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Ultraviolet Radiation and the Antarctic Coastal Marine Ecosystem

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The Antarctic marine ecosystem is one of the largest ecosystems on the planet. It is bound by the Antarctic continent to the south and by the Polar Front to the north. Physical, chemical, and biological properties are distinct to this system both by their absolute value as well as by their scale of variability. For example, low and relatively constant temperatures are characteristic of surface marine waters (from −1.84° and 2.5°C) (Hofmann et al. 1996). In contrast, solar radiation presents a large seasonal variability that reaches an extreme of 24 h of light in summer and 24 h of darkness in winter, south of the Antarctic polar circle (66.5° S). Similarly, a strong seasonal variability in sea ice coverage reaches maximum values in winter (July and August) and minimum in the fall (March), sweeping approximately half the Antarctic marine ecosystem and effectively doubling the surface of the Antarctic continent. Atmospheric circulation, a driving force on air temperatures and sea ice distribution, includes several cyclonic pressure systems that surround the continent, introducing winds, cloudiness, moisture, and heat into the marine environment and coastal regions in a scale of days to weeks.

The Antarctic aquatic ecosystem has been divided into four major biogeochemical regimes: polar front, permanent open oceanic waters, areas affected by the annual advance and retreat of sea ice, and coastal waters (Tréguer and Jacques 1992). The most productive areas are concentrated in coastal regions swept by the seasonal ice edge, such as the continental shelf west of the Antarctic Peninsula (Figure 7.1). This area is characterized by highly productive waters that sustain abundant antarctic krill, *Euphausia superba*. Several large-scale research projects have been carried out in this region to understand krill population dynamics and the marine food chain that supports large secondary production, the penguins and whales as major krill predators, and the linkages between environmental forcing and the marine ecosystem (El Sayed 1996). In addition, major studies on the effect of ultraviolet radiation (UVR, 280–400 nm) on marine organisms have originated in Western Antarctic Peninsula (e.g., Karentz, Cleaver and Mitchell 1991; Helbling et al. 1992; Smith et al. 1992; Malloy et al. 1997; Prézelin, Moline and Matlick 1998; Quetin et al. 1998). This is an area of particular scientific interest because of a 50-year warming trend, thus combining several aspects of global change research, mainly UV radiation and surface warming.

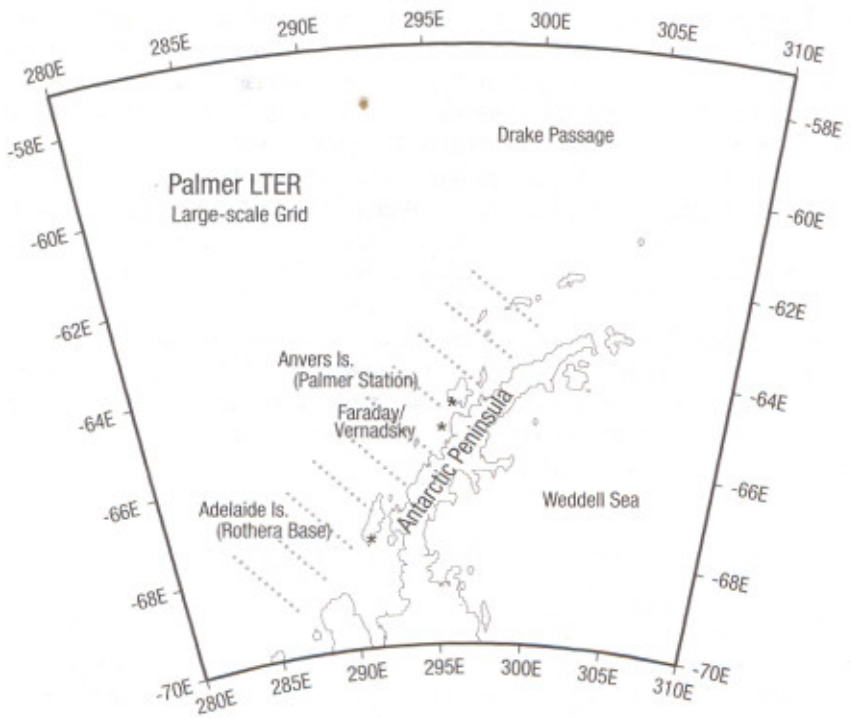

FIGURE 7.1. Map of the Western Antarctic Peninsula with location of Palmer Station, Faraday, and Rothera. The *points in the grid* indicate the stations sampled during the yearly January cruises from 1997 to 2000.

As an environmental factor, ultraviolet radiation (UVR) in Antarctica has a predictable UVR to PAR (photosynthetically available radiation, 400–700 nm) ratio as a function of latitude and time of the year. Variables that affect UVR (i.e., clouds) can affect PAR as well (Lubin and Frederick 1991) while UVR to PAR ratios remain unchanged. The presence of the ozone hole in Antarctica (Farmer, Gardiner and Shanklin 1985) causes an increase in UVB only (290–320 nm, as the ozone hole moves around the continent), independent of UVA (320–400 nm) or PAR, resulting in higher UVB:UVA:PAR ratios (Smith et al. 1992; Booth et al. 1994). This change in UVR ratios will increase damage by UVB as well as change the induction of repair by UVA and PAR, affecting short- and long-term responses of organisms and communities to UVR (Vincent and Roy 1993).

The net effect of UVR on marine organisms is a balance between photochemical damage and biologically driven processes of recovery and repair (Vincent and Neale 2000). When considering UVR effects on Antarctic organisms, and systems, we need to assess how environmental conditions affect both the rate of UVR damage (i.e., by changing exposure) and the rate of repair (i.e., by ac-

tivating enzymatic processes). UVB is known to affect a variety of cellular processes and molecules in the marine environment (Weiler and Penhale 1994; Häder 1997; de Mora, Demers and Vernet 2000). UVA is damaging to certain cellular process as well, such as photosynthesis (Helbling et al. 1992), but it is also involved in repair mechanisms (Mitchell and Karentz 1993). Thus, the change in the ratio of UVB:UVA, by both changes in stratospheric ozone and in the water column by differential attenuation of UVB and UVA with depth (Diaz, Morrow and Booth 2000), is key to our understanding of UV stress on aquatic ecosystems.

In this chapter we describe the major environmental factors influencing marine Antarctic organisms as they are exposed to possible effects of UVR. We review the effect of UVR on Antarctic marine organisms, in particular primary production and the krill-centered food web in coastal areas. Although we address what is known of UVR effects in Antarctica, we stress the Western Antarctic Peninsula because of its interest to krill recruitment and fishery and as an area undergoing climate warming.

