

Effects of solar UV and visible irradiance on photosynthesis and vertical migration of *Oscillatoria* sp. (Cyanobacteria) in an Antarctic microbial mat

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ABSTRACT: The migratory patterns of an *Oscillatoria* sp. in a hypersaline microbial mat on Antarctica's McMurdo Ice Shelf, 78° S, 166° E, were examined under the natural solar irradiance of austral summer. Upward and downward migration was monitored in response to different intensities of full solar irradiance and of selected wavelengths achieved using a series of filter and screening treatments. [¹⁴C] photoincorporation rates, using freshly collected cell material, were also measured under different intensities and spectral regions of solar irradiance, as well as at several temperatures of incubation. Our objectives were two-fold: (1) to determine whether this cyanobacterium displays a pattern of migration, photosynthesis, and photoinhibition in response to solar UV and visible irradiance similar to that displayed by motile cyanobacteria in hypersaline ponds of middle latitudes (~28° N), and (2) to examine the impact of temperature on these activities. *Oscillatoria* sp. migrated completely to the surface under low visible irradiance (<8 W m⁻²), green light, and complete darkness; none of these treatments included UV-B or more than 0.26 W m⁻² UV-A. Red light, which included ~0.5 W m⁻² UV-A, promoted a partial upward ascent. UV-A (6.9 W m⁻² UV-A, ~0.1 W m⁻² UV-B), visible irradiance >60 W m⁻², and blue light, which included 0.94 W m⁻² UV-A, caused complete downward migration. Photosynthetic saturation occurred at low visible light levels (~26 W m⁻²), and both photo- and UV-inhibition was apparent. Photosynthetic rates increased in the order 2, <10, <15 and <20°C, and there was no apparent effect of temperature on the magnitude of UV inhibition on photosynthesis. Overall trends in photosynthesis and migration patterns of *Oscillatoria* sp. parallel those described for benthic cyanobacteria of middle latitudes, though the Antarctic species appears to have a lower response threshold to visible light and UV. These results are consistent with the hypothesis that UV radiation is functioning as a primary cue for avoidance of damaging solar radiation in the *Oscillatoria* sp. population, and suggests that UV is involved in the migratory behavior of motile cyanobacteria in microbial mats worldwide.

KEY WORDS: Cyanobacterial mats · Vertical migration · Photosynthesis · *Oscillatoria* sp. · UV · Solar irradiance · Antarctica

INTRODUCTION

Contemporary microbial mats dominated by cyanobacteria exist in habitats usually labeled 'extreme', such as hot springs, desert soils, hypersaline waters, and polar lakes and ponds. Outside of these environments cyanobacterial mats are, at best, ephemeral.

Extreme habitats exclude efficient grazing fauna (e.g. Fenchel 1998) and thus resemble shallow marine ecosystems of the Proterozoic Eon in which stromatolitic cyanobacterial mats were widespread, prior to the evolution of metazoans capable of grazing mats (Farmer 1992). Extant mats are compact and often laminated, with cyanobacteria typically forming the uppermost layer, which is usually less than 1 mm thick. Photosynthesis, aerobic and anaerobic respiration, sulfate-sulfur reduction and other biological processes in these mats are tightly linked due to the mats' compact nature, resulting in steep concentration gradients of

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various chemical species (Revsbech et al. 1983, Cohen & Rosenberg 1989, Jørgensen et al. 1992). Steep gradients in irradiance and spectral quality also occur, caused by both absorption and scattering of incident radiation (Jørgensen & Des Marais 1988, Köhl et al. 1994). These spatial gradients often change dramatically on both a diurnal and seasonal basis, exposing organisms which remain at a fixed vertical position to changing chemical and physical conditions. Many of these changes are potentially harmful, as is the case for strong solar irradiance which can cause irreversible photodamage.

UV radiation, a highly reactive component of the solar radiation flux, is known to have a broad range of biologically deleterious effects. For phototrophic organisms, vulnerable because of their dependence on photosynthetically active radiation, these effects include inhibition of photosynthesis and growth, mutagenesis, and acute physiological stress that may ultimately lead to cell death. Phototrophs have 4 lines of defense against UV exposure: avoidance, screening, quenching, and repair (Garcia-Pichel & Castenholz 1994, Vincent & Quesada 1994, Wynn-Williams 1994, Castenholz & Garcia-Pichel in press). In temperate latitudes, many mat-forming filamentous cyanobacteria exhibit vertical migratory behavior, an avoidance mechanism triggered by diurnal changes in the intensity of solar irradiance (Castenholz 1968, Pentecost 1984, Richardson & Castenholz 1987, Garcia-Pichel et al. 1994, Bebout & Garcia-Pichel 1995). This behavior may also enable organisms to optimize light intensity, allowing maximum photosynthetic rate without inhibition (Garcia-Pichel et al. 1994), thereby improving fitness and competitive ability.

Recently, Kruschel & Castenholz (1998) quantified effects of different components of the natural solar irradiance spectrum on migratory behavior. They examined the effects of varying the solar environment, both UV and visible irradiance, on the vertical movements of 2 filamentous cyanobacteria, *Oscillatoria* cf. *laetevirens* and *Spirulina* cf. *subsalsa*, which are major components of mats in many hypersaline ponds near Guerrero Negro, Baja California Sur, Mexico (28°N). Upward migration of these organisms occurred under low visible (20 to 90 W m⁻²), green (~250 W m⁻²) and red (~470 W m⁻²) light, and complete darkness. Intensities of UV-A above ~1.5 to 2.0 W m⁻² and of broad visible light above ~100 W m⁻² prevented upward migration, and intensities of UV-B as low as 0.1 W m⁻² may have slowed it. Downward migration in *Oscillatoria* cf. *laetevirens* was promoted by high visible light (>400 W m⁻²) and high levels of UV-A (>~10 W m⁻²). *Oscillatoria* cf. *laetevirens* did not, however, retreat from UV-B intensities as high as 0.7 W m⁻². Kruschel & Castenholz (1998) suggested

that UV-B, even at these low light intensities, may have inhibited motility of the trichomes on the mat surface. They further found that UV radiation, as low as 0.05 W m⁻² in the case of UV-B, inhibited short-term photosynthesis of both organisms. Häder (1984) previously demonstrated that UV-B intensities as low as 200 μW m⁻² (2 h ≤ 300 nm) dramatically impaired motility and photosensory responses in some cyanobacteria. Kruschel & Castenholz (1998) concluded that UV radiation serves as an effective cue in the migratory behavior of *Oscillatoria* cf. *laetevirens* and *Spirulina* cf. *subsalsa*.

Oscillatorian cyanobacteria dominate the benthic mats that occur in the abundant meltwater ponds on the ablation moraine of Antarctica's McMurdo Ice Shelf (Vincent 1988, Wynn-Williams 1990, Vincent et al. 1993a). In these ponds, water temperatures during the short open season of 2 to 3 mo seldom rise above 8°C (Hawes et al. 1999), and many deeper ponds never lose their central ice core. In the latter, the water temperature does not rise above 4°C (Vincent 1988). Since the development of the Antarctic ozone hole, there has been much research to discern the implications of the associated increase in transmission of UV radiation, particularly on planktonic communities (see Weiler & Penhale 1994). Because benthic cyanobacteria play a major role in the lakes, ponds, and streams of the Antarctic, and since many of these communities inhabit shallow waters where they are exposed to full solar radiation in summer months, their capacity to respond to changing UV fluxes is an issue of concern (Vincent & Quesada 1994).

