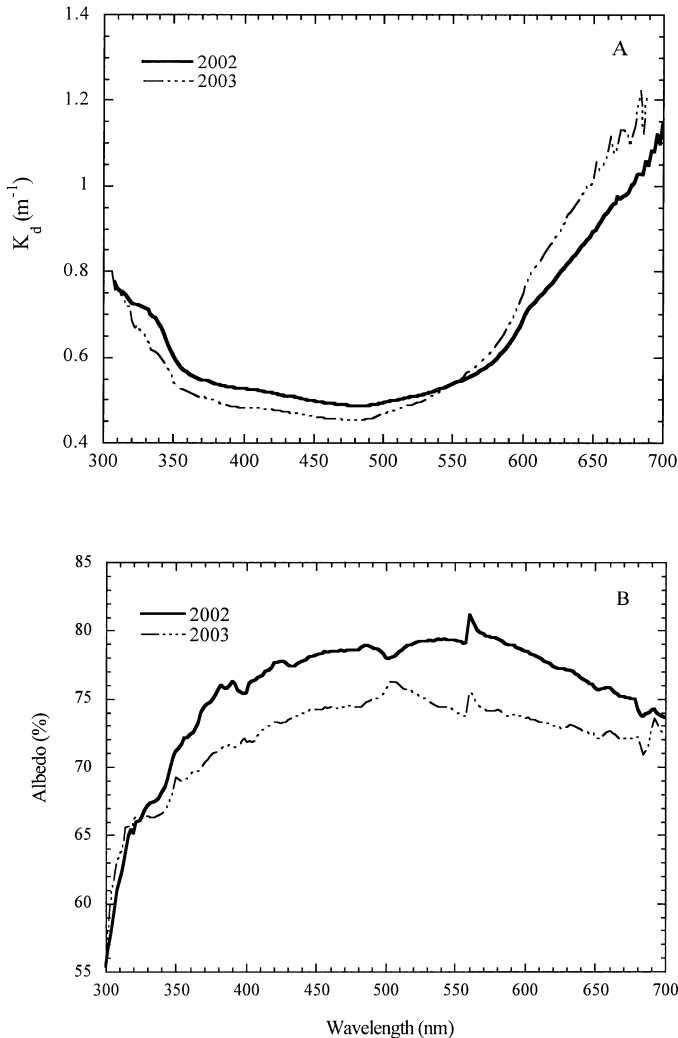


Fig. 2. (A) Spectral attenuation coefficients ($K_d \text{ m}^{-1}$) for downwelling irradiance of UVR and PAR through the ice and water column. (B) Spectral albedo for snow and sea ice at Cape Armitage in 2002 and 2003.

data). The net result of lower ozone concentrations, smaller attenuation coefficients and albedos, but greater ice thickness for the 2003 experiment was a slightly higher irradiance of UVB under the ice and larger UVB:PAR ratios in 2003 compared to 2002 values (Table 1).

Embryo survival and DNA damage—Bags containing FFE of *S. neumayeri* placed at 1, 3, and 5 m below the annual ice and exposed to UVR for 5 d exhibited significant mortality in both 2002 and 2003. In 2002 a significant effect of treatment (ANOVA: $p = 0.018$) but not depth or depth \times treatment was observed (ANOVA: $p > 0.05$, Fig. 3A), whereas similar findings for 2003 were observed with a significant effect of treatment (ANOVA: $p = 0.0005$) but not depth or depth \times treatment (ANOVA: $p > 0.05$, Fig. 3B). In 2002 only UVB effects were observed, whereas both UVA and UVB effects were observed in 2003 using post hoc multiple comparison (SNK: $p < 0.05$) testing (Fig. 3A,B). Many of the embryos that survived in both years

exhibited abnormal development (Fig. 4B) when compared to the normal development to early gastrula (Fig. 4A) in embryos not exposed to UVR at -1.8°C seawater temperature. At the end of the 5-d experiments in 2002 the embryos of *S. neumayeri* also exhibited significantly greater damage to DNA measured as CPD formation with a significant effect of treatment (ANOVA: $p < 0.0001$) and depth (ANOVA: $p < 0.0001$), and depth \times treatment (ANOVA: $p = 0.044$). In 2002 all depths and treatment groups were significantly different from each other according to post hoc multiple comparison (SNK: $p < 0.05$) tests (Fig. 5A). In 2003 we observed a significant effect of treatment (ANOVA: $p < 0.001$) and depth (ANOVA: $p = 0.017$), but not depth \times treatment (ANOVA: $p = 0.081$). Both UVA and UVB caused DNA damage in 2003. Shallow depths were significantly different from mid or deep depths but mid and deep depths were not significantly different from each other as determined by post hoc multiple comparison (SNK: $p < 0.05$) testing (Fig. 5B).

