

Impacts of Global Warming on Polar Ecosystems

Carlos M. Duarte (ed.)

Offprint of Chapter

1. THE IMPACT OF INCREASING ULTRAVIOLET RADIATION ON THE POLAR OCEANS

by

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1.1. ULTRAVIOLET RADIATION AND THE TERRESTRIAL OZONE LAYER

MORE THAN 3,000 MILLION YEARS AGO, the cyanobacteria inhabiting the oceans changed the composition of the Earth's atmosphere by producing oxygen that accumulated in the atmosphere and became ozone when it reached the stratosphere. This is the current scientific explanation for the origin of the atmospheric ozone layer, which, given the capacity of this gas to absorb ultraviolet (UV) radiation, allowed life to develop on the surface of Planet Earth.

Once it reaches the stratosphere, oxygen is exposed to the intense solar radiation that impinges on the upper layers of the atmosphere. The high energy of the ultraviolet radiation reaching the stratosphere breaks down oxygen molecules (O_2) into oxygen atoms (O), which then react with oxygen molecules to form ozone (O_3). The same ultraviolet radiation dissociates the ozone into oxygen atoms, which can again react to form molecular oxygen and ozone, making ozone formation in the stratosphere a highly dynamic process. This process is expressed by the Chapman equations, which describe the phenomena associated with the formation and dissociation of ozone and oxygen molecules and atoms in the stratosphere. The outermost layer of the stratosphere, with the highest altitude, is dominated by atomic oxygen because solar radiation is much more intense and so produces greater dissociation. Within the stratosphere, however, solar radiation is absorbed to a greater degree, favouring the formation of ozone, which attains a maximum concentration at about 20 km above the Earth's surface. By contrast, in the lowest layer of the stratosphere, that closest to the Earth, ultraviolet radiation is very weak because it has largely been absorbed in its passage through the ozone layer. Molecular oxygen predominates here, since very little ozone is formed.

◀ **Photo 1.1: Icebergs and rainbow.** This rainbow spanning the Antarctic ice shows how solar radiation is composed of bands of different colours and energy. The least visible but most energetic of these is the ultraviolet band, whose intensity has increased in the polar regions due to depletion of the ozone layer.

Today, the ozone layer continues to protect the terrestrial and ocean surfaces of the planet from the high levels of ultraviolet radiation that strike the atmosphere by absorbing radiation in the 240-320 nm range. This band includes wavelengths of solar radiation of high energy that, were it not for the ozone layer, would pass through the atmosphere with harmful effects on living organisms. The ozonosphere is thinner above the equator, where ozone is found at a concentration of approximately 260 DU (Dobson units), and thickens towards higher latitudes. The greatest seasonal variation occurs at the poles, mostly because there is no solar radiation there during the polar winter, while during the long days of the polar summer they receive solar radiation for more hours.

The extent, thickness and seasonal dynamics of the ozone layer (see, for example, Solomon 1999; Staehelin et al. 2001) is an object of study for atmospheric chemists, who, amongst other tasks, have been taking regular measurements at different locations on the planet, such as Antarctica, the Arctic Ocean and, particularly, the Arosa station in Switzerland, with records dating back to 1926. The most widely used instruments for measuring ozone are the Dobson spectrophotometer and, more recently, balloons equipped with probes and sensors that are launched into the atmosphere and which calculate the change in ozone concentration with altitude. The TOMS (total ozone mapping spectrometers) satellites, of which the Earth Probe TOMS is currently in operation, and the OMI (ozone monitoring instrument) on board the AURA satellite are devices put into orbit by NASA in order to provide an overview of the distribution of ozone around our planet. The ozone maps plotted from the data sent by these satellites can be viewed online at the NASA website (jwocky.gsfc.nasa.gov/eptoms/ep.html and aura.gsfc.nasa.gov/instruments/omi/index.html).

1.2. ATMOSPHERIC POLLUTION AND OZONE DECLINE

The equations describing the formation and destruction of ozone formulated by S. Chapman in 1930 included only oxygen and ultraviolet radiation (see, for example, Solomon 1999; Dahlback 2002), but other substances that are also naturally present in the atmosphere were subsequently discovered to combine actively with ozone (O) in the same way as Chapman described, dissociating thus: $X + O_3 \rightarrow XO + O_2$, where X may be H, NO, OH, Cl, I or Br. The natural occurrence of these compounds in the atmosphere and their role in ozone destruction processes helped explain why ozone values were lower than those predicted solely from the results of the oxygen and ultraviolet radiation interactions reported by Chapman.



Photo 1.2: Icebergs in Antarctica. The most optimistic models predict that stratospheric ozone values will not recover until after 2050. In Antarctica, bright, sunny days are accompanied by high levels of ultraviolet radiation that may have negative effects on the development of life.

