CHAPTER 15

EFFECTS OF ULTRAVIOLET RADIATION ON THE PELAGIC ANTARCTIC ECOSYSTEM

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ABSTRACT

Ultraviolet radiation (UVR) affects biotic and abiotic factors in marine ecosystems. Effects on organisms are mostly deleterious due to damage to DNA and cellular proteins that are involved in biochemical processes and which ultimately affect growth and reproduction. Differential sensitivity among microalgal species to UVR has been shown to shift community composition. As a result of this shift, the total primary production for the community may be maintained at pre-UVR levels. Similar impacts and mechanisms are expected in Antarctic waters. The overall effect of UVR on the ecosystem needs to include relevant feedback mechanisms which can diminish, and sometimes reverse, deleterious effects on population growth. For example, it has been speculated that UVR can increase iron-limited phytoplankton populations by photoinduced reduction of Fe^{3+} to Fe^{2+}, a more soluble form of iron and readily available for algal and bacterial uptake. An equally positive feedback can be attributed to diminished grazing by zooplankton. Thus, energy flow among the trophic levels can decrease as a result of damage to a certain trophic level, but overall biomass and ecosystem production might remain relatively unchanged.

Similar positive and negative feedbacks associated with UVR are related to the dissolved organic matter (DOM) pool, known to be recycled by bacterial activity. Although it could be expected that bacterial production in Antarctic surface waters would decrease when exposed to UVR, this effect can be counteracted by increased substrate nutrient availability. Photolysis of high-molecular weight molecules by UVR produces

The Effects of Ozone Depletion on Aquatic Ecosystems, edited by Donat-P. Häder.
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higher availability of low-molecular weight molecules readily taken up by bacteria. This step might be of greater importance in high latitude ecosystems where low bacterial production has been attributed to low substrate availability.

Similarly, increased nutrients for bacterial activity originate from photolysis of high-molecular weight molecules which are known to release NH_4^+ and amino acids under UVR. The DOM pool might also increase through phytoplankton excretion of organic matter, a process known to occur under algal stress. On the other hand, a decrease in DOM by diffusion from zooplankton fecal pellets is expected in surface waters due to decreased grazing.

In summary, we argue that the understanding of the effect of UVR on Antarctic ecosystems is more than the sum of the effect of radiation on individual species, given that alteration of interspecific interactions can exacerbate, diminish and sometimes reverse known physiological damage. This, plus complex and nonlinear feedback mechanisms associated with UVR effects make prediction at the ecosystem level uncertain.

INTRODUCTION

A recent characteristic phenomenon of the Antarctic ecosystem is the well-known springtime decrease in stratospheric ozone, known as the ozone hole. It is confined to the polar vortex over the Antarctic continent, from September to December of each year. However, once the winter/spring vortex breaks down, its effects reach mid latitudes, mostly during the month of December,[1] although it has also been detected in sub-antarctic environments during the spring.[2] There has been significant annual and interannual variability in Antarctic ozone, and, consequently, in changes in ozone-related incident ultraviolet radiation (UVR). During the last two decades major international efforts have focused on the physics and chemistry of the Earth's atmosphere with emphasis on understanding processes that control the ozone layer, while studies on the effects of UV on the biosphere, in particular at the community and ecosystem level, have been relatively limited.[3]

Interest in UV effects on aquatic ecosystems is increasing because ozone depletion is not restricted to the area over Antarctica and significant reductions have been reported in the Northern Hemisphere.[4-6] Hemispherical trends are superimposed on high interannual variability, as pointed out by Michaels et al,[7] where low ozone during 1992 can be associated with a drop in sunspots, a strong El Niño event and the eruption of Mount Pinatubo, all of which can potentially decrease ozone in the stratosphere. Other populated areas, such as South America, Australia, New Zealand and South Africa are affected, in particular at the time of the vortex disappearance, probably as an effect of dilution.[1,4]

It has been estimated that aquatic ecosystems fix between 30 and 50 Gt of carbon per year, which is roughly half the total global fixation of carbon.[8-10] Consequently, the threat of increased UVR on surface layers of the ocean on marine productivity is of considerable concern. Estimates for the Southern Ocean range from 1-5 Gt C y^{-1}.[11] For the Southern Ocean, ice algae are estimated to contribute up to 30% of the total primary production.[12] Traditionally, prediction of UV effects on ecosystems have assumed a linear addition of UV effects on different levels of the food chain where the final effect on higher trophic level predators, such as penguins, whales and seals, have been inferred from the cumulative effect on primary producers and grazers.[13] In other words, the total effect of UV at a given trophic level has been assumed to be the combination of UV effects on the previous trophic level added to the direct effect of UV on the level itself. For example, initial studies on UV effects on marine algal communities reported decreased total primary productivity and shifts between species towards less UV-B-sensitive species as well as a drop in total species diversity, assuming constant

grazing.[14-17] In contrast, recent trophic-level assessments suggest that differential UV sensitivity between algae and herbivores may contribute to an increase in algae by exerting a stronger UV influence on the grazers.[18,19] An analogous influence on zooplankton, thus reducing zooplankton grazing, could counteract UV photoinhibition on phytoplankton growth. In addition to biological factors, UVR affects abiotic processes which affect directly or indirectly the food web. These factors are either chemical (e.g. nutrients) or related to the dissolved organic matter (DOM) pool which is intrinsically related to the microbial loop.[20] Such an alteration of the ecosystem functioning would result in a decrease of transfer of energy through the food web.[21]

In this chapter we summarize what is known of the UVR effects on different levels of the Antarctic food web, with emphasis on the relationships between trophic species, and what is known of the UV effects on abiotic processes affecting the food web. Several recent reviews on UVR effects on aquatic and Antarctic ecosystem[13,22] have given excellent summary of the UV photobiology and that information will not be rephrased here. We present evidence to suggest that research required for understanding UV effects on Antarctic ecosystems will necessitate ecosystem studies in addition to detailed determination of UVR on specific processes related to any given trophic level.

