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Response of two Antarctic marine bacteria to different natural UV radiation doses and wavelengths

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Abstract: The aim of this work was to investigate the effect of different fractions of UVR on two Antarctic marine bacteria (*Arthrobacter* UVvi and FCB-related UVps strains) and to study the relationship between the bacterial viability and the UVB dose. Ten experiments exposing strains to natural solar radiation were conducted in Potter Cove, South Shetland Islands. The effect of different UVR wavelengths on viability was analysed by using cultures in quartz bottles covered with interferential filters. Six treatments were performed: DARK, PAR (with UVR shielded off), UVA360, UVA320, UVB305 and UVB280. In all UVR treatments, strains showed significant losses of viability under high and moderate irradiance and no differences were observed between UV treatments. Under high UVB dose (15.0 kJ m^{-2} received in only two hours), the effect of UVB treatments was significantly higher than that observed under UVA treatments. However, UVA caused a significant reduction on bacterial viability. Survival rates were negatively correlated with integrated UVB dose, FCB-related UVps being more sensitive than *Arthobacter* UVvi. The similar values observed in viability when the same dose was received in different time periods suggested that DNA repair mechanisms are not much effective in these strains. The different response to the UV wavelength ranges studied here suggests that changes in the spectral composition of natural radiation could differentially affect the components of Antarctic marine bacterial communities.

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Key words: Antarctic microorganisms, solar radiation, UV filters, ozone depletion

Introduction

Stratospheric ozone depletion produces changes in the spectral composition of solar ultraviolet radiation (UVR, 280–400 nm) reaching Antarctica and the Southern Ocean resulting in increased levels of biologically harmful, short-wavelength ultraviolet-B radiation (UVB, 280–320 nm) (Staehelin *et al*. 2001) in Spring. Previous work has shown that both, UVB and UVA radiation (320–400 nm) impact marine carbon cycling by principally affecting the phytoplankton and bacterioplankton, which represent the basis of the oceanic food webs (Herndl *et al*. 1993, 2000, Vincent & Neale 2000, Booth *et al.* 2001a, Biggs & Moody 2003). Davidson & van der Heijden (2000) found that inhibition of bacterial growth increased with dose and time exposure to UVB of the bacterioplankton from natural Antarctic microbial communities. The effect of solar UVR on bacterioplankton depends on the spectral attenuation coefficients of the water column as well as the time of exposure and protection mechanisms of the organisms when they are passively moving in the mixing layer. In this sense, Booth *et al.* (2001a) reported that the RecA protein (a regulator of the Dark Repair System) represents an important component in the ability of the marine bacterium *Vibrio natriegens* to survive exposure to solar UVR in the Gulf of Mexico. These authors reported that the increase in the cellular RecA levels shows a diel cycle caused by the UVB band but either by the UVA wavelengths.

Bacterioplankton seem to lack UV screening pigments such as mycosporines or scytonemins (Karentz 1994, Garcia-Pichel 1994). As a consequence, they are more prone to UVB stress than larger eukaryotic organisms and when exposed to UVB their DNA showed about twice the amount of cyclobutane dimers than the > 0.8 μm plankton fraction (Jeffrey *et al*. 1996). Bacterioplankton are no longer regarded solely as a final decomposer of organic material. According to the "microbial loop" hypothesis, bacterioplankton are seen in the centre of a food web, having a similar function to phytoplankton and protists (Karl 1993). Despite the crucial role of the bacterioplankton in the functioning of marine ecosystems, little is known about the effects induced by different ranges of the natural UVA and UVB wavelengths on isolated marine bacteria, as well as on the mortality caused by accumulated UVR doses. Booth *et al.* (2001a) found that *V. natriegens* viability was affected as substantially by light from which UVB was filtered as by solar radiation that contained UVB. However, RecA concentration in this strain increased in response to exposure to light of < 360 nm wavelength but not to UVA of > 360 nm wavelength. Different levels of sensitivity to UVR were observed in marine bacterial isolates by Joux

et al. (1999). In addition, Booth (personal communication, 2005) has observed a synergistic effect of UVA and UVB on several cellular processes. These reports suggest that species composition of natural marine bacterial communities could also be modified by UV stress, as was observed by Arrieta *et al*. (2000).

In a previous work, we isolated two psychrotolerant Antarctic heterotrophic marine bacteria and found that these strains showed a significant loss of viability after exposure to high levels of natural UVR (Hernández *et al*. 2002). As the response of the previously isolated strains seemed to be different under UVA and UVA + UVB radiation, the aim of this research was to investigate the spectral responses of these two Antarctic marine bacteria to different bands of UVR in the UVA and UVB ranges and to study the relationship between bacterial viability and UVB dose received by these bacteria.

