Proc. NIPR Symp. Polar Biol., 7, 53–69, 1994

COMPARATIVE IMPACT OF *IN SITU* UV EXPOSURE ON PRODUCTIVITY, GROWTH AND SURVIVAL OF ANTARCTIC *PHAEOCYSTIS* AND DIATOMS

Andrew T. DAVIDSON and Harvey J. MARCHANT

Australian Antarctic Division, Channel Highway, Kingston, Tasmania, 7050, Australia

Abstract: Depletion of stratospheric ozone over Antarctica enhances UV-B (280–320 nm) radiation reaching the Earth's surface during spring. UV-B influences the growth and survival of marine phytoplankton. The near surface UV irradiance, *in situ* growth and primary production of the prymnesiophyte *Phaeocystis* c.f. *pouchetii* (HARIOT) LAGERHEIM and three diatoms were measured during UV exposure. Survival, growth and cell diameter were also determined after exposure. The flagellate stage in the life cycle of *Phaeocystis* was the only organism examined that suffered mortality as a result of natural UV exposure, however, UV-A (320–400 nm) was responsible for most of this mortality. Interspecific differences in production, cell concentration and growth were observed at sublethal irradiances. Such differences may lead to changes in phytoplankton species composition.

1. Introduction

Ozone depletion over Antarctica has occurred between September and November since the mid-1970s (STOLARSKI *et al.*, 1986). This depletion has increased UV-B irradiances (280–320 nm) reaching the Earth's surface during spring to levels at least as high as those at the summer solstice (FREDERICK and SNELL, 1988; LUBIN *et al.*, 1989). Sea-ice algae contribute 10–50% of the primary production in some areas (VOYTEK, 1989) and phytoplankton inhabiting shallow mixed depths of the marginal ice zone (MIZ) support 25–67% of the phytoplanktonic production in the Southern Ocean (SMITH and NELSON, 1986). The Antarctic sea ice in spring can be sufficiently transparent to UV that biologically significant doses are received by the ice algal community (TRODAHL and BUCKLEY, 1989). The mixed depth during blooms in the MIZ can be 10 m or less for up to 6 days (VETH, 1991). UV-B penetrates to depths in excess 50 m in Antarctic waters (GIESKES and KRAAY, 1990; KARENTZ and LUTZE, 1990; SMITH *et al.*, 1992). Thus, much production by phytoplankton in the Southern Ocean occurs in environments vulnerable to UV-B radiation at a time when irradiances at these wavelengths are enhanced by stratospheric ozone depletion.

Phytoplankton form the base of the Antarctic food web and sustain the wealth of life for which the Southern Ocean is renown (AINLEY *et al.*, 1986). Exposure of phytoplankton to UV-B radiation reduces photosynthesis, growth, survival, nutrient uptake and photosynthetic pigment concentrations, effects

motility and phototactic orientation and increases mutagenesis in DNA and proteins (*e.g.* JITTS *et al.*, 1976; LORENZEN, 1979; CALKINS and THORDARDOTTIR, 1980; WORREST *et al.*, 1981; WORREST, 1983; DÖLER, 1984, 1985, 1987; HÄDER, 1986, 1987, 1988; JOKIEL and YORK, 1984; KARENTZ *et al.*, 1991; MARCHANT *et al.*, 1991). This has lead to concern about the effect of elevated UV-B levels on the Antarctic ecosystem. Opinions regarding the magnitude of the effect range from insignificant (HOLM-HANSEN *et al.*, 1989) to catastrophic (EL-SAYED *et al.*, 1990).

Interspecific variation in survival, growth and repair responses to UV-B exposure is reportedly high (CALKINS and THORDARDOTTIR, 1980; WORREST *et al.*, 1981; JOKIEL and YORK, 1984; KARENTZ *et al.*, 1991; SMITH *et al.*, 1992), even within a single genus (MITCHELL and KARENTZ, 1990). This has lead to the proposal that increased UV-B irradiance is likely to alter the species composition of phytoplankton communities in favor of those species with greater tolerance (WORREST *et al.*, 1981; WORREST 1983; JOKIEL and YORK, 1984; EL-SAYED *et al.*, 1990; KARENTZ, 1990, 1991; HÄDER and WORREST, 1991; KARENTZ *et al.*, 1991; MARCHANT and DAVIDSON, 1991; HELBLING *et al.*, 1992). Long term exposure of natural phytoplankton assemblages to *in situ* UV irradiances reportedly changes the community composition (WORREST *et al.*, 1981; BOTHWELL *et al.*, 1993). This could effect the trophic interactions and carbon flux rates of Antarctic waters (EL-SAYED *et al.*, 1990; KARENTZ, 1990; HÄDER and WORREST, 1991; KARENTZ *et al.*, 1991; MARCHANT and DAVIDSON, 1991) and may have far reaching effects on the Southern Ocean ecosystem (EL-SAYED *et al.*, 1990). However, there is little direct evidence that increased UV-B irradiance as a result of stratospheric ozone depletion has caused changes in phytoplankton species composition of the Southern Ocean.

CALKINS and THORDARDOTTIR (1980) suggested that temperate and sub-polar diatoms possess little reserve capacity to cope with increased UV-B exposure. THOMSON *et al.* (1980) and HANNAN *et al.* (1980) showed that UV-B could significantly reduce the growth rate of marine diatoms and in Antarctic waters. EL-SAYED *et al.* (1990) concluded that Antarctic phytoplankton are currently UV stressed and are likely to be seriously affected by any increase in UV radiation. In contrast, studies of North American phytoplankton by GALA and GIESY (1991) and HOBSON and HARTLEY (1983) found little inhibition of production by UV-B and DAVIDSON *et al.* (1994) found that selected species of Antarctic diatoms, though variable in their response, sustained no significant mortality until UV-B exposures were increased to levels almost an order of magnitude greater than those currently experienced in Antarctic surface waters. While the prospects for diatoms under increasing UV-B irradiances are uncertain, tolerance of nanoplankton to UV-B exposure is little known but apparently low (EL-SAYED *et al.*, 1990; KARENTZ *et al.*, 1991).

UV-A wavelengths are not enhanced by ozone depletion, however, they have been found to be a major factor in depressing rates of photosynthesis and growth (*e.g.* JITTS *et al.*, 1976; JOKIEL and YORK, 1984; MASKE, 1984; BUHLMANN *et al.*, 1987; HELBLING *et al.*, 1992). HOLM-HANSEN *et al.* (1989) found that in near surface Antarctic waters approximately 50% of inhibition of photosynthesis

was due to UV-A. The greater penetration of the water column by UV-A than UV-B meant that UV-A was responsible for most of the photoinhibition in these waters (HOLM-HANSEN, 1990). Long term exposures of phytoplankton have also shown UV-A is responsible for almost all inhibition of phytoplankton growth (JOKIEL and YORK, 1984).