UV RADIATION IN THE SOUTHERN OCEAN

Estimation of quantitative effects of ultraviolet radiation (UVR) on biological systems requires knowledge of the incident spectral irradiance and a biological weighting function (BWF), which provides the wavelength-dependency of biological action. Because BWFs are heavily weighted in the UV-B region of the spectrum, high spectral resolution is required for accurate estimation of effective biological doses. Smith et al[23] have developed a high spectral resolution (1 nm) air and in-water spectroradiometer and Booth et al[24] have developed the U.S. National Science Foundation UV Network which provides high resolution data at three locations in the Antarctic continent. Alternatively, narrow band instruments (e.g. Bio-Spherical Instrument PUV series) can, in conjunction with an adequate full spectral model, be used to estimate incident spectral irradiance with adequate resolution. BWFs, specific to the target unit, have been developed. For Antarctica, stepwise functions for the BWF for photosynthesis have been developed by Helbling et al,[25] Lubin et al,[26] Smith et al[23] and Boucher et al[27] which have yielded results similar to the more detailed determination of Cullen et al.[28] Other BWFs have been developed in temperate areas for plant chloroplasts[29] and DNA.[30] There is a paucity of BWFs for other processes, for other levels of the food chain, not only for Antarctica but everywhere. This is a serious constraint for modeling and predictive purposes.

Actinometry (e.g. refs. 31, 32) has not been used extensively in Antarctic studies. On the other hand, a biological dosimeter, based on the response of an organism to UVR, has been used. This method provides a relative unit to assess potential effects of UV exposure on a specific organism or target molecule. Once the response of the organism to UV is evaluated under standard conditions, i.e. by exposure to natural UV radiation, we can say the organism has been calibrated. A relative estimate of potential UV damage can then be estimated. The potential benefit of the biological dosimeter resides in being a relatively more easy and inexpensive method, once it has been carefully evaluated. The main disadvantage is the exacting dosimetry required for quantitative calibration. It can also be used to compare biological effects on very diverse environments with or without very different UV climatology. Although a biological dosimeter was carefully evaluated for an Antarctic coastal site it has not been used extensively use in the

region.[33] Both the actinometry and the biological dosimeter give broad band estimates of UVR unless the incident radiation is differentially screened, usually with filters.[33]

Climatology of UV Radiation

Ultraviolet radiation (UVR) levels are mostly controlled by atmospheric ozone, cloud cover, and solar zenith angle with ozone concentration being relatively specific to the UV-B region.[34] Natural variability in these environmental variables give rise to a very high natural variability in UVR, with ozone primarily affecting the relative ratios of UV-B to UVR, photosynthetic available radiation (PAR), or total irradiance. The dynamic nature of the polar vortex containing the ozone hole has given rise to large changes in these UV-B ratios on time scales of several days or less (Fig. 15.1). The polar vortex, and correspondingly, the ozone hole, is often elongated in shape, giving rise to an uneven distribution of UV-B at locations within the Antarctic continent.[35] The natural-short term variability (hours to days) due to changes in cloud cover and solar zenith angle compounds the difficulty in assessing the influence of increased UV-B levels on natural systems.[23,36] The resultant effect is that natural variability (cloudiness) can counteract UVR increases. Further, recent work (Gautier et al, University of California Santa Barbara, U.S., personal communication) suggests that the combined influence of cloud cover and surface reflectance influences these UV-B ratios. As not much is known with respect to the effect of this variability on organisms and processes, it is too soon to predict the effect of this variability either to enhance or decrease UV effects on Antarctic ecosystems.

Transmission of UV in Surface Waters and Ice

Transmission of UVR within the water column is a key element in assessing UV effects in marine systems. Light transmission is affected by water itself, as well as particulate and dissolved organic matter (POM and DOM, respectively) within the water column. Water is known to be a relatively strong UV absorber[37-39] and spectral attenuation coefficients have been published for clear natural waters.[38] However, in natural waters, particulate and dissolved organic matter strongly absorb UVR and these in-water constituents are highly variable. In blue, more transparent oligotrophic waters, biologically significant UV doses can penetrate several tens of meters. In contrast, more productive coastal waters,

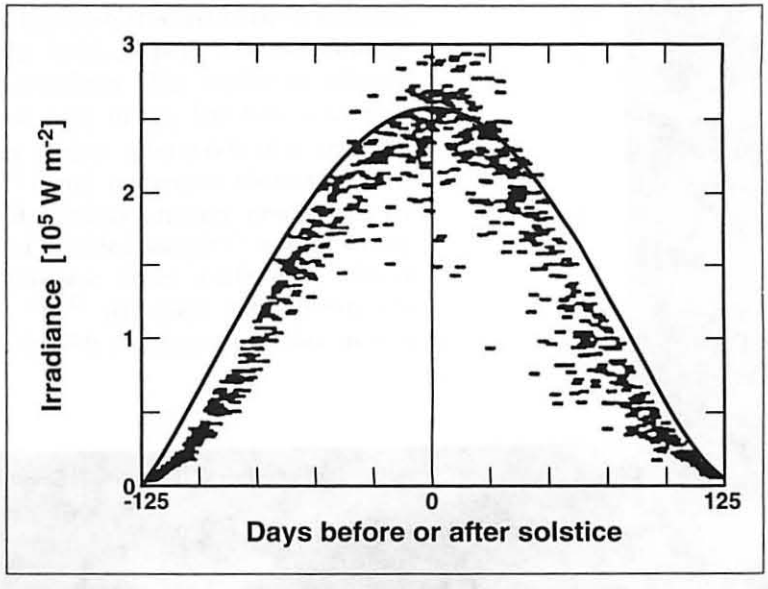

Fig. 15.1. Daily maximum UV-A irradiances (360-400 nm) from 15 December 1989 to 7 February 1993 at McMurdo Station (77.51°S, 166.40°E) shown as a function of days before and after solstice. Redrawn from Booth et al, 1994.