Materials and methods

Study area

Both strains were isolated from surface water at Potter Cove, King George Island (62°14'S, 58°40'W, South Shetland Islands). Field experiments were carried out on a beach there and laboratory experiments were conducted in the Argentinean-German Dallman Laboratory (Jubany Station). In summer, this area presents an average cloud cover of 6.4 octas (80%). Average daily dose of UVB of 40.8 kJ m^{-2} and 29.9 kJ m^{-2} were reported by Hoyer *et al*. (2001) for December and January respectively.

Bacterial strains

Strains were psychrotolerant and both showed a growth temperature range of 0–30ºC and an optimum temperature between 20ºC and 25ºC. The selected strains were *Arthrobacter* UVvi and UVps, a strain related to *Flavobacterium–Cytophaga–Bacteroides* (FCB) group, which is a complex group in the *Bacteroidetes* division (Hernández *et al*. 2004). Partial 16S rDNA sequences of FCB-related UVps and *Arthrobacter* UVvi are deposited in the GeneBank under the accession numbers AY220353 and AY220354 respectively.

Irradiance measurements

Incident UVR was measured continuously using a multichannel UV spectroradiometer developed at the Alfred Wegener Institute for Polar and Marine Research and distributed by Isitec Bremerhaven (Germany). This instrument is based on a Bentham DM 150 double monochromator, with a multichannel detector system. UVB data were recorded every second from 290 nm to 320 nm range with a data point every 1.35 nm. Data were stored as 1 min average. The 290–320 nm range was used as experimental wavelengths because < 290 nm is below the detection limit for the solar altitudes reached at Potter Peninsula. PAR and UVA radiation data were obtained using a PUV-510 spectroradiometer (Biospherical Instrument Inc). UVA doses were calculated using irradiances at 340–380 nm.

Evaluation of the solar radiation effect

Ten solar exposure experiments were performed on days with different irradiance regime during the Antarctic summers 2001–02 and 2002–03. Bacterial suspensions from cultures grown on marine agar 2216 (Difco) plates were prepared for each strain using artificial seawater. A mixed bacterial suspension (50 ml in seawater supplemented with 0.1% peptone) was used in each quartz bottle in an incubation chamber. This chamber was immersed in a continuous water circulation bath in order to minimise temperature fluctuations in the flasks (average temperature during the assays was 5.5 ± 1.0ºC). Interferential quartz filters (Schott R) were used to cover the flasks in the different irradiance treatments (triplicates). Treatments considered were:

a) DARK (control system with a black filter),

b) PAR, 420 nm cut-off filter,

c) UVA360, (PAR + UV-A >360 nm) (360 nm cut-off filter),

d) UVA320, (PAR + UV-A) (320 nm cut-off filter),

e) UVB305, (PAR + UV-A + UV-B > 305 nm) (305 nm cut-off filter),

f) UVB280, (PAR + UV-A + UV-B) (no filters).

Samples from treatments were taken at times which differ between the experiments due to the different solar radiation regimes existing during each one. Serial dilutions of the samples were plated (0.1 ml) on marine agar 2216 and incubated in dark for 7 days at 20 °C. This temperature was chosen because in previous analysis it proved to shorten the incubation period of these psychrotolerant bacterial strains and yielded the same results as those obtained using lower temperatures (data not shown). Between 30 and 300 colonies were counted on each plate and results are expressed as Colony Forming Units per ml (CFU ml^{-1}).

The viability of the strains under different treatments was analysed and compared using Specific Death Rate (SDR). SDR represents the slope of the curves describing the loss of viability during a given time interval, and is expressed in units of the reciprocal of time (Pirt 1975, chapter 7).

Statistical analysis

Bacterial counts data were analysed by Repeated Measures ANOVA and Tukey's Multiple Comparison Test. Individual

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comparisons of pairs of values at the end of the assays were made using an Unpaired t-test. Viability values of different sampling times from ten experiments were analysed by Non-linear Regression Analysis, using survival (expressed as percentage of the dark treatments) as the dependent variable and UVB integrated dose as the independent one (n = 29 for each strain).

Results

Although ten independent experiments were performed during the study (all of which have been considered for the regression analysis and the 3D plots presented below in this section), here we show the results obtained from three representative experiments. Results obtained from these three experiments represent the pattern of responses observed in all the experiments carried out. Experiment 1 was carried out on a partially cloudy day and represents a "moderate dose" situation. Total UVB dose was 17.06 kJ m^{-2} and the dose rate was 2.83 kJ m^{-2} h^{-1}. Experiment 2 was carried out on a sunny day and was selected as a "high dose" situation because it showed the highest UVB radiation levels among all the ten experiments. Total UVB dose was 30.45 kJ m^{-2} and the dose rate was 3.81 kJ m^{-2} h^{-1}. This UVB dose was accumulated in 8 h, and represents a high UVB radiation level for Potter Peninsula, where a maximum UVB dose of 52.4 kJ m^{-2} was reported by Hoyer *et al*.