The nanoplanktonic prymnesiophyte *Phaeocystis* c.f. *pouchetii* is arguably the most abundant and widespread phytoplankter of the Antarctic marine ecosystem (FRYXELL and KENDRICK, 1988). It is a frequent member of the ice-algal assemblage and one of the first species to bloom in the top few meters of the water column (GARRISON *et al.*, 1987; FRYXELL and KENDRICK, 1988). Together with diatoms, principally of the genus *Nitzschia, Phaeocystis* frequently dominates the phytoplankton of the ice-edge bloom and plays a pivotal role in determining the structure and function of the planktonic community (GARRISON *et al.*, 1987; FRYXELL and KENDRICK, 1988; GARRISON and BUCK, 1989; DAVIDSON and MARCHANT, 1992a). Any UV mediated change in the abundance of *Phaeocystis* relative to diatoms would significantly alter the particle size, form and availability of carbon to higher trophic levels and is likely to change vertical carbon flux rates (MARCHANT and DAVIDSON, 1991). Here we report the *in situ* primary production, growth and survival of Antarctic isolates of *Phaeocystis* and selected species of diatoms and their post-irradiance growth at an Antarctic coastal site.

2. Materials and Methods

Unialgal cultures of *Chaetoceros simplex* OSTENFELD, *Stellarima microtrias* (EHRENBERG) HASLE and SIMS, *Nitzschia curta* (V.H.) HASLE and a *Phaeocystis* c.f. *pouchetii* (HARIOT) LAGERHEIM were isolated from Prydz Bay, Antarctica in 1991/92 and were maintained in culture under cool white fluorescent light at photosynthetically active radiation (PAR) intensity of 5.11 Wm^{-2}. *C. simplex, S. microtrias* and *N. curta* were grown in f/2 medium (GUILLARD and RYTHER, 1962) and a mixed flagellate and colonial life stage culture of *Phaeocystis pouchetii* was grown in GP5 (LOEBLICH and SMITH, 1968). An exponentially growth phase culture of each species of was diluted 1:6 with fresh nutrient medium two days before *in situ* incubation. Immediately before irradiation the cultures were thoroughly mixed and two hundred and fifty m*l* of each species transferred to each of three Whirlpak bags which transmitted light above 220 nm (PAR, UV-A and UV-B treatment). One bag remained unscreened while the remainder were screened with mylar (which transmitted wavelengths above 320 nm–PAR and UV-A treatment) or polycarbonate (which transmitted wavelengths above 370 nm–PAR treatment). Like PRÉZELIN and SMITH (1993) we found no evidence of inhibition of growth or photosynthesis by UV-B induced toxicity of Whirlpaks (HOLM-HANSEN and HELBLING, 1993). Interspecific differences in growth and photosynthesis were species specific rather than treatment dependant. Bags were then incubated at 0.30 m depth in near-shore waters off Davis between 19th February and 26th February 1992.

A further seven 50 m*l* subsamples of each species were transferred to 100 m*l*

Whirlpak bags for primary production incubations. Three bags were screened as above, one was screened with opaque black plastic as a dark bag control and a further three were immediately acidified with 200 μl of 6 N HCl as time zero blanks. Primary production was estimated using the methods of SCHINDLER *et al.* (1972) modified after GRIFFITH (pers. comm.). At the conclusion of the production incubation a 7 m*l* subsample from each Whirlpak was transferred to a 20 m*l* scintillation vial and acidified as above. The vials were then shaken at 200 rpm for 2 hours to remove inorganic ^{14}C. Counts were performed in Lumagel using a LKB 1215 Rackbeta II liquid scintillation counter. Estimates of count efficiency were performed each sample day before performing decay counts. The mean of triplicate time zero blanks and dark bag uptake were subtracted from counts in calculation of primary production. *In situ* incubations were performed at 0.30 m depth for 4 hours between 10.30 and 12.30 solar time. Determination of primary production by each species and under each light treatment was repeated after 4 and 8 days *in situ* incubation. The light treatment of each primary production incubation was the same as that from which the subsample was removed.

Surface UV-A and UV-B irradiance was integrated *in situ* using an International Light IL 1700 Radiometer. Primary calibration of detector response was made using a National Institute of Standards and Technology intercomparison package (NIST Test # 534/240436-88) with further calibration using four International Light primary transfer standards.

A 5 m*l* subsample of each *in situ* incubated treatment for each species was inoculated into 30 m*l* of fresh growth medium. These cultures were returned to culture maintenance conditions for estimation of growth rate and survival and will henceforth be referred to as "ongrowth" cultures. A further 10 m*l* was removed at each sample time and fixed with Lugol's iodine for estimation of cell concentration using inverted microscope cell counts over 15 replicate fields. Cell concentration in ongrown cultures was estimated 3 and 9 days after subculturing and the growth rate of the control culture then used to calculate the number of surviving cells immediately after irradiation from the final cell concentration in irradiated treatments (DAVIDSON *et al.*, 1994). Calculations ensure that only viable cells capable of contributing to population growth are included in the survival of each species under each light treatment. After 2, 4, and 8 days *in situ* exposure subsamples were removed from each 250 m*l* Whirlpak and the *in situ* cell concentration, survival and rate of ongrowth again estimated.

The equivalent spherical diameters of *P. pouchetii* flagellate and colonial cells were measured microscopically using a Zeiss Photomicroscope II at 1000× magnification. A total of 200 equivalent spherical diameters were measured from each light treatment which had been irradiated for 8 days and ongrown for a further 9 days.

3. Results

Surface UV-A and UV-B irradiances were integrated during the duration of the 8 days *in situ* incubation (Figs. 1, 3 and 4) and during each 4 hour primary

production incubation (Figs. 5 and 6). Surface irradiances were high during the first 2 days of incubation as were irradiances during the primary production incubations. Between days 2 and 4 conditions were frequently overcast and surface irradiances were low, particularly at UV-B wavelengths. Irradiances during primary production incubation were similarly low. Between day 4 and 8 integrated UV-A and UV-B irradiance increased again and surface irradiances integrated over the duration of the primary production incubation were the highest observed.

