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Abstract

Depletion of stratospheric ozone over Antarctica for the past two decades has caused an increase in ultraviolet B (UVB) radiation reaching Antarctic marine habitats. Research efforts to evaluate the impact of enhanced UVB radiation have initially focused on phytoplankton under the assumption that whole ecosystem effects will most likely originate through reductions in primary productivity. However, phytoplankton do not represent the only significant component in Antarctic marine ecosystem response to enhanced levels of UVB radiation. Antarctic bacterioplankton, sea ice microalgae, macroalgae, zooplankton and benthic invertebrates (particularly early developmental stages) are also sensitive to UVB. Little information exists on UVB responses of larger Antarctic marine vertebrates (e.g., birds, seals and whales). Although the effects of ozone depletion on Antarctic marine organisms have not been catastrophic, the long-term consequences of possible alterations in taxonomic structure and trophic interactions remain uncertain.

Introduction

Environmental concerns about ozone depletion arise from the fact that the primary responsibility of the ozone layer is to absorb biologically damaging ultraviolet B radiation (UVB). UVB is able to penetrate well into the lower atmosphere and surface waters of the oceans, even without ozone depletion, providing a potential daily stress to many marine organisms (Buma *et al*., 2001). Therefore, enhanced ultraviolet radiation (UVR) associated with concurrent anthropogenic induced seasonal declines in stratospheric ozone is expected to have ecological effects on marine communities. This is a matter of particular concern in the Antarctic region, where the most extensive destruction of ozone occurs. For the past two decades, significant ozone depletion (>50%) has occurred over Antarctica and parts of the Southern Ocean during the austral spring (September- November), causing increased levels of UVB to reach Antarctic marine environments (Madronich, 1998).

The aim of this review is to build on previous reviews relating to the ecological effects of ozone depletion over Antarctica and the Southern Ocean (e.g., Karentz, 1991; Karentz and Bosch, 2001) and update our understanding of how enhanced UVB radiation resulting from ozone depletion affects Antarctic marine organisms.

Stratospheric ozone depletion in Antarctica

The Antarctic ozone problem has received considerable international attention since Farman *et al*., (1985), initially described it. Their data from Halley Bay indicated that the spring values of total ozone in Antarctica had steadily declined since the late 1970s. This has become a predictable event in the springtime over Antarctica, with minima values indicating decreases of over 50% from ‘normal’ column ozone levels and up to 90% at specific altitudes (Hofmann *et al*., 1987). It is thought that the ‘normal’ pre-1980 ozone concentration over the Antarctic averaged approximately 300 Dobson units (DU) or higher (Karentz, 1991).

The Antarctic ozone hole

The term ‘Antarctic ozone hole’ was coined to refer to regions with large stratospheric ozone losses, and is now generally applied to ozone concentrations of 220 DU or less (WMO, 2002). Ozone values over the Antarctic before the early 1980s were never less than 220 DU (NIWA, 2003). However, in September 2003, a record loss of 47.3 million tons of ozone was recorded over Antarctica (Figure 1) with ozone concentrations as low as 105 DU at the centre of the hole (NIWA, 2003). The areal extent of ozone depletion over Antarctica varies greatly from year to year (Figure 1), and although normally formed between September and November, the Antarctic ozone hole has started earlier and persisted for longer in recent years (WMO, 2002). In addition to these annual trends, short-term changes in ozone levels over coastal regions of Antarctica have been observed due to daily and locally dynamic processes such as the rotation of the polar vortex (Karentz and Bosch, 2001). The polar vortex is an atmospheric circumpolar current that is believed to isolate a large cold core of air from the global atmosphere- the ‘containment vessel’ hypothesis (Keys, 1997)- which enables ozone depletion to occur without the influence of mixing of air from adjacent air masses to the north.