Discussion

Attenuation of solar UVB irradiance and changes in spectral composition as UVR is transmitted through the annual ice have not received adequate attention. Modeling studies on the transmission characteristics of annual ice for McMurdo Sound have shown that the 2-m-thick annual ice and snow cover can dramatically reduce UVR transmission through the ice into the water column and that the attenuation of UVR, as well as PAR, is greater with snow cover or older annual ice (Trodahl and Buckley 1989; Perovich 1993). Modeling of UVB (305 nm) penetration through the early Austral spring sea ice, without snow cover, of McMurdo Sound shows a 20-fold increase in UVB transmission during the occurrence of the ozone hole that is coincident with the high transmission characteristics of snow-free early spring sea ice (Trodahl and Buckley 1989, 1990). Large areas of McMurdo Sound are either snow-free or have little snow cover during the ozone hole (Perovich 1993; personal observation). Our measurements during the Austral spring show that UVB wavelengths can reach to a depth of 6.7 m after being transmitted through 2.5 to 3.1 m of annual sea ice. Given these results, the planktonic phases of benthic invertebrates under the annual ice in McMurdo Sound will be exposed to UVR, both UVB and UVA, during the Austral spring, the amount of which will be greatly affected by snow cover, the presence of the sea-ice microbial community, the extent and persistence of the ozone hole, and the optical properties of the ice. Recent data have also shown that not only can UVR be transmitted through the >4.0 m perennial ice of lakes in the Dry Valleys but that sufficient UVR penetrates to potentially cause the inhibition of phytoplankton growth (Vincent et al. 1998).

We observed significant mortality and DNA damage to urchin embryos from exposure to UVR under the annual ice in 2002 and 2003. The higher mortality and DNA damage observed in 2003 were associated with slightly greater irradiances of UVB, but more importantly higher UVB:PAR ratios, and therefore lower irradiances of visible radiation

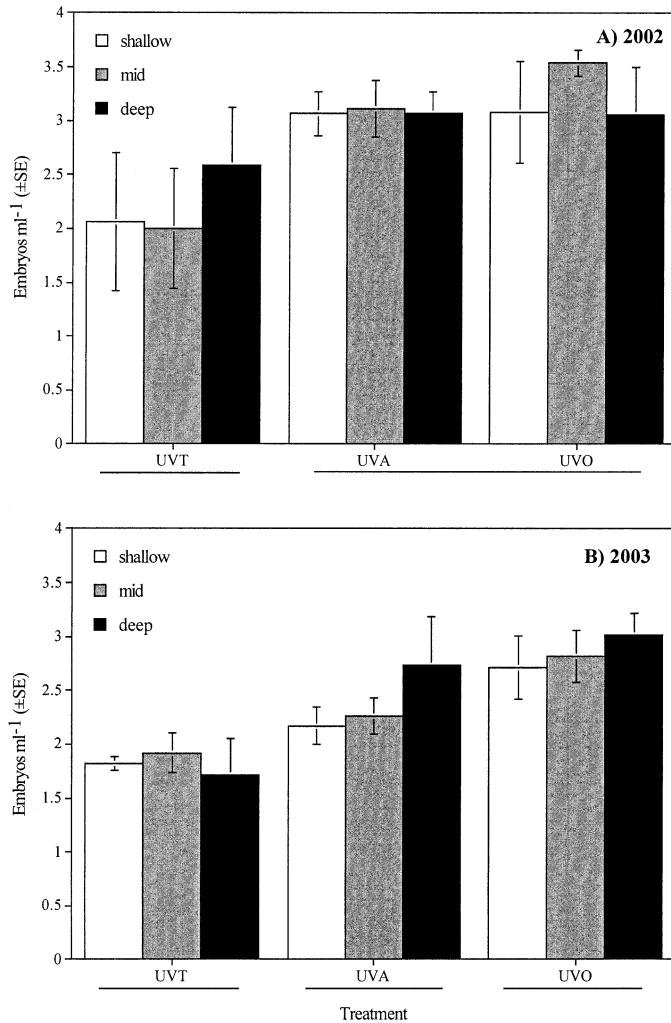
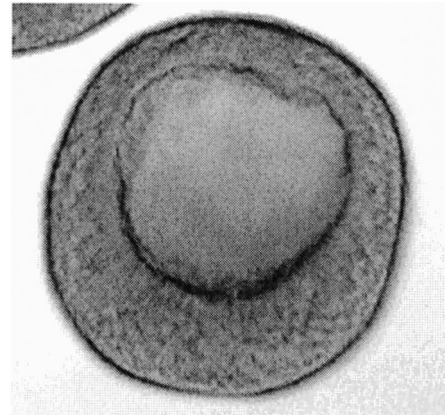