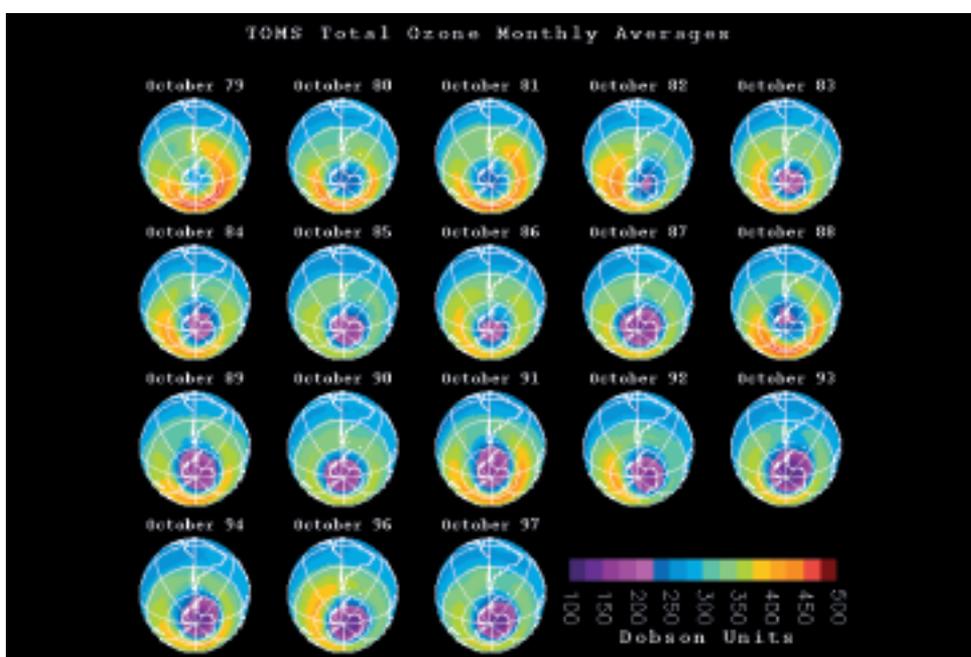
In 1970, Professor P. Crutzen not only described the NO-mediated ozone dissociation reactions, but also pinpointed a problem whereby emissions of nitrous oxide, a stable and long-lived gas produced by soil bacteria, had increased as a consequence of widespread fertilizer use and could cause an increase of NO in the atmosphere, leading to a reduction in the amount of ozone. Not long after, Crutzen and H. Johnston independently realised that supersonic aeroplane flights contributed to NO emissions. In 1974, Rowland and Molina described the role of atmospheric Cl in O₃ dissociation equations and also showed that organic chlorofluorocarbons (long-lived gases, such as the CFCs used in cooling systems) could be contributing to the reduction in the concentration of stratospheric ozone. When CFCs enter the stratosphere, they are dissociated by the action of UV radiation, forming free Cl that in turn reacts with ozone, destroying it. The Rowland-Molina theory met with fierce opposition from the aerosol and halocarbon industries, who branded it as “science fiction”. Nevertheless, laboratory evidence from other researchers and measurements of chlo-

rine radicals in the atmosphere did link CFCs with the deterioration of the ozone layer. Predictions at that point were not optimistic: if CFC emissions continued, the ozone layer could decrease 30-50% by the year 2050.

1.2.1. An ozone hole over Antarctica

During the 1980s, scientists studying the ozone layer at the British Halley Station in Antarctica verified that the concentration of ozone was dropping fast; in fact, the decrease they measured was so large they thought it must be due to probe malfunction. Yet measurements taken with new instruments at the same station confirmed that the concentration of ozone over Antarctica had indeed fallen to alarmingly low levels. In 1985, the journal *Nature* reported the discovery by Farman, Gardiner and Shanklin of the Antarctic ozone hole, so called because of the huge fall in stratospheric ozone concentration. The decrease occurred at the end of winter and in the spring, with peak values reached in October (map 1.1). This discov-

Map 1.1: Distribution of ozone concentrations over Antarctica in the month of October from 1979 to 1997



The ozone hole above Antarctica is easily appreciable in the ozone maps (measured in Dobson units) plotted with data from the TOMS satellite launched by NASA. The minimum ozone concentrations over Antarctica are recorded in October, and have been declining notably since 1980.

Source: NASA.

ery was a wake-up call for the scientific community, who realised the far-reaching consequences that the loss of the ozone layer could have for life on our planet.

This drop in ozone levels was not only recorded in Antarctica (see, for example, Dahlback 2002). Satellite data making the same prediction were dismissed as incorrect, because the decrease in ozone concentration coincided with the placing in orbit of the new TOMS satellite. The chronological series of ozone layer measurements taken above Arosa (Switzerland), dating from 1926, also showed an unequivocal fall in ozone concentration as of 1980, which has continued at a rate of approximately 2.9% per decade. The conclusion was that the ozonosphere was deteriorating. Evidence from other latitudes helped confirm this realisation. The Arosa time series showed that ozone levels had held relatively stable in the stratosphere over long periods, so the recent depletion of the ozone layer was a global reality. A number of governments signed the Montreal Protocol in 1987, committing to a reduction in their CFC emissions and ushering in a period of severe restrictions. Crutzen, Molina and Rowland won the Nobel Prize for Chemistry in 1995 for their work on stratospheric ozone.