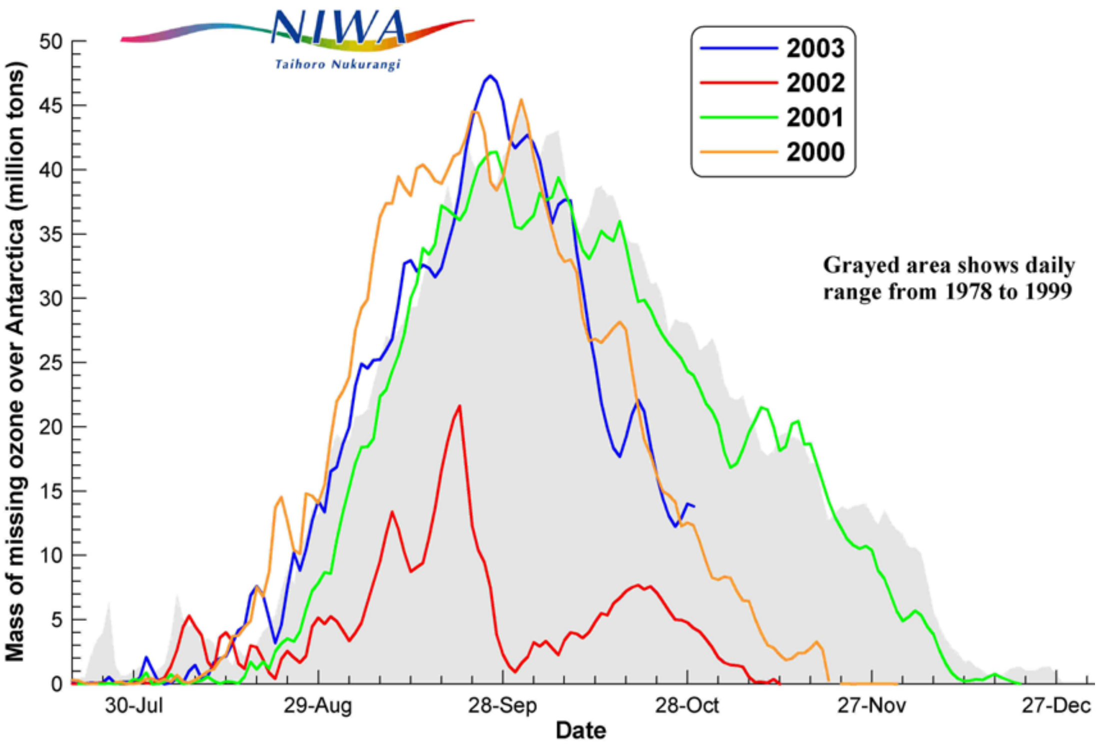

Fig. 1 The mass of missing ozone (million tons) from the Antarctic stratosphere in 2000, 2001, 2002 and 2003. Also shown in grey shading is the daily range of values for the period 1978 to 2000. Source: NIWA, (2003).

Causes of ozone depletion

The consensus amongst atmospheric scientists is that the major factor responsible for ozone depletion is anthropogenic and industrial emissions of chlorofluorohydrocarbons (CFCs), halons and other atmospheric anthropogenic pollutants such as nitrogen oxides (NO_x) (Solomon, 1990). Both CFCs and halons are very stable and inert reservoir species in the troposphere, but are converted in the stratosphere into highly reactive chlorine and bromine atoms respectively (Whitehead *et al*., 2000). One free atom of chlorine in the stratosphere can potentially destroy as many as 100,000 molecules of ozone during its chemical lifetime (Bunyard, 1999). This has triggered alarm as, since the 1970s, the concentration of CFCs in the air has increased five-fold (Bunyard, 1999).

Although releases of CFCs have been concentrated in developed and developing countries, their long chemical lifetimes mean that their impact is felt globally as the gas is transported polewards via atmospheric circulation.

According to the 2001 State of the Environment Report for the Ross Sea Region of Antarctica, “the Antarctic region currently shows the strongest regional response to the increased concentrations of human-made ozone depleting chemicals” (NZAI, 2001).

Causes of the Antarctic ozone hole

This annual phenomenon is caused by a special combination of physical and chemical features unique to the springtime Antarctic atmosphere. These include the presence of the polar vortex; extremely cold temperatures in the stratosphere; formation of polar stratospheric clouds (PSCs) that provide the necessary substrates for the heterogenous (gas/ liquid/ solid phase) chemistry; and after a long dark winter period, solar radiation that is required to activate ozone depleting chemicals (Hoyer, 2003; Karentz and Bosch, 2001; NZAI, 2001). Normal ozone concentrations are only restored with the breakdown of the polar vortex by summer tropospheric wave activity (Keys, 1993).