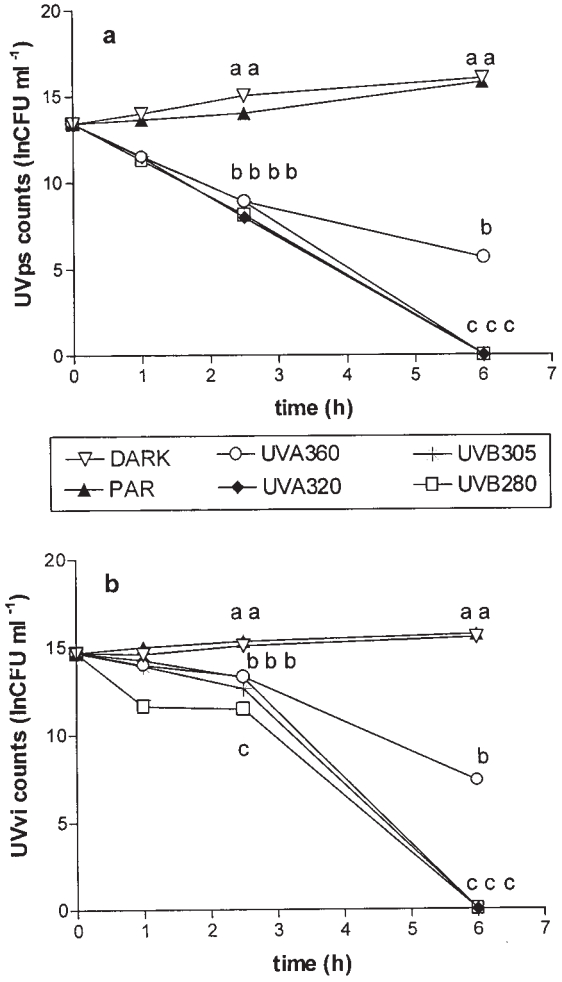

Fig. 1. Effect of solar radiation dose on viability of **a.** FCB-related UVps, and **b.** *Arthrobacter* UVvi registered on Experiment 1, carried out on 23 December 2001 (12h30–18h30) at Jubany Station. Treatments tested were DARK (∇), PAR (▲), UVA360 (O), UVA320 (♦), UVB305 (✻), UVB280 (□). Different letters represent significant differences among samples from the same sampling time. Error bars indicate standard deviation (SD) of triplicates. When bars of the SD are not visible then the SD is smaller than the symbol.

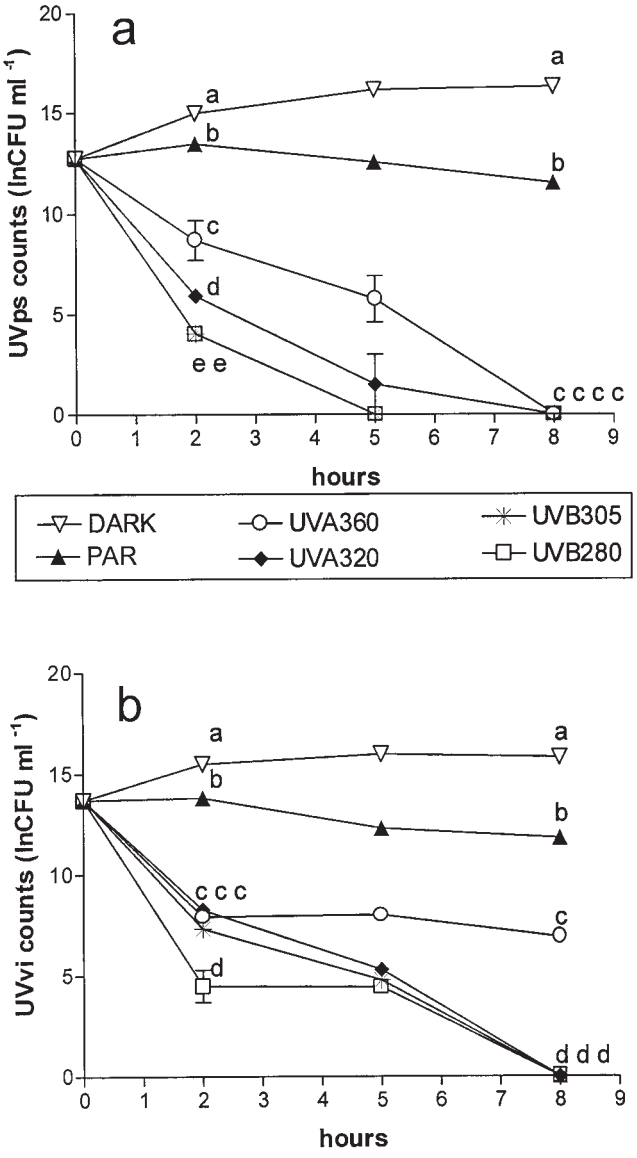

Fig. 2. Effect of solar radiation dose on viability of **a.** FCB-related UVps and **b.** *Arthrobacter* UVvi registered on Experiment 2, carried out on 27 December 2001 (11h30–19h30) at Jubany Station. Details as in Fig. 1.