The Antarctic Coastal Marine Environment

Atmospheric Processes

Average winter and summer air temperatures in the Western Antarctic Peninsula are −5.5°C and 2.9°C, respectively (Smith et al. 1995). Superimposed on seasonal and interannual variability, a period of rapid warming has been observed in the Antarctic Peninsula in the last half-century. Based on records collected at Faraday (65° 15′ S, 64° 15′ W; see Figure 7.1) by the British Antarctic Survey, the average annual air temperature has increased by 2.4°C (Figure 7.2). Most of

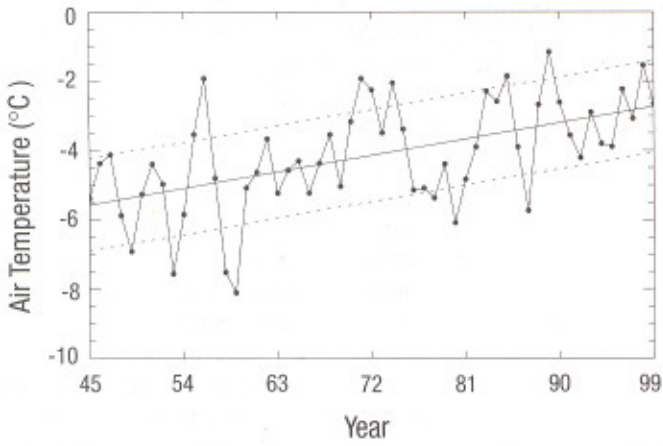

FIGURE 7.2. Faraday annual average air temperatures from 1945 to 1999 (n = 54). *Lines* indicate the least-squares regression line ± 1 SD. (significant at the 90% confidence level). (From Smith and Stammerjohn, in press.)

the warming is caused by an increase of about 6°C in the average monthly air temperature in June (Smith, Stammerjohn and Baker 1996). Spring and summer trends are comparatively smaller. The same warming trend is observed further south in the data collected at Rothera (67° 34′ S, 68° 08′ W). Enhanced meridional flows from mid- to high latitudes during winter are responsible for above-average winter temperatures observed in the past (van Loon 1967). The warming trend indicates an increase in maritime, as opposed to continental, influence in the region (Smith and Stammerjohn, in press). Paleoecological records collected from sediment and ice cores indicate that the region has experienced other warming periods of similar magnitude in the past 7000 years (Smith et al. 1999). Thus, the present-day warming seems to be within the boundaries of climate change observed in the past. In addition to magnitude, climate variability is characterized by the rate of change. It has not been ascertained yet if the warming we observe now is occurring at a faster rate of change than previous events.

Sea Ice Dynamics

Sea ice formation in Antarctica is driven by the cooling of surface seawater by air temperature in the fall and winter months. Conversely, the ocean provides the heat to melt sea ice in the spring and summer (Figure 7.3). Sea ice extent (or maximum area covered during the season) in the Western Antarctic Peninsula is closely coupled with winter air temperature (Jacka and Budd 1991; Smith, Stammerjohn and Baker 1996). In contrast to the Southern Ocean as a whole, the warming of winter air temperature in the Western Antarctic Peninsula has resulted in decreased winter sea ice in this region, based on a 21-year record of satellite passive microwave (Smith and Stammerjohn, in press). On average, the sea ice in spring and fall during the 1990s was lower than in the 1980s as the result of its slower advance and faster retreat. A consequence of this trend of higher winter air temperatures and faster melting of sea ice is to expose plankton to UVR in this region earlier in the spring season than in previous years.

Ultraviolet and Photosynthetically Active Radiation

Background information about the solar spectrum and fundamental physical concepts related to UVR in the atmosphere and underwater have been summarized recently by Diaz, Morrow and Booth (2000). On average, only 1.5% of extraterrestrial UVB reaches the Earth's surface. Solar elevation is the most important factor governing surface UVR in the world, followed by total column ozone, which absorbs UVB strongly at 280–310 nm (Lubin, Jensen and Gies 1998). In Antarctica, irradiance is at a maximum in December and at a minimum in June (Figure 7.4). Within Antarctica, UVR variability is also driven by cloudiness. The ratio of UVB:UVA:PAR also changes seasonally because of changes in ozone concentration and differential path length through the atmosphere. As UVB is mostly absorbed in the stratosphere by ozone, the depletion of ozone (ozone hole) occurs in late winter and spring when the Antarctic vortex closes. The chlorofluorocarbons destroy the ozone on ice particle surfaces (Solomon 1988).

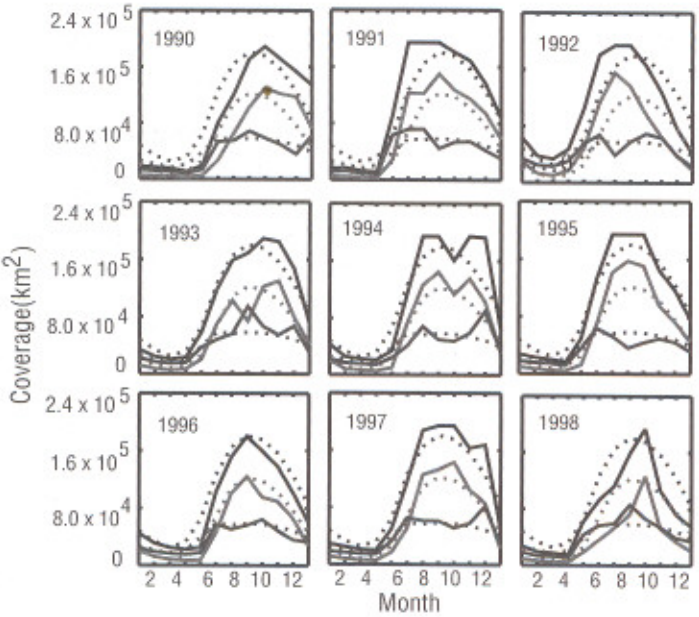

FIGURE 7.3. Monthly ice coverage of the Western Antarctic Peninsula area. *Dotted line* represents monthly averages based on the October 1977 to August 1998 monthly record derived from passive microwave satellite data (Smith and Stammerjohn, in press); *continuous lines* represent monthly averages for that year; *top line* in each square is total area covered by ice within the grid in the Western Antarctic Peninsula (see Figure 7.1); *middle line* represents the area of 100% ice coverage; *lower line* is the difference between total area and area with 100% ice coverage, or the area of open water.

Changes in total column ozone, due to decreases in stratospheric ozone, noticeably increase the ratio of UVB to UVA and PAR (Booth et al. 1994). Overall, up to 60% higher UVB increases are expected in high latitudes in October due to total column ozone variability (Sabziparvar, Forster and Shine 1998). Other natural and anthropogenically induced factors can also change UVB reaching the Earth's surface. Increased aerosols in the atmosphere are thought to decrease surface UVB up to 2% globally. Conversely, feedback effects of enhanced greenhouse gases can cool the polar stratosphere, resulting in a more stable polar vortex; this will lead to enhanced ozone depletion by chemical reactions and to reduced transport of ozone from lower latitudes (Taalas et al. 2000), resulting in increased UVB reaching Antarctica.