Despite the dominance of benthic filamentous cyanobacteria, there have been no empirical studies examining the possible role of vertical migratory behavior as a mechanism to minimize the adverse effects of UV radiation in Antarctic microbial mats. Migratory behavior of a motile oscillatorian has previously been observed in a hypersaline pond in the Bratina Island region of the McMurdo Ice Shelf (Vincent et al. 1993a). In the present study, we sought to elucidate patterns of migration, photosynthesis, and photo- and UV-inhibition in response to both ambient and modified natural solar irradiance in this organism, and to compare these patterns to those of the motile cyanobacteria of Guerrero Negro (Kruschel & Castenholz 1998). A corollary objective was to examine the impact of temperature on these activities. Results provide insight into the direct effects of solar UV radiation on the migratory strategy of this oscillatorian in an Antarctic benthic mat, as well as our larger objective to ascertain whether UV radiation is a migratory cue common to motile cyanobacteria which are prevalent in microbial systems of extreme habitats worldwide.

MATERIALS AND METHODS

Research site. Salt Pond is one of thousands of meltwater ponds occurring on the ablation zone of Antarctica's McMurdo Ice Shelf, $\sim 78^\circ$ S, 166° E. Although migratory behavior by cyanobacteria was observed in benthic mats in other meltwater ponds, it was most pronounced in Salt Pond, the site chosen for this study.

Salt Pond is a shallow, hypersaline pond covering an area of ~ 220 m² (Fig. 1A) and surrounded by a salt deposit enriched in mirabilite ($\text{Na}_2\text{SO}_4 \cdot 10\text{H}_2\text{O}$; Howard-Williams et al. 1989). In January 1998, when this study was conducted, it had a salinity of $\sim 53\%$ (American Optical Refractometer). Unlike the thick, laminated, gelatinous benthic mats commonly associated with other hypersaline waters, this thin benthic mat con-

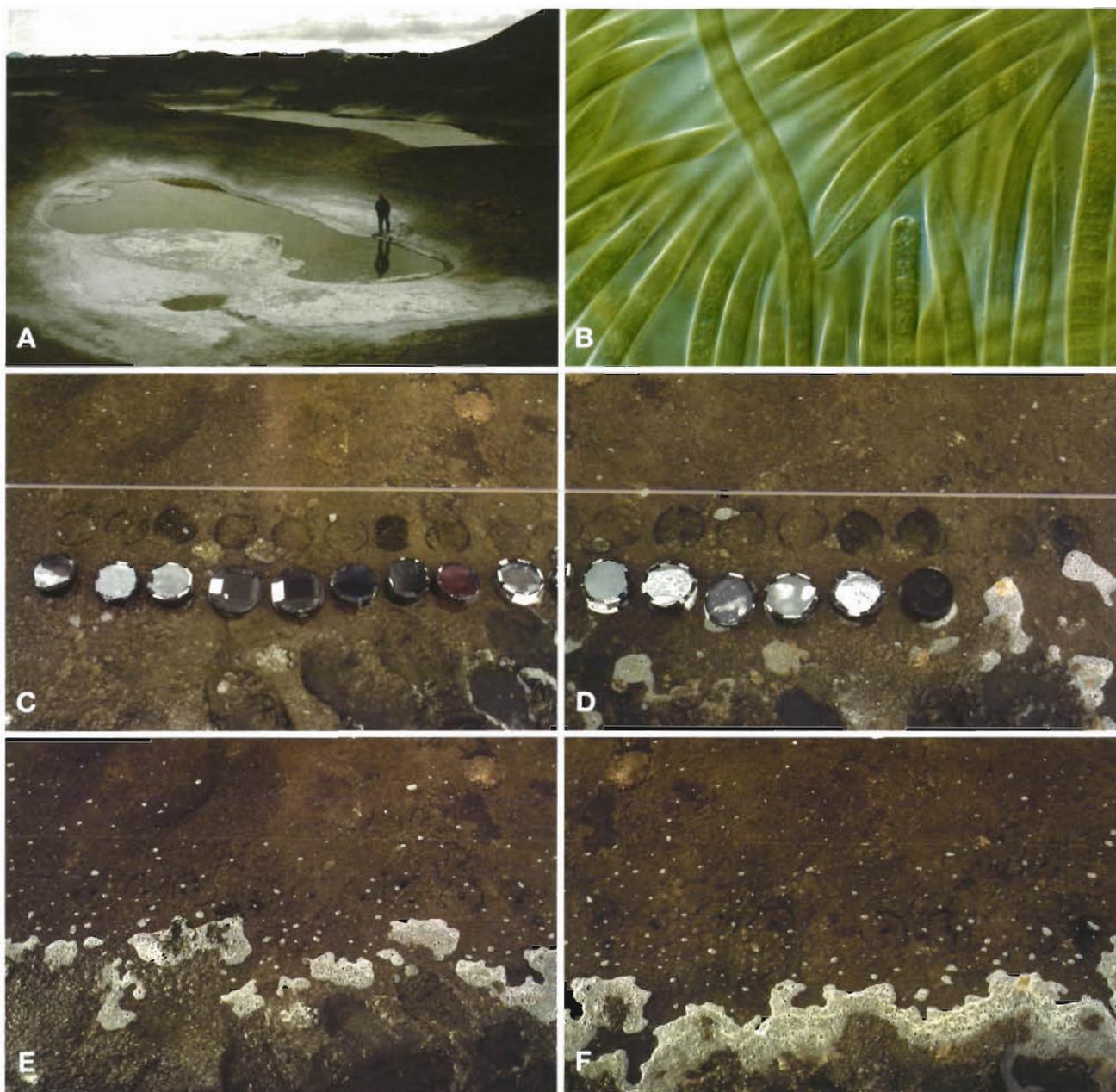


Fig. 1. (A) Salt Pond, McMurdo Ice Shelf (Brack Pond and Bratina Island in the background). (B) *Oscillatoria* sp. 'K' trichomes (~ 7 μm in diameter). (C,D) Upward migration of *Oscillatoria* sp. 'K' in Salt Pond, after 3 h of treatment, from left to right: D, D+3, D+6, UV-A, UV-A/B, blue, green, red, P, P+3, P+6, S, S+3, S+6, dark (see Table 1 and 'Materials and methods' for description). (E,F) In response to the removal of filter treatments from (C,D) and exposure to full solar irradiance for several hours, *Oscillatoria* sp. 'K' migrated back below the surface of the mat (note ring and central coring marks)

tains much inorganic sediment composed of silt and sand. A large, motile oscillatorian, 6 to 7 μm in diameter, dominates the mat (Fig. 1B). Previously referred to as *Oscillatoria* cf. *priestleyi* (e.g. Vincent et al. 1993a,b), it is morphologically classified as morphotype K in Broady & Kibblewhite's (1991) characterization of Antarctic oscillatoriales. *Phormidium* (= *Leptolyngbya*) sp., *Amphipleura* sp., a smaller naviculoid diatom and a unicellular eukaryote were other photosynthetic members of the mat. These, however, were rare in comparison to the dominant cyanobacterium, herein referred to as *Oscillatoria* sp. 'K'. Sequence analysis of 16S rDNA indicates that *Oscillatoria* sp. 'K' is the same organism that was dominant in the pond in January 1990 (Nadeau & Castenholz unpubl. data), when the migratory behavior was first observed. Growth studies performed in the laboratory on isolates of this organism indicate that it is psychrotolerant (Castenholz & Schneider 1993, Nadeau & Castenholz unpubl. data), capable of growth near the freezing point of water yet having a temperature optimum $>15^\circ\text{C}$. During the period of this study, the temperature of Salt Pond, in the shallow region where experiments were conducted, ranged from 1.6 to 10.7°C and averaged $\sim 6.0^\circ\text{C}$. Over 24 h on a sunny day, the temperature commonly ranged from ~ 2 to $\sim 8^\circ\text{C}$.