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(2001) for December 1997 for a daily period of 20 h. Experiment 3 was selected as representative of a low radiation situation. It was carried out a totally cloudy day, receiving a total UVB dose of 9.13 kJ m^{-2}. Dose rate in this experiment was 0.76 kJ m^{-2} h^{-1}.

Experiment 1 (23 December 2001) was made under moderate irradiance regime and bacterial viability at different sampling times for this experiment is shown in Fig. 1. During the first 2.5 h the UVB dose was 12.2 kJ m^{-2} (UVA dose 134.2 kJ m^{-2}). At that time only 0.5% and 4% of the populations of FCB-related UVps and *Arthrobacter* UVvi respectively survived in the UVB280 treatment. When we compared the effect of the six treatments, we observed no significant differences between PAR and DARK for both strains. These two treatments differed from all the UVR treatments ($P < 0.05$). In addition, at the initial period, whereas FCB-related UVps (Fig. 1a) showed no significant difference between any of the UVR treatments (UVA360, UVA320, UVB305 and UVB280) *Arthrobacter* UVvi showed a significant decrease in viability ($P < 0.05$) in the UVB280 compared with the rest of UV treatments (Fig. 1b). Despite the fact that UVA360 showed no differences compared with the others UV treatments at the initial period, at the end of the assay this treatment showed higher ($P < 0.05$) survival values. This was observed for both strains.

Experiment 2 (27 December 2001) was carried out under a high irradiance regime. After 2 h of exposure (UVB dose 15.0 kJ m^{-2} and UVA dose 169.5 kJ m^{-2}), *Arthrobacter* UVvi and FCB-related UVps showed 0.01% of survival in UVB280 treatment (Fig. 2). During this initial period, as was observed in the first experiment, both strains showed differences in viability between the UVR treatments and PAR and DARK ($P < 0.01$). In contrast with the moderate radiation regime, both UVB treatments (UVB280 and UVB305) showed similar effects on FCB-related UVps viability and differed ($P < 0.05$) from the UVA320 and UVA360 (Fig 2a). For *Arthrobacter* UVvi, even though UVB treatments caused a greater reduction in viability than the UVA treatments, the effect of UVB280 was more pronounced ($P < 0.05$) than that induced by the UVB305 and UVA treatments (Fig. 2b). Viability observed under PAR was significantly lower than under DARK ($P < 0.05$). This difference was more evident at the end of the period due to a decrease in viability of the PAR treatment. At the end of this assay, PAR dose was 3520 kJ m^{-2}, more than twice the amount received by the strains during Experiment 1 (1580 kJ m^{-2}) which showed no differences in viability between PAR and DARK treatments.

Experiment 3 (24 February 2002) was carried out under a low irradiance regime (Fig. 3). Over the first 5 h of exposure the UVB and UVA doses were 6.3 kJ m^{-2} and 76.8 kJ m^{-2} respectively. While *Arthrobacter* UVvi was only slightly affected (91% survival after full UVR exposure), FCB-related UVps showed a major impact (15% survival after full UVR exposure). When all treatments were compared at this time, *Arthrobacter* UVvi showed no significant differences ($P > 0.05$) between irradiated treatments, all of which showed significantly lower CFU values compared with DARK (Fig. 3b). For FCB-related UVps the DARK and PAR treatments were not significantly different in terms of CFU while CFU for the UVA320, UVB305 and UVB280 treatments were significantly lower than of the PAR treatment ($P < 0.05$) with the UVB280 being the most deleterious. The remaining viability of FCB-related UVps after 5 h under UVA360 was similar to that observed under DARK or PAR, but at the end of assay UVA360 showed a