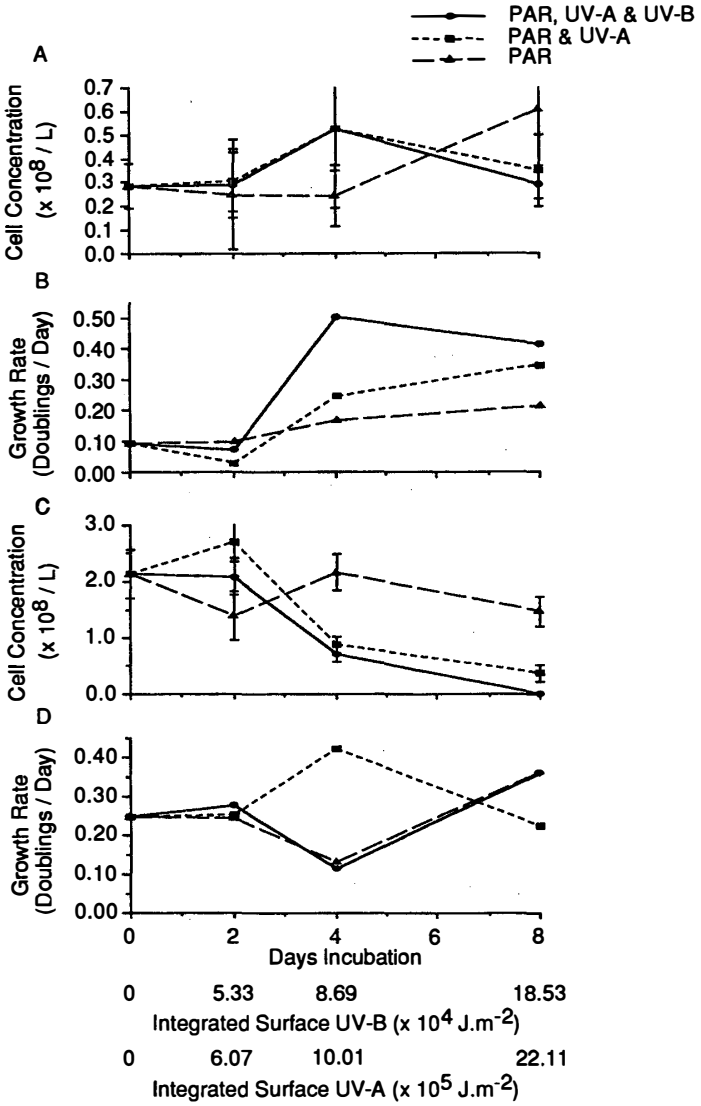

Fig. 1. Colonial Phaeocystis *(A) cell concentration during* in situ *irradiation and (B) growth rate of cells incubated for 0, 2, 4 and 8 days, subcultured, returned to culture maintenance conditions and ongrown for 9 days. Flagellate stage* Phaeocystis *(C) cell concentration during* in situ *irradiation and (D) growth rate after irradiation (as above). Growth rate calculated after* VERITY *et al. (1988). Total integrated UV-A and UV-B dose at each* in situ *sample period are given. Error bars represent standard deviation.*

The concentration of colonial *Phaeocystis* changed little during *in situ* incubations (Fig. 1A). Samples which received UV-B in the irradiance did not differ significantly from those that received PAR and UV-A. Only in the incubation which received PAR alone may cell concentration have increased but this never differed significantly from UV exposed treatments. Exposure of colonial *Phaeocystis* to unscreened solar irradiance (PAR, UV-A and UV-B) for periods of more than 2 days greatly increased their rate of post-irradiance ongrowth (Fig. 1B). Colonial cells which received PAR and UV-A also showed a marked but lesser promotion of growth rate while growth of PAR irradiated control samples showed little increase in growth rate with incubation time.

The concentration of flagellate cells fell as a result of *in situ* UV radiation.

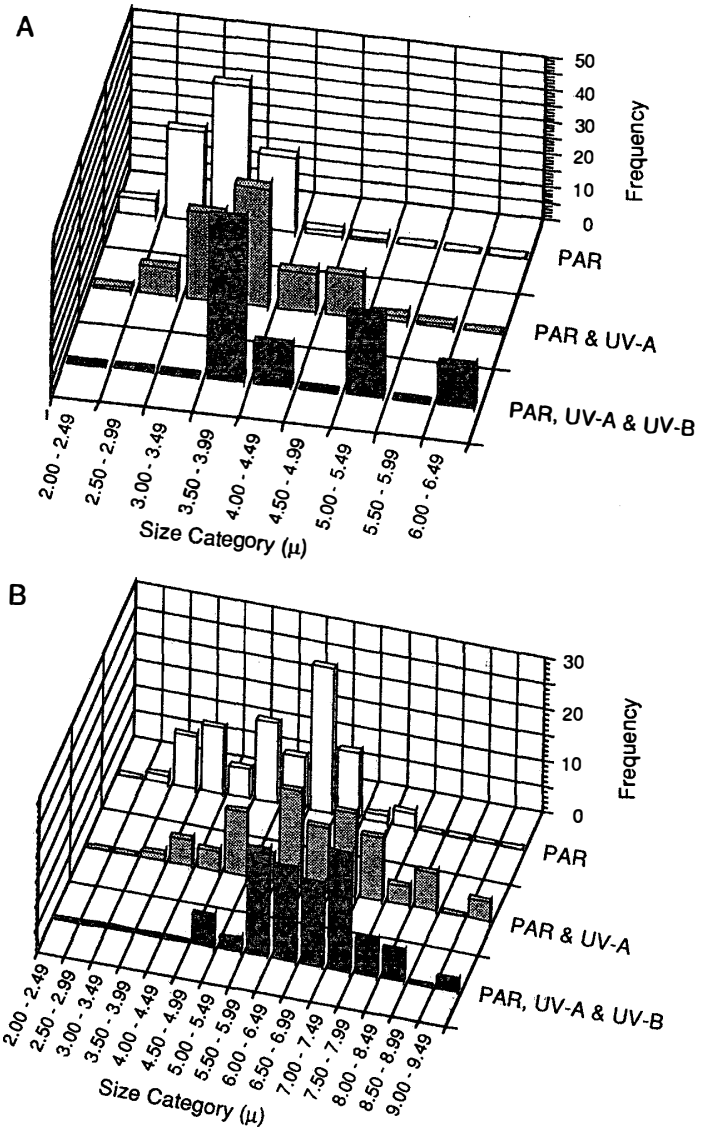

Fig. 2. Cell size distribution of (A) flagellate and (B) colonial cells incubated in situ *at 0.30 m depth for 8 days exposed to PAR, PAR and UV-A or PAR, UV-A and UV-B subcultured and ongrown in culture maintenance conditions for 9 days.*

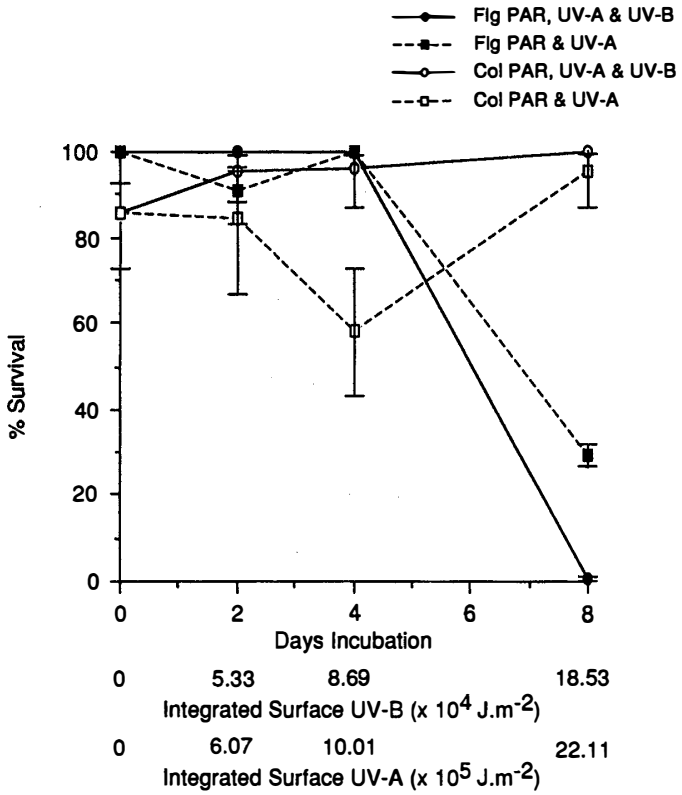

Fig. 3. Percent survival of unscreened (Flg PAR, UV-A & UV-B) or mylar screened (Flg PAR & UV-A) flagellate stage and unscreened (Col PAR, UV-A & UV-B) or mylar screened (Col PAR & UV-A) colonial stage Antarctic Phaeocystis *culture during near surface* in situ *incubations. Error bars represent standard error calculated after* Zar *(1984).*

Flagellate concentrations in the PAR irradiated treatment remained approximately constant (Fig. 1C). Cells subject to PAR and UV-A declined to around 20% of their original numbers over the 8 day period while flagellate concentrations exposed to PAR, UV-A and UV-B declined at a similar rate but where almost absent after 8 days incubation. The rate of ongrowth of the flagellate stage after irradiation changed little with time irrespective of irradiance treatment (Fig. 1D). The only exception was the PAR and UV-A treatment after 4 days incubation, the reasons for which are uncertain.