UVR is further modified through the air–water interface at the sea surface and after entering the water. Overall transmission in the water follows an exponential decrease with depth for both UVR and PAR (Holm-Hansen, Lubin and Helbling 1993). UVB is differentially absorbed and can reach depths of 50 m with an average effective irradiance of 20–30 m. Light transmission is inversely pro-

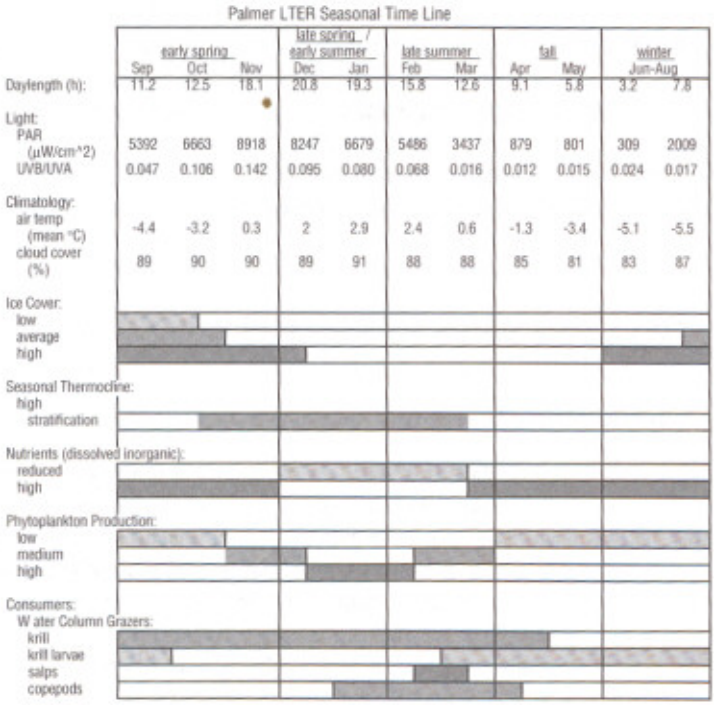

FIGURE 7.4. Seasonal development of physical and biological components of the coastal Antarctic ecosystem based on what is known of the area. General physical and biological parameters are extracted from Smith et al. (1995) and are based on known interannual variability (see text). UV radiation is based on data from the UV network of National Science Foundation, sea ice data from Smith and Stammerjohn (in press), and phytoplankton development data from Kozlowski et al. (1995).

portional to the diffuse attenuation coefficient, which is mostly controlled by the absorption of particles (i.e., phytoplankton), dissolved organic matter (i.e., Gelstoff), and water itself (Diaz, Morrow and Booth 2000).

Through the seasons, UVR starts in the Western Antarctic Peninsula in August (Booth et al. 1994). At this time, we can expect maximum sea ice cover in the area (see Figure 7.3) (Stammerjohn and Smith 1996). UVR transmission through the ice varies with physical conditions, in particular, ice thickness and snow cover. For an average 40-cm-thick first-year ice, only 0.5%–9% of surface UVB reaches the underside of ice, with an average of 2% (Perovich 1993). UVR can affect photosynthesis and a variety of cellular processes in sea ice populations (Prézelin, Moline and Matlick 1998). In ice-free areas, UVR can penetrate the water column, affecting phytoplankton and other components of the aquatic food chain (see Figure 7.4). It is not known, and probably it is difficult to measure, if a decrease in sea ice cover in the spring that increases UVR exposure of plankton will result in increased net UVR damage to the system. As the ozone

hole develops early in the season (Roscoe, Jones and Lee 1997), any biological activity during late winter and early spring will be exposed to high UVB. Possible negative feedback mechanisms are also present. The reduced melting of sea ice will have an opposite effect on UVR exposure as well. It is believed that the melting of ice increases water column stratification and favors early springtime phytoplankton development (Smith and Nelson 1986). Decreased ice melting could delay phytoplankton development in the water column and thus reduce phytoplankton UVR exposure in early spring.

UVR Effects on Primary Production in the Western Antarctic Peninsula

Phytoplankton Development

In the vicinity of Palmer Station (64° 46.7′ S, 64° 04.0′ W), midway through the Antarctic Peninsula (see Figure 7.1), phytoplankton growth starts in October and measurable accumulation (>1 mg chlorophyll *a* m^{-3}) is seen in October or November (see Figure 7.4). Phytoplankton concentration, measured as chlorophyll *a* (chl *a*), is low through the winter (0.001–0.04 mg m^{-3}; Vernet, unpublished data) and early spring (0.04–0.12 mg chl *a* m^{-3}; Kelley et al. 1999). Phytoplankton develops through the summer (December to February) and lasts until March or April (Smith, Baker and Vernet 1998). The area is swept by several biomass peaks centered at the month of January. In years of high production, chl *a* can reach concentrations of 40 mg m^{-3} in the mixed layer while in years of low production the accumulation does not surpass 3–4 mg m^{-3}. On the continental shelf, a large gradient is observed from high values near the shore to low values on the continental slope, about 200 km offshore. Thus, phytoplankton can reach high accumulations in this region through spring and summer, under high UVR and PAR.

Large interannual variability in phytoplankton accumulations and corresponding primary productivity are characteristic of this region. During the 1990s (1991–2000), estimated annual primary production in the vicinity of Palmer Station varied by a factor of 8 (54–380 g C m^{-2} $year^{-1}$). This variability is associated also with changes in phytoplankton composition. The main microphytoplankton groups (>2 m) dominating in the region, in order of importance, are diatoms, cryptomonads, and prymnesiophytes. The northern coastal areas in the Peninsula are characterized by high diatom concentrations and sometimes cryptomonads (Vernet et al. 1994; Moline and Prézelin 1996; Ross et al. 2000) whereas further south, in the region of Marguerite Bay, summer populations are dominated by prymnesiophytes (e.g., *Phaeocystis sp.*).

UVR Effect on Primary Production

The overall effect of UVR on phytoplankton is to decrease rates of primary production (Smith 1989; Holm-Hansen, Helbling and Lubin 1993; Cullen and Neale 1994; Prézelin, Boucher and Schofield 1994; Weiler and Penhale 1994; Smith

and Cullen 1995; Cullen and Neale 1997). UVB and UVA inhibit both light-limited and light-saturated carbon uptake (Steemann-Nielsen 1964; Maske 1984; Cullen, Neale and Lesser 1992; Ekelund 1994; Lesser 1996). In Antarctic phytoplankton, UVB inhibits carbon incorporation by 25%–50% of shielded samples (Holm-Hansen, Villafañe and Helbling 1997). A strong depth gradient is observed in UVR inhibition from the surface to depth. Measurable UVB inhibition of primary production is usually constrained to the upper 20–25 m of the water column (Holm-Hansen, Mitchell and Vernet 1989; Karentz and Lutze 1990; Smith et al. 1992), as expected from UVB transmission.