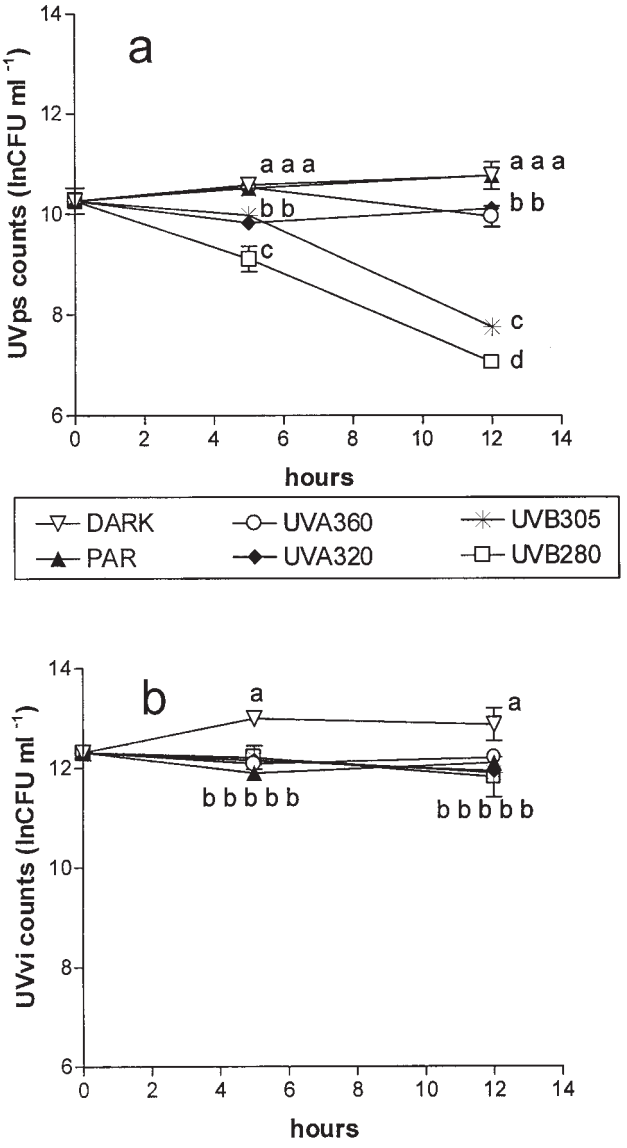

Fig. 3. Effect of solar radiation dose on viability of **a.** FCB-related UVps, and **b.** *Arthrobacter* UVvi registered on Experiment 3, carried out on 24 February 2002, (8h30–20h30) at Jubany Station. Details as in Fig. 1.

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significant decrease in viability ($P < 0.05$) compared with those treatments (Fig. 3a). Figure 4 shows the SDR values observed in the initial period of exposure for the three experiments. Initial exposure time for the high, moderate and low radiation regimes was 2 h, 2.5 h and 5 h respectively. Results obtained with the FCB-related strain are shown in Fig. 4a. In the moderate irradiance experiment only UVA360 showed differences from the rest of the UV treatments ($P < 0.05$) whereas in high irradiance experiment SDR showed significant differences ($P < 0.05$) between UVB and UVA treatments. For *Arthrobacter* UVvi significant differences ($P < 0.01$) between UVR treatments and PAR were observed in the SDR values under moderate and high irradiance (Fig. 4b). SDR values were significantly different ($P < 0.05$) between UVB and UVA treatments in the high and moderate irradiance assays. In these assays significant differences ($P < 0.05$) were also observed between UVB305 and UVB280 treatments, but no differences were detected between UVA320 and UVA360. *Arthrobacter* UVvi showed higher SDR values than FCB-related UVps for all UVR treatments in the high and moderate irradiance experiments except for UVA360 under high irradiance condition. Bacterial viability (expressed as the ratio between CFU observed in UVB280 or UVB305 and DARK) obtained from 10 experiments with different radiation regimes decreased exponentially with the increase in UVB dose (Fig. 5). A significant logistic regression ($P < 0.05$) was obtained for UVps under both UVB280 ($r^2 = 0.8811$) and UVB305 ($r^2 = 0.9451$) treatments (Fig. 5a).