Irradiance measurements and radiation alteration.

Throughout each of the experiments, incident radiation was repeatedly measured with an International Light Research Radiometer (IL 1700) for 3 wavebands: visible+IR (400 to >1000 nm), UV-A (320 to 400 nm), and UV-B (280 to 320 nm). Reported values were measured for the surface of the water, which was a few cm above the mat. Incident solar radiation was altered using broad band transmission screens with sharp UV cut-offs, as well as zero to 6 neutral density screens. The combinations and intensities (in W m^{-2}) are noted in figure legends. The styrene filter (K-lite UVF CS, Plaskolite Inc, Columbus, OH) blocks most UV radiation (50% T at 395 nm, 5% T at 385 nm), whereas the polyester filter (Cadillac Plastics, Baltimore, MD) mostly blocks the UV-B region (46% T at 330 nm, $<1\%$ T at 310 nm). Control cellulose diacetate filters transmit both UV-A and UV-B ($\sim 5\%$ T at 287 nm, 50% T at 295 nm). All 3 filters transmit $\sim 90\%$ of visible light. Transmittance spectra for UV-blocking and colored filter materials are shown in Fig. 2.

Data shown in Fig. 6 were collected continuously, at 10 min intervals, with a Campbell CR10 data logger, using sensors (Macam Photometrics Ltd, Livingston, Scotland, UK) mounted 3 m above the surface of the McMurdo Ice Shelf. Calibration was by comparison with output from an UVM spectrometer maintained at the National Institute of Water and Atmospheric Research, Lauder, New Zealand.

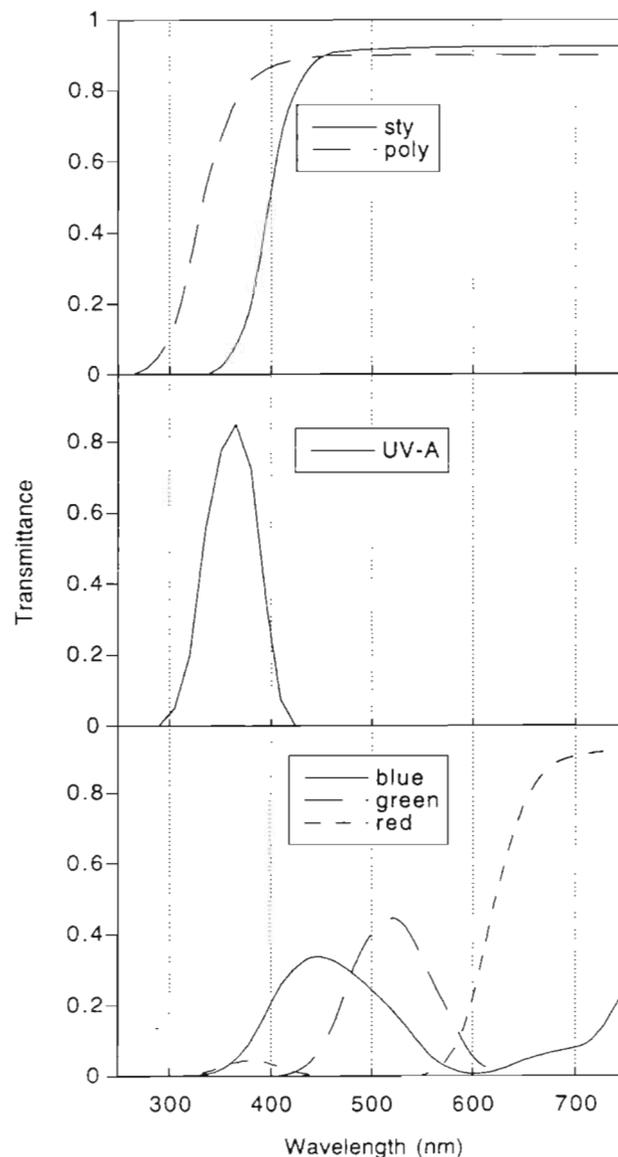


Fig. 2. Transmittance spectra for filter materials

Migration experiments. Filtering devices were constructed by mounting round pieces of filter, with or without neutral density screens, onto thin plastic cylinders (8 cm in diameter, 3 cm high) which are opaque except for 2 bottom-side openings cut for water exchange. The cylinders were pushed part way into the soft mat material for the 3 to 6 h duration of each experiment, exposing the encircled mat to whatever radiation was transmitted by the filter. No preparatory treatment was necessary prior to upward migration experiments, in that the motile population of trichomes was below the surface of the mat during the 24 h daylight of austral summer. However, prior to downward migration experiments, the mat was covered with a dark filter for several hours,

which allowed ascent of the motile trichomes to the mat surface. The composition of this mat, with its high silt and sand content, made it impossible to use the minicore technique of Garcia-Pichel et al. (1994) to quantify the vertical position of the migrating cyanobacterial band. Instead, the migration response was graded on a scale of 0 to 4 based on visual observation. Core samples, 1 cm in diameter and ~5 cm in thickness, were taken for chlorophyll *a* (chl *a*) measurements. These were mechanically disrupted, extracted overnight in 95% methanol, and quantified spectrophotometrically using the equation of Lenz & Zeitschel (1968).

Irradiance, UV, and temperature effects on photosynthesis. Photoincorporation of [^{14}C] NaHCO_3 was used as a measure of photosynthesis in 3 different types of experiments: (1) quantification of photo- and UV-inhibition on photosynthetic capacity under 3 different ranges of the solar spectrum (visible alone, visible+UV-A, visible+UV-A/B) and 3 different intensities (using neutral density screens), (2) characterization of the time course of photosynthetic uptake under the same 3 regions of the solar spectrum after 30, 60, 90, and 120 min of incubation, and (3) determination of the effects of these solar spectral ranges as a function of incubation temperature. Prior to these experiments, an opaque cover was placed over a portion of the mat for >7 h during the low sun period of 24 h daylight which allowed the *Oscillatoria* sp. 'K' population to migrate to the mat surface. The population of freely dissociating trichomes was harvested, using a wide-bore syringe, and resuspended uniformly in native pond water which had been filtered 3 to 5 times through WhatmanTM GF/C filters to remove phytoplankton. Cell suspensions were used within 1 to 3 h of collection. Aliquots (7.5 ml) of the diluted suspension were distributed to 2 oz Whirl-PakTM bags (NASCO), followed by addition of [^{14}C] sodium bicarbonate to achieve a final activity of 2.96 kBq ml⁻¹ (0.08 μCi). Each light treatment included duplicate samples, with dark samples used as controls.

Microscopic examination of fixed subsamples from cell suspensions showed the presence of a small photosynthetic flagellate, a probable cryptomonad, ~4 μm in diameter. Cell counts combined with stereometric formulae, in which trichomes were considered cylinders and flagellates were considered spheres, were used to calculate biovolume. By these calculations *Oscillatoria* sp. 'K' constituted 98.9% of the biovolume; thus, results were attributed to this species.

Type 1 incubations were for 1.5 h and those for the time series (Type 2) were as indicated in the figure legend. Both Type 1 and Type 2 incubations were performed in trays in a shallow pond at ambient temperature, which remained constant, $\pm 1.5^\circ\text{C}$, within each experiment. Replicate experiments were carried out on different days; temperature of incubation among the

experiments varied from about 5 to 11°C. Type 3 experiments were incubated on the surface of water-filled insulated coolers which were maintained at temperatures of 2 to 3, 10, 15, and 20°C by frequent additions of hot water. Samples were acclimated for 2 h at the incubation temperature prior to 2 h photoincorporation incubations.