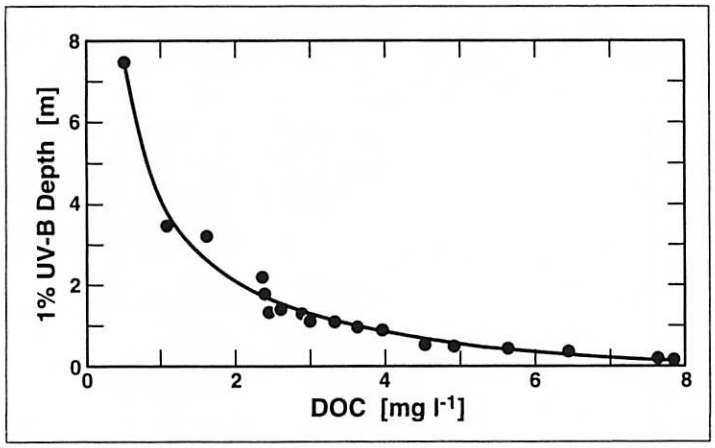

Fig. 15.2. Relationship between the depth of 1% UV incident radiation and dissolved organic carbon (DOC) in lakes. Reprinted with permission from Schindler et al, Nature 1996; 379:706, ©1996 MacMillan Magazines Limited.

with higher particle concentration (e.g. >3 mg chlorophyll *a* m^{-3}) can have attenuation coefficients nearly an order of magnitude higher, limiting significant penetration depths to the order of meters.[40] DOM shows an even stronger attenuation in the UVR[40,41] and can effectively limit significant penetration depths to a meter or less. For example, Kramer[42] estimated that the combination of high POM and DOM in Dutch coastal waters would limit UVR transmission in the water column to such an extent that no UV effects or planktonic organisms were expected. High POM absorption in Antarctic waters[43] and probably in ice-edge blooms,[44] would limit UV transmission in late spring and summer due to high production, but not during early spring (e.g. October) where chlorophyll (chl) *a* levels are usually lower than 0.5 mg m^{-3}.[45] The paucity of absorption estimates for POM, and in particular for DOM, make it difficult to speculate on their effect in Antarctic waters, although similar levels of DOM as in other parts of the world would support the hypothesis of important UVR absorption by DOM (Fig. 15.2).[46] Estimated UV effects at depths of about 20 m in the vicinity of Palmer might be due in part to the contribution of DOM absorption.[33,47]

The role of DOC in light attenuation is intimately related to other environmental changes. For example, in boreal lakes, the decreased amount of DOC, caused by an increase in average temperature and acidification in the last 20 years, was related to increased UVR in the water column.[48] In the case of Antarctic waters, a complex mix of competing feedback mechanisms make estimating changes in UVR, due to environmental change, speculative.

There are relatively few direct observations on the optical properties of Antarctic ice and snow. These observations suggest that UV transmission in the ice is maximum in October due to relatively high transparency in spring. Based on these observations, it is expected that ice algae, associated with bottom communities in ice flows, potentially can be exposed to relatively high levels of UV-B. These UV-B levels have increased by as much as an order of magnitude under the ozone hole.[49]

THE FOOD WEB

PHYTOPLANKTON

Photosynthesis

Deleterious effect of UV-B on photosynthesis has been studied both in cultures and in the field, in particular for Antarctic phytoplankton. The reader is referred to reviews done in the last few years that cover this subject extensively (e.g. refs. 22, 36, 50, 51 and references therein). Overall, UV-B inhibits primary production by 30-50% of shielded samples[52] with a strong depth gradient from surface to about 20-50 m.[23,33,53] All these experiments are based on 6-24 h incubations, either in situ

or in incubators exposed to sunlight. On the average for the water column, primary production decreases by 6-12%[25,24] during springtime ozone depletion over Antarctic water resulting in a 2% reduction in the yearly primary production estimates for the marginal ice zone.[25]Helbling et al[54] based on different assumptions and methodology, estimate the decrease in primary production to be 0.15% for the entire ice-free waters south of the Polar Front. A UV inhibition function for photosynthesis has been described by Cullen and Neale.[55] The biological weighting function for Antarctic phytoplankton, necessary to scale UVR to biological effective irradiance, has been determined for natural populations by Lubin et al,[26] Helbling et al,[24] Smith et al,[23] Boucher et al[27] and Neale et al.[56]

Nutrient uptake

Very little is known of the effect of UVR on nutrient uptake in Antarctic phytoplankton. Studies on temperate species suggest that nitrogenase, the enzyme related to nitrogen assimilation in phytoplankton, is activated by PAR[57] and inactivated by UV-B radiation.[58] In contrast, ammonium uptake seems less affected.[59,60] Overall, amino acid concentration in the cell decreased under UV-B.[61] The effect is also felt on enzymes related to amino acid metabolism. UVR diminishes synthesis and intracellular accumulation of alanine and valine[62] while synthesis and accumulation of glutamic acid increase due to inhibition of glutamate synthase[58] or glutamate dehydrogenase.[60] These results are similar to metabolic changes observed in phytoplankton under nitrogen stress, suggesting that UV-B suppresses nitrogen assimilation into cells.[63] Decreased NH_4^+ uptake by *Pavlova* spp. under UV-B and high intensity UV-A was interpreted as reduced supply of ATP and NADPH from direct effects of UV-B on the photosynthetic apparatus and pigment bleaching.[60] Similar effects of UVR on Antarctic species will have to be assumed until experiments are carried out for Antarctic, or at least, polar phytoplankton.