1.2.2. The current situation: predictions and global warming

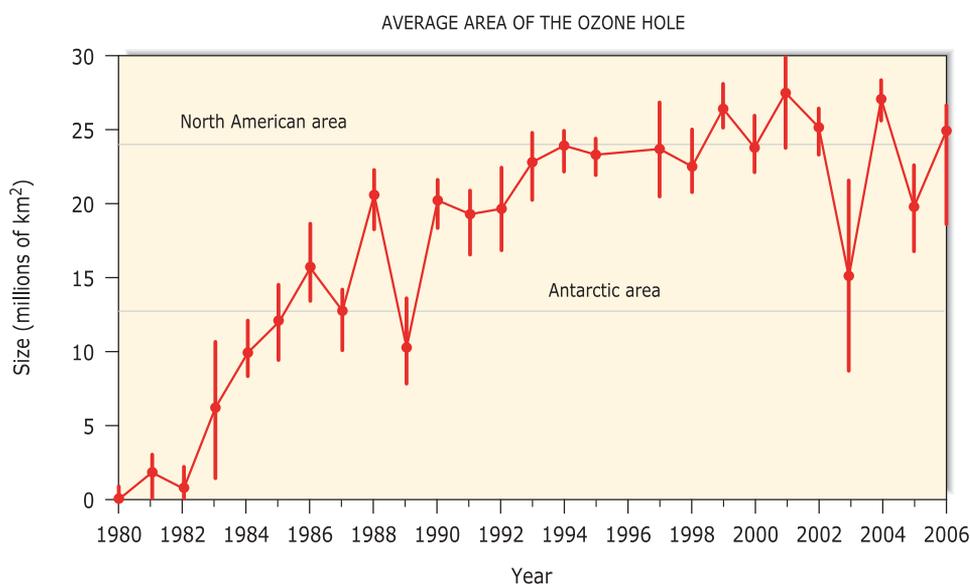
The decline in stratospheric ozone concentration was arrested by the Montreal Protocol, but, so far, the gas has not recouped the levels recorded before the decline set in in the 1970s. Current predictions based on the rate of CFC disappearance from the atmosphere suggest that recovery of ozone to its 1960s and 1970s levels will not be achieved until 2050 (Weatherhead and Andersen 2006). If this is correct, the increased UV radiation reaching the terrestrial and marine surface will persist for at least 80 years from the onset of depletion, which may represent a significant impact with unforeseeable consequences. Recently, predictions about ozone recovery have been questioned (Shindell, Rind and Lonergan 1998; Weatherhead and Andersen 2006) on account of the considerable uncertainty that surrounds them; firstly, due to the continuing emission of polluting substances—such as nitrous oxide and new compounds that appear every year for various uses—that are prone to destroy ozone, and secondly, because the global warming generated by the accumulation of greenhouse gases in the atmosphere may also be hindering the recovery of the ozone layer. The warming of lower atmospheric strata has a deleterious effect on the ozone layer, because the temperature of the troposphere influences that of the stratosphere: the more heat accumulating in the troposphere the colder the stratosphere becomes, and the colder the stratosphere, the more ozone is lost from it (Shindell, Rind and Lonergan 1998).



Photo 1.3: Ice masses drifting in open waters. The increase in ultraviolet radiation reaching the poles, especially in Antarctica, is reducing the biological productivity of their waters.

The combination of these factors has prevented the polar areas and intermediate latitudes from recovering historical ozone concentrations; instead, the values recorded now are lower than those existing before CFC emissions began. In the polar regions, where ozone concentration is strongly seasonal, an ozone hole still forms every winter-spring; of immense proportions in the case of Antarctica. The rate of ozone decline and the size of the hole are greater over Antarctica than the Arctic Ocean, since the gas's natural concentration tends to be lower in the first case due to topographic differences. The Arctic is a frozen ocean surrounded by continents, while Antarctica is a frozen continent surrounded by oceanic waters. This essential difference is of prime importance for the atmospheric circulation—including that of the stratosphere—generated over the two poles. With the coming of winter, the lack of solar radiation at the poles causes a slowing of ozone production-destruction dynamics, exposing levels of the gas to the influence of the circulating air masses. The lack of solar radiation leads to a cooling of the air at the poles, creating a steep temperature gradient that sends it circulating vigorously in an east-west direction, encircling the area of the polar atmosphere. This whirlwind effect, known as the circumpolar vortex, prevents the ozone-rich air of lower latitudes from penetrating the interior, isolating the atmosphere above the poles. The vortex is much less powerful in the Arctic than over Antarctica, because the Arctic Ocean suffers frequent disturbances that

Figure 1.1: Changes in the size of the ozone hole over Antarctica from 1979, when it did not exist, up to the present day



The graph shows the average values in the size of the Antarctic ozone hole observed in successive months of October. The ozone hole is defined as the area where the concentration is equal to or less than 220 Dobson units. The vertical lines show the errors of the monthly averages. The horizontal lines are equivalent to the area of the Antarctic continent—surpassed by the ozone hole since 1990—and to the area of the North American land mass to which the ozone hole area is equivalent in the present time.

allow ozone-rich air to penetrate from lower latitudes. For this reason, although ozone concentration has diminished over the Arctic, an ozone hole does not always appear. In contrast, the Antarctic ozone hole persists to this day, with the lowest levels recorded in October, coinciding with the arrival of the southern spring. In effect, the hole reached its record minimum concentration in October 2006, according to measurements kept since the 1980s, before its existence (figure 1.1). This was accompanied, moreover by a recent-year low in ozone concentration, confirming that recovery is still far from sight.

Global warming is no longer a prediction but a reality. It is also having a dramatic effect on the polar areas; the most sensitive to global temperature changes, as we explain in other chapters of this book. Importantly, today's diminishing ozone values, with polar regions especially affected, mean that the impact of global warming and the melting of the polar ice is being felt in an environment subjected to high levels of UV radiation. The combined effects of high UV radiation, ice melt and increased ambient temperature are still very much an unknown quantity.

1.3. INCREASED UV RADIATION OVER THE POLAR REGIONS

The climatological conditions of the polar areas are inauspicious for the development of life, not only for their low temperatures, but also because the lack of liquid water means they are ice deserts devoid of vegetation. The polar oceans, on the other hand, are a less extreme environment and experience smaller temperature variations, between approximately +5 and -2.3°C in polar waters, making them a more stable environment for life than the terrestrial habitat. In addition, polar waters are rich in nutrients that favour plankton proliferation. Life in the polar regions accordingly unfolds in the oceans, which serve as the source of food for their bird and large mammalian inhabitants. This is why any impacts on the polar oceans have serious consequences for the development and the maintenance of the system as a whole.