Incubations were stopped by the addition of formalin to ~5% final concentration. Samples were stored in the dark, for 1 to 3 wk, until processed. This involved filtration onto Gelman GN-6 membrane filters, acidification with 2% (v/v) concentrated HCl, and rinsing with double-distilled water. Filters were transferred to scintillation vials to which 7.5 ml of OptiPhase 'HighSafe' 3 (Wallac) scintillation cocktail was added, and stored overnight at 4°C. [^{14}C] photoincorporation was quantified by liquid scintillation counting (Wallac LKB 1217 Rackbeta). Resulting disintegrations per minute (DPM) data were normalized to chl *a* content, determined spectrophotometrically from methanol extracted samples (Lenz & Zeitschel 1968).

Statistical analyses. Analysis of variance (ANOVA), analysis of covariance (ANCOVA), and regression analyses (Sokal & Rohlf 1995) were made using SuperANOVA (Abacus Concepts 1989). Two-factor ANOVA models for each photoincorporation experiment type, using [^{14}C] uptake data, were categorized as follows: (1) groups of irradiance quality (visible, visible+UV-A, visible+UV-A/B) and intensity (2.2, 14, 38, 85%), (2) groups of radiation intensity/quality (85% visible+UV-A/B, 85% visible, 14% visible) and incubation time (30, 60, 90, 120 min), and (3) groups of radiation intensity/quality (85% visible+UV-A/B, 85% visible+UV-A, 85% visible or 85% visible+UV-A/B, 38% visible+UV-A/B, 9% visible+UV-A/B) and incubation temperature (2.2, 10, 15, 20°C). Mean percent UV inhibition and 95% interval estimates were calculated using the Bliss theorem (Hubert 1992), as previously described (Miller et al. 1998). Other analyses are described below in the 'Results' section.

RESULTS

Migration

Migration of *Oscillatoria* sp. 'K' was vividly evidenced by changes in coloration of the mat surface in response to various treatments (Fig. 1C to F). The mat was grayish-yellow during the 24 h daylight of the austral summer, but changed to dark green when the motile component migrated upward. Migration was apparent after 2 to 3 h under filters which elicited the most rapid response. Table 1 presents the results of migration experiments, as well as incident and treatment irradiance values.

Table 1. Results of upward and downward migration experiments and key to irradiance transmitted through filter/screening combinations used as treatments. Scoring on a scale of 0 to 4, with 0 = no migration and 4 = maximum migration; thus a score of 4 for upward migration means the trichomes came completely to the surface of the mat, but in downward migration it means the trichomes completely left the mat surface. Upward migration irradiance values represent the range in measurements from 3 experiments. During duplicate downward migration experiments, full incident radiation was essentially the same. All experiments were ~4 h in duration. D: diacetate, transmits UV-A/B. P: polyester, blocks UV-B. S: styrene, blocks nearly all UV. ND: no data. Numbers in treatment column denote number of neutral density screens used

Treatment	Upward migration Score	Irradiance transmitted through filters ($W m^{-2}$)			Downward migration Score	Irradiance transmitted through filters ($W m^{-2}$)		
		VIS	UV-A	UV-B		VIS	UV-A	UV-B
Full irradiance		230–360	13.4–14.4	0.78–0.81		459	18.6	1.1
D	0	203–318	11.5–12.4	0.63–0.72	4	405	16	0.89
D+3	0	34.2–53.4	1.7–1.8	0.09–0.1	3–4	68.2	2.7	0.14
D+4	1	12–18.8	0.62–0.67	0	3	24	1.0	0
D+6	3–4	4.8–7.6	0.2–0.25	0	0	9.6	0.34	0
P	0	193–302	9.4–10	0.25–0.27	4	385	13	0.36
P+3	0	29.3–45.7	1.5–1.6	0	4	58.5	2.1	0
P+6	3–4	4.4–7.8	0.24–0.26	0	ND	10	0.33	0
S	0	140–220	1.3–1.4	0	4	279	1.8	0
S+3	0–1	30–47	0.2–0.22	0	1–2	60.1	0.28	0
S+4	1	12.9–20	0.1	0	1	25.9	0.14	0
S+6	4	4.2–6.5	0	0	0	8.4	0.04	0
UV-A	0	13.0–20	4.9–5.3	0	4	26	6.9	0.1
Blue	0	87.6–137	0.68–0.7	0	4	175	0.94	0
Green	4	55.6–87	0	0	0	111	0	0
Red	2–3	108–169	0.5	0	0–2	216	0.66	0
Dark	3–4				0			

To insure that negative results were due to prevention of upward vertical movement, and not distributional heterogeneity in the *Oscillatoria* sp. 'K' population, chl *a* was used as a correlative to estimate biomass of *Oscillatoria* sp. 'K' under each treatment in the upward migration experiments. To this end, core samples were taken from under all filters at the end of each experiment. The average concentration (μg chl *a* $cm^{-2} \pm SE$) for the upward migration experiments shown in Table 1 were 36.3 (2.54), 20.0 (1.20), and 26.3 (2.25). Relative homogeneity of the population within each experiment is demonstrated by the low variance in chlorophyll measurements.

The *Oscillatoria* sp. 'K' population migrated completely to the surface under low visible irradiance ($<8 W m^{-2}$), green light, and complete darkness (Table 1). None of these treatments included UV-B or more than $0.26 W m^{-2}$ UV-A. Red light, which included $\sim 0.5 W m^{-2}$ UV-A, also allowed a considerable upward ascent, but to a lesser extent. Green light elicited the most pronounced response. Noticeable upward migration occurred at a higher visible irradiance when most of the UV was blocked (S+3; $\sim 0.22 W m^{-2}$ UV-A, $0 W m^{-2}$ UV-B) in contrast to treatments with the same neutral density screening which transmitted UV-A/B (D+3; $\sim 1.7 W m^{-2}$ UV-A, $\sim 0.1 W m^{-2}$ UV-B) or only UV-A (P+3; $\sim 1.5 W m^{-2}$ UV-A). Even partial upward ascent did not occur under any treatments which included a measurable UV-B component.

The sections of mat used for downward migration experiments were uniformly dark green due to the forced upward migration of *Oscillatoria* sp. 'K' prior to the start of these experiments, indicating relative homogeneity of trichome distribution. Filters which elicited the most pronounced responses resulted in the disappearance of *Oscillatoria* sp. 'K' from the surface within 2 to 3 h of treatment. *Oscillatoria* sp. 'K' displayed a maximal downward migratory response to UV-A ($6.9 W m^{-2}$ UV-A, $\sim 0.1 W m^{-2}$ UV-B), high visible irradiance ($>60 W m^{-2}$) and blue light, which included $0.94 W m^{-2}$ UV-A (Table 1). Responses to high visible light are difficult to interpret, in that these treatments also included a UV-A component. However, several filter combinations which transmitted low visible light and some UV-A (e.g. D+6, S+4, S+6; Table 1) did not cause extensive downward migration, yet any treatment which transmitted UV-B did. Trichomes remained on the surface of the mat under treatments which had allowed upward migration in the experiments described earlier.

Photosynthetic carbon assimilation

Type 1

This was a 2-way factorial design in which spectral quality and irradiance level were varied. There were 3

light quality treatments (visible+UV-A/B, visible+UV-A, and visible alone) and 4 irradiance levels (85, 38, 14, and 2.2%). Results from experiments performed under incident solar irradiance encountered during both a clear and an overcast day, 460 W m⁻² and 186 W m⁻² respectively, are shown (Fig. 3A,B). In both cases, 2-way ANOVA resulted in highly significant effects ($p \leq 0.0005$) of both spectral quality and irradiance level on photosynthetic carbon assimilation. However, there was also a significant interaction term between these factors ($p < 0.01$), indicating that cells respond differently to UV at different irradiance levels.