Exudation

The amount of extracellular carbon produced by phytoplankton has been a controversial subject for several decades.[64,65] Excretion of carbon by photosynthetic organisms is a widespread process associated with photosynthesis.[66] On the average, phytoplankton excretes 5-25% of the carbon incorporated in particulate matter, both in monospecific cultures and in natural populations[65,68] and the amount excreted is a constant proportion of photosynthetic rates. Several studies have pointed out that a large proportion of photosynthetic carbon goes through a DOC phase[69] for at least short periods of time.[70] Under these conditions, between 20-60% of photosynthate must go into the DOC pool to explain the DOC changes observed,[70] mainly during spring bloom events in temperate waters. Additional organic carbon excretion in phytoplankton seems associated with physiological imbalance due to events such as nitrogen limitation,[71-73] in particular under high-light conditions.[73] In the field, the transfer of cells to higher irradiance might produce excess photosynthate.[67,68] Nutrient limitation is observed during late growth stages in batch cultures[74] or at the end of the spring bloom. High DOC concentrations have also been observed after a *Phaeocystis* sp. bloom.[75,76] This excess carbon excreted might be associated with increased intracellular carbohydrate, as in diatoms[74,77] but not observed in dinoflagellates.[72]

Very little is known of exudation by Antarctic phytoplankton and the consequent implication for the DOC pool. Recent results in the Arctic suggest a large amount of extracellular carbon observed seemed to be related to phytoplankton composition (i.e. cells which produce mucilage for colonial formation) and to a lesser extent to in situ nitrate limitation.[78] In Arctic Water, *Chaetoceros socialis* allocated 40% of total carbon incorporated as extracellular under conditions of low silicic acid (<0.2 µM) and measurable nitrate concentrations (0.5-2.5 µM). Similar extracellular carbon production was found in a mixture

of *C. socialis* and *P. pouchetii* at the Polar Front and the marginal ice zone with higher nutrient concentrations (5-10 µM nitrate).

These results suggest that species composition and their physiological state may largely control extracellular carbon production in the field.[79] Although low nitrate is known to increase exudation,[74] this effect is not expected in Antarctic open waters; however, this effect might be observed during or after massive coastal blooms.[45,80]

In spite of the obvious importance of phytoplankton exudation on the carbon cycle and as substrate for the microbial loop, no studies have been carried out on the effect of UV-B on exudation, for either temperate or polar phytoplankton. In general, exudation increases when algae are stressed and it can be speculated that UV-B stress would act in a similar way.

Respiration

Changes in $\delta^{13}C$ in ΣCO_2 observed in the Bellinghausen Sea in the spring of 1990 combined with changes in cell abundance in the colonial prymnesiophyte *Phaeocystis* sp. suggest that under increased UV-B radiation, as measured under decreased ozone concentration, there is an increase in the ratio of total community respiration to photosynthesis.[81] Heterotrophic respiration increases were attributed to increased bacterial substrate due to cell lysis.

Growth

The effect of UV-B on marine phytoplankton growth has been shown to be species-specific. For several cultures of temperate species, specific growth rate was affected negatively by UV-B.[82-84] In the diatom *Phaeodactylum tricornutum*, no decrease in UVR sensitivity was observed with time.[82] Similar results were observed on 3D experiments on Antarctic phytoplankton dominated by *Corethron criophylum* where growth rates decreased by 100% on cells exposed to UV-A + UV-B + PAR and by 50% when exposed to UV-A + PAR, as compared to controls exposed to PAR only.[85] On the other hand, active growth of coastal species was observed for 12 days at Palmer Station where diatom cultures were kept at in situ solar radiation.[86] No difference was found also between treatments (UVR + PAR vs. PAR only) for the colonial prymnesiophyte *Phaeocystis* sp., although these cultures did not grow. This lack of effect was observed in spite of the well-documented inhibition of photosynthesis[23,26-28] for Antarctic phytoplankton in experiments from 2-24 h and points towards different controls of photosynthesis and growth and between short- vs. long-term effects of UV-B. It has been noted for some time that caution must be used when inferring longer term ecological consequences from short-term observations.[87]

Mixing of cells in the upper water column, in particular within the mixed layer, affects the average irradiance in which a cell is exposed during the day.[35,88,89] Several studies have speculated about the possible role of alleviation from UVR in Antarctic waters if cells are mixed deeper in the water column.[50,90,91] Experiments where UVR intensity was manipulated to resemble mixing in the upper water column showed increased production in cloudy days while the effect was opposite on sunny days.[51] Phytoplankton dominated by the diatom *Thalassiosira gravida* showed less photoinhibition when exposed to variable radiation,[92] supporting the hypothesis that mixing might provide UV-B protection.[36]

Cell size

Coastal waters have, on the average, a higher proportion of larger cells than open waters.[93] For example, more than 80% of the nearshore phytoplankton biomass was associated with cells >10 µm in Terre Adélie during summer while 70 km offshore, cells >10 µm represented only 30% of the total biomass and 59% of the cells were between 1-10 µm.[94] Within coastal waters, high Chl *a* accumulations (i.e. blooms) are dominated by large cells (e.g. >20 µm) while low Chl *a* concentrations are dominated by smaller cells.[80,95] A differential effect of UVR on cell size, as

observed for diatom cultures,[96] show higher damage on smaller cells, and we might speculate that oceanic phytoplankton may have a higher sensitivity to UV-B. In addition, UVR increases cell size[82] associated with a concomitant reduction in specific growth rates.