The evidence of increased UV radiation on polar ecosystems must be urgently checked and quantified. It is estimated that for every 1% reduction in stratospheric ozone, the transmission of ultraviolet B light to the surface of the Earth will increase by 1-2% (see, for example, Dahlback 2002). However, to assess the impact of UV radiation on these ecosystems, it is not enough just to consider the incident radiation, we also need to determine the effective doses organisms are receiving and how sensitive they are.

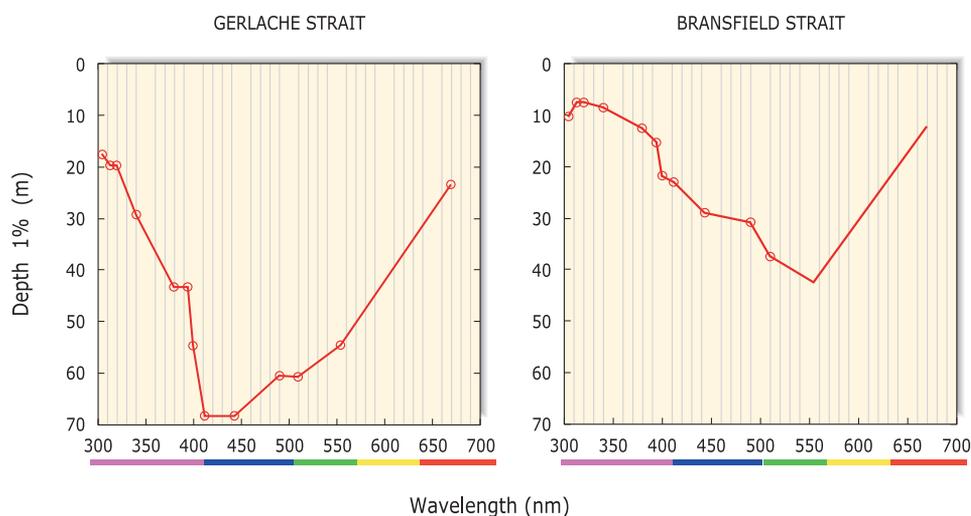
UV radiation absorption and reflection can operate through various processes, generating considerable variation in the doses received at a given place and by a particular organism. The intensity of this radiation varies according to the angle of the sun and therefore the latitude, the season of the year and the time of day (60% of total radiation is received between 10 a.m. and 2 p.m.). Cloud cover may influence the doses received since clouds absorb ultraviolet radiation, but only when cover is very dense does it provide an effective filter—90% of UV radiation can penetrate light cloud cover. The concentration of aerosols in the atmosphere is another factor, since these substances absorb UV radiation; and altitude too, with an extra 10-12% received for every 1,000 metres gained. Different surfaces have different capacities for reflecting ultraviolet radiation; so, while the Earth reflects around 25%, snow can reflect up to 80% of incident UV radiation. Finally, UV radiation penetrates water and can also have a significant effect on marine organisms.

Ultraviolet light, like visible light, is absorbed in the oceans by water, suspended particles and dissolved substances. Organic carbon compounds are the main agents of underwater attenuation of UV light. Wavelengths in the UVB band, despite containing more energy, are absorbed to a greater extent and do not penetrate as deeply as UVA band wavelengths. There are still few meas-

urements of the penetrative capacity of UV light in ocean waters. The equipment required for its underwater quantification is novel and sophisticated, and in possession of only a handful of laboratories.

Measurements taken in polar waters show that UV radiation can penetrate down to significant depths, particularly in comparison with visible radiation. For instance, during the Spanish ICEPOS-2005 project in Antarctic waters in the southern summer of 2005, aboard the oceanographic research vessel *BIO Hespérides*, measurements were taken of underwater solar radiation in the Weddell and Bellingshausen seas and the Bransfield, Gerlache and Antarctic straits. The size of the illuminated layer, which, in oceanographic terms is calculated as the depth at which 1% of the light reaching the surface of the water is received, varied between 10 and 70 m in the waters sampled during the ICEPOS-2005 expedition. It was found that 1% of ultraviolet radiation penetrated to depths of 5 to 19 m for the UVB band (at 305 nm) and 45 m for the UVA band (380 nm) (figure 1.2). This means that ultraviolet radiation reaches considerable depths in the illuminated layer of Antarctic waters and is present in up to 50% of the photic layer, for which reason its impact on aquatic organisms may be significant.

Figure 1.2: Penetration depth (in metres) of solar radiation in two areas of the Southern Ocean, measured during the ICEPOS-2005 Spanish oceanographic expedition



The red line represents the depth reached by 1% of the solar radiation received at the ocean surface and shows how it varies as a function of the spectrum band (wavelength), each labelled with the corresponding colour of the visible spectrum. The colour violet (300-400 nm), for instance, represents radiation in the ultraviolet band.

Source: Data provided by S. Agustí and M. Llabrés.