In the experiment conducted at the higher absolute irradiance level (Fig. 3A), post hoc tests of 2-way ANOVA indicated no significant differences between visible+UV-A/B and visible+UV-A, though both differ significantly ($p = 0.0001$) from the treatment in which only visible light was available. In the absence of UV, photosynthetic saturation was reached at 60 W m⁻². An increase to 365 W m⁻² resulted in photoinhibition. Inhibition was already apparent at the 14% irradiance level in the visible+UV-A (~54.8 W m⁻² vis, ~1.8 W m⁻²

UV-A) and visible+UV-A/B (~63.9 W m⁻² vis, ~2.3 W m⁻² UV-A, ~0.14 W m⁻² UV-B) treatments.

In the experiment conducted during overcast conditions (Fig. 3B) the photosynthetic rate saturated between 26 W m⁻² and 70 W m⁻² under visible light alone. Post hoc tests of 2-way ANOVA indicated no significant difference between these 2 treatments, however, so saturation was likely reached near 26 W m⁻². There was only slight inhibition at 158 W m⁻², the 85% irradiance level. Maximal photosynthesis was reached at 14% irradiance under both visible+UV-A (~23.7 W m⁻² vis, ~1.1 W m⁻² UV-A) and visible+UV-A/B (~27.6 W m⁻² vis, ~1.5 W m⁻² UV-A, ~0.01 W m⁻² UV-B), while further increases in both treatments caused inhibition.

To further investigate the interaction term in these experiments, 2-factor ANOVA was repeated using data from the 2 lowest light intensities, 2.2 and 14%, including all 3 UV treatments. For the experiment performed at the higher absolute light level (Fig. 3A), this analysis showed no significant effects ($p > 0.13$) of either radiation quality or intensity. Furthermore, the significance level of the interaction term was greatly

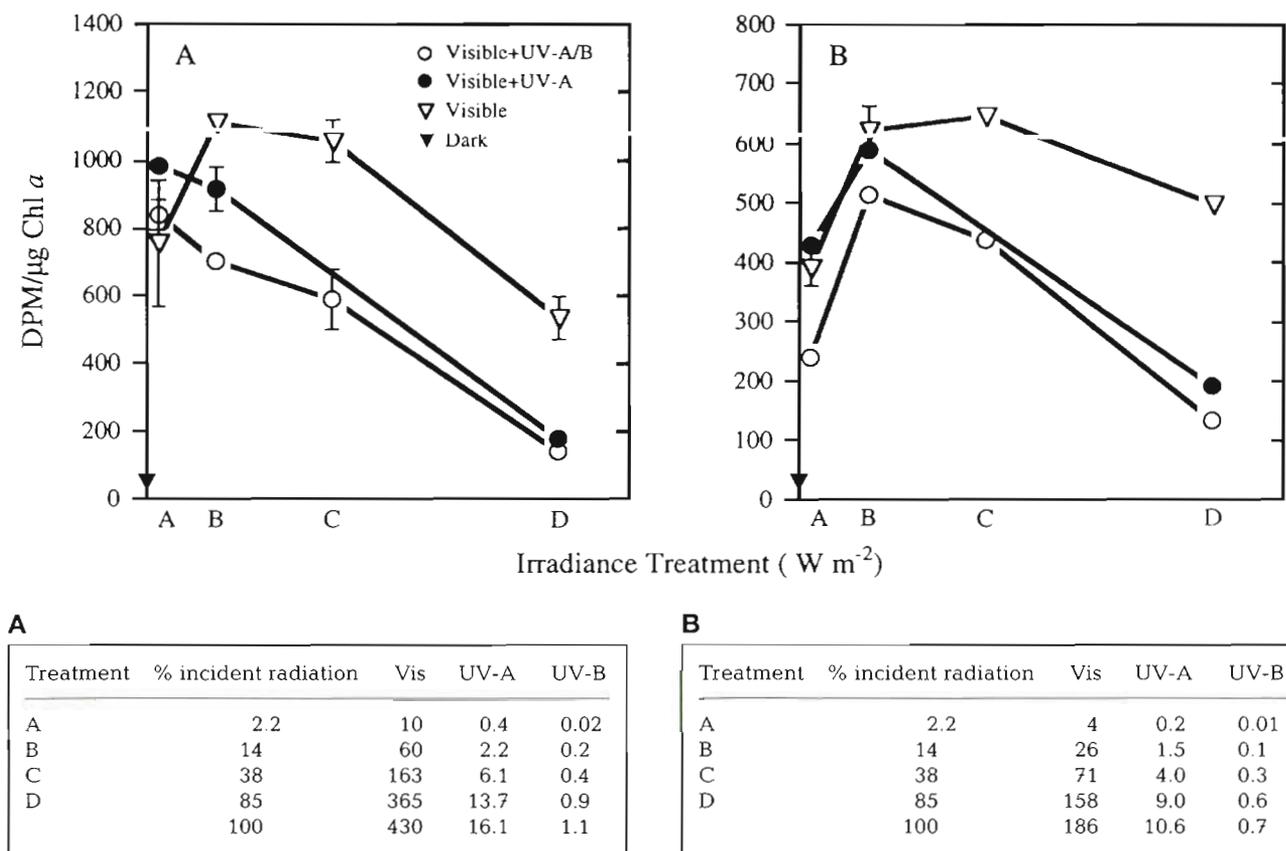


Fig. 3. Chl a normalized photosynthetic [¹⁴C]-bicarbonate incorporation of *Oscillatoria* sp. 'K' over 1.5 h. Cells were assayed at the irradiances indicated under diacetate (visible+UV-A/B), polyester (visible+UV-A), and styrene (visible) filters. Weather conditions were (A) clear and sunny, incubation temperature ~5.6°C, and (B) overcast, incubation temperature ~5.2°C. There are no data for the 38% visible+UV-A treatment. Error bars represent SE

reduced ($p > 0.05$). However, in the lower absolute light level experiment (Fig. 3B) both radiation quality and intensity still had significant effects ($p = 0.001$), and the interaction term was not significant. In the latter experiment, the cells were under subsaturating light conditions at the 2 lower light treatments.

Type 2

These experiments evaluated the time course of inhibitory effects under 3 different solar environments (Fig. 4). A 2-way ANOVA resulted in a highly significant effect ($p = 0.0001$) of both solar environment and incubation time, though the interaction of the 2 terms was also significant ($p = 0.008$). The lowest irradiance treatment, 64 W m⁻² of visible light alone, gave the highest photoincorporation rates. For this treatment, [¹⁴C] uptake fits a linear model ($r^2 = 0.885$, $p = 0.001$) over the 120 min incubation period. Photoinhibition occurred by 60 min of incubation at the highest intensity (85%; 391 W m⁻²) of visible irradiance. Application of 85% visible+UV-A/B (17.2 W m⁻² UV-A, ~0.97 W m⁻² UV-B) caused inhibition after only 30 min of incubation. Relative to the highest uptake rates achieved at 14% of visible light alone, uptake under the 85% visible+UV-A/B treatment was only 10% greater than that of the dark control throughout the 2 h incubation.