The cell diameter of the colonial and flagellate cells increased with addition of UV-A and UV-B to the irradiance (Fig. 2A and B). Mean flagellate cell diameter in cultures receiving PAR were 3.18 μm (Fig. 2A). This increased to 3.71 μm with addition of UV-A to the exposure and reached 4.50 μm when also exposed to UV-B. The mean cell diameter of the colonial stage was 5.03 μm after exposure to PAR only (Fig. 2B). This increased to 6.18 μm with the introduction of UV-A and further increased to 6.59 μm after exposure to UV-A and UV-B.

Exposure of colonial stage *Phaeocystis* to natural irradiances over a period of 8 days caused no decline in survival (Fig. 3). Survival of flagellate stage

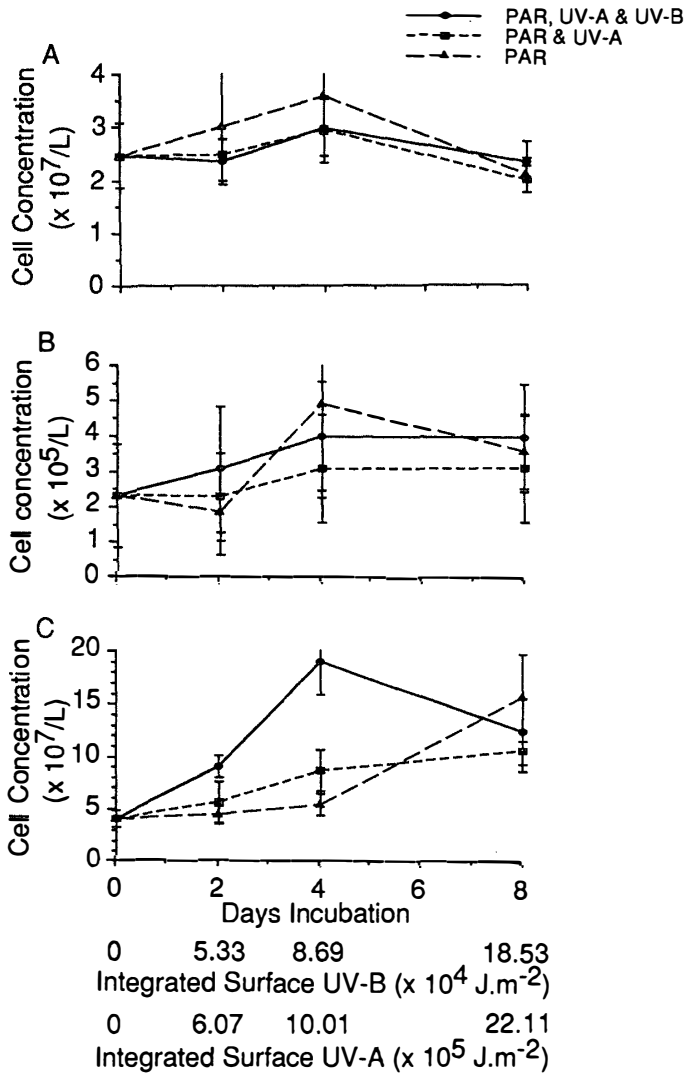

Fig. 4. Cell concentration of (A) C. simplex, *(B)* S. microtrias *and (C)* N. curta *exposed to PAR, PAR and UV-A or PAR, UV-A & UV-B during near surface* in situ *incubations. Total integrated UV-A and UV-B dose at each* in situ *sample period are given. Error bars represent standard deviation*

Table 1. Percent survival of PAR and UV-A or PAR,UV-A and UV-B irradiated diatoms exposed to near surface in situ *irradiance for 8 days calculated after* DAVIDSON et al. *(1994). L1 and L2 represent upper and lowe standard errors calculated after* ZAR *(1984).*

Species	PAR & UV-A			PAR, UV-A & UV-B		
	Mean	L1	L2	Mean	L1	L2
S. microtrias	95.88	99.87	86.77	93.53	98.55	85.28
C. simplex	99.17	99.97	96.04	98.59	99.91	95.70
N. curta	100.00	100.00	100.00	100.00	100.00	100.00

Table 2. Growth rate of diatoms after 8 days near surface in situ *exposure to PAR, PAR and UV-A or PAR, UV-A and UV-B, subcultured and ongrown in culture maintenance conditions for 9 days. Growth rate calculated after* VERITY et al. *(1988).*

	Growth rate		
Species	PAR	PAR & UV-A	PAR, UV-A & UV-B
S. microtrias	0.263	0.218	0.122
C. simplex	0.674	0.336	0.266
N. curta	0.253	0.289	0.657

Phaeocystis also remained high for the first 4 days incubation but declined markedly between days 4 and 8. The decline was greatest when cultures were exposed to the PAR, UV-A and UV-B but a major decline was also observed in the treatment with PAR and UV-A.

The concentration of *C. simplex* and *S. microtrias* cells did not increase significantly during *in situ* incubation (Fig. 4A and B). Concentrations of *N. curta* did significantly increase in all treatments. The greatest increase was observed in the unscreened treatment during the first 4 days of irradiation after which the concentration declined toward day 8 (Fig. 4C). None of the diatom species exhibited any significant decline in the survival as a result of UV irradiance (Table 1). Interspecific differences were observed in the growth rate of cultures established and ongrown after irradiance treatments (Table 2). Growth of *S. microtrias* and *C. simplex* declined with the addition of UV-A and UV-B to the irradiance. UV-B was responsible for the greatest decline in the growth rate of *S. microtrias* while the greatest decline in growth rate of *C. simplex* was caused by UV-A. *N. curta* showed a promotion of growth rate in the unscreened treatment similar to that observed for *Phaeocystis*. Unlike *Phaeocystis*, little promotion of growth rate resulted from addition of UV-A to the irradiance.