1.4. DAMAGE INDUCED BY UV RADIATION AND PROTECTION MECHANISMS

The energy associated with a photon is inversely proportional to its wavelength; the higher the energy, the greater the capacity of UV radiation to cause damage. The UVC band (200-280 nm) has the highest energy, and is accordingly the most harmful; even so, if ozone concentration levels were to lower dramatically and the ozone layer to thin to a few centimetres, the atmosphere would still be capable of filtering out all the incident UVC solar radiation. The current loss of ozone, however, is sufficient to diminish absorption of UVB light (280-315 nm), which is the ultraviolet band mostly absorbed by ozone gas. This has given rise to an increase in the amount of UVB radiation received on the Earth's surface. Ozone absorbs little of bands of longer wavelength like the UVA band (315-400 nm), so changes in the ozonosphere do not greatly affect the amount of UVA radiation reaching the Earth. The difficulty in determining the scale of the increase in ultraviolet radiation striking the polar oceans and ecosystems is basically a lack of data, because records of UV radiation incidence prior to ozone layer depletion are practically non-existent.

UVB is a high-energy radiation that acts at the molecular level, denaturing many organic compounds that are essential for live organisms. UVA radiation is considered less harmful because it has less energy. It is also thought to play an important role in activating a range of photoprotection and repair mechanisms; nevertheless, at high doses, it can have the same harmful effects as UVB light.

The damages ultraviolet radiation causes living organisms are many and diverse (see, for example, Roy 2000; Vincent and Neale 2000; Buma, Boelen and Jeffrey 2003; Banaszak 2003). UV radiation denatures cellular DNA (a molecule particularly sensitive to ultraviolet light, given its capacity to absorb radiation in this band), causing transcription and replication errors, and is thus capable of producing mutations. It also denatures other compounds, such as proteins and pigments, destroys the cell membrane, inhibits nutrient absorption in photosynthesising plankton, affects the mobility and navigation systems of aquatic organisms, inhibits photosynthesis and the growth of unicellular plankton organisms and causes cell death in phytoplankton. All these effects indicate that UV radiation may be a direct cause of plankton population losses (Llabrés and Agustí 2006). In addition to the direct harm it causes, UV radiation reacts strongly with organic matter dissolved in the ocean and with other chemical compounds—such as nitrates—that are common in polar

waters, forming so-called reactive oxygen species (ROS), like the hydroxyl radical (OH^\cdot) and hydrogen peroxide (H_2O_2). Such substances are highly reactive and toxic to living organisms since they react with biomolecules (proteins, lipids, DNA, etc.), modifying or destroying them. ROS form in water and even inside the cells of organisms. UV radiation may also increase the toxicity of certain compounds. This is the case with some persistent polluting substances like aromatic polycyclic hydrocarbons, petroleum-derived compounds whose toxicity increases after exposure to UV radiation, in a process known as phototoxicity or photoactivation (Banaszak 2003).

Higher organisms have a greater capacity to generate protective structures against the damage caused by exposure to UV radiation, but this does not shield them completely from its harmful effects. Many marine invertebrates with shells and hard, highly protective exostructures lack such defences in the egg and larval stages, when they are as vulnerable to UV radiation as the larvae of aquatic vertebrates. UV radiation damage has also been documented in some aquatic vertebrates. For example, the eyes of some fish have developed cataracts due to exposure, and sunburn of the skin is common in fish living in high-altitude water bodies or confined in fish farm cages, since both are more exposed to UV rays. Although these burns are not lethal in themselves, they enormously increase the likelihood of the fish succumbing to infections, so may cause their death by indirect means (see, for example, Zagarese and Williamson 2000; Leech and Johnsen 2003).

Although currently exacerbated by diminishing ozone levels, exposure to certain levels of UV radiation has been a natural occurrence for the Earth's inhabitants since life first began. Millions of years of evolution have enabled species to develop mechanisms to minimise the harmful effects of UV radiation that are efficient for certain levels of radiation and exposure.

1.4.1. Avoiding exposure to UV radiation: plankton migrations

Only the surface layer of the oceans receives radiation, and this photic layer extends down to a maximum depth of 200 m in the planet's most transparent waters. The dark area of the ocean encompasses thousands of metres and provides a safe haven for organisms against UV radiation. Hence, one of the protection mechanisms available to aquatic species is directly to avoid exposure to UV radiation (see, for example, Leech and Johnsen 2003). Migrations through the water column and similar light-responsive behaviours are common in aquatic organisms. Zooplankton, for instance, migrate during the day to the

dark region of the water column and only rise at night to feed in the surface layer, where photosynthetic plankton live. These daily migrations up and down the water column are so widespread that they have spawned new variants of predatory behaviour. Many aquatic species are equipped with sensors to detect light and ultraviolet radiation and react with negative or positive phototactic behaviour; some even have what is known as UV vision. And numerous organisms, fish amongst them, have vision within the UVA or UVB wavelength band, which is useful for navigation and communication and for identifying prey, especially those enriched by substances that protect against UV radiation, which are absorbed in large quantities in these bands. UV vision undoubtedly also helps to identify and avoid the depths to which the harmful wavelengths of UV light penetrate (Leech and Johnsen 2003).

1.4.2. Protection and repair systems

Not all aquatic organisms have the mobility or capacity to choose their position in the water column. A case in point are the photosynthetic plankton. These organisms (photo 1.4) have to absorb the light in the visible range to photosynthesise, and are forced to remain in the layer of the ocean lit by solar radiation and exposed to the UV spectrum. Their only defence is to develop protection mechanisms and, after years and years of evolution, these have become as many as they are varied (see, for example, Roy 2000; Banaszak 2003).

1.4.2.1. PROTECTIVE CELLULAR STRUCTURES OR “PARASOLS”

These are physical protection mechanisms involving the production of structures that act as barriers to prevent ultraviolet radiation from penetrating. One example is the mucus secreted by microalgae like *Phaeocystis pouchetii*, whose primary function is to bring cells together into colonies, but which also serves to reflect and prevent the penetration of UV radiation (Banaszak 2003). Other such structures are based on the creation of special cell walls or the formation of crystals on the outside of the cell. And certain variations in the shape or arrangement of the crystals making up the cell wall may also be useful for reflecting UV radiation. For instance, it has recently been found that holococcoliths (planktonic microalgae) have crystalline structures in their calcite sheaths that efficiently reflect UV radiation (Quintero-Torres et al. 2006), preventing it from entering the cell.