A greenhouse gas connection

It has been suggested that increasing levels of greenhouse gases may serve to worsen the areal extent and persistence of the Antarctic ozone hole by warming the Earth’s surface but cooling the stratosphere (Salawitch, 1998; Shindell *et al*., 1998). This occurs as more of the heat radiated from Earth’s surface is trapped in the troposphere (a process known as global warming), resulting in less heat reaching the overlying stratosphere (Salawitch, 1998). Stratospheric ozone is itself considered a greenhouse gas. In the process of blocking UVB from the Sun, ozone breaks down to form oxygen while the UVB loses some of its energy and degrades to heat (Bunyard, 1999). However, with ozone depletion occurring over the Antarctic, the stratosphere can retain less heat and cools as the lower atmosphere warms.

This stratospheric cooling leads to increased formation of PSCs that attract and hold the chlorine breakdown products of CFCs (Bunyard, 1999). This is a matter of considerable concern as, on a weight per weight basis, CFCs trap thousands of times more heat than other greenhouse gases like carbon dioxide and already account for 17% of greenhouse gas activity (Bunyard, 1999).

Antarctic ozone hole recovery

Despite international efforts to see the reduction and eventual elimination of emissions of ozone depleting chemicals in accordance with the Montreal Protocol, uncertainties remain about the exact timing of Antarctic ozone hole recovery. Shindell *et al*., (1998) predict that ozone levels will continue to decrease over the next century, especially in the years 2010-2019. Madronich *et al*., (1998), give a slightly more positive prognosis. They expect that within 40-60 years, global ozone levels will return to normal and springtime ozone depletion over the Antarctic will no longer occur. While this may seem encouraging, the impact of the past 20 years of ozone depletion and of the 40-60 years of continued ozone losses on the Antarctic ecosystem is still uncertain.

Incident UVB radiation in Antarctica

Regardless of the cause, stratospheric ozone depletion results in increased UVR, particularly UVB, at the Earth's surface. UVR consists of three subdivisions which are defined as follows; UVA (315-400 nm), UVB (280-315 nm) and UVC (100-280 nm). Under 'normal' stratospheric ozone conditions, the ozone layer completely absorbs the high energy UVC and most, but not all, of the UVB (Hoyer, 2003). Longer wavelength UVA and photosynthetically active radiation (PAR: 400-700 nm) pass through the ozone layer relatively unaffected (Hoyer 2003). Although UVB represents less than 0.8% of the total energy reaching the surface of the Earth, it is responsible for almost half of the photochemical effects in marine environments (Whitehead *et al*., 2000). Further, it has been predicted that the projected long-term increase in UVB radiation will affect the marine environment for at least the next 25 years (Madronich *et al*., 1998).

Seawater clarity around Antarctica is extremely high in early spring, partly due to the limited terrestrial riverine influx. PAR can penetrate the water column to depths of 40 m (Gómez *et al*., 1997), while solar UVR can penetrate the water column to depths of at least 30 m for UVB and 60-70 m for UVA (Holm-Hansen *et al*., 1993; Smith *et al*., 1992). This penetration increases as stratospheric ozone declines (Smith *et al*., 1992). Although UVB radiation is more strongly absorbed than UVA and PAR even in clear Antarctic waters, biologically effective intensities of UVB radiation may penetrate the water column as deep as 25 m (Holm-Hansen *et al*., 1989; Karentz, 1989; Smith *et al*., 1992).

Consequently, the incident and in water ratios of UVB:UVA:PAR vary with ozone levels and depth (Smith *et al*., 1992). With a reduction in ozone, there may be an increase in damaging UVB wavelengths without a proportional increase in longer wavelengths involved in photoreactivation and photorepair (Smith, 1989). Indeed, the relative change in UVB radiation in Antarctica is the greatest of anywhere in the world (NZAI, 2001). It is important to note that other factors such as clouds, sea ice (which is most extensive in early spring), albedo, aerosols, haze, pollutants and solar zenith angle may also influence the absorption and reflection of UVB in Antarctica (Kerr and McElroy, 1993). UVB radiation is therefore most likely to affect shallow sessile benthic organisms beneath areas of clear ice and pelagic marine communities in open water.

