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UV B-Induced Vertical Migrations of Cyanobacteria in a Microbial Mat

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Exposure to moderate doses of UV B (0.35 to 0.79 W m^{-2} s^{-1} or 0.98 to 2.2 μmol of photons m^{-2} s^{-1} at 310 nm) caused the surface layers of microbial mats from Solar Lake, Sinai, Egypt, to become visibly lighter green. Concurrent with the color change were rapid and dramatic reductions in gross photosynthesis and in the resultant high porewater oxygen concentrations in the surface layers of the mats. The depths at which both maximum gross photosynthesis and maximum oxygen concentrations occurred were displaced downward. In contrast, gross photosynthesis in the deeper layers of the mats increased in response to UV B incident upon the surface. The cessation of exposure to UV B partially reversed all of these changes. Taken together, these responses suggest that photoautotrophic members of the mat community, most likely the dominant cyanobacterium *Microcoleus chthonoplastes*, were migrating in response to the added UV B. The migration phenomenon was also observed in response to increases in visible radiation and UV A, but UV B was ca. 100-fold more effective than visible radiation and ca. 20-fold more effective than UV A in provoking the response. Migrating microorganisms within this mat are apparently able to sense UV B directly and respond behaviorally to limit their exposure to UV. Because of strong vertical gradients of light and dissolved substances in microbial mats, the migration and the resultant vertical redistribution of photosynthetic activity have important consequences for both the photobiology of the cyanobacteria and the net primary productivity of the mat ecosystem.

Photosynthetic microbial mats commonly develop in environments in which solar UV (wavelengths shorter than 400 nm) may be a significant physiological stress. These benthic photosynthetic communities are common in tropical and subtropical regions, usually occurring in very shallow waters. Many benthic photosynthetic communities are completely emergent during low tides or for several tidal cycles or longer. Solar UV, and particularly solar UV B (wavelengths between 280 and 315 nm), has well-documented detrimental effects on oxygenic phototrophic organisms (6), including those from microbial mats (30). While it has been generally assumed that UV did not penetrate these communities and that the organisms below the very surface were protected, direct measurements of UV penetration in several types of benthic photosynthetic communities (10) have shown that UV B penetrates deeply enough to significantly affect a large portion of the euphotic zone.

The reduction of stratospheric ozone and resultant increases in UV reaching the planet surface have been shown to negatively affect phytoplankton primary productivity (27). Less is known about the effects of UV on benthic photosynthetic communities, including microbial mats. Some studies indicate that periphyton communities may be susceptible to UV increases (2, 3, 32). Microbial mats may also be affected in a number of ways (13). Benthic photosynthetic communities are capable of extremely high rates of photosynthesis and contribute significantly to the very high primary productivity of shallow-water environments (21, 28, 29, 33). It is therefore important to understand the effects of UV, and in particular those of changes in UV, on benthic photosynthesis in these environments.

A number of mechanisms are employed by mat microorganisms to minimize the adverse effects of UV B. It has been previously observed that organisms present within microbial mats produce sunscreen compounds, i.e., substances which absorb UV B and decrease the likelihood that the radiation will be absorbed by target cellular constituents (11, 12). Manipulations of UV in field studies of microbial mats indicate that mat microorganisms may also migrate in response to changes in the amount of natural UV A incident upon the surface of the community (4, 13). In this contribution, we examine the effects of UV on a microbial mat collected in Solar Lake, Sinai, Egypt. A mechanistic approach, using artificial sources of UV, was used to examine the phenomenon of UV-induced vertical migrations. These mats were chosen primarily because they contain extremely high abundances of *Microcoleus chthonoplastes*. This filamentous cyanobacterium is probably the most common builder of marine microbial mats, and it has a truly global distribution (22).

MATERIALS AND METHODS

Microbial mats were from Solar Lake, Sinai, Egypt (see references 5, 17, and 24 for a description of the environment and ecology). The mats were airlifted to Bremen, Germany, in plastic tubs and then maintained in glass aquaria in an aerated artificial seawater mix (Hugo Schmidt, Lünen, Germany) made up to a salinity of 85‰. Light was provided by halogen flood lamps; the photosynthetically active radiation (400 to 700 nm) at the surfaces of the mats was 200 ± 20 μmol of photons m^{-2} s^{-1}. The experiments described here were performed at various times between 1 week and 1 month after collection of the mats. After an initial "greening" in color upon collection, the mats maintained under halogen lamps changed little in appearance over the time that the experiments were conducted.

Experiments were performed on cores obtained from the larger pieces of mat by using acrylic core tubes (46-mm inside diameter). The cores were mounted in a small acrylic flow chamber (248 mm long by 78 mm wide) with an agarose gel made up by using the artificial seawater solution (20 g of agarose $liter^{-1}$). The surfaces of the cores were made flush with the surface of the agar. Flow was provided by recirculating the artificial seawater in the flume (and a reservoir) through a flow collimator consisting of a symmetrical pattern of holes (1-mm diameter) drilled through an acrylic plate (6-mm thickness). This experimental setup provided nearly laminar flow over the surfaces of the cores, at a flow speed of approximately 5 cm s^{-1}.