Species composition

Initial experiments with temperate phytoplankton, showing differential sensitivity to UV-B by different species,[17] suggest a change in species composition in long-term UV-B exposure with more UV-tolerant species ultimately dominating.[16] As mentioned above, there is a wide range of interspecific UV-B sensitivity on growth and survival, with smaller cells being more sensitive, due to a higher surface to volume ratio as a result of cell size and cell shape.[96] In addition to size, an increased UV-B sensitivity in flagellates, as compared with diatoms, was observed in natural populations of Antarctic phytoplankton.[54,97] This difference can be attributed in part to size (flagellates are on the average smaller than Antarctic diatoms) and to increased UV-absorbing properties of diatoms[97] related to the presence of mycosporine-like amino acids which are believed to reduce deleterious effects by UV-B on growth.[84] The predicted shift from less to more resistant species (e.g. from flagellates to diatoms) was observed in a 2-week experiment of natural Antarctic populations exposed to ambient UVR, although similar Chl *a* and particulate carbon accumulation were observed under UVR and UVR + PAR.[52] Under UVR the amount of UV absorbing compounds (e.g. mycosporine-like amino acids) increased as well. As a result of this shift in species composition, a decreased sensitivity of photosynthesis was observed in the phytoplankton exposed to UVR. The higher resistance by diatoms, as compared with flagellates (in particular the colonial prymnesiophyte, *Phaeocystis pouchetii*, ref. 81), seems to be related to a lower effect on photosynthesis as well as nitrate uptake.[59]

Few studies are available on effects of UVR at longer time scales. McMinn et al[98] documented no changes in diatom species composition in laminated sediments in Antarctic anoxic fjords for the last 20 years, coinciding with the decrease of ozone. However, as noted by Bothwell and coworkers[18] the limited data provided by McMinn et al[98] do not substantiate their implied lack of a UV-B effect.

Zooplankton

UV effects on zooplankton, under normal and decreased ozone conditions in temperate waters, affect zooplankton survival, reproduction and grazing.[99] It is not clear from these results if decreased grazing would result in a reversal of UV effects on phytoplankton, as observed for a chronomid/diatom interaction in temperate freshwater stream beds (Fig. 15.3). We can expect that a 50% mortality of a grazer would decrease grazing pressure and favor phytoplankton growth. The possibility of grazing reversing deleterious effects of UV on phytoplankton and the relative importance of grazing in controlling phytoplankton population growth in any given community is currently a matter of speculation. Under current UV irradiance, overall decrease in primary production by UV in the Antarctic euphotic zone is estimated at 6-23% of marginal ice zone production.[25,35] The overall result would depend on the effect of UVR on Antarctic grazers, averaged for the euphotic zone, and on time scales representative of phytoplankton accumulation at ambient temperature (days to weeks, if we assume a specific growth rate of 0.1-0.3 d^{-1}).[44]

Sedimentation

Potential changes in grazing pressure will affect sedimentation of particulate matter. In areas where organic matter sedimentation out of the euphotic zone is due to grazer (i.e. krill) fecal pellets,[100] we might expect a shift to cell sedimentation, assuming no change in primary production. Thus, the pulse of organic matter after a bloom could consist mainly of intact cells.