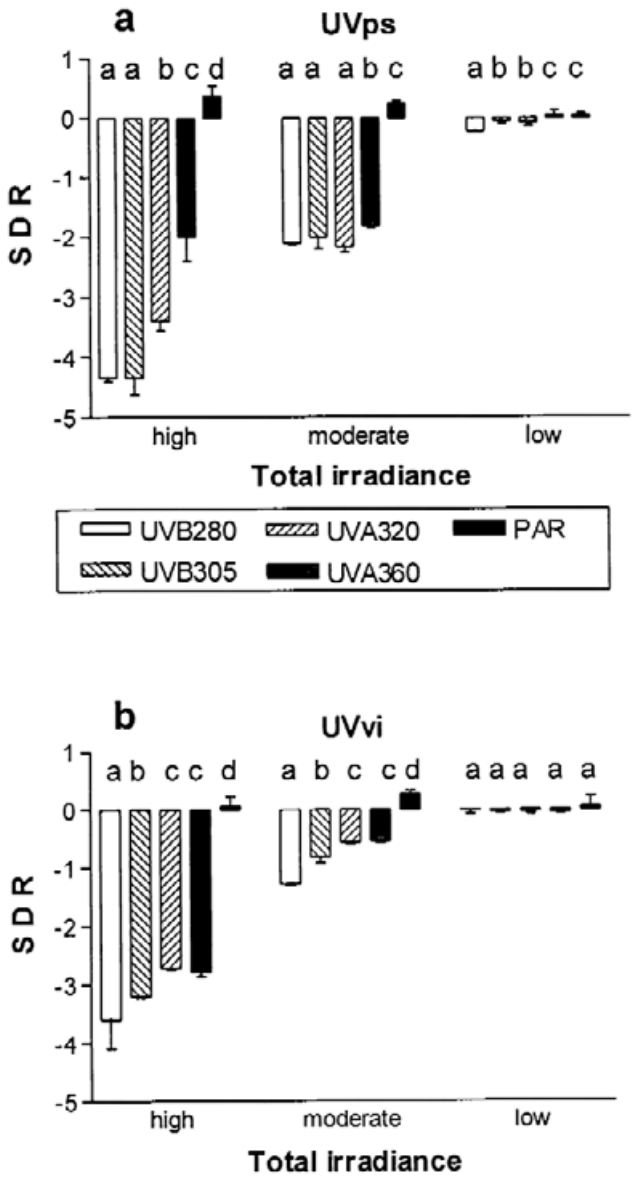

Fig. 4. Specific Death Rate (SDR) values observed in the initial period of exposure for the low (UVB dose rate: 0.76 kJ m^{-2} h^{-1}), moderate (UVB dose rate: 2.83 kJ m^{-2} h^{-1}) and high (dose rate: 3.81 kJ m^{-2} h^{-1}) radiation doses experiments. **a.** FCB-related UVps and **b.** *Arthrobacter* UVvi. Significant differences ($P < 0.01$) between UVR treatments and PAR, for each experiment are indicated with different letters.

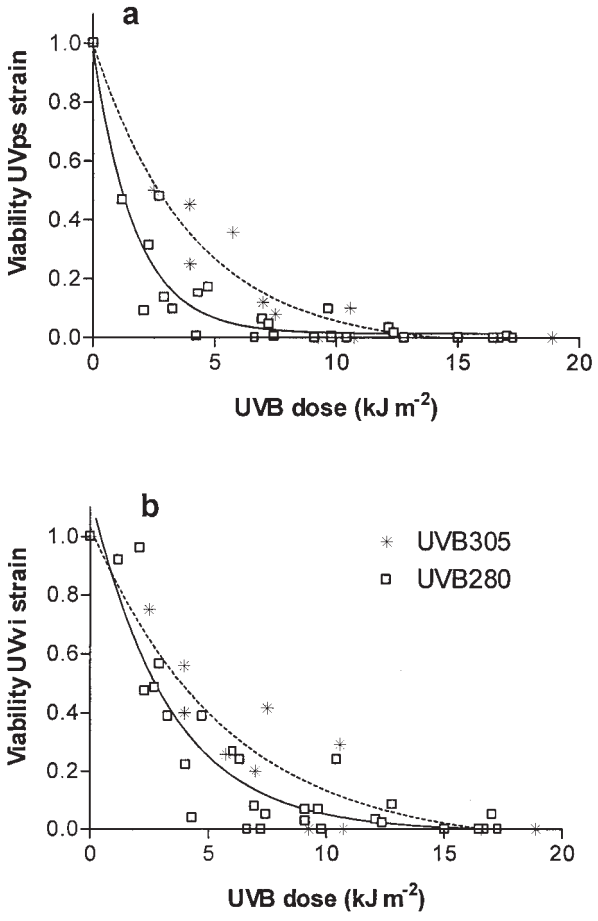

Fig. 5. Significant logistic regression ($P < 0.05$) plotted between bacterial viability values (expressed as the ratio between UVB280 or UVB305 and DARK treatments) and UVB integrated dose for **a.** FCB-related UVps, and **b.** *Arthrobacter* UVvi strains, obtained from 10 experiments performed under different radiation regimes.

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Values of lethal dose 50 (LD 50) for UVB280 (1.2 kJ m^{-2}) and UVB305 (2.8 kJ m^{-2}) showed significant differences ($P < 0.05$) in this strain. Similar logistic regressions (Fig. 5b) were observed for UVvi ($r^2 = 0.8477$ under UVB280 and $r^2 = 0.8813$ under UVB305). In this case LD50 were 2.3 kJ m^{-2} for UVB280 and 4.0 kJ m^{-2} for UVB305 ($P < 0.05$). When the response of the strains was compared using the LD 50, UVps proved to be more sensitive to UVB radiation than UVvi and significant differences ($P < 0.05$) were observed under both UVB280 and UVB305 treatments. In addition, under UVB280, UVps showed 10% of remaining viability at 4.0 kJ m^{-2} and UVvi showed the same remaining viability at 7.5 kJ m^{-2}. Under UVB305 UVps and UVvi showed 10% of initial viability at 8.4 kJ m^{-2} and 11.1 kJ m^{-2} respectively.