Irradiation. Experimental cores were illuminated with visible light provided by a fiber optic light source (Schott, Wiesbaden, Germany) positioned at a 90° angle

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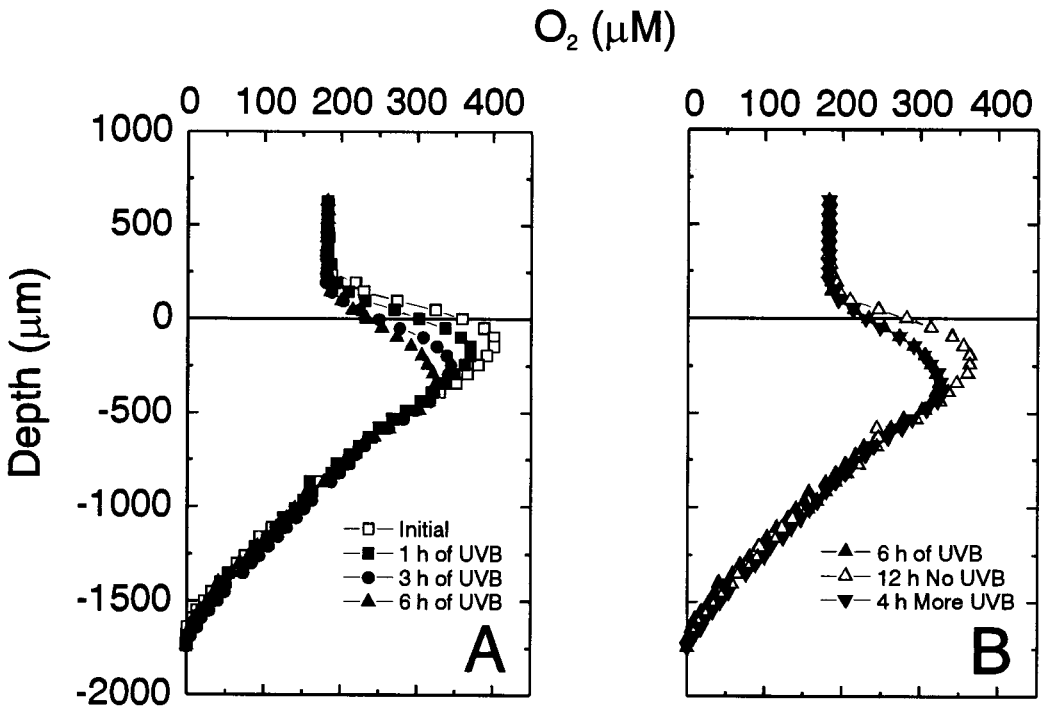

FIG. 1. Changes in oxygen concentration in the surface layers of the Solar Lake microbial mat community upon exposure to UV B (2.2 μmol of photons m^{-2} s^{-1} at 310 nm). (A) Measurements made before the start of UV B exposure and after 1, 3, and 6 h of exposure. (B) Profiles recorded 12 h after termination of UV B and then after an additional 4 h of exposure. The location was the same for both panels, and the profile obtained after 6 h of exposure to UV B is plotted in both panels.

to the surface of the mats (directly overhead). The light beam was passed through a collimating lens and a daylight correction filter (Schott). The irradiance was adjusted with neutral density filters (Oriel Corporation, Stratford, Conn.) positioned just below the collimating lens. The irradiance reaching the mat surface was measured by positioning a Li-Cor quantum sensor (model LI-190SA coupled to a Li-Cor model LI-189) in the light beam at the same height as the surface of the microbial mat.

UV. UV B was provided by a single 20-W suntanning fluorescence tube (Philips TL 12), which emitted light mainly in the UV B range (280 to 320 nm), with a maximum at 312 nm. UV B photon fluxes at the surfaces of the mats in these experiments ranged from 0.35 to 0.79 W m^{-2} (0.98 to 2.2 μmol of photons m^{-2} s^{-1} at 310 nm). UV A (320 to 400 nm) was provided by a Philips TLD 08 black-light fluorescence tube, which emitted light with a maximum at 365 nm. UV A photon fluxes at the surfaces of the mats ranged from 1.3 to 1.6 W m^{-2} s^{-1} (3.9 to 4.8 μmol of photons m^{-2} s^{-1} at 365 nm). UV A and UV B fluxes incident on the surface of the mat were measured with an International Light radiometer (IL1700) and appropriate sensors by placing the sensors on the same plane as the sample after its removal. The readings were corrected for the spectral output of the lamps and the spectral sensitivity of the sensor.

Oxygen concentration, flux, and photosynthesis measurements. Rates of photosynthesis (oxygen evolution) and oxygen concentrations were measured with microelectrodes. The microelectrodes used were of the Clark type, incorporating guard cathodes (23). Microelectrodes were coupled to a custom-built low-noise picoammeter interfaced with a microcomputer for data acquisition and were positioned by using motorized micromanipulators. A two-point calibration of the electrode was performed by using (i) a zero value obtained from the asymptotic minimum of the $[O_2]$ within the mats and (ii) a value for air-saturated water obtained in the aerated water circulating in the flume. The oxygen concentration in the air-saturated water in the flumes at a given temperature and salinity was calculated (8).

Rates of gross photosynthesis were determined by using the dark-shift technique (25) within the first second after darkening. This technique results in a measurement of volumetric gross photosynthesis (i.e., units of change in amount of oxygen per unit volume per unit time). In some instances, we also calculated the gross photosynthesis attributable to the entire photic zone below a given area of mat by vertically integrating the nonzero rates of gross photosynthesis measured at ~93-μm intervals.

Gradients in oxygen concentration can be used to calculate the diffusive flux J of oxygen according to the one-dimensional form of Fick's First Law of Diffusion (1), $J = -D\,\partial C/\partial Z$, where D is the diffusion coefficient, C is the concentration, and Z is the depth. We used the portion of the oxygen profile within the diffusive boundary layer because the diffusion coefficient of oxygen in water is known (20). Linear regressions of the profiles of oxygen concentrations across the diffusive boundary layer were used to determine $\partial C/\partial Z$. Slopes were calculated by the least-squares method with at least four datum points. Goodness-of-fit estimates (r^2) were generally greater than 0.8. We present our data in units of percent change in concentration gradients. These gradients are directly proportional to the flux across the diffusive boundary layer. Since the flux of oxygen out of a photosynthetic community in the light is equal to the amount of oxygen produced minus the amount of oxygen consumed by respiration, this measurement is also equal to the net primary productivity of the community in the light (15).