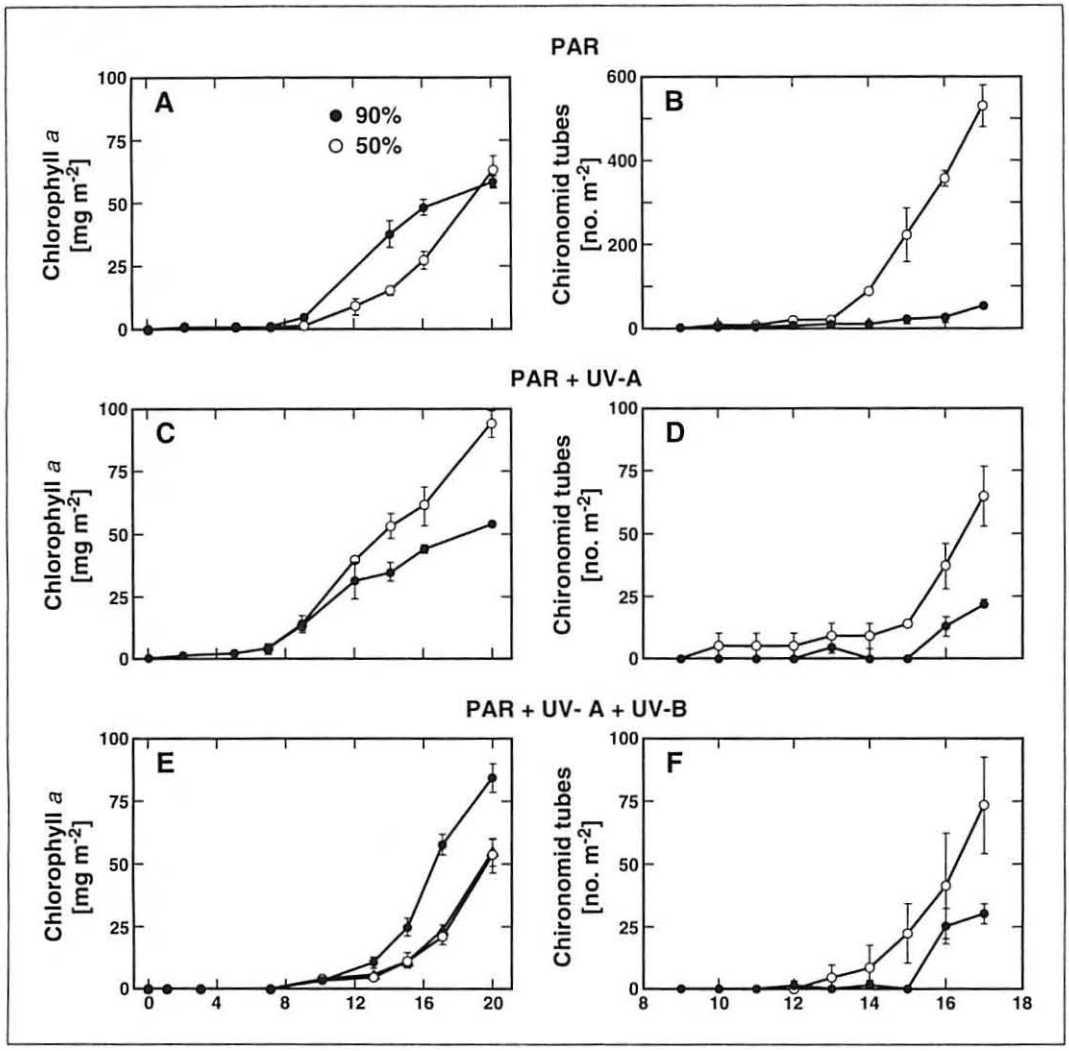

Fig. 15.3. Changes in phytoplankton (chlorophyll a concentration, left panels) and chironomid larval abundance (chironomid tubes, right panels) with time in streams. Experiments carried out at two irradiance levels (filled symbols, 90% of incident irradiance, and open circles, 50% of incident irradiance) at three treatments (PAR: top panels; PAR + UV-A: middle panels; and PAR + UV-A + UV-B: low panels). Reprinted with permission from Bothwell et al, Science 265:97-100. © 1994 American Association for the Advancement of Science.

This effect will be maximum in coastal areas where larger cells[94] and higher production are found.[45] Secondary effects will include alteration of elemental ratios, heterotrophic substrate and nutrient recycling below the euphotic zone. If, on the other hand, a large proportion of sedimenting matter is due to cell sinking then the quality of organic matter to depth would not be substantially altered.[101] The quantity and timing might be affected if, as discussed before, UVR would alter species composition and/or species size.

THE MICROBIAL LOOP

Bacteria

Bacterial biomass in Antarctic waters can reach 9% of the net plankton biomass in the top 50 m and increase with depth up to 50%, as measured in Bransfield Strait and Drake Passage in summer.[46] Different

from other parts of the ocean, there is no correlation between phytoplankton and bacterial biomass in Antarctic waters[94,102] and the reason for this difference is unclear.[103]

UVR reduces bacterial activity in temperate coastal waters in the top 5 m of the water column, with no indication of higher resistance in surface populations as opposed to those from depth.[104] Inhibition was observed at an irradiance equal to 0.7 W m^{-2}. UV-B was also found to photochemically degrade bacterial extracellular enzymes.[104] The combination of decreased bacterial activity and the degradation of extracellular enzymes reduces the flow of energy through the microbial loop. This effect is counteracted, or at least diminished, by the increase in bacterial substrate due to photodegradation of DOM. Increased bacterial activity at low UV-B irradiance with respect to dark uptake (Fig. 15.4) was attributed to this process.

Photo-oxidation of DOM

UV-B interaction with DOM is known to produce oxygen radicals and hydrogen peroxide (H_2O_2) which can be considered oxidative agents of biological membranes and have a negative impact on planktonic communities.[105] In addition, multiple studies have documented the photo-oxidation of DOM responsible for degrading high-molecular weight DOM into low-molecular weight DOM (e.g. Fig. 15.5)[105,106] which is readily available for bacterial consumption.[107,108]

The importance of the size class on bacterial productivity is still a matter of debate, as Amon and Benner[109] found that although bacterial growth efficiencies were higher at low-molecular weight DOM, total bacterial growth and respiration was higher at high-molecular weight DOM (>1000 daltons), resulting in a higher carbon based rate of utilization. It is too early to assess the degree to which UV photo-oxidation of DOM would be of importance in Antarctic surface waters. Given the debate on whether bacterial activity is depressed at low temperature,[110,111] and the potential role of substrate on polar bacterial metabolism,[112] the role of phytoplankton as providers of labile DOC and photo-oxidation of DOM by UVR are both critical to Antarctic ecosystems.

Photochemical production of dissolved amino acids from humic substances have been shown to increase bacterial production in temperate coastal waters.[113] UV-B was found to be the most active portion of the solar spectrum for this process which could be due both to higher energy and higher absorption by the target molecule. Although no or low humic acids are expected in Antarctica, Lara and Thomas[114] have identified recalcitrant DOM production by marine phytoplankton with