Total photosynthetic rates of *Phaeocystis* only declined slightly with incubation time and little difference was observed between the irradiance treatments (Fig. 5A). The carbon fixation rate per cell in the PAR screened treatment also exhibited little change with time (Fig. 5B), however, fixation rates per cell in treatments which receiving UV-A or UV-A and UV-B increased rapidly. This resulted from the decrease in flagellate cell concentration (Fig. 1C). In addition, the irradiance treatment and the flux rate during the production incubation appear to have little effect on the rate of production by the colonial stage (Fig. 5A). The diatom species investigated showed differing responses in production to the irradiance treatment. Although rates of production were frequently lowest in treatments which received UV-B, inhibition of photosynthesis was only slight. The rate of production per cell by the diatom species investigated was not reflected in changes in cell concentration during *in situ* incubation. Little difference was observed in primary production per cell of *C. simplex* between light treatments, however, the production by each cell approximately doubled during

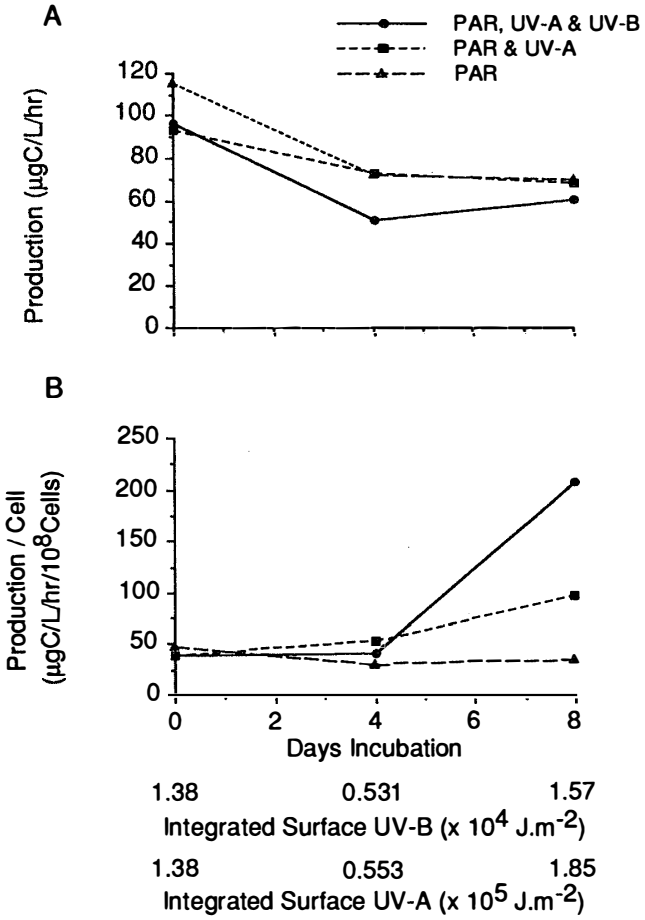

Fig. 5. The rate of (A) primary production and (B) production per cell by cultured Phaeocystis *taken from near surface* in situ *incubations. 50 ml sub-samples were removed from polycarbonate, mylar or unscreened light treatments and replaced* in situ *beneath the same screen for 4 hr incubations to estimate primary production. Surface UV-A and UV-B irradiance was integrated for the duration of the production incubations.*

in situ incubation (Fig. 6A). Production per cell by *S. microtrias* appeared to decline slightly during incubation (Fig. 6B), while that by *N. curta* declined by approximately 90% in all treatments (Fig. 6C).

4. Discussion

4.1. Survival

Flagellate stage *Phaeocystis* was the only organism examined which demonstrated a significant decline in cell concentration during *in situ* exposure and survival after irradiation. UV-A was responsible for most of this decline. JOKIEL and YORK (1984) found that long term inhibition of growth was due almost entirely to UV-A. Our results indicate that it can also account for most of the mortality. Addition of UV-B to the irradiance further reduced the cell concentration of the flagellate stage but differences were slight and only significant after 8

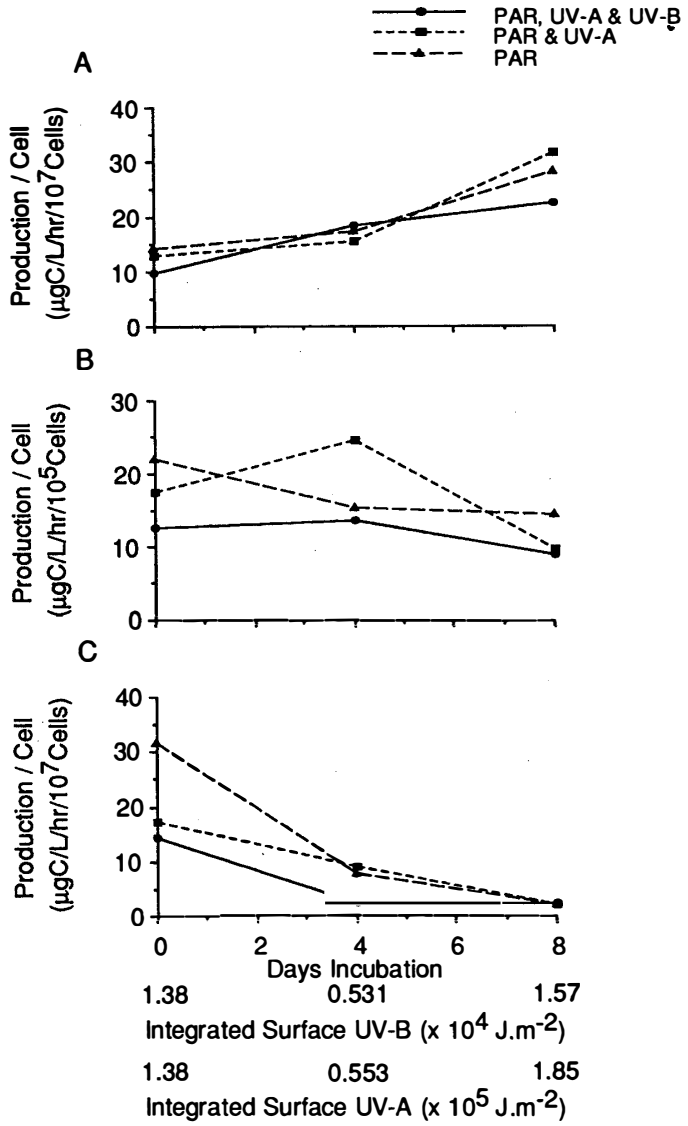

Fig. 6. The rate of *primary production per cell by (A)* C. simplex, *(B)* S. microtrias *and (C)* N. curta *during near surface* in situ *incubations performed as for Phaeocystis.*

days irradiation. KARENTZ *et al.* (1991) and CALKINS and THORDARDOTTIR (1980), indicate that UV-B induced mortality would act as a selective pressure on the species composition of the phytoplankton community. As UV-A irradiances are not significantly enhanced as a result of ozone depletion, our results indicate that no major decline in *Phaeocystis* or diatom abundance as a result of UV-B induced mortality is likely.

Antarctic colonial *Phaeocystis* possesses high concentrations of UV absorbing compounds which provided substantial protection from UV radiation (MARCHANT *et al.*, 1991). The flagellate stage lacks these compounds and exhibited greater vulnerability to UV radiation. Our results support this finding. Antarctic near surface UV irradiances are sufficient to cause mortality in flagellate *Phaeocystis* populations but the colonial stage maintains its photosynthetic production during

exposure to UV and exhibits increased growth and cell size and high survival after irradiation with UV-A and UV-B.