Measurement of penetration of UV B into mats. The penetration of UV B into microbial mats was measured with a recently developed fiber optic microsensor (9). Cores of the microbial mat were illuminated with a highly UV-enriched collimated beam from a xenon arc lamp (Oriel Corporation). The sensors were positioned at an angle of 30° to the surface of the mat and were moved by using motorized micromanipulators. The detector used was an International Light radiometer (IL1700), which was attached to the fiber optic sensors by a custom-built coupling (9).

Optical monitoring of cyanobacterial migrations. Spectral reflectance (radiance reflectance) measurements were made by using light sensors constructed from flat-cut tapered optical fibers (16). The tips of the fibers were placed at a distance of 5 mm from the surface of the mat at an angle of 45° to the mat surface. Optical fibers were coupled to a photodiode array-based detector system (optical spectral multichannel analyzer; Spectroscopy Instruments). This unit and the relevant optical couplings have been previously described in detail (18).

Replication and experimental design. The experiments presented here investigated the time course response of a microbial mat community to the application of UV. This was generally done in a single location; repeated measurements of oxygen concentration and gross photosynthesis were made by moving the microelectrode only in a vertical direction. The spectral reflectance measurements presented here integrated a 15- to 20-mm^2 area of the mat, within which the oxygen microelectrode measurements were also made. All of the experiments described here were replicated in full at least twice, with similar results.

RESULTS

Visible changes in mat surface color. Exposure of the Solar Lake mat to a moderate level of UV B (0.98 to 2.2 μmol of photons m^{-2} s^{-1} at 310 nm) resulted in a change in the surface coloration of the mat. Although there was a great deal of variability in the initial coloration and also variability in the

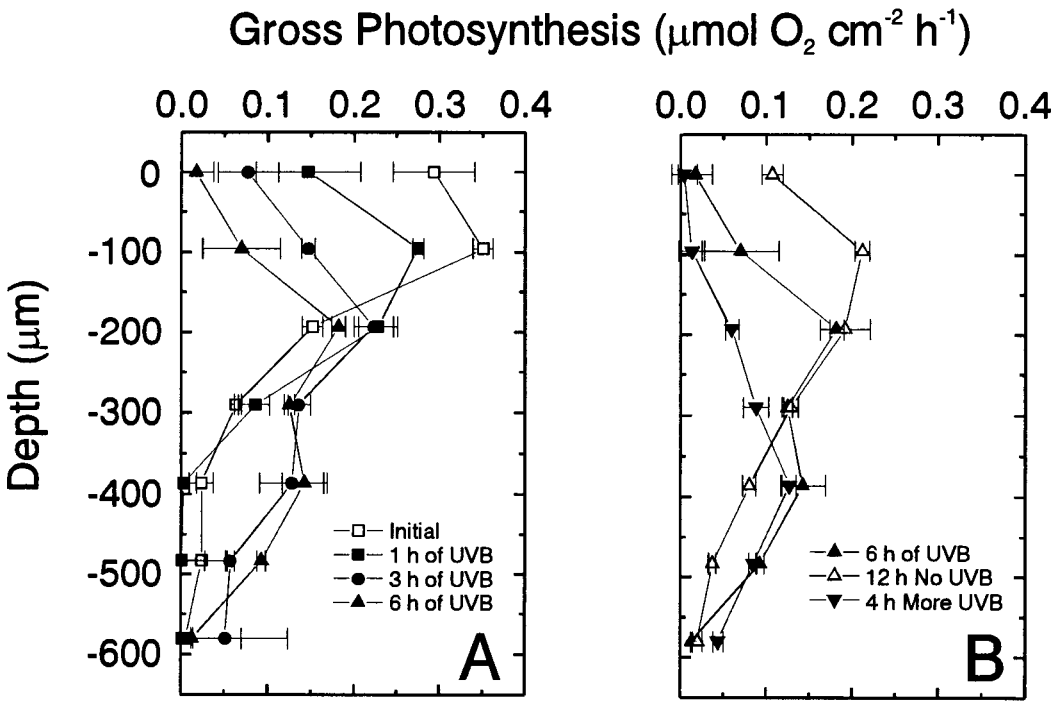

FIG. 2. Changes in the depth distribution of gross photosynthesis within the Solar Lake microbial mat community before and after exposure of the surface to UV B (2.2 μmol of photons m^{-2} s^{-1} at 310 nm). Error bars indicate the standard deviations from two to four rate determinations at each depth. (A) Measurements made after 1, 3, and 6 h of exposure to UV B. (B) Measurements made 12 h after the termination of UV B and then after a second 4-h exposure. The location was the same for both panels, and the rate measurements made after 6 h of exposure to UV B are plotted in both panels.

color change which was observed, the change itself was evident in every sample examined (eight cores). In general, the surface changed from a dark blue-green to a lighter blue-green (with some brown areas). The changes were usually evident within less than 1 h of exposure to UV B.

Oxygen concentration dynamics. Upon exposure to UV B (2.2 μmol of photons m^{-2} s^{-1} at 310 nm), there were decreases in the porewater oxygen concentration in the surface layers (above 400 μm) of the microbial mat (Fig. 1). A change in the shape of the profile of oxygen concentration was also evident, with the depth at which the maximum concentration occurred moving downward. Six hours of irradiation depressed the maximal O_2 concentration by ca. 20% and moved the position at which it occurred downward by 250 μm. These changes were reversible, to an extent. After 12 h without UV B, the depth at which the maximum concentration occurred moved back upward, and the maximum concentration in the profile increased by ca. 5% (Fig. 1).