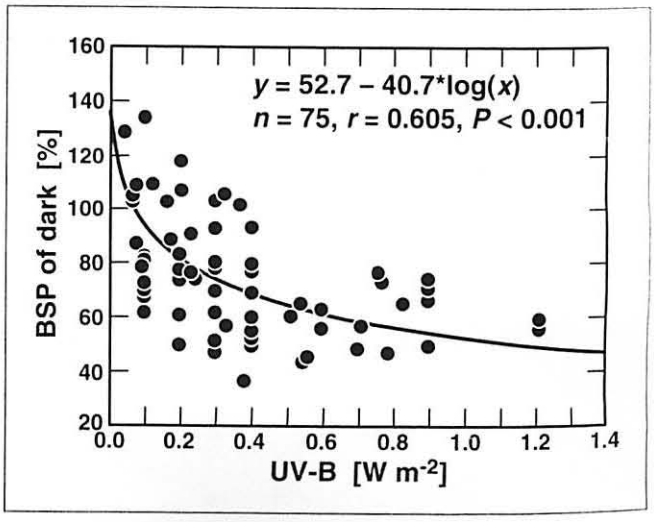

Fig. 15.4. Bacterial secondary production (BSP) as a function of UV-B radiation. Note higher production at low UV-B with respect to dark uptake. Redrawn from Herndl et al. Nature 361:717-719. Copyright, MacMillan Magazines Limited.

chemical characteristics previously associated only with humic substances. The source of this pool of DOM seem to be degradation of cellular membranes and can be assumed to be produced anywhere in the ocean.

NUTRIENTS

Macronutrients

DOM exposed to UV-B releases NH_4^+ into the surrounding waters, thus becoming a nutrient source in coastal waters.[113] This larger availability of ammonium, of major importance in areas of nitrogen limitation, can counteract decreased N uptake and metabolism by phytoplankton,[59,63] and potentially bacteria, as a result of UV-B inhibition. In spite of high nitrate concentrations in most Antarctic open waters during the growth season, phytoplankton has shown low specific nitrate uptake rates[115] and differential uptake of NH_4^+ when present,[116] suggesting that a potential effect of UV-B in releasing NH_4^+ may be of interest in the Southern Ocean.

Micronutrients

The potential interaction of iron (Fe) and UV-B as a source of dissolved iron is important in the Southern Ocean as it has been hypothesized that Fe limitation may be controlling primary production in Antarctic open waters characterized with low chlorophyll accumulation and high macronutrient concentration.[117] For example, the gradient of higher productivity in coastal waters as opposed to open waters observed in the Western Antarctic Peninsula[15,80] is correlated with observed iron concentrations (4.7 nM and 0.16 nM, respectively).[118] A similar approach was taken by de Baar et al[119] to explain high primary productivity at the Polar Front (1200-3000 mg C m^{-2} d^{-1}) with high Fe concentration in surface waters (2-4 nM at 60-100 m) as opposed to lower primary production (80-300 mg C m^{-2} d^{-1}) at the Antarctic Circumpolar Current with subnanomolar concentrations (0.17 nM at 40 m). On the other hand, de Baar et al[120] and Buma et al[121] did not find rapid Chl *a* accumulation with Fe addition with respect

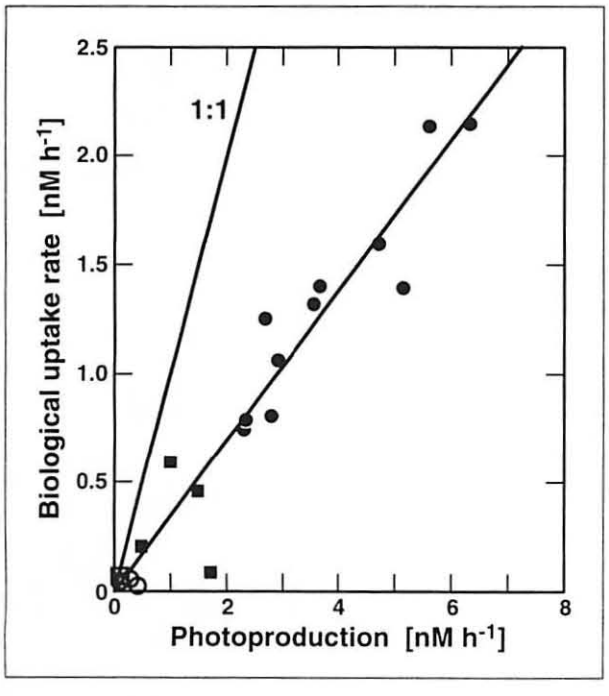

Fig. 15.5. Photochemical production of pyruvate after irradiation of dissolved organic matter (DOM) plotted against the rate of uptake of pyruvate by bacteria in coastal waters (filled circles) and in the Sargasso Sea (open circles). Reprinted with permission from Kieber et al, Nature 1989; 341:637-639, © 1989 MacMillan Magazines Limited.

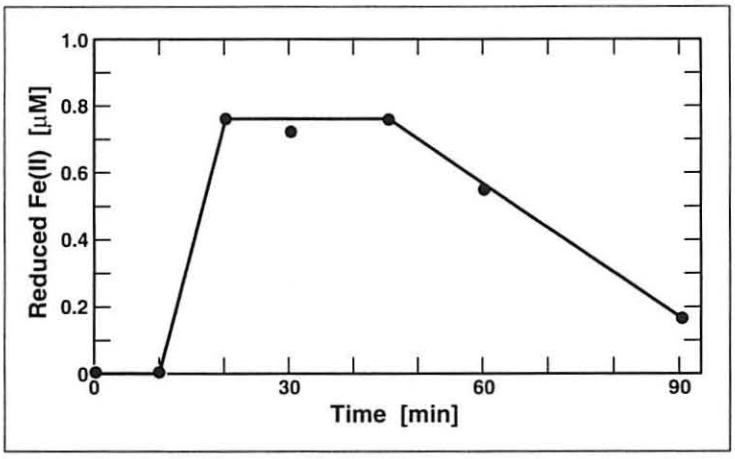

Fig. 15.6. Photoreduction of Fe(III) in seawater (pH 8.0-8.1) in the presence of the diatom Phaeodactylum tricornutum *under UVR. Fe(III) concentration of 5 µM; diatom concentration of 10^5 cells ml^{-1}. Redrawn from Kuma et al, Marine Chemistry 37:15-27. Copyright 1992, with kind permission from Elsevier NL.*