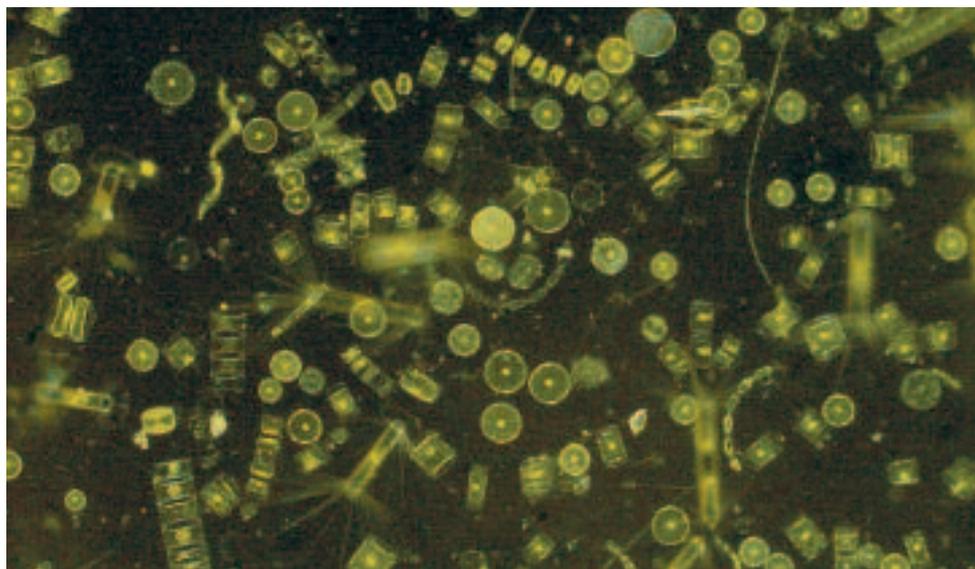


Photo 1.4: A sample of Antarctic phytoplankton dominated by a diversity of diatomea species, viewed under a phase-contrast microscope (x100)

1.4.2.2. “SUN FILTER” PRODUCTION

This is one of the most important protection mechanisms. It is based on the production by phytoplankton cells of chemical substances that absorb ultraviolet radiation to protect the cells from its harmful effects (Roy 2000; Banaszak 2003). Among the most important sun filters is mycosporine, a substance with a strong solar protective function that is secreted by fungi, and the mycosporine-like aminoacids (MAAs), sun filters produced by other organisms. These aminoacids are hydrosoluble and have a maximum absorption capacity at 320 nm, i.e., between the UVA and UVB bands, although different types can be synthesised with the ability to absorb light in the 309-360 nm range. Only bacteria, fungi and algae have the capacity to synthesise these compounds, but they can be passed onto and accumulate within other organisms that feed on planktonic algae. These predators benefit from their function as a solar filter and also transmit them along the food chain.

Other pigments also act as sun filters, including scytonemin, which is secreted by cyanobacteria growing on the polar ice sheet. This substance sticks to the surface of cells, forming a mucus film that acts as a powerful solar filter. Melanin-type pigments too provide protection from UV radiation and, although not synthesised by algae, they are synthesised by other zooplankton organisms, as has been described in the cladocerans of the Arctic Ocean.

Many of these sun-filtering substances have been copied by industry for a range of applications.

1.4.2.3. ANTIOXIDANTS

An indirect effect of ultraviolet radiation is the toxicity of the ROS formed by the action of UV radiation on the molecules of organic substances, or on the oxygen present in the water or the cells themselves. These toxic photoproducts may be more harmful to cells than UV radiation itself. Toxic photoproducts are neutralised by certain antioxidants (Roy 2000; Banaszak 2003), including substances like ascorbate, cleaning enzymes and carotenoids, which act as oxidant traps by combining with and neutralising the free radicals of the ROS. The quantities of antioxidants in a given organism are directly related to its exposure to UV radiation, and their concentration increases with the dose of UV radiation received.

Carotenoids are pigments that can only be synthesised by photosynthetic organisms, such as photosynthetic plankton, but can accumulate in species that feed on phytoplankton. Thus, some copepods (small crustaceans that make up part of the zooplankton) may be transparent or red, in the latter case if they have accumulated carotenoids as part of their diet. And these red copepods are more resistant to UV radiation than their paler fellows. The algae that grow on ice and snow give them a characteristic reddish hue, caused by the large amounts of carotenoid pigments they contain to shield themselves from the strong solar radiation reflected off these surfaces.