The effect of UVR on the inhibition of carbon uptake is not constant across the spectrum (280–390 nm) (Neale 2000). In some populations, UVA can have twice the inhibitory effect as UVB (Holm-Hansen, Villafañe and Helbling 1997) whereas other populations are more sensitive to UVB (Boucher and Prézelin 1996a). This difference is of importance to assess possible effects of decreased stratospheric ozone, affecting only UVB. The response of phytoplankton is not linear across UVR irradiance levels; the threshold for photosynthetic inhibition of Antarctic coastal phytoplankton has been determined to be 0.5 W m^{-2} for UVB and 10 W m^{-2} for UVA (Booth et al. 1997). In contrast, an order of magnitude higher sensitivity and no threshold was observed for Arctic phytoplankton sampled from a deep mixed layer (Helbling et al. 1996). The variability has been attributed to differences in phytoplankton composition and to the degree of adaptation to in situ conditions.

Variability in UV Inhibition of Primary Production

To date, the effect of UVR on Antarctic phytoplankton has been studied in monospecific cultures and in a variety of field assemblages. Most of the projects have been carried out in late winter and spring (September to December), coinciding with the period of ozone depletion. These experiments are short term and difficult to extrapolate to other time or space scales.

To assess the effect of UVR on primary production at longer time and space scales, recent experiments were carried out in four consecutive summers (January to mid-February), from 1997 to 2000, in the Western Antarctic Peninsula. Samples were taken randomly within the grid shown in Figure 7.1, between Palmer Station and Rothera. Each experiment was incubated for 24 h and sampled every 2, 4, 8, and 24 h. UVB and PAR irradiance were measured during the incubations with a GUV-511 from Biospherical Instruments Inc. Dose was calculated by integrating 305-nm irradiance (μJ cm^{-2}) over the time of the incubations. Ambient temperature was maintained with running seawater from the ship's seawater intake sampled at 3-m depth. Inhibition of primary production is expressed as the ratio of primary production exposed to UVR and PAR to primary production when UVR was blocked ($PP_{UVR+PAR}/PP_{PAR}$).

The experiments showed inhibition of primary production by UVR, as indicated by a negative ratio of $PP_{UVR\ +\ PAR}/PP_{PAR}$ (Figure 7.5). For any given time of incubation, there was a negative linear correlation between inhibition and 305-nm dose, showing higher inhibition at higher dose. The inhibition decreased

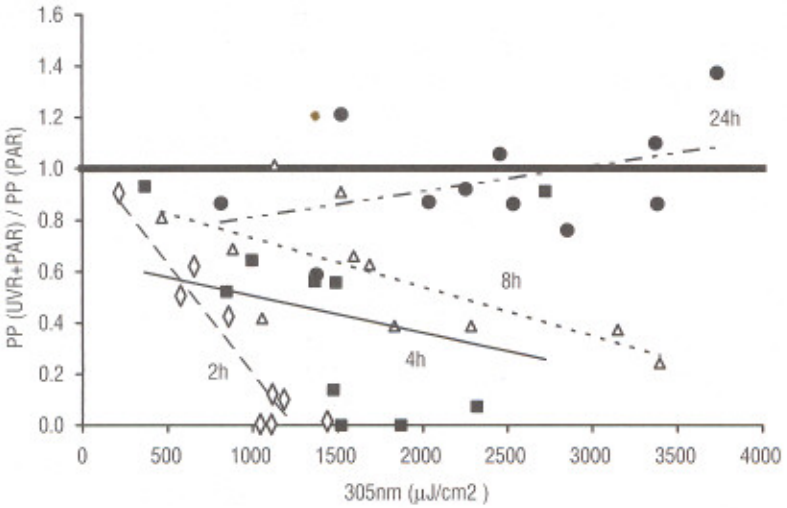

FIGURE 7.5. Effect of UVR on primary production (PP). Experiments were carried out with surface waters sampled from the Western Antarctic Peninsula, within the LTER grid (see Figure 7.1), in January 1997. Incubations were done in Teflon bottles (73.2% reduction of incident UVR at 305 nm). Doses are 305-nm irradiances integrated over 2, 4, 8, and 24 h of on-deck incubations.

with time, as seen by a decrease in the slope at time intervals of 4, 8, and 24 h. After 24 h, some samples showed slightly higher production under UVR + PAR than under PAR alone.

Large variability in daily 305-nm doses was observed for all 4 years (Table 7.1). Changes in dose are related to variability in irradiance as all incubations were integrated by the same time interval (2, 4, 8, and 24 h). For low daily 305-nm doses ($\leq$3,736 μJ cm^{-2}), as observed in January 1997, there was acclimation by phytoplankton carbon uptake to UVR. We observed a decrease in sur-

TABLE 7.1. Average UVR inhibition of primary production observed in surface waters of the Western Antarctic Peninsula.

Incubation (h)	1997	1998	1999	2000	Average
2	0.29 ± 0.32	0.65 ± 0.33	0.80 ± 0.20	0.88 ± 0.84	0.66 ± 0.26
4	0.43 ± 0.36	0.83 ± 0.37	0.71 ± 0.27	0.74 ± 0.36	0.68 ± 0.17
8	0.59 ± 0.25	0.74 ± 0.22	0.67 ± 0.29	0.62 ± 0.24	0.65 ± 0.07
24	0.95 ± 0.23	1.05 ± 0.21	0.56 ± 0.25	0.61 ± 0.23	0.79 ± 0.24

PAR, photosynthetic active radiation.

Data are Primary production$_{UVR + PAR}$/primary production$_{PAR}$.

Phytoplankton inoculated with radioactive carbon were incubated on the ship's deck, under sunlight, and sampled at 2, 4, 8, and 24 h. UVR was screened out with plexiglas (similar to UF3). Incubations started at mid- to late morning and were completed the next day at the same time. Average day length at this time of year is 16–19 h, depending on latitude (64.5° S to 68° S).

face inhibition with time, with maximum inhibition of 0.27 ± 0.32 after 2 h incubation and a final inhibition of 0.95 ± 0.23 after 24 h (Figure 7.5 and Table 7.1). With intermediate 305-nm UV doses (≤9617 μJ cm^{-2} and ≤9,697 μJ cm^{-2}, respectively) there was acclimation in 1998 and a lack of acclimation in 1999. In 2000, with maximum 24-h 305-nm UV doses ≤27,067 μJ cm^{-2}, no acclimation was observed. As all experiments were carried out from mid-January to mid-February of 1997 to 2000, changes in 305-nm UV doses were not caused by variability in sun angle or difference in total ozone column but by changes in weather patterns affecting UVR reaching the ocean surface. The observed variability in UVR is attributed mainly to variability in cloud cover.