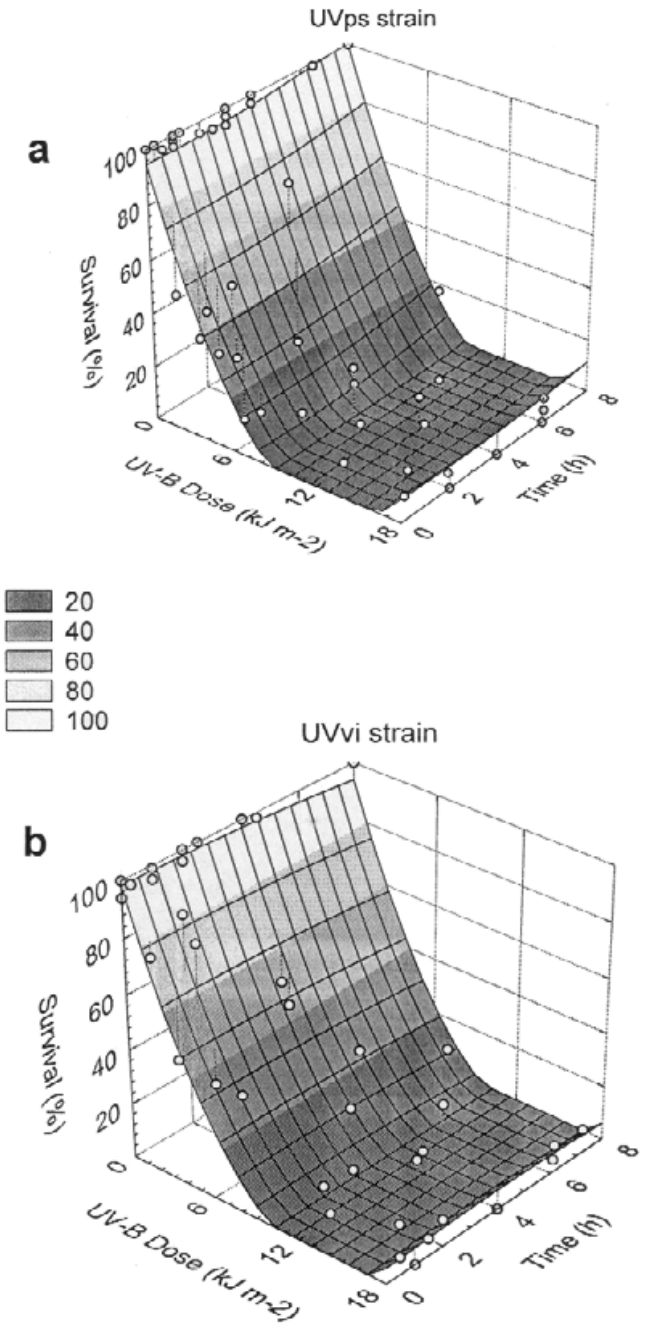

Fig. 6. 3 D plot obtained between the UVB dose, bacterial mortality and time of exposure for **a.** FCB-related UVps, and **b.** *Arthrobacter* UVvi strains. Survival values are expressed as the percentage ratio between CFU in UVB280 and DARK treatments.

We suggested previously (Hernández *et al*. 2002) that the mortality values for the strains studied were dependent on the UVB dose but independent of the time in which such dose was accumulated. Results obtained in this work seems to support this assumption, as can be observed in Fig. 6 where the UVB dose, bacterial mortality and time are shown simultaneously in a 3D plot.

Discussion

The UVB radiation reaching the Antarctic surface causes deleterious effect on the natural bacterial strains (Davidson & van der Heijden 2000, Booth *et al.* 2001b). We previously observed a negative effect of the UVR on FCB-related UVps and *Arthrobacter* UVvi (Hernández *et al*. 2002) reporting values of bacterial mortality greater than those observed by Davidson & van der Heijden (2000). However, similar bacterial mortality was reported by Helbling *et al*. (1995) working with both, isolated strains and natural bacterial assemblages and Booth *et al.* (2001b) using microcosms systems. The deleterious effect of UVA on marine heterotrophic bacteria, which has been previously observed, was also observed for both studied strains (Kim & Watanabe 1994, Sommaruga *et al.* 1997, Booth *et al.* 2001b, Hernández *et al*. 2004). Portions of the UVA spectrum are involved in DNA damage repair by activation of the photoenzymatic repair mechanism (Kaiser & Herndl 1997, Huot *et al*. 2000). Our previous results suggested that in *Arthrobacter* UVvi and FCB-related UVps the DNA repair mechanisms were not effective in reducing the effect of UV during the exposure period and one of them even failed to recover after 24 h in the dark (Hernández *et al* 2004). It is remarkable that in our experiments, although the strains were growing for seven days in the dark after exposure to solar radiation, differences in CFU were still detectable. Even though under this condition photoenzymatic repair was not possible, the dark repair mechanism should still work. This fact reinforces the assumption that, under the experimental conditions, such dark repair mechanisms were not effective.

The effect on the bacterial viability of the different wavelength ranges of UVA and UVB studied showed a complex interaction among λ, irradiance and the individual strain. Similar interactions have been observed by Booth *et al*. (unpublished data) in laboratory studies with *Vibrio natriegens* using discrete wavelengths from an artificial UVR source. Data obtained from the experiment showed in the result section highlight the behaviour of UVA360

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treatment. Although it comprises the UVA wavelengths closest to PAR, it showed a significant deleterious effect on both strains under high and moderate irradiance. This suggests inefficient photoenzymatic repair in these strains. Despite the fact that the UVA320 treatment showed high mortality under moderate and high irradiance conditions, mortality was lower than under the UVB treatments.