UVB radiation effects on Antarctic marine organisms

UVB radiation is known to have a wide range of negative effects on marine organisms (Karentz and Bosch, 2001; references therein). These effects can be both direct and indirect. Direct effects include structural damage to DNA that cause photoproducts such as cyclobutane pyrimidine dimers (CPD) (Lesser and Barry, 2003). Lipids, proteins and nucleic acids may also be affected (Hoyer, 2003). Indirect effects are caused by reactive oxygen species (ROS) such as hydrogen peroxide, hydroxyl radicals and superoxide radicals.

ROS are oxidants capable of damaging DNA, RNA, proteins, pigments and inhibiting physiological processes like photosynthesis (Hoyer, 2003). In addition, UVB may deleteriously affect community structure in ways that are not apparent through studies based on individual species or trophic levels (e.g., Bothwell *et al*., 1994).

The remainder of this review will introduce the effects of enhanced UVB radiation on Antarctic marine organisms, including bacterioplankton, phytoplankton, sea ice microalgae, macroalgae, zooplankton, benthic invertebrates and vertebrates. Ecosystem responses are also discussed briefly.

Bacterioplankton

Although relatively little work has been conducted on the impact of ozone depletion on Antarctic marine heterotrophic bacteria, a logarithmic relationship between loss of viability and UVB dose has been demonstrated for two Antarctic marine bacterial strains (Hermandez *et al*., 2002). These results suggest that even though the changing UVB flux over Antarctica is unlikely to cause an abrupt decline in productivity, microbial community composition in Antarctic surface waters could be significantly affected. It is well known that heterotrophic bacteria are a significant component of the Antarctic marine ecosystem. They play a major role in the cycling of nutrients and organic matter in the sea and are one of the major determinants of inorganic and organic nutrient availability (Hermandez *et al*., 2002). Therefore, changes in microbial viability and community structure caused by variations in UVB exposure could potentially have a variety of effects that transmit through the entire Antarctic marine food web.

Phytoplankton

Antarctic ozone depletion coincides with the initiation of seasonal phytoplankton blooms in the high-light, high-nutrient regime of the marginal ice zone (MIZ), polynyas, and coastal waters of the Antarctic Peninsula

(Moisan and Mitchell, 2001). Springtime blooms in the MIZ account for 25-67% of primary production in Antarctic waters (Smith and Nelson, 1986). Much of the work on UV photobiology of Antarctic marine organisms has focused on phytoplankton under the assumption that whole ecosystem effects will most likely originate through reductions in this primary production. It is also significant that phytoplankton are small single-celled organisms with short generation times and little control over their positioning in the water column. They would therefore be expected to be more exposed and more vulnerable to UVB than larger multicellular species with longer generation times and yearly reproductive cycles.

Several studies have reported a decline in phytoplankton production when exposed to ambient levels of UVB without ozone depletion (e.g., Helbling *et al*., 1992; Smith *et al*., 1992). Increased exposure under ozone depleted conditions exacerbated responses, reducing phytoplankton productivity by <1-15%, depending on the temporal and spatial sampling pattern used (Arrigo, 1994; Boucher and Prézelin, 1996; Neale *et al*., 1998). However, primary production is not the only factor that needs to be considered when evaluating the effects of enhanced UVB on Antarctic phytoplankton. Species-specific responses to UVB have been reported with larger cells being more resistant to exposure than smaller cells (Karentz *et al*., 1991). Alterations in taxonomic structure and size distribution within Antarctic phytoplankton communities may therefore be a significant effect of ozone depletion over Antarctica requiring further investigation.

Sea ice microalgae

A major concern with the assessment of the effects of enhanced UVB radiation on marine phytoplankton is the effect of vertical movement of the algal cells in the water column due to mixing. Sea ice microalgae however, remain in a fixed position in the ice where exposure to UVB cannot be avoided. Furthermore, sea ice can be quite transparent to UVB radiation during spring, when the Antarctic ozone hole is at its maximum (Ryan *et al*., 2002). During this time, the amount of incident UVR penetrating the sea ice increases from 1-5% to 10% due to the increase in incident UVB but not higher wavelengths (Ryan and Beaglehole, 1994). Under these higher UVB exposures, Ryan and Beaglehole, (1994), observed a 5% reduction in sea ice microalgal photosynthetic production. Although this indicates a minor effect on primary productivity, stronger effects have been reported on standing crop (up to 40% decline) and species successional patterns that depend on the amount of snow cover and the initial species composition (McMinn *et al*., 1999).