4.2. Growth

UV is reportedly responsible for significant decreases in the growth rate of phytoplankton (THOMSON *et al.*, 1980; HANNAN *et al.*, 1980; JOKIEL and YORK, 1984; DÖHLER, 1984, 1985). WORREST *et al.* (1981) attributed this to interspecific differences in genetic limits of photoadaptation. During *in situ* incubations using diluted exponentially growth phase cultures we found only *N. curta* sustained significant growth. This suggests that growth may have been inhibited as a result of PAR, however, JOKIEL and YORK (1984) found high levels of PAR were not inhibitory to growth. Alternatively, features of the *in situ* environment such as temperature may have reduced growth rates. SMITH *et al.* (1992) found that growth of *Phaeocystis* (presumably colonial) in Antarctic waters was inhibited by inclusion of UV-B in the natural solar irradiance while the growth of *Chaetoceros socialis* was not. We did not observe significant inhibition of colonial *Phaeocystis* growth by UV-B but this may have been due to our use of monospecific nutrient enriched cultures or differences in experimental methods and strain.

In situ exposure of *Phaeocystis* to UV resulted in an increase in cell diameter in both the flagellate and colonial life stages of subcultures established immediately after irradiation and allowed to grow in culture maintenance conditions for a further 9 days. An increase in cell size may be caused by inhibition of cell division (BADOUR, 1968) or an increase in light intensity (THOMSON *et al.*, 1991). The concentration of flagellate cells decreased in irradiances treatments including UV-A or UV-A and B but their growth rate after irradiation did not differ markedly between irradiance treatments indicating that flagellate cells which survived irradiation were able to sustain normal growth. No significant change in colonial cell concentration was observed in any of the irradiance treatments during *in situ* irradiation and those that received UV-A or UV-A and UV-B exhibited enhanced growth rates after irradiation. Thus, unlike BADOUR (1968), the observed increase in cell size as a result of exposure to UV radiation appear not to be as a result of inhibition of cell division. The increase in cell size observed by THOMSON *et al.* (1991) were reversible after 12 hours while the increase we observed was wavelength dependant and persisted for at least the 9 days of ongrowth. Our results indicate a sustained change in cell metabolism of UV irradiated *Phaeocystis*. Changes in size of the flagellate cells may, however, also reflect UV induced changes in flagellate cell stage (KORNMANN, 1955; L. PEPERZAK pers. comm.) or formation of flagellates from the colonial stage (VELDHUIS *et al.*, 1986; VERITY *et al.*, 1988; DAVIDSON and MARCHANT, 1992b).

Exposure of *N. curta* to PAR, UV-A and UV-B caused a rapid increase in cell concentrations for the first 4 days of incubation suggesting high UV tolerance by this species. UV irradiances between days 4 and 8 were high. During this time the concentration of *N. curta* in this treatment declined suggesting that exposure of the cells beyond an upper threshold becomes inhibitory to their growth or that the UV exposure may impose cumulative stress on cell physiology which is

expressed only after extended periods of irradiation (CALKINS and THORDARDOTTIR, 1980; JOKIEL and YORK, 1984; DÖHLER, 1984; VOSJAN *et al.*, 1990; MARCHANT *et al.*, 1991).

Interspecific differences were observed in the growth rate of cultures established and ongrown after irradiance treatments. Ongrowth of *N. curta* showed the division rate of the PAR, UV-A and UV-B irradiated treatment for this species was more than twice that of other treatments despite its rates of primary production during incubation being low. To sustain growth after irradiation the photosynthetic rate of *N. curta* must recover rapidly, however, the differences in the rate of ongrowth by *N. curta* must largely reflect UV-B induced effects on processes other than photosynthesis. DAVIDSON *et al.* (1994) suggests the possibility of UV-B being involved in repair of UV-A related damage. This may explain the higher growth rate of the unscreened treatment than that receiving UV-A. The reason for the lower growth rate of the PAR irradiated ongrowth culture is unclear but, like colonial *Phaeocystis*, exposure to UV may promote growth after irradiation. Laboratory studies will be undertaken to further investigate the apparently contradictory responses of *N. curta* to UV-B exposure. Ongrowth of *S. microtrias* showed greatest reduction in growth rate as a result of UV-B irradiance. That of *C. simplex* was reduced most by UV-A but declined further with addition of UV-B to the irradiance. The reduced rate of ongrowth by these species may, at least in part, reflect the degree of inhibition of photosynthesis by UV during *in situ* incubation.

The photobiological strategy favored as a result of UV-B exposure would depend on the duration and intensity of the irradiance received. Though the diatoms we have examined survive high UV irradiances for a short time (DAVIDSON *et al.*, 1994) their long term survival and growth during and after irradiation may not advantage them over species that appear more vulnerable. For example, *S. microtrias* is able to survive UV-B intensities approximately an order of magnitude higher than that of *Phaeocystis* (DAVIDSON *et al.*, 1994), however, it grows little better than *Phaeocystis* during *in situ* incubation and irradiation with UV-B results in depression of growth after exposure. The rate of ongrowth for *Phaeocystis* after exposure to UV-B irradiation was approximately 3 times that of the PAR irradiated culture and this species would likely be favored at sublethal irradiances.

4.3. Production

UV is widely reported as being inhibitory to photosynthesis (*e.g.* LORENZEN, 1979; JITTS *et al.*, 1976; JOKIEL and YORK, 1984; WORREST *et al.*, 1981; SMITH and BAKER, 1989; WORREST, 1986; HÄDER and WORREST, 1991; VOYTEK, 1989). Estimates of inhibition by near surface UV-B irradiances range from 15–30% while UV-A resulted in a further decline of around 50% (HELBLING *et al.*, 1992; HOLM-HANSEN, 1990; HOLM-HANSEN *et al.*, 1989; MASKE, 1984). In Antarctic waters the increase in UV-B as a result of ozone depletion apparently result in a reduction of at least 6–12 % in primary production (SMITH *et al.*, 1992). We found inhibition of production was variable, probably as a result of variations in

tolerance and photoadaptive ability of each species and changes in the *in situ* irradiance received. Photoinhibition was frequently greatest for treatments which received UV-B in the irradiance but differences between light treatments were slight and percent inhibition seldom reached the magnitude reported above. However, we used nutrient enriched monospecific cultures in our investigation and the lower sensitivity may reflect the high nutrient environment (CULLEN and LESSER, 1991)

The colonial *Phaeocystis* cell concentration remained relatively constant during the 8 days of irradiation. Exposure of flagellate cells to UV for periods exceeding 2 days significantly reduced their concentration in culture. However, in comparison with the PAR irradiated control, the rate of production in UV irradiated treatments did not markedly decline and the production per *Phaeocystis* cell greatly increased. Although no size fractionated production was conducted to separate the flagellate and colonial stages of *Phaeocystis*, the colonial stage in the life cycle of this alga appears largely responsibly for photosynthesis during *in situ* incubation. This may be as a result of possessing UV absorbing compounds (MARCHANT *et al.*, 1991) which protect the photosynthetic apparatus and/or the sustained changes in physiology as a result of UV exposure. *C. simplex* was the only diatom which increased its rate of photosynthesis per cell during *in situ* incubation suggesting photoadaptation of this species to the near surface light environment. Primary production by *N. curta* declined markedly but this was apparently largely due to PAR irradiance rather than UV wavelengths. This contrasts with the finding of previous authors that PAR has little inhibitory effect upon photosynthesis (JOKIEL and YORK, 1984; BUHLMANN *et al.*, 1987).