Analysis of the response of the strains to the different UVB wavelengths (which are directly affected by changes in stratospheric ozone concentration) is an important point in inferring the effects that the presence of the ozone hole and the subsequent increase in the incident UVB radiation can exert on the Antarctic marine bacterioplankton. The trials under different solar irradiance presented here highlight the interspecific differences between the strains. Stepanova (2004), working with heterotrophic bacteria from the Black Sea, reported that tolerance of marine bacteria to UVR is conditioned by their seasonal adaptation to increasing levels of UVR and also suggested that there might be a seasonal substitution of the sensitive species by the tolerant ones. Other authors also reported significant interspecific differences in UVB sensitivity of marine bacteria (Joux *et al*. 1999, Arrieta *et al*. 2000, Booth *et al*. 2001b). On the other hand, Winter *et al*. (2001), using denaturing gradient gel electrophoresis (DGGE), found that only 10% of the operational taxonomic units (OTUs) detected in North Sea bacterioplankton appeared to be affected by both UVB and UVA exposure. One of the OTUs constantly affected in Winter *et al.* assays belonged to the FCB group, indicating that this member of the bacterial community was highly sensitive to the UVR. However, the authors did not say if this OTU represented an important member of the natural bacterioplankton community.

Under the low radiation treatment, there was a positive effect on the survival of FCB-related UVps when the UVB $\lambda < 305$ was screened out. The more resistant strain *Arthrobacter* UVvi showed no difference in responses under the different UVB wavelength ranges, suggesting that although there exists a differential effect of the diverse UVB wavelengths ranges, this is only evident when the accumulated dose is low and the strain is markedly sensitive to the UVB.

Under the moderate and high radiation treatments, where the solar radiation dose was higher, the effects of UVB wavelength ranges on FCB-related UVps at the end of the experiments were difficult to differentiate and the effects of the total UV and UV with $\lambda > 305$ were similar. Only in some of the assays and at the initial periods of exposure were differences observed for $\lambda > 320$. When working with a more UV-resistant strain, *Arthrobacter* UVvi, the general pattern of response to the different wavelengths was similar. However, during the initial period of exposure, there seems to exist a higher tolerance to the UV wavelengths present under the UVB305 treatment. The higher viability values and dose-mortality plots support this assertion.

Greater deleterious effects observed under the UVB305 treatment compared with the UVA320 agree with those reported by Wilhelm *et al*. (2002) who found twice the damage in DNA (expressed as CPDs concentration in calf thymus DNA segments) exposed to UVB $\lambda > 305$ than in those observed under the same dose of UVA $\lambda > 320$. This differential effect could have important consequences for the aquatic environment. In the surface layer, as an example, on a cloudy day and hence under low solar irradiance, bacterial strains as FCB-related UVps could be differentially affected in comparison with other relatively more resistant strains like *Arthrobacter* UVvi, leading to changes in the bacterial community composition.

The regression observed when all the data for bacterial survival from ten experiments were plotted against UVB integrated dose supports the hypothesis that the studied strains lack efficient mechanisms to repair the deleterious effect of the UVB. This confirms the different sensitivity of the strains, evidenced by the differences in the values of LD50. In addition, despite that in some of the experiments we did not observe differences between the effect of UVB280 and UVB320, when all the data were plotted together, regression analysis showed that significant doses of UVB $\lambda < 305$ reached the earth surface and cause higher mortality than those caused by UVB $\lambda > 305$.

It is important to highlight that for the strains studied under these treatments, the phenomenon of reciprocity seems to be satisfied. The reciprocity is fulfilled when the effect of the applied dose of radiation is independent from the time over which the exposure occurred (Grad *et al*. 2001). Previous studies using different biological models reported the existence of reciprocity (Smith & Baker 1982, Kouwenberg *et al*. 1999). Trocine *et al*. (1981) found reciprocity in two out of three species of seagrass. The third species showed no reciprocity and it was attributed to the presence of a significant photoenzymatic repair activity. In this study we observed that both strains showed similar survival levels when receiving similar UVB dose of radiation independently of the elapsed time for the accumulation of such dose. This fact might be related to the lack of effective repair mechanisms in the strains studied under the assayed conditions and would suggest the existence of the phenomenon of reciprocity.

In conclusion, the Antarctic marine bacterial strains studied here showed a differential response to UVR wavelength ranges. However, for both strains, UVA wavelengths are sufficient to suppress bacterial viability significantly in marine situations, principally UVA $\lambda < 360$. When exposed to the UVB wavelengths, both strains lose viability exponentially with the dose. Similar UVB doses, even accumulated in different time periods, caused similar decreases in viability. The UVB filtering action of the water column and the role of vertical mixing should be analysed using the same biological model in order to build a general overview of the response of these strains to UV in Potter

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Cove, when they are under a complex combination of factors that attenuate or enhance the effects of this part of the solar radiation.

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