Macroalgae

As primary producers, macrolagae are important organisms for coastal ecosystems. However, until relatively recently, the literature contained very few studies relating to the UV photobiology of Antarctic macroalgae. Most of the investigated species from polar regions are affected by UVR, particularly UVB. In general, Antarctic red algal species exhibit stronger inhibiting effects of UVB radiation on growth and photosynthetic activity than green and brown algal species that do not have strong absorption in the UV wavelengths (Bischof *et al*., 1998). Red algal species have also been found to contain more of the UV absorbing mycosporine-like amino acids (MAAs) than green and brown algal species, which is a typical pattern for these groups at other latitudes (Hoyer *et al*., 2001; Hoyer *et al*., 2002; Karentz *et al*., 1991). These responses appear to be species-specific, especially for the less UV tolerant red algae (Bischof *et al*., 1998; Hoyer *et al*., 2002).

The observed differences in individual UV tolerance suggest that an increase in UVB radiation because of ozone depletion may be a factor in affecting the vertical distribution of polar macroalgae species (Bischof *et al*., 1998). The dependence of MAA formation and accumulation on depth distribution has also been demonstrated (Hoyer *et al*., 2001).

Zooplankton

Little work has been conducted on the effects of UVB on primary consumers among the zooplankton, mainly due to the assumption that the major effect on zooplankton populations would be indirect due to disruptions in their phytoplankton diet. Antarctic krill are voracious consumers of phytoplankton and, at times, other zooplankters, and are a major prey item for higher trophic levels. This makes them a key species in the Southern Ocean. Detrimental effects on the krill population due to increased UVB are therefore likely to have consequential effects on both upper and lower trophic levels. Newman *et al*., (1999) provide the first evidence “that the mortality of juvenile Antarctic krill is accelerated by comparatively low levels (2-5 times below ambient 12 noon surface levels) of UVB radiation”.

The Antarctic ozone hole coincides with the timing of spawning, and embryo and larval development of many Antarctic benthic invertebrates. These include the sea star *Odontaster validus*, the sea urchin *Sterechinus neumayeri* and the ribbon worm *Parborlasia corrugatus* which all produce eggs <0.2 mm diameter and have planktotrophic larval development (Pearse *et al*., 1991). Their small size, lack of protective tegument, high rate of cell division, and distribution (upper part of the water column), makes these planktonic stages vulnerable to UVR that penetrates the annual sea ice cover in spring (Lamare *et al*., 2004).

Recent *in vitro* experiments indicated that the embryos and larvae of *S. neumayeri* are sensitive to UVR, and that the sensitivity is inversely related to the UV wavelength (i.e., more sensitive to the shorter most biologically damaging wavelengths, <320 nm) (Lamare *et al*., 2004). *In situ* experiments indicated that *S. neumayeri* embryos and larvae were damaged when exposed to ambient levels of UVR without ozone depletion. Increased exposure under ozone depleted conditions exacerbated responses, reducing the survival rate of newly hatched *S. neumayeri* eggs by 30-40% (Lamare *et al*., 2004). The degree of damage was found to be dependent on both wavelength (being greatest in the shorter UVB wavelengths) and depth (being greatest 0.5 m below the sea ice and generally no UV effects observed at depths below 5 m) (Lamare *et al*., 2004). These results suggest that the short wavelength UVR penetrating through the sea ice is intense enough to have damaging effects on sensitive *S. neumayeri* larval stages.

Similar results have been obtained for the sea star *Psilaster charcoti*, which produces large (0.7 mm diameter) yolk-laden eggs and free-swimming non-feeding larvae (Pearse *et al*., 1991). However, the implications of these results are quite different due to this species developmental strategy. The eggs released by *P. charcoti* float towards the surface at rates of up to 2.0 m/hr *in situ*, allowing them to move from depths occupied by adults to depths at which they are vulnerable to UV damage in less than one day (Pearse *et al*., 1991).