To understand the factors controlling inhibition of carbon uptake and the ability of phytoplankton to acclimate, a linear least-squares regression was calculated to the average inhibition of primary production (primary production$_{UVR+PAR}$)/primary production$_{PAR}$) as a function of incubation time (2, 4, 8, and 24 h) for each of the 4 years (Table 7.2). A positive slope indicates a decrease in inhibition with time (see Table 7.1) whereas a negative slope indicates higher inhibition after 24 h or an absence of acclimation. The total average 305-nm dose per year explains 79% of the variance in acclimation observed interannually (Figure 7.6a) and temperature can explain 54% of the variance (Figure 7.6b).

Similar to our results in Antarctic phytoplankton, acclimation to UVR was also observed in the cyanobacterium *Phormidium murayi* (Roos and Vincent 1998) as growth increased from day 1 to day 5 in cells incubated under UVR and PAR. Acclimation within 24 h of exposure to ambient UVR, as seen in the Western Antarctic Peninsula in 1997, is comparable to responses by the subtropical diatom *Chaetoceros gracilis* Schutt (Hazzard, Lesser and Kinzie 1997). Antarctic coastal phytoplankton from the vicinity of McMurdo Station showed a 22% decrease in maximum photosynthetic rate (mg C (mg chl a)$^{-1}$ h^{-1}) after 9 days of UVR exposure (Lesser, Neale and Cullen 1996).

How representative are the experiments performed with surface phytoplankton to overall primary production in the water column? As discussed earlier, UVR and PAR decrease exponentially with depth, and UVB is differentially absorbed with respect to UVA and PAR. We can expect UVB to decrease to 1% of sur-

TABLE 7.2. Lease-squares linear regression of the average UVR inhibition of primary production.

Year	Slope	Intercept	r^2	Average 24-h 305-nm dose (mJ cm^{-2})	Average temperature (°C)	Acclimation
1997	0.106	0.14	0.94	2395 ± 915	1.17 ± 0.61	Yes
1998	0.055	0.60	0.69	5858 ± 2776	1.62 ± 0.56	Yes
1999	−0.038	0.83	0.97	7957 ± 1595	0.86 ± 0.18	No
2000	−0.047	0.90	0.90	23998 ± 3100	0.17 ± 1.33	No

Primary production$_{UVR+PAR}$/primary production$_{PAR}$ as a function of incubation time (2, 4, 8, and 24 h) in the Western Antarctic Peninsula experiment for each of the four years (data in Table 7.1).

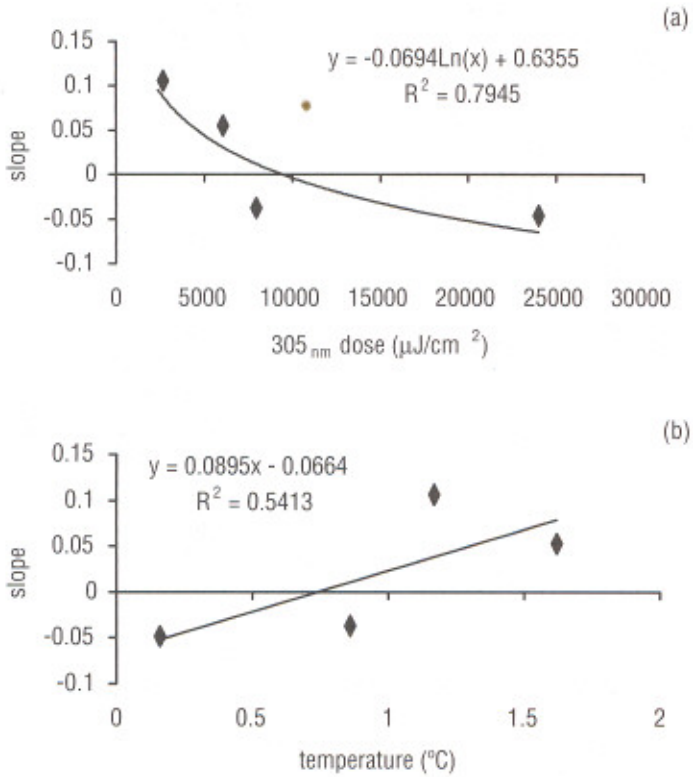

FIGURE 7.6a,b. Environmental factors controlling UVR inhibition and acclimation of primary production in four consecutive summers (1997–2000). (a) Rate of change of inhibition of primary production by UVR in 24-h experiments as a function of average daily 305-nm UV doses for each year (data in Tables 7.1 and 7.2). (b) Rate of change of inhibition of primary production by UVR in 24-h experiments as a function of temperature of incubation

face irradiance at 30-m depth in low productive Antarctic waters where chl *a* concentration is approximately 0.25 mg m^{-3} (Holm-Hansen, Helbling and Lubin 1993). The results presented in Figure 7.5 and Tables 7.1 and 7.2 would be representative of UVB at 30% of surface irradiance or about 5-m depth and thus representative of irradiance encountered in the mixed layer. For more productive, less clear waters, this represents shallower depth (2–3 m).

On average, daily depth-integrated primary production decreases by 6%–12% in the presence of UVB (Holm-Hansen, Mitchell and Vernet 1989; Smith et al. 1992; Helbling et al. 1992) during springtime ozone depletion over Antarctic coastal waters, although higher water column inhibition has been measured also (i.e., 25%; Boucher and Prézelin 1996b). UVR inhibition of annual primary production was calculated as 2% for the Southern Ocean (Smith et al. 1992). Hel-

bling, Villafañe and Holm-Hansen (1994), on the basis of different assumptions and methodology, calculated the decrease in primary production to be 0.15% for the entire icefree waters south of the Polar Front. The degree of uncertainty of these measurements increases with area- and time-integrated calculations, as they are based on discrete hourly or daily measurements (i.e., depths) taken in a short period of time (i.e., month-long cruise) and space (i.e., several hundred square kilometers as opposed to the whole Southern Ocean).

Temperature

Low ambient temperatures are characteristic of the marine environment in the Antarctic. Lowest, freezing temperature is −1.84°C. In late spring and summer, low temperatures in the Western Antarctic Peninsula are associated with melting ice (−1.61°C) and warmer waters are offshore, 2.5°C. For any given location, the melting and formation of ice drive the distribution of low surface temperature. Furthermore, melting of continental ice decreases temperature and salinity in nearshore areas.

Overall response of the UVR inhibition of primary production was also influenced by the ambient (incubation) temperature during the 1997–2000 experiments. Average temperature for all the experiments was 1.29° ± 0.72°C, varying from −1.5° to 2.5°C. The ability of the phytoplankton to acclimate carbon uptake to ambient UVR was enhanced at higher temperatures (Figure 7.6b and Table 7.2). The influence of temperature on acclimation could result from the influence of temperature on repair mechanisms (Vincent and Neale 2000) because the higher temperature should promote higher enzymatic activity.