5. Conclusion

The net effect of survival, photo-protective mechanisms, photosynthetic rate and growth would determine the niche available to each species in the UV environment. The nature and duration of UV exposure in Antarctic waters is yet to be fully determined. The shallow blooms of the MIZ, which are responsible for much of the primary production in the Southern Ocean, appear vulnerable to increased UV-B radiation as a result of stratospheric ozone depletion (MARCHANT and DAVIDSON, 1991). Interspecific differences in the responses of the phytoplankton to UV exposure have led to the suggestion that species or strains possessing greater tolerance to UV will be favored (HÄDER and WORREST, 1991; KARENTZ, 1991; MARCHANT and DAVIDSON, 1991). However, our results indicate that the interaction of UV intensity, dose and the photobiology of each species is complex and the impact on the organisms is not great. The consequent changes in phytoplankton species composition may be sufficiently slow or slight that they are undiscernible from spatial and interannual variability.

Acknowledgments

We gratefully acknowledge John GIBSON and Andrew MCMINN for their comments on the manuscript and Jeff HUNT, Paul SYNNOT, Lionel WHITEHORN, Peter SPRUNK and Fiona SCOTT for their assistance with field operations.

References

AINLEY, D. G., FRASER, W. R., SULLIVAN, C. W., TORRES, J. J., HOPKINS, T. L. and SMITH, W. O. (1986): Antarctic mesopelagic micronekton: Evidence from seabirds that pack ice affects community structure. Science, **232**, 847–849.

BADOUR, S. S. (1968): Experimental separation of cell division and silica shell formation in *Cyclotella cryptica*. Microbiology, **62**, 17–33.

BOTHWELL, M. L., SHERBOT, D., ROBERGE, A. C. and DALEY, R. J. (1993): Influence of natural ultraviolet radiation on lotic periphytic diatom community growth, biomass accrual, and species composition: short-term versus long-term effects. J. Phycol., **29**, 24-35.

BUHLMANN, B., BOSSARD, P. and UEHLINGER, U. (1987): The influence of longwave ultraviolet radiation (UV-A) on the photosynthetic activity (^{14}C-assimilation) of phytoplankton. J. Plankton Res., **9**, 935–943.

CALKINS, J. and THORDARDOTTIR, T. (1980): The ecological significance of solar UV radiation on aquatic organisms. Nature, **283**, 563–566.

CULLEN, J. J. and Lesser, M. P. (1991): Inhibition of photosynthesis by ultraviolet radiation as a function of dose and dosage rate: results for a marine diatom. Mar. Biol., **111**, 183-190.

DAVIDSON, A. T. and MARCHANT, H. J. (1992a): Protist abundance and carbon concentration during a *Phaeocystis*-dominated bloom at an Antarctic coastal site. Polar Biol., **12**, 387–395.

DAVIDSON, A. T. and MARCHANT, H. J. (1992b): The biology and ecology of *Phaeocystis* (Prymnesiophyceae). Progress in Phycological Research, Vol. 8, ed. by F. E. ROUND and D. J. CHAPMAN. Bristol, Biopress, 1–45.

DAVIDSON, A. T., BRAMICH, D., MARCHANT, H. J. and MCMINN, A. (1994): Effects of UV-B irradiation on growth and survival of Antarctic marine diatoms. to be published in Mar. Biol.

DÖHLER, G. (1984): Effect of UV-B radiation on the marine diatoms Lauderia annulata and *Thalassiosira rotula* grown in different salinities. Mar. Biol., **83**, 247–253.

DÖHLER, G. (1985): Effect of UV-B radiation (290-320 nm) on the nitrogen metabolism of several diatoms. J. Plant Physiol., **118**, 391–400.

DÖHLER, G. (1987): Effect of irradiation on nitrogen metabolism in marine diatoms and phytoplankton. Oceanis, **13**, 487–493.

EL-SAYED, S. Z., STEPHENS, F. C., BIDIGARE, R. R. and ONDRUSEK, M. E. (1990): Effect of ultraviolet radiation on Antarctic marine phytoplankton. Antarctic Ecosystems; Ecological Change and Conservation, ed. by K. R. KERRY and G. HEMPEL. Berlin, Springer, 379–385.

FREDERICK, J. E. and SNELL, H. E. (1988): Ultraviolet radiation levels during the antarctic spring. Science, **241**, 438–440.

FRYXELL, G. A. and KENDRICK, G. A. (1988): Austral spring microalgae across the Weddell Sea ice edge: Spatial relationships found along a northward transect during AMERIEZ 83. Deep Sea Res., **35**, 1–20.

GALA, W. R. and GIESY, J. P. (1991): Effects of ultraviolet radiation on the primary production of natural phytoplankton assemblages in Lake Michigan. Ecotoxicol. Environ. Saf., **22**, 345-361.

GARRISON, D. L. and BUCK, K. R. (1989): The biota of Antarctic pack ice in the Weddell Sea and Antarctic Peninsular regions. Polar Biol., **10**, 211-219.

GARRISON, D. L., BUCK, K. R. and FRYXELL, G. A. (1987): Algal assemblages in the antarctic pack ice and in ice-edge plankton. J. Phycol., **23**, 564–572.

GIESKES, W. W. C. and KRAAY, G. W. (1990): Transmission of ultraviolet light in the Weddell Sea:

Report of the first measurements made in the Antarctic. BIOMASS Newsl., **12**, 12–14.

GUILLARD, R. R. L. and RYTHER, J. H. (1962): Studies of the marine plankton diatoms *Cyclotella nana* HUSTEDT and *Detonula confervaceae* (CLEVE) GRAN. Can. J. Microbiol., **8**, 229–239.

HÄDER, D.-P. (1986): Effects of solar and artificial UV radiation on motility and phototaxis in the flagellate *Euglena gracilis*. Photochem. Photobiol., **44**, 651–656.

HÄDER, D.-P. (1987): Effects of UV-B radiation on photomovement in the desmid, *Cosmarium cucumis*. Photochem. Photobiol., **46**, 121–126.

HÄDER D.-P. (1988): Ecological consequences of photomovement in microorganisms. Photochem. Photobiol., **1** (B), 385–414.

HÄDER, D.-P. and WORREST, R. C. (1991): Effects of enhanced solar ultraviolet radiation on aquatic ecosystems. Photochem. Photobiol., **53**, 717–725.

HANNAN, P. J., SWINNERTON, J. W., LAMONTAGNE, R. A. and PATOUILLET, C. (1980): Effect of UV-B on algal growth rate and trace gas production. Aquatic Toxicology, ed. by J. G. EATON *et al.* American Society for Testing and Materials, 177–190 (ISBN 0-686-76097-2).

HELBLING, E. W., VILLAFANE, V., FERRARIO, M. and HOLM-HANSEN, O. (1992): Impact of natural ultraviolet radiation on specific marine phytoplankton species. Mar. Ecol. Prog. Ser., **80**, 89–100.

HOBSON, L. A. and HARTLEY, F. A. (1983): Ultraviolet irradiance and primary production in a Vancouver Island fjord, British Columbia, Canada. J. Plankton Res., **5**, 325–331.

HOLM-HANSEN, O. (1990): Effects of ultraviolet-B and ultraviolet-A on photosynthetic rates on Antarctic phytoplankton. Antarct. J. U. S., **25**, 177–178.