Antarctic icthyoplankton, including the floating eggs of *Chaenocephalus aceratus* (icefish) could potentially be exposed to biologically damaging levels of UV radiation during the most crucial stages of early development. Malloy *et al*., (1997) report a significant correlation between DNA damage levels in icefish eggs collected from surface waters and total daily incident UVB irradiance. Other near-surface Southern Ocean zooplankton such as chaetognaths and transparent planktonic polychaetes responded in a similar way to enhanced UVB, providing the first evidence that ozone depletion may be causing DNA damage in Antarctic heterotrophs (Malloy *et al*., 1997).

Benthic invertebrates

MAAs have been found in the majority (~90%) of Antarctic benthic marine invertebrates in McMurdo Sound, including sponges, cnidarians, nemerteans, molluscs, bryozoans, arthropods, echinoderms and tunicates (Karentz *et al*., 1991; McClintock and Karentz, 1997). However, MAAs were generally found in low levels and abundances which may reflect a reduced need for UV protectants in marine organisms inhabiting subtidal benthic environments that experience seasonal sea ice cover. During spring, sea ice scours most inter- and subtidal areas and so the majority of benthic organisms reside in relatively deep (>20 m depth) water where they are protected from UV exposure by both the sea ice and the overlying water column (Karentz and Bosch, 2001).

While Antarctic invertebrates lack the biosynthetic pathways to produce MAAs, they are able to acquire them via their diet (Karentz *et al*., 1997). The low levels of MAAs may therefore be a function of food supply, since the majority of benthic species in McMurdo Sound are not herbivorous (McClintock and Karentz, 1997). However, along the Antarctic Peninsula where the food supply is more likely to be live algal material, there is a consistent vertical gradient of MAA concentration in benthic Antarctic species from the intertidal to subtidal depths of 30 m (Karentz *et al*., 1997).

Vertebrates

There have been no direct studies undertaken on the effects of enhanced UVB on higher animals, aside from those that included larval stages of fish (Karentz *et al*., 1997; Malloy *et al*., 1997; McClintock and Karentz, 1997). Fish, birds, seals and whales are physically protected from UVB induced damage by scales, feathers, fur and thick skin layers respectively (Karentz and Bosch, 2001). Therefore, any impact of enhanced UVB radiation on higher marine organisms is expected to occur indirectly through changes in community structure of lower trophic levels, which has the potential to limit food sources.

Ecosystem responses

It has been strongly suggested that enhanced UVB radiation may perturb marine ecosystems as a whole (Karentz, 1991), however this has not yet been systematically investigated. In a study carried out in shallow temperate streams, Bothwell *et al*., (1994) demonstrated that herbivorous grazers were the keystone species affected by UVB. It was therefore concluded “that predictions of the response of entire ecosystems to enhanced UVB cannot be made on single trophic-level assessments”.

It has also been suggested that enhanced UVB radiation may affect whole ecosystem responses to some forms of pollution, such as diesel fuel. Even though UVR dramatically shortens the survival time of faecal bacteria in Antarctic waters (Statham and McMeekin, 1994), it also reduces marine bacterial decomposition of diesel fuel (Delille *et al*., 1998). Furthermore, the toxicity of certain Polycyclic Aromatic Hydrocarbons (PAHs) to Antarctic marine organisms may be enhanced by several orders of magnitude by the presence of UVR (Ling *et al*., 1998).

Conclusions

Antarctica is a unique location for ozone-related research, as it is the only place on Earth where such large predictable ozone losses occur. The results of studies conducted so far have indicated the potential for increased UVB, as a result of seasonal ozone depletion over Antarctica, to change the species composition of the plankton community and hence overall productivity of the marine environment. Therefore, it is most likely that the greatest effect of ozone depletion on larger animals will be through their food sources. There is also evidence that enhanced UVB radiation may have already resulted in changes in the Antarctic marine environment. Future research should focus on gaining a more detailed understanding of UV effects on the complex interactions within the entire ecosystem, rather than single-trophic levels.

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