Temperature influences also the effect of UVR on primary production (as measured by carbon uptake) in polar mat-forming cyanobacteria. Cyanobacteria are psychotrophs, growing slowly (0.23 + 0.069 day^{-1}) at the optimum temperature of 19.9°C (Tang, Tremblay and Vincent 1997). Experiments carried out on the polar cyanobacterium *Phormidium murayi* West and West showed a synergistic effect of temperature and UVR inhibition (Roos and Vincent 1998). Cyanobacteria were grown at 5°, 10°, 15°, 20°, and 25°C. Photosynthesis versus irradiance (P versus I) curves showed that maximum photosynthetic rate (P_{max}) was a function of temperature (a factor of 2.7 higher at 35°C than at 5°C), but no effect of temperature was observed on the light-limited response. After several days of acclimation under UVR, P_{max} was reduced by 30% but there was no effect by temperature on P_{max} or α. From Table 7.1 of Roos and Vincent, we can calculate that temperature reduced P_{max} by 78% (0.22 of optimal photosynthesis) from 20°C to 5°C for incubations under PAR only. Cultures grown at 20°C under UVR showed decreased photosynthesis by 21% or 0.79 of optimal. When both factors were combined, P_{max} was 0.146 of optimal photosynthesis or resulted in a 85% reduction.

The combined effect of temperature and UVR inhibition can be compared to models of multiple stressors (Folt et al. 1999). The comparative model implies that the dominant limiting factor will be expressed when more than two stres-

sors are present. The additive model predicts that the combined effect of two stressors will be equal to the sum of the effect of each factor separately. The multiplicative model predicts that the final result in the presence of both factors will be equal to the multiplication of the effect of the two independent factors. Synergism occurs when the observed effect of both factors is larger than that predicted by a model, and antagonism among multiple stressors is present when the combined effect is less than predicted by a model. In the example of the cyanobacteria, comparing temperature effect (from 20° to 5°C) and UVR effect at optimal photosynthesis (at 20°C), the additive model predicts a 78% + 21% = 99% reduction in P_{max} (78% + 21% reduction). The multiplicative model predicts P_{max} to be 0.17 (0.22 * 0.79) of optimal values, and the comparative model predicts that the dominant stress factor, in this case temperature, will predominate and that the combined effect of both stressors would be 0.22 of optimal photosynthesis. In the experiment, the observed P_{max} for both factors (temperature and UVR) combined was 0.146 of optimal photosynthesis (85% reduction), better than the 98% reduction predicted by the additive model and worse than the 0.17 (83% reduction) predicted by the multiplicative model. Thus, for this case, there was a multiplicative synergistic effect of both stressors. The authors interpreted their result as a decrease in repair mechanisms at low temperatures.

Similar multiplicative effect for temperature and UVR combined was also observed in *Nostoc* sp. (Aráoz, Lebert and Häder 1998) grown at 18°C and exposed to temperatures up to 47°C and to UVB of 0–150 kJ m^{-2}. Cells could survive high temperature (84% survival or 16% reduction at 42°C and 20% survival at 47°C) but were more sensitive to UVR at 18°C (40% survival at 50 kJ m^{-2} or 60% reduction). When both factors were combined at 42°C and 50 kJ m^{-2}, they observed a 12% survival or 88% reduction. The comparative model predicts a 60% reduction in survival, the multiplicative model predicts a 67% reduction, and the additive model predicts a 76% reduction. Thus, high temperature and UVR have a synergistic effect on *Nostoc* sp., as concluded by the authors. In the case of *Nostoc* sp., this is an additive synergistic effect, with a higher reduction than for the multiplicative synergistic model.

No experiments are yet available to calculate synergism or antagonism by temperature and UVR on primary production in antarctic phytoplankton. The results presented here (Figures 7.5, 7.6 and Tables 7.1, 7.2) suggest that temperature might have an effect on acclimation to UVR. Thus, there is a suggestion that ambient low temperatures decrease the rate of repair and that a similar synergistic effect of temperature and UVR can be expected, as for polar and temperate cyanobacteria.

Nutrient Metabolism

UVR affects nutrient uptake and nitrogen metabolism in marine phytoplankton (see Vernet 2000). Furthermore, recent studies show that nutrient limitation might affect UVR inhibition on population growth. In an experiment carried out with natural phytoplankton for 7 days, onset of UVB effect on phytoplankton at 5-m

depth or greater was observed on day 3, once nitrate concentration decreased appreciably (Figure 7.7) (Mostajir et al. 1999). Similar to the combined effects of temperature and UVR, nutrient limitation and UVR might have a synergistic effect. Cullen and Lesser (1991) found that nitrate-limited *Thalassiosira pseudonana* was 8.6 times more sensitive to UVB than nitrate-replete cells.

In contrast, other long-term exposure experiments showed mixed results. The marine diatom *Phaeodactylum tricornutum* exposed to UVR showed a lack of growth inhibition due to nitrogen limitation (Behrenfeld, Hardy and Lee 1992). The freshwater green alga *Selenastrum capricornutum* grown under UVB and phosphate limitation showed higher inhibition of photosynthesis and growth than for short-term exposure (hours) but a relaxation in the inhibition of nutrient limitation (Veen, Reuvers and Rونçak 1997).

Community Composition

Damage to organisms exposed to UVB varies by 100 fold between species (Ekelund 1990; Karentz, Cleaver and Mitchell 1991). The differential sensitivity to UVB suggests a change in species composition caused by long-term UVB exposure, with species that are more UV tolerant ultimately dominating (Worrest et al. 1981). In general, based on culture studies, diatoms are the most resistant to UVR, followed by prymnesiophytes and other flagellates, such as cryptomonads. Green algae and cyanobacteria are usually considered as resistant as diatoms. This differential sensitivity among phyla has been established based on

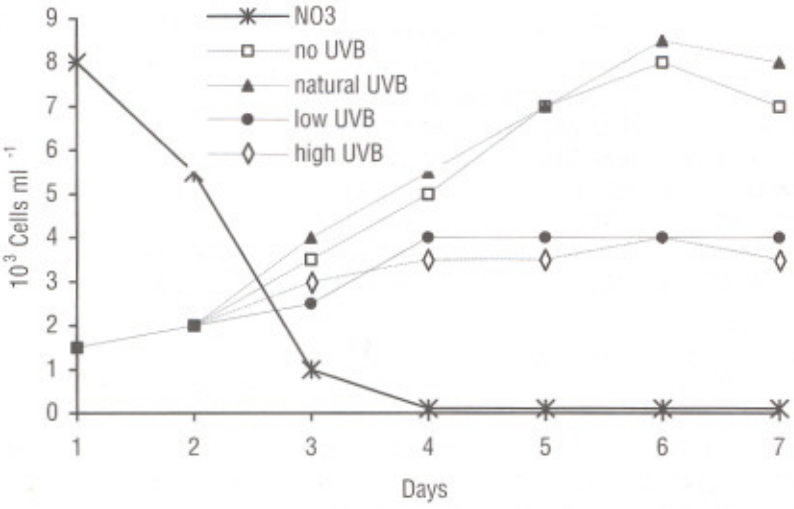

FIGURE 7.7. Phytoplankton (5- to 30-μm cells) abundance and nitrate concentration during a 7-day experiment in a 1500-l mesocosm with St. Lawrence River water under four UVB treatments. (Drawn from Mostajir et al. 1999.)