Changes in gross photosynthesis and net productivity. Exposure to UV B (2.2 μmol of photons m^{-2} s^{-1} at 310 nm) immediately reduced the rates of gross photosynthesis in the upper layers of the mat (Fig. 2). Photosynthesis in the deeper layers (below 200 μm) of the mat, however, actually increased upon exposure of the surface to UV B (Fig. 2 and 3). Therefore, the depth at which the highest rates of photosynthesis occurred was displaced downward (Fig. 2). Although these changes were reversible, a complete recovery to the initial rates of gross photosynthesis did not occur. A cessation in UV B exposure resulted in some recovery of gross photosynthesis and an upward movement of the depth of maximum photosynthesis (Fig. 2). The oxygen concentration gradient across the diffusive boundary layer also decreased upon UV B exposure (Fig. 4). The flux of oxygen across this concentration gradient (the net oxygen export from the mat), which may be used as a measure of net photosynthesis in benthic photosynthetic communities (15), decreased more (as a percentage of the initial value) than the integrated gross photosynthesis.

Penetration of UV B. Below a small surface maximum in scalar irradiance, UV B was attenuated exponentially with depth in the Solar Lake microbial mat, with an apparent (subsurface) attenuation coefficient of 10.5 mm^{-1} (at 310 nm). The depth at which 1% of the incident radiation remained was ca. 500 μm (Fig. 5). The depth at which photosynthesis was observed to change from a decrease to an increase upon exposure to UV B corresponded to the depth at which ca. 30% of the incident UV B remained (Fig. 3 and 5).

Spectral reflectance. Measurements of spectral reflectance (radiance reflectance) at the surface of the mat were made in an attempt to quantify the color change which we observed. In order to enable comparison of the spectral reflectance measurements with oxygen microelectrode measurements, which integrate very small areas of the mat, we positioned the fiber optic sensor to collect the light reflected from a small (15 to 20-mm^2) area. The spectral reflectance of the mat was similar to previously reported spectra of microbial mats (16), with minima corresponding to major photosynthetic pigment absorption maxima (data not shown). The spectral reflectance across almost all wavelengths from 450 to 800 nm increased upon exposure to UV B. The spectral reflectances at 620 nm (the absorption maximum for phycocyanin), 577 nm (the absorption maximum for phycoerythrocyanin, a pigment characteristic of *M. chthonoplastes* [22]), and 680 nm (the absorption maximum for chlorophyll *a*) all showed a similar pattern of change upon UV B exposure. Microscopic examination of the mats revealed that the overwhelmingly dominant microorganisms were filamentous cyanobacteria, primarily *M. chthono-*

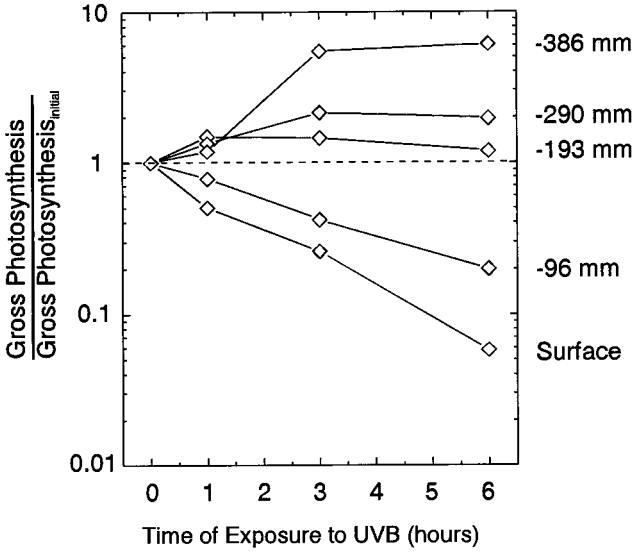

FIG. 3. Changes in gross photosynthesis at various depths in the Solar Lake microbial mat community during exposure to UV B. Data are the same as used for Fig. 2 and are expressed as fractions of the initial rates of photosynthesis (dose-response relationship). Gross photosynthesis is plotted on a log scale; numbers greater than 1 indicate increases in photosynthesis at a particular depth.

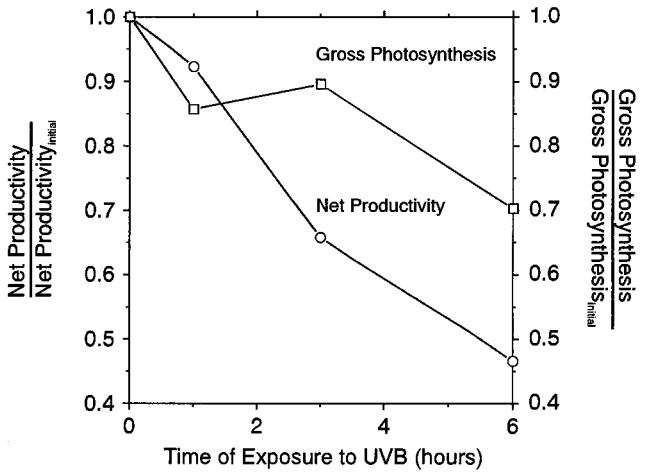

FIG. 4. Effect of exposure to UV B (2.2 μmol of photons m^{-2} s^{-1} at 310 nm) on gross and net photosyntheses in the Solar Lake microbial mat. Gross photosynthesis is expressed as the depth-integrated rate of gross photosynthesis for the entire photic zone. Net photosynthesis is calculated on the basis of the oxygen concentration gradient across the diffusive boundary layer. This gradient is proportional to the flux of oxygen across the mat-water interface and is therefore a measure of net community productivity by the mat (amount of oxygen produced by photosynthesis minus amount of oxygen consumed by respiration).