1.4.2.4. REPAIR SYSTEMS

Photoprotection systems are not infallible, nor can all the harmful effects of UV radiation be avoided. Living organisms have accordingly evolved systems to repair the cell damage caused by ultraviolet radiation (see, for example, Vincent and Neale 2000; Buma, Boelen and Jeffrey 2003; Banaszak 2003). Protein repair systems are triggered when cells are exposed to ultraviolet light. It is also thought that accelerating protein renewal is a way to replace damaged proteins with new versions. But the main systems in use are those of DNA repair (see, for example, Vincent and Neale 2000; Buma, Boelen and Jeffrey 2003), given this molecule's vital importance for cell function. UV radiation-induced DNA damage consists mainly of the chemical alteration of its bases. One of the most common changes occurs through the dimerization of adjacent pyrimidine

bases, producing photoproducts known as cyclobutane pyrimidine dimers (CPDs) which account for between 50% and 80% of all photoproducts induced by the exposure of DNA to UV radiation. CPDs are not mutagenic but they do inhibit replication. Repair systems are of two main kinds: photoreactivation, which involves stimulation by blue light and UVA, and dark repair, which is a light-independent mechanism. Both systems require the organism to synthesise enzymes that can act on the damaged area. Photolyase, for instance, identifies CPDs and uses light energy to repair damaged bases. Dark repair systems require the synthesis of a series of replication enzymes that act on the damaged area to identify them, cut the chain, synthesise the correct sequence and insert it at the appropriate location after excising the damaged sequence. All eukaryote and prokaryote cells are equipped with these repair systems, which have evolved over time to occupy a key place in mammal biology: for example, it has been calculated that the DNA of a human cell experiences about 500,000 lesions a day, almost all of them repairable by these systems.

1.5. IMPACT OF INCREASING UV RADIATION ON THE POLAR OCEANS

The impact of increasing UV radiation on the polar oceans depends on the dose received and the relative effectiveness of protection and repair systems. These are not common to all organisms; rather, distinct species display different sensitivities to UV radiation depending on the efficacy of the systems they employ. Furthermore, the use of these systems exacts an energetic and nutritional cost.

As a consequence, ultraviolet radiation has a considerable impact on the polar oceans, especially the Southern Ocean, which is prone to receive a larger amount of radiation. This impact has been demonstrated in a range of studies.

UV radiation inhibits photosynthesis and, therefore, the production of photosynthetic plankton. In 1992, Smith et al. calculated that increased UV radiation on the Antarctic waters was responsible for a 6-12% reduction in primary production. Given that primary production forms the base of the food chain, a reduction of this magnitude may have consequences for total production in Antarctica. Since the publication of this study, the ozone concentration has continued to decline (by 2006, the ozone hole was 25% larger than in the early 1990s), suggesting that its 1992 estimates need to be urgently revised.

The impact of UV radiation on Antarctic plankton has also been detected from the presence of CPDs in the DNA of natural samples of planktonic compounds

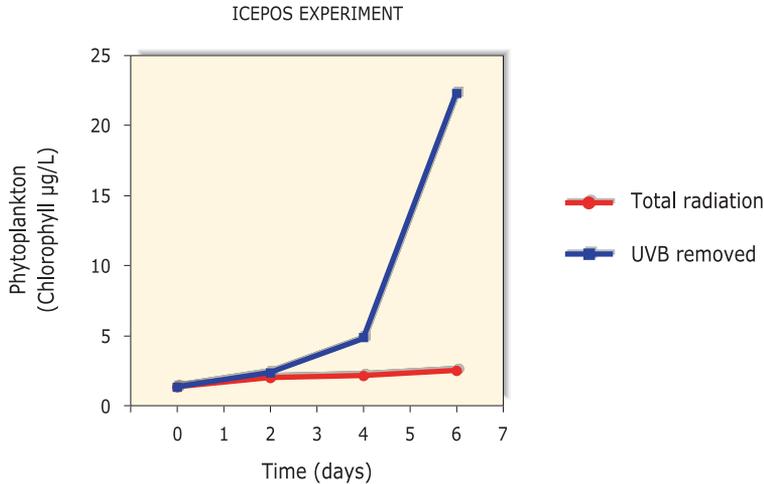
even at depths below 20 m. CPD accumulation has been found in certain algae growing under the sea ice (Buma, Boelen and Jeffrey 2003), and it has been confirmed that DNA damage is present throughout the Antarctic summer in both phytoplankton and bacterioplankton (Buma, De Boer and Boelen 2001).

This suggests that UV radiation has a control function for the development of phytoplankton populations. We recently confirmed this in experiments conducted with Antarctic phytoplankton during the Spanish ICEPOS mission at the Spanish Antarctic Base Juan Carlos I on Livingston Island (South Shetland archipelago in the Antarctic Ocean) during the southern summer of 2003–2004. The experiments consisted simply of incubating surface seawater samples taken from South Bay near the Spanish Base. The samples contained natural plankton populations and were incubated in 2-litre bottles hermetically sealed and submerged in large tanks. Water from the bay was circulated through the tanks to maintain a similar water temperature, and the tanks were exposed to natural solar radiation, to keep the plankton exposed to similar natural conditions to those of plankton growing in the surface waters of South Bay. The incubating bottles were made of different materials of varying transparency to solar radiation. Quartz bottles, which are transparent to all visible and ultraviolet light spectra, let in all the solar radiation the plankton naturally receive in their underwater habitat, while polycarbonate plastic bottles are opaque to UVB radiation, thus simulating an environment from which the B band of the UV spectrum has been eliminated. The results show that ultraviolet light strongly controls the abundance of plankton (figure 1.3). Plankton populations incubated in the quartz bottles did not exhibit any significant changes in abundance, but plankton growing in the polycarbonate bottles, which filtered out all the UVB radiation, showed a more than 15-fold increase in abundance in only 6 days (figure 1.3). These experiments demonstrate that UVB radiation exerts a significant control over the abundance of Antarctic photosynthetic plankton, and that this radiation impedes generation of the biomass volume that might otherwise be expected from the high nutrient concentrations in Antarctic waters.