Fig. 3. Embryo survivorship at Cape Armitage (A) in 2002 and (B) in 2003. Bars underneath similar treatment groups or common superscripts indicate no significant difference ($p > 0.05$) by post hoc multiple comparison tests (SNK).

available for repair processes (Table 1). Changes in the UVB:PAR ratios are an important indicator of the effectiveness of DNA repair processes because photolyase, which repairs UVR-induced photolesions, requires UVA and visible radiation to be catalytically active (Kim and Sancar 1993; Roy 2000). Malloy et al. (1997) measured significant increases in net DNA damage in Antarctic ice fish and krill collected from shallow open waters during the occurrence of the ozone hole despite the fact that rates of repair were high for these species. In 2003 there was a ~25% increase in UVB irradiance and embryos at 1 m below the ice incurred over twice as much DNA damage as in 2002. This did not change embryo survival at shallower depths between years, suggesting that the rate of repair for DNA damage may have been sufficient despite the greater UVB:PAR ratios. It is also clear that UVA has significant effects on the amount of DNA damage, and this pattern has been reported for other species of sea urchins (Lesser and Barry 2003; Lesser et al. 2003).

A) Normal development



B) Abnormal development

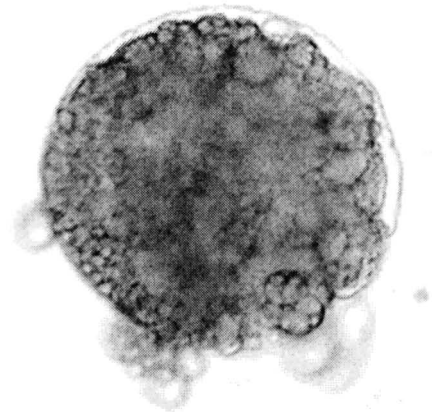


Fig. 4. Photomicrographs of *S. neumayeri* developing embryos from field experiments. (A) Normal late blastula from UVO treatments. (B) Abnormal "packed" blastula resembling apoptotic morphology from UVT treatments. $\times 1000$.

As reported for the embryos of the temperate sea urchin *Strongylocentrotus droebachiensis* exhibiting DNA damage after exposure to UVR, we observed delays in cell division and abnormal morphologies for the embryos of *S. neumayeri* (e.g., "packed" blastula, Fig. 4B) that were consistent with the cells of developing embryos undergoing programmed cell death or apoptosis (Adams and Shick 1996; Lesser and Barry 2003; Lesser et al. 2003). In these urchin embryos the DNA damage led to an increased expression of markers of the cell cycle, p53 and p21, that cause delays in cell division while DNA repair is taking place (Lesser et al. 2003). If DNA repair is unsuccessful then the affected cells of the developing embryo are slated for apoptosis or programmed cell death (Lesser et al. 2003). The UVR irradiances experienced by the developing embryos of *S. neumayeri* are lower compared to the UVR irradiances that temperate sea urchin embryos are exposed to (Adams and Shick 1996; Lesser et al. 2003). Nonetheless, this results in DNA damage, high mortality, and abnormal development, suggesting that the embryos of *S. neumayeri* can tolerate the loss of only a very