plastes. We chose, therefore, to monitor the changes in spectral reflectance at 577 nm (hereafter termed reflectance$_{577}$) in all subsequent experiments in order to monitor changes in the spectral reflectance of the mat attributable to this particular cyanobacterium. The cessation of exposure to UV B resulted in an immediate reversal of the change in reflectance$_{577}$, and these changes were repeatable over several UV B treatments. Increases in reflectance$_{577}$ were faster than decreases in reflectance$_{577}$. Changes in reflectance$_{577}$ were correlated with net community productivity, as measured by changes in oxygen flux across the diffusive boundary layer (Fig. 6).

Wavelength dependency of response. The UV B source that we used also provided some UV A. In order to make sure that the effects we observed were attributable to UV B alone, we used an acetate filter (cutoff, 315 nm) to remove all UV B from the source. We then monitored the changes in the reflectance$_{577}$ both with and without the acetate filter in place between the UV source and the mat. The responses that we observed were apparently due to the UV B portion of the spectrum, since migrations occurred much more slowly, or not at all, until the acetate filter was removed (Fig. 7).

Reflectance changes were induced by irradiance changes in various wavebands. Preliminary experimentation had revealed that a shift of 100 μmol of photons m^{-2} s^{-1} in visible light (shift-up) was the minimum necessary to produce a detectable response, whereas much smaller shifts in the flux of UV (particularly UV B) would produce a similar response (data not shown). Figure 8 shows the results of an experiment in which visible light (a shift in the amount of photosynthetically active radiation from 56 to 166 μmol of photons m^{-2} s^{-1}), UV A (a shift from undetectable to 3.9 and then to 4.8 μmol of photons m^{-2} s^{-1}), and UV B (a shift from undetectable to 0.98 μmol of photons m^{-2} s^{-1}) were all manipulated over the same mat core in a single time course experiment. At photon fluxes above the thresholds necessary to produce the response, all three treatments did result in rapid migratory movements. UV B was the most effective wave band (per photon) in provoking migration. Much higher photon fluxes in UV A (3.9 to 4.8 μmol of photons m^{-2} s^{-1}) were necessary to produce a change in reflectance$_{577}$ of less than half of that produced by UV B at 0.98 μmol of photons m^{-2} s^{-1}. An increase in UV A from 3.9 to 4.8 μmol of photons m^{-2} s^{-1} did not increase the magnitude of the change in reflectance$_{577}$ (Fig. 8). Decreases in reflectance$_{577}$ (due to an upward migration of pigment-containing organisms) were generally slower than the increases in reflectance$_{577}$ we observed in response to the onset of UV A and UV B, as well as increases in visible light.

DISCUSSION

Evidence for migration and alternative hypotheses. The changes which occurred in the Solar Lake microbial mat upon exposure to UV included (i) a change in the color of the surface, (ii) a decrease in the porewater oxygen concentration in the surface layers, (iii) a shift downward of the depth at which the maximum porewater oxygen concentration occurred, (iv) decreases in gross photosynthesis in the surface layers, (v) increases in gross photosynthesis below a depth of ca. 200 μm, (vi) a decrease in reflectance$_{577}$, and (vii) rapid reversibility of all of the above-mentioned changes. These changes, and particularly the rapid reversibility of the observed changes, are consistent with a migration of cyanobacterial primary producers. We will examine some possible alternatives to this migration hypothesis in the following discussion.

We observed a decrease in porewater oxygen concentrations in response to exposure to UV B. Mat porewater oxygen concentrations are controlled by the relative rates of photosynthetic production of oxygen and respiratory consumption of oxygen by both photosynthetic and heterotrophic organisms. The decrease in porewater [O_2] upon exposure to UV B could therefore be caused by an increase in rates of respiration, which we consider to be unlikely given that UV B exposure should damage respiration and not enhance it, or by a decrease in rates of photosynthesis, which we measured. The measured decrease in gross photosynthesis at the surface of the mat could certainly result from UV-mediated damage instead of, or in addition to, a migration, and indeed some portion of the

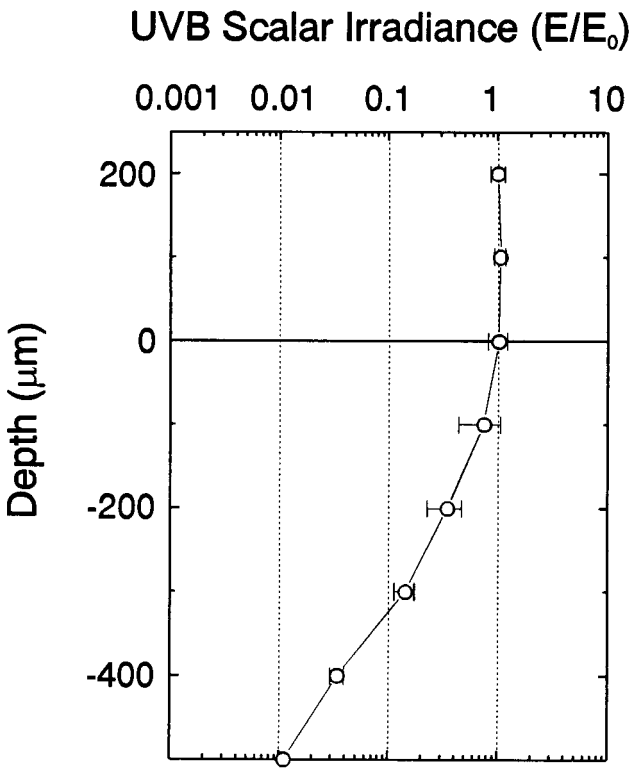

FIG. 5. Profile of diffuse UV B (scalar irradiance at 310 nm) in the Solar Lake microbial mat community, measured by using a recently developed fiber optic microsensor. Scalar irradiance is a measurement of radiation incident upon a point from all angles.