several cellular processes, such as nitrogen assimilation (Döhler 1997), radiocarbon uptake (Davidson and Marchant 1994; Helbling, Villafañe and Holm-Hansen 1994; Vernet et al. 1994; Villafañe et al. 1995a), specific growth rate (Karentz 1994; Davidson et al. 1994; Villafañe et al. 1995b), and cell abundance in natural populations (Karentz and Spero 1995).

Experiments with mixed populations can be used to test predictions on phytoplankton succession based on differential UVR sensitivity established in the laboratory and from short-term field experiments. Davidson, Marchant and de la Mare (1996) found that 2-day UVB exposures of exponentially growing mixed cultures at 0°C favored *Phaeocystis antarctica* over diatoms. They rejected a hypothesis based on previous experiments in which they found diatoms were three to five times more resistant than *P. antarctica* (Davidson et al. 1994). Part of the discrepancy can be attributed to differences in experimental design: this latter experiment used 9150 J m^{-2} erythemal UVB in a 2-day exposure whereas previous cultures had been exposed to 20%–650% of average springtime UVB radiation in the area.

Cell Size

A differential effect of UVR on cell size has been observed for diatom cultures (Karentz, Cleaver and Mitchell 1991), with greater damage being associated with smaller cells. Small cells have a shorter light path length with reduced absorption and refraction by cytoplasmic components between the cell membrane and nuclear DNA, which results in increased UVB reaching the DNA (Raven 1991; García-Pichel 1994; Booth et al. 1997).

Increases in cell size have been observed in cultures under UVB exposure (Döhler 1985; Behrenfeld, Hardy and Lee 1992; Veen, Reuvers and Ronçak 1997) and are a consequence of the reduction in specific growth rates. Buma, Engelen and Gieskes (1997) attributed the increased cell size to an arrested cell cycle caused by residual DNA damage, as measured by concentration of thymidine dimer cellular content. The increase in cell size results from carbon uptake in the absence of cell division. Coastal waters have, on average, a higher proportion of larger cells than open waters (Malone 1980). For example, more than 80% of the nearshore phytoplankton biomass was associated with cells larger than 10 μm in Terre Adélie, Antarctica, during summer whereas 70 km offshore, cells larger than 10 μm represented only 30% of the total biomass and 59% of the cells were between 1 and 10 μm (Fiala and Delille 1992). Within Antarctic coastal waters, high chl *a* accumulations are dominated by large cells (e.g., >20 μm) while low chl *a* concentrations are dominated by smaller cells (Holm-Hansen and Mitchell 1991; Bidigare et al. 1996). Based on increased inhibition found in smaller cells, presumably due to their smaller light path length, we might hypothesize that oceanic Antarctic phytoplankton may have a higher sensitivity to UVB.

The differential effects of UVR on phytoplankton populations, resulting from their composition or size, are relevant to the spatial, seasonal, and interannual variability in phytoplankton (Ross et al. 2000) and also result from the conse-

quences of global change that could influence a shift in coastal phytoplankton composition. It has been suggested that increased air temperature is increasing continental glacial melt in the region of the Western Antarctic Peninsula and, as a consequence, decreasing surface salinity and increasing stratification. From the dominant phytoplankton groups in the area, Cryptophyceae (also known as cryptomonads) seem to favor shallow mixed layers, with lower salinity and a stratified water column. These algae are unicellular, flagellate cells, 13–20 μm in length. They are not selected by krill in a mixed assemblage, probably due to the small size (Haberman 1998). In addition, they are known to be more sensitive to UVR (Vernet et al. 1994). Such a shift in phytoplankton composition, an indirect effect of climate warming, could not only affect the efficiency of the food chain but also increase the overall inhibition of primary production in the area.

Effect of UVR on the Antarctic Food Chain in the Western Antarctic Peninsula

The phytoplankton growth that supports krill populations in the Western Antarctic Peninsula is composed of large cells (>20 μm) that prefer calm conditions and shallow mixed layers. Phytoplankton under these conditions are usually less sensitive to UVR (Karentz et al. 1991) or have a faster recovery rate (shallow mixed layers). Once the phytoplankton accumulation reaches high particle concentration, there is a shielding of UVR for cells at depth due to increased UVR absorption by surface populations. Thus, it seems phytoplankton can grow under high UVR but that once the populations are established they can acclimate to, or avoid, damaging UVR.

Before experiments in mesocosms, prediction of UVR effects on ecosystems had assumed a linear addition of UV effects on different trophic levels. More recent experiments suggest that UVE might change carbon and energy flows in an ecosystem, thus favoring some pathways at the expense of others. For example, differential UVR sensitivity between algae and herbivores can increase algal populations by decreased grazing pressure (Bothwell et al. 1993). Similarly, increase in substrate due to photooxidation of dissolved organic matter has been reported as enhancing bacterial populations exposed to low levels of UVB (Herndl, Muller-Niklas and Frick 1993). Thus, changing the interaction between biotic and abiotic components or between different components of the food web can sometimes decrease or reverse the deleterious effect of UVB on a known organism (Vernet and Smith 1997).

Research on the effect of UVR at the ecosystem level is a demanding task. Mostajir et al. (1999) cite five criteria necessary to extend results from laboratory and mesocosms into whole ecosystems. First, the experiment must have organisms representative of natural environments. Second, it is the relative sensitivity of the different elements of the community that determines the net effect of UV on the ecosystem, not the absolute response. Thus, experiments need to be carried out with all the elements of the system under study present. Third, en-

hanced UVB irradiances and doses must be plausible, i.e., not too high, but representative of ozone-depleted conditions at that location. Fourth, the effect of UVB must be carried out under environmentally representative conditions, e.g., nutrient depletion for surface summer populations. Fifth, natural mixing rates should be included in the experiment.