Another important impact of increased UV radiation has to do with species diversity, since a continuing increase will inhibit development of the less vs. more resistant species. This, in turn, could have consequences for the food chain, impairing the efficiency of matter transfer to predators or even altering the make-up of species occupying other trophic strata (Keller et al. 1997).

Ultraviolet light also affects the macroalgae; organisms vital for coastal ecosystems and that dominate primary production on the seabed of the Arctic and Southern Oceans. As with the phytoplankton, a variety of impacts have been detected in

Figure 1.3: Result of experiments to determine the impact of ultraviolet radiation on the phytoplankton populations of South Bay, Livingston Island; an island forming part of the South Shetland archipelago (Antarctica)



The plankton collected and exposed to the natural full spectrum of solar radiation—including visible and ultraviolet light—did not increase in abundance, as measured by changes in chlorophyll concentration, which remained within the usual range of values observed in the Bay. However, when UVB radiation was eliminated with special filters (blue line), the abundance of plankton augmented (in this assay, by over 15 times in just 6 days). These experiments were carried out at the Spanish Antarctic Base Juan Carlos I as part of the work of the ICEPOS Spanish Antarctic Project, led by Carlos M. Duarte.

Source: Data provided by M. Llabrés and S. Agustí.

polar macroalgae populations, including the inhibition of photosynthesis and damage to DNA (see, for example, Bischof, Hanelt and Wiencke 2002). Nevertheless, they are far better equipped than phytoplankton to protect themselves from and adapt to an environment with higher UVB radiation. There is evidence that some macroalgae, despite suffering initial damage, manage to adapt efficiently to the new conditions by, for instance, increasing their production of solar filter substances such as mycosporine-like aminoacids (MAAs) (Bischof, Hanelt and Wiencke 2002). However, we still lack data quantifying the impact of increased UVB radiation on the biomass production of these polar organisms. Laboratory experiments have shown that ultraviolet radiation limits macroalgae growth and their capacity to increase their biomass, but no similar experiments have been conducted on polar populations under natural conditions. For this reason, it remains difficult to assess the impact of UV radiation on the growth and biomass production of this group of primary producers (Bischof, Hanelt and Wiencke 2002).

Non-photosynthetic organisms also experience the effects of ultraviolet light. Marine bacteria, which play an important role in the use and regeneration of



Photo 1.5: Adélie penguins (*Pygoscelis adeliae*). All living organisms inhabiting the polar regions will need to strengthen their defence systems to counter the negative effects of the higher ultraviolet radiation caused by ozone layer depletion.

organic matter processes, have been shown to suffer mortality in Antarctica when subjected to UVB radiation (Helbling et al. 1995). Nor are the deleterious effects of UV radiation confined to microorganisms: higher organisms inhabiting the polar oceans also suffer from UV radiation. Vertebrates and invertebrates like fish and crustaceans that in adulthood are well equipped to avoid and resist the damaging effects of UV light are nevertheless extremely sensitive to it during their egg and larval stages. Several studies have confirmed this sensitivity of fish and crustacean eggs and larvae in both Antarctica and the Arctic Ocean. In the waters north of the Arctic Circle, which are very productive and rich in fish species, the presence of CPDs has been detected in Norwegian and Canadian cod eggs and larvae (Browman and Vetter 2002). Experiments have also shown the capacity of UVB rays to induce significant mortality in Arctic cod eggs and larvae, with all eggs dying after four days' exposure to natural UVB radiation levels in northern Norwegian waters (latitude 70° north), and all larvae dying after six days of exposure. In experiments in which UVB radiation was filtered out from the natural solar radiation, there was no increase in the natural mortality rate of either eggs or larvae (Browman and Vetter 2002). DNA damage meas-

ured by CPD detection has also been found in icefish eggs in Antarctica and in the larvae of other organisms such as krill (Malloy et al. 1997). The degree of damage sustained by the eggs of these species is correlated with the incident UVB radiation (Malloy et al. 1997). Although the level of stress induced in krill by this exposure is not known, the increase in UVB radiation has been identified as a possible causal factor in the reduction of the yearly recruitment of new individuals to fish and plankton populations in Antarctica (Malloy et al. 1997). In other words, polar productivity is threatened not only by a reduction in the production of planktonic microalgae, but also by the direct effects of UV radiation on consumers at different trophic levels in the ocean. The impact of increased UV radiation on the polar oceans in the current context of global warming will give it a dominant role in the control of biological production, organism stress and the overall dynamics of polar ecosystems.

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LIST OF PHOTOGRAPHS

Photo 1.1: Icebergs and rainbow. © Juan Carlos Muñoz	24
Photo 1.2: Icebergs in Antarctica. © Juan Carlos Muñoz	27
Photo 1.3: Ice masses drifting in open waters. © Jordi Bas	30
Photo 1.4: A sample of Antarctic phytoplankton dominated by a diversity of diatomea species, viewed under a phase-contrast microscope (x100)	37
Photo 1.5: Adélie penguins (<i>Pygoscelis adeliae</i>). © Juan Carlos Muñoz	42

LIST OF ILLUSTRATIONS

Map 1.1: Distribution of ozone concentrations over Antarctica in the month of October from 1979 to 1997	28
Figure 1.1: Changes in the size of the ozone hole over Antarctica from 1979, when it did not exist, up to the present day	31
Figure 1.2: Penetration depth (in metres) of solar radiation in two areas of the Southern Ocean, measured during the ICEPOS-2005 Spanish oceanographic expedition	33
Figure 1.3: Result of experiments to determine the impact of ultraviolet radiation on the phytoplankton populations of South Bay, Livingston Island; an island forming part of the South Shetland archipelago (Antarctica)	41

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