activity of the surface layer of the mat is lost upon the first exposure to the UV. However, we did see activity return to these surface layers upon cessation of UV B exposure on time scales that could not be explained by repair mechanisms. We conclude that this return of activity to the surface layers was due to an upward migration of phototrophic organisms. The increase in gross photosynthesis which we observed in the deeper layers of the mat could be explained by (i) a migration to that depth, (ii) increased light availability due to UV-mediated bleaching of the surface layers, or (iii) growth at the deeper layers. The bleaching hypothesis is an unlikely explanation, as the photic zone did not deepen. Growth is equally unlikely. To obtain the observed sixfold increase of gross photosynthesis in the 3-h time period (Fig. 3; 400-μm depth measurements) would require *Escherichia coli*-like doubling times (slightly more than 1.5 h). Doubling times on this order are far shorter than those of any known cyanobacterium. The redistribution of photosynthetic activity upon cessation of UV also argues strongly against both bleaching and growth. Short-term changes in mat coloration due to variations in environmental conditions are usually associated with migrations (13, 14, 19, 26, 31). We saw a decrease in the green color of the surface of the mat upon exposure of the community to UV. That means that something green (which was at the surface before) was not there after UV B exposure. This could be due to UV-mediated bleaching of pigments or to green cells leaving the near-surface areas. We also, however, observed a greening of the surface upon UV shutoff. This means that either whole cells were coming back to the surface or pigments were being resynthesized (almost fully) within 2 to 3 h by a nonmigrating surface layer which had its photosynthetic capabilities damaged (Fig. 2). Repigmentation of bleached cyanobacteria usually takes place on time scales of days. The rapidity of the changes argues for a migration phenomenon, which is known to occur in other microbial mats on time scales of hours (31). Thus, we conclude that the photoautotrophic members of intact samples of Solar Lake microbial mat migrate in response to exposure to UV B.

We note that our results do contrast with the preliminary results of Garcia-Pichel and Castenholz, which suggest that UV A may be more important in the case of intact mats composed of *Oscillatoria* sp.-*Spirulina* sp. assemblages (4, 13). It seems likely that there is a complex relationship between the various wavelengths which are important in regulating the migratory responses of microorganisms exposed to solar UV. Solar UV incident upon naturally occurring microbial mat communities contains both UV A and UV B, and the relative proportions of these wave bands are not simulated by our artificial UV sources. That cyanobacteria may sense and respond to UV, however, has previously been rigorously demonstrated; e.g., some cyanobacteria have been shown to respond directly to UV B by synthesizing sunscreen pigments (11, 13). The implication of our results (i.e., that some cyanobacteria are able to sense UV B directly and respond "behaviorally" to it) now needs to be rigorously tested by direct measurements of motility in isolated cultures or field populations. This may be a difficult enterprise and is not within the scope of the present contribution. In future experiments with isolated organisms, optical conditions similar to those found in the mat environment, containing a steep gradient of UV exposure within the measuring setup, should be sought in order to allow the motile cells to reach safe areas within time scales that permit survival.

UV B-induced migrations as a strategy for protection against UV. UV B exposure dramatically reduced the integrated community gross photosynthetic rates and net productivity in the Solar Lake microbial mats, but some portion of the total mat photosynthetic activity (at least over the time frame investigated in the course of these experiments) recovered quickly. These data demonstrate that there is a portion of the population of *M. chthonoplastes* which was able to use a vertical migration response to avoid damage by UV B. This occurs in intact Solar Lake microbial mats in spite of previously reported inhibitory effects of UV on motility in cyanobacteria (7). Measurements of UV B penetration revealed that organisms migrating to a depth of 300 μm would reduce the UV B irradiance they experienced to 10% of the surface irradiance. The migratory movement is a mechanism by which these organisms may avoid the negative effects of the higher UV doses present at the surface of the mat.

Our results indicate that UV B is by far the most effective wave band in promoting the migration response of *M. chthonoplastes*. It is a common opinion that photoprotective mechanisms implicated in the acclimation to UV B exposure in microorganisms may actually be triggered by the sensing of wavelengths in the UV A band. This would imply that microorganisms would not be able to respond to ozone-mediated climatic changes in UV regimen because these would alter the ground levels of UV B, but not those of the UV A which is sensed. Our present experiments imply that these populations of *M. chthonoplastes* were able to sense UV B directly and to behaviorally respond to it through motility in a manner that is physiologically beneficial.