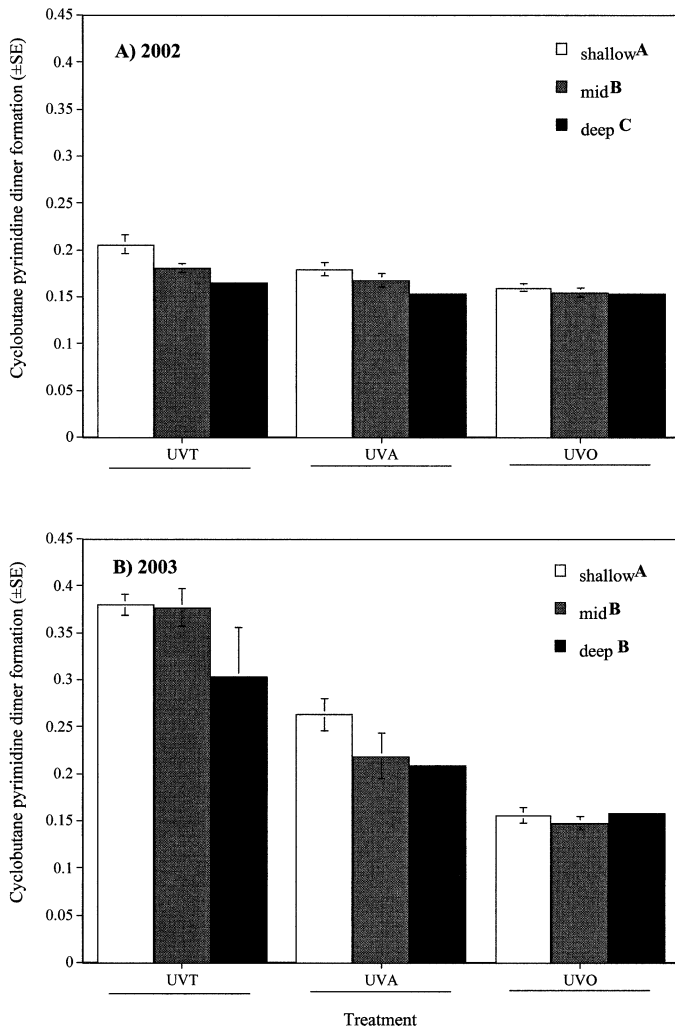


Fig. 5. CPD formation in embryos deployed as described in Fig. 2. Cape Armitage (A) in 2002 and (B) in 2003. $n = 3$ for each treatment at each depth. Treatment groups with similar bars underneath or common superscripts are not significantly different from each other ($p > 0.05$) according to post hoc multiple comparison tests (SNK).

few cells via apoptosis and still complete their developmental program.

One potential mechanism of protection against the biological effects of UVR is the presence of UVR-absorbing compounds such as mycosporine-like amino acids (MAAs), which have strong absorption at 310–360 nm. Embryos of sea urchins contain MAAs transferred specifically to the eggs from parents that have fed on macrophytes containing MAAs (Carroll and Shick 1996). These MAAs can provide significant protection from the biological effects of UVR in developing sea urchin embryos (Adams and Shick 1996, 2001). Many Antarctic marine organisms contain MAAs, including *S. neumayeri* (Karentz et al. 1991; McClintock and Karentz 1997). The female gonads of the Antarctic sea urchin *S. neumayeri* from Cape Armitage also contain MAAs, including mycosporine-glycine, shinorine, porphyra-334, and palythine but in lower concentrations (McClintock and

Karentz 1997; Lesser and Lamare unpubl. data) than observed for *S. neumayeri* from the Antarctic peninsula (Karentz et al. 1997) collected from approximately the same depth and time of year. Two common red macrophytes, *Iridaea cordata* and *Phyllophora antarctica*, occur in McMurdo Sound and contain significant concentrations of MAAs (McClintock and Karentz 1997), but little or no herbivory on these species by sea urchins has been observed (Miller and Pearse 1991). Whatever accumulation of MAAs occurs from consuming these macrophytes is probably incidental to grazing upon the urchin's primary food source of benthic diatoms (Miller and Pearse 1991) that generally contain low concentrations of MAAs (Karentz et al. 1991). Because the principal food of this omnivore is low in MAAs, the developing planktonic embryos of *S. neumayeri* obtain less protection against UVR from trophically acquired MAAs. The embryos and larvae of *S. neumayeri* are found throughout the water column of McMurdo Sound during the Austral spring (Bosch et al. 1987) where they are exposed to both UVA and UVB that is transmitted through as much as 3 m of annual ice. In addition to having low concentrations of MAAs the embryos of *S. neumayeri* also have extremely low metabolic rates, which may constrain how much energy can be diverted to repair processes (Marsh et al. 2001).

Although we have shown UVR effects on the embryos of *S. neumayeri* in their natural environment we do not yet know what, if any, effects UVR exposure over the last 20 years has had on the population biology of *S. neumayeri* or community dynamics of the Antarctic benthos. A study of several populations of *S. neumayeri* in McMurdo Sound concluded that the size frequency distribution of urchins at several locations and depths showed that despite the large amount of energy invested in reproduction no successful recruitment had occurred for 4–7 years (Brey et al. 1995). It has been suggested that the variation in recruitment success for Antarctic benthic invertebrates is on decadal time scales and is caused by variations in current regime, the extension of sea ice cover, or the formation of anchor ice (Dayton 1989; Brey et al. 1995; Gutt 2000). During the mid 1980s the annual “ozone hole” had already begun to occur with its increase in Austral spring UVB irradiances equivalent to those measured during the Austral summer (Frederick and Snell 1988). The infrequent recruitment events in McMurdo Sound could also be affected by exposure to UVB during springtime ozone depletions, with its potential to cause significant mortality of embryos and larvae in the plankton and further reduce settlement and recruitment to the adult population. Any additional cause of embryo or larval mortality could be significant for the long-term dynamics of benthic communities in McMurdo Sound. The influence of UVB irradiances over long time scales on the benthic communities is unknown, but continued measurements of UVR, development of biological weighting functions for DNA damage in urchin embryos and larvae, monitoring of settlement and recruitment dynamics of Antarctic benthic communities, or dominant species of those communities such as *S. neumayeri*, would be an important undertaking, as the “ozone hole” over the Antarctic continent is predicted to continue for the next half century (Madronich et al. 1998).

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