HOLM-HANSEN, O. and HELBLING, E. W. (1993): Polythene bags and solar ultraviolet radiation. Science, **259**, 534.

HOLM-HANSEN, O., MITCHELL, B. G. and VERNET, M. (1989): Ultraviolet radiation in antarctic waters: Effects on rates of primary production. Antarct. J. U. S., **24**, 177–178.

JITTS, H. R., MOREL, A. and SAIJO, Y. (1976): The relation of oceanic primary production to available photosynthetic irradiance. Aust. J. Mar. Freshwater Res., **27**, 441–454.

JOKIEL, P. L. and YORK R. H., Jr. (1984): Importance of ultraviolet radiation in photoinhibition of microalgal growth. Limnol. Oceanogr., **29**, 192–199.

KARENTZ, D. (1990): Ecological considerations of the Antarctic ozone hole in the marine environment. Effects of solar ultraviolet radiation on biogeochemical dynamics in aquatic environments, ed. by N. V. BLOUGH and R. G. ZEPP. 137–140

KARENTZ, D. (1991): Ecological considerations of Antarctic ozone depletion. Antarctic Science, **3**, 3–11.

KARENTZ, D. and LUTZE, L. H. (1990): Evaluation of biologically harmful ultraviolet radiation in Antarctica with a biological dosimeter designed for aquatic environments. Limnol. Oceanogr., **35**, 549–561.

KARENTZ, D., CLEAVER, J. E. and MITCHELL, D. L. (1991): Cell survival characteristics and molecular responses of Antarctic phytoplankton to ultraviolet-B radiation. J. Phycol., **27**, 326–341.

KORNMANN, P. (1955): Beobachtungen an *Phaeocystis*-kulturen. Helgoländer Wiss. Meeresunters., **5**, 218–233.

LEOBLICH, A. R. III and SMITH, V. E. (1968): Chloroplast pigments of the marine dinoflagellate *Gymnodinium resplendens*. Lipids, **3**, 3–15.

LORENZEN, C. J. (1979): Ultraviolet radiation and phytoplankton photosynthesis. Limnol. Oceanogr., **24**, 1117–1120.

LUBIN, D., FREDERICK, J. E., BOOTH, C. R., LUCAS, T. and NEUSCHULER, D. (1989): Measurements of enhanced springtime ultraviolet radiation at Palmer Station Antarctica. Geophys. Res. Lett., **16**, 783–785.

MARCHANT, H. J. and DAVIDSON, A. T. (1991): Possible impacts of ozone depletion on trophic interactions and biogenic vertical carbon flux in the Southern Ocean. Proceedings of the International Conference on the Role of Polar Regions in Global Change, ed. by G. WELLER *et al.* Fairbanks, Geophysical Institute, 397–400.

MARCHANT, H. J., DAVIDSON, A. T. and KELLY, G. J. (1991): UV-B protecting pigments in the

marine alga *Phaeocystis pouchetii* from Antarctica. Mar. Biol., **109**, 391–395.

MASKE, H. (1984): Daylight ultraviolet radiation and the photoinhibition of phytoplankton carbon uptake. J. Plankton Res., **6**, 351–357.

MITCHELL, D. L. and KARENTZ, D. (1990): Molecular and biological responses of Antarctic phytoplankton to ultraviolet radiation. Antarct. J. U. S., **25**, 174–175.

PRÉZELIN, B. B. and SMITH, R. C. (1993): Polythene bags and solar radiation: Response. Science, **259**, 534–535.

SCHINDLER, D. W., SCHMIDT, R. V. and RIED, R. A. (1972): Acidification and bubbling as an alternative to filtration in determining phytoplankton production by the ^{14}C method. J. Fish. Res. Board Can., **29**, 1627–1631.

SMITH, R. C. and BAKER, K. S. (1989): Stratospheric ozone, middle ultraviolet radiation and phytoplankton productivity. Oceanography, **2**, 4–10.

SMITH, R. C., PRÉZELIN, B. B., BAKER, K. S., BIDIGARE, R. R., BOUCHER, N. P., COLEY, T., KARENTZ, D., MACINTYRE, S., MATLICK, H. A., MENZIES, D., ONDRUSEK, M., WAN, Z. AND WATERS, K. J. (1992): Ozone depletion: Ultraviolet radiation and phytoplankton biology in Antarctic waters. Science, **255**, 952–959.

SMITH, W. O., Jr. and NELSON, D. M. (1986): Importance of ice edge phytoplankton production in the Southern Ocean. BioScience, **36**, 251–257.

STOLARSKI, R. S., KRUEGER, A. J., SCHOEBERL, M. R., MCPETERS, R. D., NEWMAN, P. A. and ALPERT, J. C. (1986): Nimbus 7 satellite measurements of the springtime Antarctic ozone decrease. Nature, **322**, 808–811.

THOMSON, B. E., WORREST, R. C. and VAN DYKE, H. (1980): The growth response of an estuarine diatom (*Melosira nummuloides* [Dillw.] Ag.) to UV-B (290–320 nm) radiation. Estuaries, **3**, 69–72.

THOMSON, P. A., HARRISON, P. J. and PARSLOW, J. S. (1991): Influence of irradiance on cell volume and carbon quota for ten species of marine phytoplankton. J. Phycol., **27**, 351–360.

TRODAHL, H. J. and BUCKLEY, R. G. (1989): Ultraviolet levels under sea ice during the Antarctic spring. Science, **245**, 194–195.

VELDHUIS, M. J. W., COLIJN, F. and VENEKAMP, L. A. H. (1986): The spring bloom of *Phaeocystis pouchetii* (Haptophyceae) in Dutch coastal waters. Neth. J. Sea Res., **20**, 37–48.

VERITY, P. G., VILLAREAL, T. A. and SMAYDA, T. J. (1988): Ecological investigations of blooms of *Phaeocystis pouchetii*-1. Abundance, biochemical composition and metabolic rates. J. Plankton Res., **10**, 219–248.

VETH, C. (1991): The evolution of the upper water layer in the marginal ice zone, austral spring 1988, Scotia-Weddell Sea. J. Mar. Sys., **2**, 451–464.

VOSJAN, J. H., DÖHLER, G. and NIEUWLAND, G. (1990): Effect of UV-B irradiance on the ATP content of microorganisms of the Weddell Sea (Antarctica). Neth. J. Sea Res., **25**, 391–393.

VOYTEK, M. A. (1989): Ominous future under the ozone hole: Assessing biological impacts in Antarctica. Washington, Environmental Defence Fund, 1–69.

WORREST, R. C. (1983): Impact of solar ultraviolet-B radiation (290–320 nm) upon marine microalgae. Physiol. Plant., **58**, 428–434.

WORREST, R. C. (1986): The effect of solar UV-B radiation on aquatic systems: An overview. Effects of Changes in Stratospheric Ozone and Global Climate, ed. by J. G. TITUS. 175–199.

WORREST, R. C., THOMSON, B. E. and VAN DYKE, H. (1981): Impact of UV-B radiation upon estuarine microcosms. Phytochem. Phytobiol., **33**, 861–867.

ZAR, J. H. (1984): Biostastical analysis. 2nd ed. New Jersey, Prentice-Hall, 653 p.

(Received May 6, 1993; Revised manuscript received September 7, 1993)