Fitness changes associated with UV-induced vertical migrations. Our experiments did not address potential costs of migration to migrating organisms. Microbial mat organisms live in extremely steep vertical gradients of light and nutrients. A migration downward, away from the surface of the community, decreases the exposure of the organisms to potentially harmful

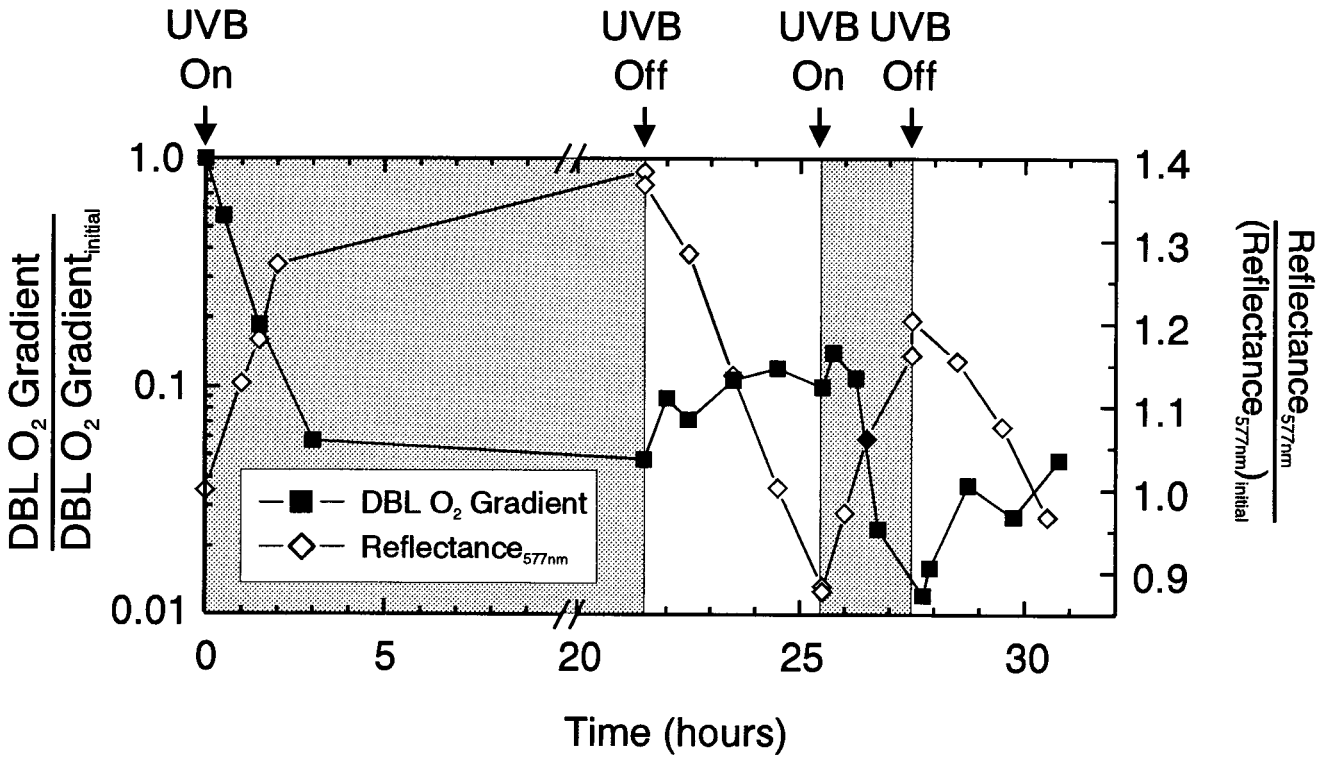

FIG. 6. Effects of UV B on the oxygen concentration gradient across the diffusive boundary layer (DBL) and reflectance$_{577}$ (radiance reflectance) of the Solar Lake microbial mat community. The oxygen concentration gradient across the DBL is directly proportional to the flux of oxygen across the mat-water interface and is therefore a measure of net community productivity (amount of oxygen produced by photosynthesis minus amount of oxygen consumed by respiration). Results from a 32-h experiment are shown. Reflectance$_{577}$ was recorded with a fiber optic light microprobe positioned 5 mm from the surface of the mat.

UV B but also to potentially growth-limiting light energy. The overall change in fitness of migrating organisms, relative to that of organisms which do not migrate, is presumably a function of the relative importances of these and other factors. Further work is needed in order to evaluate the potential of the migratory response as a long-term strategy for UV protection. Certainly the existence of the migratory response and the relative effectiveness of the UV B portion of the spectrum in causing it argue in favor of its importance as a photoprotective adaptation.

Experimental considerations. It is difficult to extrapolate data obtained from experimental manipulations of UV B to a predictive understanding of the effects of UV B (or of changes in UV B) in nature. Our studies were performed in the laboratory with samples that had been collected days to weeks prior to the start of the experiments. There is often a greening of the surface of microbial mats which occurs upon their transfer from the site of collection to laboratories, even when the mats are maintained under high-intensity light sources. The greening (which was also evident in the mats used for our experiments) results from a migration of cyanobacteria to the surface layers of the mat. Our results indicate that it may be the absence of UV in the artificial light sources used which allows the greening to occur.

Although the position of the cyanobacteria in our samples (nearer the surface than they would be in nature) may have rendered them more sensitive to applications of UV, the UV treatment we employed was an immediate "switch on." UV was immediately increased from a nearly undetectable level to an irradiance representative of natural in situ irradiance at midday at the field site. Natural (solar) UV increases gradually