To test the effect of UV inclusion at the 85% intensity level, a 1-factor ANCOVA model was used in which uptake was treated as the dependent variable with

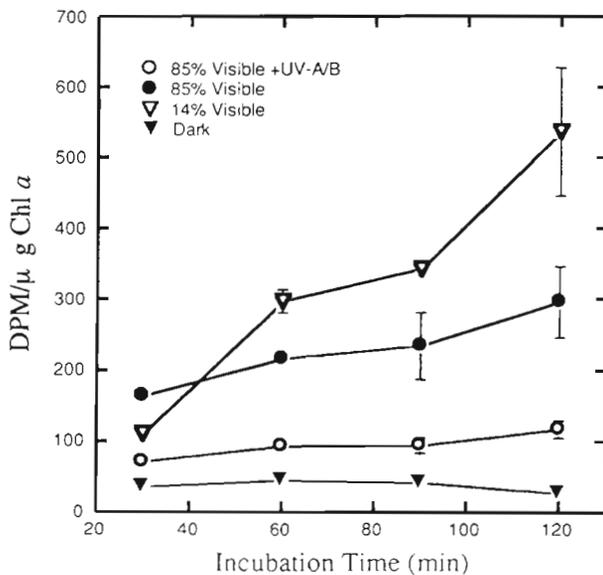


Fig. 4. Time course of chl a normalized photosynthetic [¹⁴C]-bicarbonate incorporation of *Oscillatoria* sp. 'K' over 2 h at -8°C. Mean 100% irradiance values are 402 W m⁻² visible, 17.8 W m⁻² UV-A, 1.1 W m⁻² UV-B. Error bars represent SE

UV as the factor and incubation time as the regressor. The hypothesis of homogeneity of slopes could not be rejected ($p = 0.06$), so the interaction involving the covariate was eliminated from the model. The resulting F -value was highly significant ($F_{[1,13]} = 63.07$, $p = 0.0001$), indicating that the means of the 85% visible±UV treatments vary significantly. Because there is no interaction of light quality with time, the absolute difference between these 2 light treatments stayed the same over the incubation period. The mean UV inhibition of carbon uptake was estimated at 58% ± 12%.

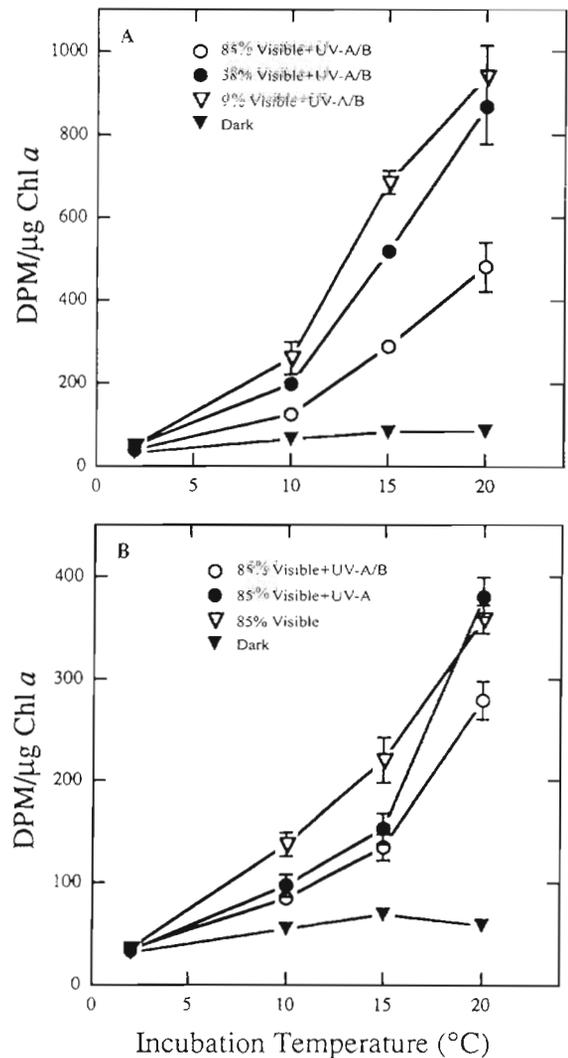


Fig. 5. Effect of visible and UV irradiance on photosynthetic carbon uptake of *Oscillatoria* sp. 'K' as a function of incubation temperature. Cells were acclimated for 2 h at the appropriate temperatures prior to 2 h incubations. (A) Treatments vary in percent radiation; UV-A/B was transmitted for all treatments. Mean 100% irradiance values were 163 W m⁻² visible, 9.3 W m⁻² UV-A, 0.5 W m⁻² UV-B. (B) Treatments vary in UV component transmitted. Mean 100% irradiance values were 300 W m⁻² visible, 12.5 W m⁻² UV-A, 0.63 W m⁻² UV-B. Error bars represent SE

Type 3

These experiments evaluated the effects of temperature and irradiance on photosynthesis (Fig. 5). Absolute irradiance values were low during these experiments because of overcast conditions. 2-factor ANOVA resulted in highly significant effects of both irradiance and temperature ($p \leq 0.0003$ both experiments), though there was a significant irradiance-by-incubation temperature interaction term ($p \leq 0.01$). At 2°C (Fig. 5) uptake did not differ significantly from the dark control for any of the irradiance treatments. Thus, 2-factor ANOVA was repeated excluding these data, which resulted in a much reduced significance level ($p \geq 0.05$ for both experiments) for the interaction term. In each experiment, photosynthetic rates increased in the order 2, <10, <15 and <20°C; within any given light treatment the greatest [¹⁴C] uptake was always at 20°C.

Varying the percent irradiance, while transmitting UV (Fig. 5A), resulted in the lowest carbon assimilation rates at the highest light treatment (85%; 143 W m⁻² vis, 8 W m⁻² UV-A, 0.4 W m⁻² UV-B). The highest carbon assimilation rates occurred under the 9% visible+UV-A/B treatment (14.6 W m⁻² vis, 0.5 W m⁻² UV-A, 0 W m⁻² UV-B), although at 20°C this rate did not differ significantly from that of the 38% visible+UV-A/B treatment (61.9 W m⁻² vis, 1.65 W m⁻² UV-A, 0.09 W m⁻² UV-B).

Results of a similar experiment, in which the intensity of visible irradiance remained constant while the UV conditions varied (Fig. 5B), showed lowest photosynthetic rates in the visible+UV-A/B treatment (255 W m⁻² vis, 10.7 W m⁻² UV-A, 0.5 W m⁻² UV-B). Visible+UV-A resulted in equally low rates at 10 and 15°C, but at 20°C did not significantly differ from the visible only treatment. A 1-factor ANCOVA model was used to test the effect of temperature on the magnitude of UV inhibition in this experiment. In this model, uptake was treated as the dependent variable with UV as the factor and incubation temperature as the regressor. The homogeneity of slopes hypothesis could not be rejected ($p = 0.3$), indicating no interaction of light quality with temperature. Thus, there was no apparent effect of temperature on the magnitude (percent) of UV inhibition on photosynthesis.

DISCUSSION

Photosynthetic activity

The solar irradiance values presented in Fig. 3A are among the highest recorded during the month of January 1998. UV-inhibition was detected as low as

~60 W m⁻² visible irradiance plus ~2.5 W m⁻² UV-A/B (Fig. 3A), but with visible light only *Oscillatoria* sp. 'K' showed no inhibition at this intensity. The rate of convergence towards the dark uptake values was significantly higher when UV was included. At the highest light level, uptake rates for both UV-A and UV-A/B treatments were not much higher than the dark control, i.e. the cells were almost completely inhibited. In the Baja cyanobacteria (Kruschel & Castenholz 1998) the inclusion of UV-A or UV-A/B radiation with high visible irradiance similarly inhibited photosynthesis almost to dark levels.