Mesoscosm experiments have not been carried out for Antarctic systems but in temperate, subarctic, and arctic environments. Subarctic experiments lasting 7 days in St. Lawrence Estuary surface water (screened by a 240-mm mesh) maintained between 8.5° and 11.4°C in summer (July) at four UVB treatments (no UVB, natural UVB, low UVB, and high UVB) showed a shift from herbivory to microbial food web. Ciliates and large (5–20 μm) phytoplankton were differentially sensitive to UVB. Ciliates showed decreased abundance at all UVB levels while large phytoplankton did not show inhibition at natural UVB but decreased in number at both levels of enhanced UVB (low UVB and high UVB, which enhanced by a factor of 1.23 and 1.79, respectively, the natural UVB levels). As a consequence of decreased predation, ciliate prey increased: bacteria, heterotrophic flagellates, and small (<5 μm) phytoplankton showed higher abundance under UVR. These results suggest that enhanced UVB levels at realistic doses expected under severe ozone depletion can change the food web structure.

Ciliates are particularly sensitive to UVB. Experiments in freshwater systems in the Arctic, at 3.8° to 5.2°C, showed species-specific ciliate and rotifer inhibition of growth by UVB (Wickman and Carstens 1998). Not all species were inhibited; some showed no UVB effect whereas others were enhanced under UVB. Heterotrophic flagellates and bacteria were not sensitive to UVB, similar to the results from the St. Lawrence Estuary (see also Rae and Vincent 1998). In temperate areas, experiments show either no effect of UVB (Hill et al. 1997, Lange et al. 1999) or show that some predators or some grazers are more sensitive than their prey to UVB exposure (Bothwell et al. 1993; Williamson et al. 1999; Zagarese and Williamson 2000).

In the Western Antarctic Peninsula, krill, salps, and copepods are the main components of the macrozooplankton assemblages (see Figure 7.4). Years of abundant krill seem to alternate with years of salp dominance, and the two groups do not overlap geographically (Ross et al. 1996). This alternation correlates with years of higher and lower ice coverage in the previous winter, with krill dominating after winters with high ice (Loeb et al. 1997). Natural UVB fluxes in ice-free areas during springtime are high enough to cause DNA damage in krill, although no quantitative relationship was found between DNA damage and UVB flux in the field (Malloy et al. 1997). Krill and Antarctic fish that reproduce in spring and summer showed, on average, higher rates of DNA repair than species that reproduce in the winter.

Under experimental conditions, PAR radiation, three to five times lower than noon surface irradiance caused captive juvenile krill to die within 1 week (Newman et al. 1999). The addition of UVB radiation, similar to exposure at 0- to 15-m depth, increased krill mortality and decreased overall activity. Krill exposed to sublethal UVA doses also showed decreased activity. As these organisms had been kept in darkness for several months before the experiments, it is not known

if they were more susceptible than wild krill to UVR. Thus, field experiments are needed to ascertain overall UVR effect on krill. To date, indications are that they might be highly susceptible but, as their repair rate is also high, net damage is unknown.

It is not known and probably is difficult to measure if a decrease in sea ice cover in the spring that increases UVR exposure will result in increased net UVR damage to the coastal Antarctic food web. The obligatory association of young krill (less than 1 year) with the under-ice surface during winter protects these larvae from UVR in early spring and provides protection from exposure until the ice retreats. As the ice melts, the young larvae are in an environment that promotes phytoplankton growth and provides food for the young krill (Ross et al. 2000). It is not known if the shallow mixed layer associated with the ice edge phytoplankton accumulation is also an environment conducive to high zooplankton DNA repair rates, as in the case of phytoplankton.

Years of early ice retreat, as in 1998 (see Figure 7.3), not only decrease the chances of developing an ice-edge phytoplankton bloom because of low PAR but also expose young krill to high UVR:PAR during periods of low ozone. If ice protects krill larvae feeding underneath the ice, then earlier melting increases UVR exposure in a vulnerable time when larvae might be subject to low food levels until the bloom develops.

Naganobu et al. (1999) showed a positive correlation between krill recruitment and ozone depletion when years of high ozone depletion and expected higher UVB irradiance coincided with years of lower year 1 class. Thus, directly or indirectly, UVB may affect krill recruitment, either through decreased primary production or by direct net damage on krill larvae. Data interpretation is further limited by the fact that years of low recruitment coincided with years of low winter sea ice cover. These results, based on correlations between UVB variability resulting from stratospheric ozone depletion and krill recruitment, do not show causal effect by UVB. Further research on the physiological and environmental factors influencing UVB damage in krill is needed to ascertain if UVB affects krill recruitment.

The effect of UVR on Antarctic salps and copepods is unknown. Salps become abundant in the summers following a low ice winter (Loeb et al. 1997; see Figure 7.4). They are abundant in oceanic Antarctic waters and are associated with small phytoplankton cells characteristic of offshore assemblages. UVR can be more damaging to small cells (Karentz, Cleaver and Mitchell 1991; Villafañe et al. 1995a,b), thus indirectly affecting salp food source. In addition, offshore locations have deeper mixed layers than coastal environments where phytoplankton and zooplankton could be more susceptible to UVR because of their decreased ability to repair (Neale, Davis and Cullen 1998).

In summary, recent studies have shown the susceptibility of Antarctic zooplankton to UVR. The knowledge of the effect of UVR on the Antarctic food web has not yet been approached systematically nor has the experimental design been done to detect possible changes in the energy flow within the ecosystem. Studies on abiotic factors (Mopper and Kieber 2000), bacteria (Jeffrey, Kase and Wilhelm 2000), phytoplankton, and krill are starting to emerge. However, we

need a more comprehensive approach such as those obtained from microcosms experiments in other areas.

Conclusions

In conclusion, the damage caused by UVR to the marine ecosystem in coastal environments (seasonally swept by the advance and retreat of sea ice) in Antarctica is tightly coupled to the meteorology (i.e., clouds) and sea ice dynamics of the area. Large interannual variability from January 1997 to January 2000 on the effect of UVR on primary production is caused by a factor of 5 on UVR exposure resulting from cloud cover. Because of the rapid absorption of UVB by ice, maximum UVB exposure will occur under icefree conditions. Those conditions will be subject to large interannual variability on total area covered by sea ice and by the specifics of sea ice formation and retreat, which can vary as much as several months for any given location. Melting of sea ice in spring exposes krill larvae to higher UVB and higher predation but also provides the conditions for phytoplankton development necessary for production of food. Higher sea ice in winter is related to higher krill abundance in the following growth season, either by direct effect on UVR protection or indirectly by higher food availability.

The balance between repair and damage in phytoplankton in this area is primarily controlled by UVR radiation and also by water temperature. As radiation affects damage and because temperature might be related to repair processes, we can speculate that changes in UVR, caused either by anthropogenically induced changes or by natural variability, might control net damage. Finally, although large strides have been accomplished in Antarctica with respect to understanding the overall effect of abiotic and biotic components of the ecosystem, a more systematic approach is needed to characterize the relative effect of UVR on the interacting elements.

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