to controls in the Weddell/Scotia Seas (both treatments grew at similar levels). The authors concluded that incubation effects overrode metal, and in particular, Fe addition due in part to the exclusion of large grazers from the experimental vessels. Iron additions shifts phytoplankton composition from flagellates to diatoms, both in Antarctic[121] and in equatorial Pacific waters.[122] Their results were not as dramatic as those observed by Helbling et al[123] who found increased primary productivity and microzooplankton population in surface pelagic waters after addition of Fe. No effect was observed in deep pelagic waters or coastal waters off Seal Island. A shift to larger cells is similar to other experiments of phytoplankton exposed to UVR[19,96] which were attributed to differential cell survival and DNA damage.

In marine oxic waters, Fe^{3+} is the more stable form while Fe^{2+} is more soluble and readily available to phytoplankton and bacterial uptake.[124] The concentration of Fe (III)' (the sum of dissolved inorganic species) is the relevant factor to consider with respect to the uptake of inorganic iron.[125] Its concentration varies from 10^{-8} to 10^{-9} M. Recent data indicates that 99.9% of the dissolved iron in surface waters is bound within organic complexes, resulting in subpicomolar concentration of dissolved Fe(III). It is believed that the ligands for iron may originate from phytoplankton.[125]

Sunlight increases rates of oxidation and reduction of iron, enhancing labile Fe concentrations and phytoplankton uptake. Although UV-B photoreduces Fe(III) to Fe(II) associated to inorganic ligand complexes, a larger reduction power is expected from organic chromophores.[125] Reduction of organic ligands may occur by the photoproduced superoxide radical (O^{2-}). In addition, oxidation of Fe(II) can occur with photoproduced H_2O_2.

Photo-reduction of Fe(III) to Fe(II) is also attributed to the action of marine phytoplankton (Fig. 15.6). High concentrations of Fe(II) were observed during phytoplankton spring blooms in Japanese coastal waters.[126] Experiments with filtrate from a diatom culture resulted in photoreduction of Fe(II) after addition of 5 µM Fe(III). This process was attributed to the release of hydrocarboxylic acids by phytoplankton, known to reduce Fe(III) to Fe(II) in the presence of sunlight[124] and is more pronounced at lower temperatures (5° vs. 20°C), important for Antarctic waters (surface water temperature varies from -1.8° to +2.5°C).

CONCLUSIONS

Two important conclusions can be drawn from this discussion. First, evidence has accumulated to indicate that an assessment of UV effects on Antarctic ecosystems or marine ecosystems in general, will

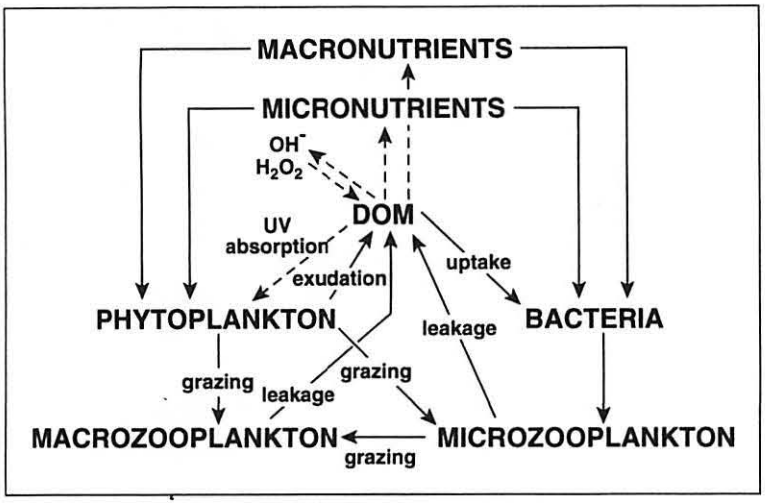

Fig. 15.7. Scheme showing biotic (full line) and abiotic (dashed line) relationships in the upper water column in the ocean, based on interactions discussed in the text. The arrow shows the direction of energy flow.

require experimentation on the ecosystem as a whole, or at least, isolate parts of it which include several interactions (i.e. the microbial loop). The predictive capability of adding effects on individual pools in the system is limited and experiments in temperate areas suggest that this can even be erroneous. Each level or species is not acting in a vacuum and biotic and abiotic interactions will modify its genotypic response to UVR. Second, it is not possible to estimate UV effects on ecosystems without concurrent effort toward understanding environmental and biological forces which drive the system. Thus, UV effects are an added stress upon the system and need to be considered in conjunction with other potential limiting factors, such as nutrients, and other driving forces, such as mixing and ice cover.

In general, we speculate that a more profound and permanent effect of UVR might be the alteration of interaction between singular elements in the ecosystem than the direct effect of UV in inhibition of that same element (Fig. 15.7). For example, changes in species composition might overshadow decrease in total primary production;[16,19] increased substrate for heterotrophic activity might balance UV inhibition of bacterial growth;[105] changes in iron availability[125] could counteract photosynthetic photoinhibition. The consequences are far reaching in that the overall carbon balance might change due to different proportions of carbon burial related to potential changes in cell size, grazing and subsequent sedimentation altering the CO_2 interaction between atmosphere and oceans.

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ENVIRONMENTAL
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THE EFFECTS OF OZONE DEPLETION ON AQUATIC ECOSYSTEMS

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