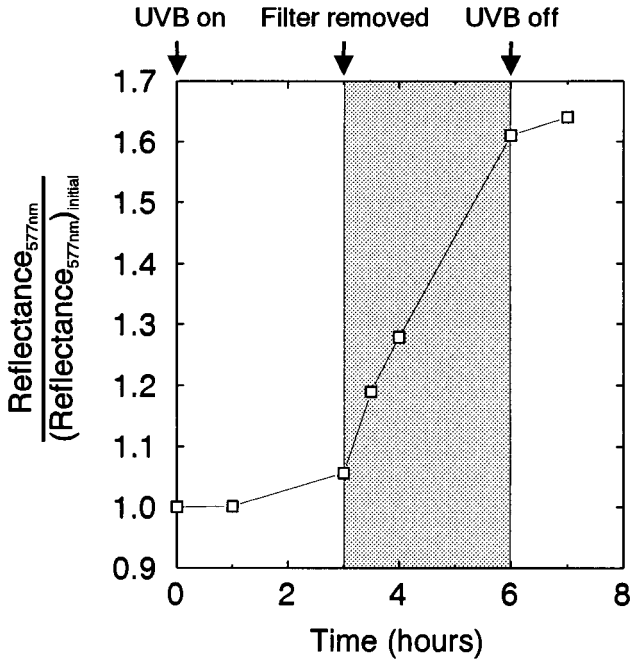

FIG. 7. Reflectance$_{577}$ (radiance reflectance) of the Solar Lake microbial mat community during exposure to UV B emitted from a fluorescence suntanning bulb. An acetate filter which allowed only UV A to pass through to the mat was in place at the start of the experiment but was removed 3 h after the start of exposure.

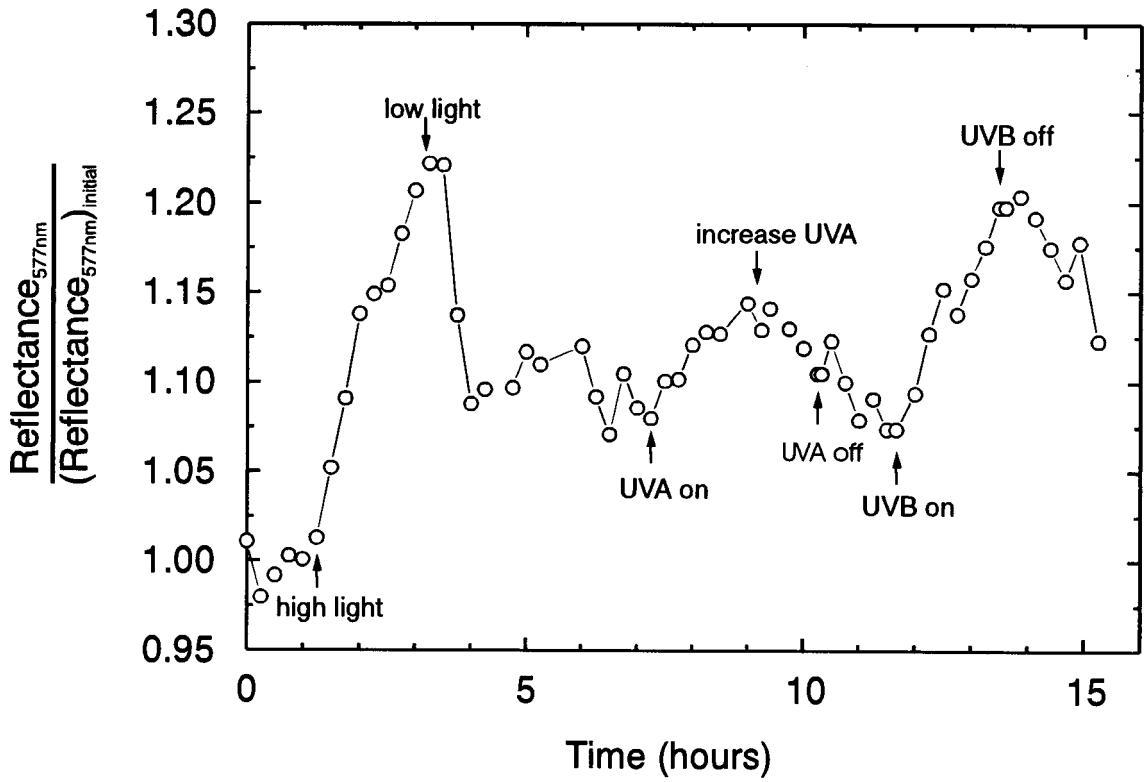

FIG. 8. Reflectance$_{577}$ (radiance reflectance) of the Solar Lake microbial mat community throughout a 15-h experiment. The effects of a shift to a higher light intensity (shift in the amount of photosynthetically active radiation from 56 to 166 μmol of photons m^{-2} s^{-1}) as well as of irradiation with both UV A (3.9 to 4.8 μmol of photons m^{-2} s^{-1} at 365 nm) and UV B (0.98 μmol of photons m^{-2} s^{-1} at 310 nm) are shown.

with the visible spectrum to a midday maximum and then decreases gradually after the midday maximum. A more natural pattern of UV B might allow the migratory response to reduce the amount of damage (a decrease in photosynthesis, [1]which was not recovered after the UV B source was switched off) observed in these experiments. Consequently, UV B-induced vertical migrations should be far more effective as a protective strategy in field populations than our laboratory experiments indicate.

Ecosystem level effects of UV-induced vertical migrations. A clear effect of the downward migration of phototrophic organisms was a relaxation of the gradient in oxygen concentration across the diffusive boundary layer (Fig. 4). This gradient is directly proportional to the net flux of oxygen out of the mat community, a commonly used measurement of net productivity in benthic photosynthetic communities. Therefore, although the migration response may allow mat microorganisms to minimize UV B-induced damage, the overall productivity of the ecosystem is decreased. This decrease could be attributable to a number of factors, including (i) a decrease in the amount of light available for photosynthesis at greater depths and (ii) an increased diffusional distance over which water column nutrients and inorganic carbon must be transported to the photosynthetic organisms. This has implications for studies of the effects of ozone-mediated increases in UV B in benthic photosynthetic communities, many of which include organisms with the ability to undergo vertical migrations. Several benthic diatoms and cyanobacteria migrate in response to a number of environmental influences. Their ability to migrate in response to UV B, as well as the effects of that migration on net community primary productivity, needs to be investigated.

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