Under overcast conditions (Fig. 3B), there is evidence that cells of *Oscillatoria* sp. 'K' were photosynthetically saturated at visible light intensity as low as ~26 W m⁻², and photoinhibited by ~158 W m⁻² of visible light alone. However, the inclusion of UV radiation was clearly detrimental to photosynthetic uptake, even at extremely low intensities (~0.25 W m⁻² UV-A and ~0.02 W m⁻² UV-B). In contrast, visible intensities above ~350 W m⁻², and inclusion of ~0.8 W m⁻² UV-A plus ~0.05 W m⁻² UV-B, caused inhibition in the migrating cyanobacteria (i.e. *Oscillatoria* cf. *laetevirens*) of the Baja ponds (Kruschel & Castenholz 1998). It would appear then, on the basis of these few experiments, that the Antarctic *Oscillatoria* is somewhat more sensitive to visible and UV irradiance than the Baja counterpart. In cyanobacteria from both locations it is unknown whether exposure over a longer period would allow recovery through repair processes. In a laboratory experiment, Vincent & Quesada (1994) showed that 5 d growth of a culture of *Oscillatoria* cf. *priestleyi* (= *Oscillatoria* sp. 'K') was completely suppressed by 5 W m⁻² UV-B, as compared to the control which doubled at 0.44 d⁻¹. However, this UV-B value is considerably higher than would be experienced in the Antarctic pond.

The detrimental effect of UV on photosynthetic uptake began soon, if not immediately, after exposure (Fig. 4). However, at a photoinhibiting visible light level (~390 W m⁻²) an increase in UV dose (i.e. time of exposure) did not alter the degree of UV inhibition. Given the high level of UV inhibition experienced by these field samples of *Oscillatoria* sp. 'K', it obviously benefits the trichomes to remain deeper in the mat and thus avoid even moderate solar UV radiation.

At 2.2°C (Fig. 5A,B), a temperature which *Oscillatoria* sp. 'K' probably experiences often during the austral summer, there was no measurable effect of irradiance because the photoincorporation rates were no greater than the dark values. There was active photosynthesis, however, at the average temperature measured in Salt Pond (6.0°C) in January. Even at the highest temperature recorded in Salt Pond, 10.7°C, it is apparent that *Oscillatoria* sp. 'K' was existing at sub-

optimal temperatures. These data agree with those obtained for a laboratory clone of this organism, which showed that both growth and photosynthetic rates reach an optimum at temperatures above 20°C (Castenholz & Schneider 1993, Nadeau & Castenholz unpubl. data).

Results of photosynthetic activity in *Oscillatoria* sp. 'K' differ from those of laboratory experiments performed on a cultured oscillatorian, *Phormidium murrayi* West & West, isolated from an Antarctic microbial mat (Roos & Vincent 1998). Roos & Vincent found no significant effect of UV radiation (1.25 W m⁻² UV-A, 0.25 W m⁻² UV-B and up to 500 μmol photons m⁻² s⁻¹ visible) on short-term (1 h) photosynthesis at 5, 10, 15, and 20°C in cultures grown under non-UV radiation and low light conditions at 20°C. They attribute these results to UV radiation dosage rates which were too low to elicit a detectable response. However, after 5 d of growth under the same visible irradiance levels and temperatures, ±UV, they did find that photosynthetic carbon uptake rates (1 h) were reduced an average of 30% by the presence of UV radiation. In both sets of experiments, there was little evidence of photoinhibition up to 500 μmol m⁻² s⁻¹ of visible irradiance alone in *Phormidium murrayi*. *Oscillatoria* sp. 'K' was photo-inhibited at much lower irradiance levels (Fig. 5A). These differences, though, are not surprising given the migratory capabilities of *Oscillatoria* sp. 'K'. If migratory behavior is a mechanism to avoid damage from high solar and UV irradiance, having maximal photosynthetic capabilities at low light levels, due to a high light-harvesting pigment content, is a necessary counterpart which allows optimization of this physical parameter. There was no significant effect of temperature on the magnitude (percent) of UV inhibition of photosynthesis for either *Phormidium murrayi* or *Oscillatoria* sp. 'K' (the latter in our experiments; Fig. 5B).

Migration

There is a broad range of incident visible wavelengths and intensities that allow or promote upward migration of *Oscillatoria* sp. 'K' to the mat surface (Table 1). The most pronounced upward response occurred under treatments which had neither a UV-A or UV-B component, although the population did move partially, or fully, to the surface under treatments of low visible irradiance that had some UV-A (<~0.6 W m⁻²). However, removal of UV was not sufficient to promote upward migration, in that higher levels of full spectrum visible irradiance also prevented upward movement. Downward migration occurred most significantly in response to high visible (>60 W m⁻²) or UV (6.9 W m⁻² UV-A, ~0.1 W m⁻² UV-B) treatments. Low visible light (<~10 W m⁻²) in combination with a low

intensity of UV-A (<~0.34 W m⁻²) did not force this cyanobacterium down from the mat surface.

Migration experiments were performed on migratory cyanobacteria in hypersaline ponds of Guerrero Negro (Kruschel & Castenholz 1998) at near optimal temperatures, whereas comparable experiments on *Oscillatoria* sp. 'K' were at suboptimal temperatures for motility in this cyanobacterium. The motility rate of the Baja *Oscillatoria* at 25 to 30°C was ~1 μm s⁻¹, while *Oscillatoria* sp. 'K' moved at speeds of 2.4 (0.24), 0.9 (0.18), and 0.4 (0.12) μm s⁻¹ at 22, 12, and 4°C, respectively. Distances from the top of the cyanobacterial band to the surface was ~0.4 to 0.5 mm in mats at both sites. Even though *Oscillatoria* sp. 'K' would have moved somewhat more slowly at the temperatures at which migration experiments were performed (~4 to 8°C), sufficient time was allowed for a full migratory response, making it possible to compare results.

Although we could not quantify exact vertical positions within the mat, our results corroborate the results of Kruschel & Castenholz (1998). They found that complete upward migration did not take place if UV-A was >~2 W m⁻² for *Spirulina* cf. *subsalsa*, and that no upward migration occurred for *Oscillatoria* cf. *laetevirens* if UV-A was above 1.5 W m⁻². The Antarctic cyanobacterium *Oscillatoria* sp. 'K' responded with similar sensitivity to both visible and UV radiation, but appears to have a somewhat lower threshold for eliciting upward or downward migratory behavior. For instance, *Spirulina* cf. *subsalsa* fully ascended to the surface under 22 W m⁻² visible and 0.8 W m⁻² UV-A, whereas *Oscillatoria* sp. 'K' only partially rose to the surface under 20 W m⁻² visible and 0.1 W m⁻² UV-A (Table 1). Furthermore, a treatment of 24 W m⁻² visible and 1.0 W m⁻² UV-A caused nearly total downward migration in the Antarctic cyanobacterium, whereas even 350 W m⁻² of visible plus 1.4 W m⁻² UV-A had little effect on *Oscillatoria* cf. *laetevirens*, although *Spirulina* cf. *subsalsa* was somewhat more sensitive (Kruschel & Castenholz 1998).

Oscillatoria sp. 'K' displayed a response to colored light similar to that of the Baja cyanobacteria, in which green light promoted the fastest ascent, red light promoted a slower ascent, with no ascent under blue light. This has been described in other motile cyanobacteria, as well, with the probable implication of positive phototaxis under green light which hastens the ascent (Castenholz 1982).

Ecological implications

Photosynthesis is one of the prime processes inhibited by UV (see Holm-Hansen et al. 1993). As primary productivity in Antarctic ponds is mainly that of filamentous

cyanobacteria which dominate these microbial benthic habitats, the severity of UV stress is a factor in the composition of these mat systems. Natural levels of UV radiation drastically inhibit photosynthesis in *Oscillatoria* sp. 'K'; this inhibition begins immediately upon exposure and is constant over the range of temperatures which this microorganism experiences in its natural habitat.

Overall trends in photosynthesis and migration patterns of *Oscillatoria* sp. 'K' parallel those described for *Spirulina* cf. *subsalsa* and *Oscillatoria* cf. *laetevirens*, which dominate soft mats of many hypersaline ponds of Guerrero Negro (Kruschel & Castenholz 1998). The most surprising aspect of this study, in view of their disparate environments and geographic locations, is the similarity of the Antarctic cyanobacterial responses to those of the Baja organisms. *Oscillatoria* sp. 'K' is quite different from *Oscillatoria* cf. *laetevirens* both with respect to morphology and 16S rDNA nucleotide sequences (Nadeau & Castenholz unpubl. data). The slight differences observed in the irradiance level thresholds that are required to elicit a response in these cyanobacteria may be due to genetic differences or to the different solar environments of their respective habitats. At 78°S the clear sky fluence density of UV radiation and of visible irradiance is only about half that of middle latitudes. This is due to the low sun angle at high latitudes. Although the sun remains above the horizon for 24 h during austral summer, the diel accumulative dosage of UV may not be as important as the midday intensity level, which may be seriously detrimental even in the few hours of maximum intensity.

Although Antarctic microbial communities are not subjected to as severe UV intensities as occur in many lower latitudes, they may nevertheless be encountering increasing intensities to which they have not been previously adapted. In the case of natural populations of *Oscillatoria* sp. 'K', it appears that this cyanobacterium is more sensitive to UV radiation than the *Oscillatoria* cf. *laetevirens* and *Spirulina* cf. *subsalsa* at 28°N in Baja California, both with regard to vertical migratory behavior and inhibition of photosynthesis. This small difference, however, may simply reflect a greater sensitivity of photosynthesis to UV radiation at low temperatures, which might also apply to the Baja cyanobacteria at suboptimal temperatures. Laboratory isolates of *Oscillatoria* sp. 'K' showed relatively poor photosynthesis and growth at the normal, but suboptimal, temperatures of the field (Castenholz & Schneider 1993, Nadeau & Castenholz unpubl. data). In field experiments (Fig. 5B), this cyanobacterium showed significantly lower UV-A inhibition of photosynthesis when the temperature was raised to 20°C, close to its temperature optimum.

In the Baja mats, migratory cyanobacteria come to the surface at dusk and remain there through dawn;

they are also seen at the surface during periods of high turbidity. It is possible that the UV avoidance strategy is not used frequently, or at all, by the Baja cyanobacteria because of the usual turbidity of the hypersaline waters where they now commonly occur. Thus, it may be that these responses evolved in other, more UV-exposed habitats, but have been retained in these specialized environments. *Oscillatoria* sp. 'K', however, makes good use of its response system in Salt Pond. During the 24 h daylight of austral summer (Fig. 6), solar irradiance is high enough, even on overcast days or during turbid conditions, to prevent *Oscillatoria* sp. 'K' from ascending to the surface. Results from our experiments, in which this cyanobacterium showed >50% UV-inhibition of photosynthesis on a clear day, suggest that a surface population would probably deteriorate as a result of UV-inhibition. *Oscillatoria* sp. 'K' has neither UV-absorbing microsporine amino acid (MAA)-like compounds nor the extracellular sunscreen pigment scytonemin, UV defense mechanisms used by other cyanobacteria (Garcia-Pichel & Castenholz 1993); its migratory strategy is a primary defense mechanism against UV exposure. This is also true of the migratory cyanobacteria of Baja.

Like the Baja populations, not only avoidance, but actual optimization of the photosynthetic light field may also exist in the Salt Pond population. During the low sun period of austral summer both PAR and UV levels can drop significantly (Fig. 6), and some upward movement towards the mat surface may occur. Nonetheless, the only time that *Oscillatoria* sp. 'K' populations are likely to be found on the mat surface would be during the transition periods of spring or fall. For

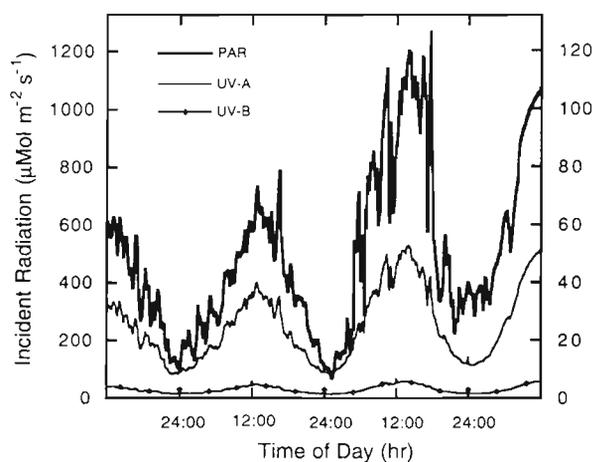


Fig. 6. PAR, UV-A, and UV-B at the study site for the 72 h period from 12:00 h on 8 January to 12:00 h on 10 January 1998, illustrating irradiance values for both an (A) overcast and a (B) clear, sunny day. Note order of magnitude difference in scale between PAR and UV values. In general, $\sim 1 \text{ W m}^{-2} \text{ PAR} = 2.15 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$

instance, during the 1997 summer/winter transition the shallow area of 2 McMurdo Ice Shelf ponds, generally the zone of maximal biomass, froze between late February and early March; into late March, however, the surface incident irradiance was still at a daily average of 40 to 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (~19 to 46 W m^{-2} PAR), suggesting 12 to 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at mat depth (Hawes et al. 1999). Furthermore, liquid water temperatures in a brackish pond stayed over $\sim 2^\circ\text{C}$ until late February (Hawes et al. 1999). Under such an environmental scenario, it is conceivable that the motile population of Salt Pond migrates to the mat surface to optimize photosynthesis, until that point when temperatures become physiologically prohibitive.

It is probable that *Oscillatoria* sp. 'K' occurs in habitats which are thermally suboptimal because it is neither grazed by herbivores, which are excluded from this extreme habitat, nor outcompeted by other photosynthetic organisms. While migratory capabilities contribute to its success, the monospecific dominance of *Oscillatoria* sp. 'K' in Salt Pond may be partially explained by the hypersalinity of this habitat, which appears to exclude the other common species growing in the fresher water ponds of the region. Though isolates of *Oscillatoria* sp. 'K' grow well in freshwater medium (Nadeau & Castenholz unpubl. data), this morphotype is usually found only in high conductivity waters of the McMurdo Ice Shelf (Broady & Kibblewhite 1991, Nadeau & Castenholz unpubl. data).

It is tempting to predict that migratory filamentous cyanobacteria have a common ancestor that possessed a UV/high light avoidance response, perhaps during an earlier period in the Earth's history (Proterozoic) when UV-B flux was considerably higher than at present. The alternative view is less attractive, since the similarity in response sensitivity shared by *Oscillatoria* sp. 'K', *Oscillatoria* cf. *laetevirens*, and *Spirulina* cf. *subsalsa* would suggest that 3 or more cyanobacteria independently evolved almost identical, complex response systems to UV and high visible irradiance.

In conclusion, our results are consistent with the hypothesis that UV radiation is functioning as a primary cue for avoidance of damaging solar radiation in the oscillatorian population of Salt Pond. This study, considered together with research conducted in middle (Kruschel & Castenholz 1998) and lower (Bebout & Garcia-Pichel 1995) latitudes, strongly suggests that UV is involved in the migratory behavior of motile cyanobacteria in soft mats worldwide. Further work is necessary, however, to fully understand the interactions between high solar irradiance, UV radiation, and temperature as stress factors which impact the physiological status of benthic Antarctic cyanobacteria, and therefore their migratory behavior and the ecology of the aquatic ecosystems which they dominate.

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