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Rapid Recovery of Marine Bacterioplankton Activity after Inhibition by UV Radiation in Coastal Waters

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Laboratory and in situ experiments were performed in order to evaluate the role of UV radiation on bacterial activity. Particular attention was given to the determination of the role of UV-A and photosynthetic active radiation (PAR) and different nutrient conditions on the recovery of bacterial activity. Laboratory experiments with nearly natural radiation intensities indicated a 20 to 40% reduction from the initial level of bacterial activity after UV-B exposure for 2 to 4 h. Bacterial activity in freshly collected seawater showed a more pronounced inhibition and faster recovery than bacterial activity in aged, nutrient-depleted seawater. The results of in situ experiments with filtered water (0.8-μm-pore-size filter) and natural surface solar radiation levels agreed with those of the laboratory experiments and revealed that UV-A and PAR are important for the recovery of bacterial activity and result in levels of bacterial activity that are higher than those prior to exposure to full solar radiation. Bacterioplankton exposed to full solar radiation for 3 h and subsequently incubated at different depths within the upper mixed water column showed an increase in bacterial activity with increased depth; the highest bacterial activity was detected at depths of 5.5 to 10.5 m, where the short-wavelength UV-B was already largely attenuated, but enough long wavelength UV-A and short PAR were available to allow recovery. This elevated bacterial activity following exposure to UV-B was attributed to the photolysis of dissolved organic matter (DOM) exposed to near-surface radiation and to the rapid recovery of bacteria from UV stress once they were mixed into deeper layers of the upper mixed water column, where they efficiently utilize the photolytically cleaved DOM. It is concluded that studies on the role of UV on the carbon and energy flux through the upper layer of the ocean should take into account the highly dynamic radiation conditions.

Although UV radiation is known to have direct detrimental effects on organisms, its role in aquatic ecosystems has not received adequate attention. The main reason for this neglect of the potential role of UV probably stems from earlier studies in which it was reported that UV penetration is limited to the top layers of the water column, even in the open ocean (12). With more sensitive instruments, however, it has been demonstrated that UV radiation penetrates to depths of >20 m (1, 4, 44).

On the one hand, solar radiation cleaves dissolved organic matter (DOM) in the top layer of the ocean and produces low-molecular-weight compounds (19, 33, 34) which are taken up efficiently by bacterioplankton (24, 25, 45); on the other hand, photolytic activity might lead to the formation of radicals (28, 48), retarding the growth of bacterioplankton. Thus, it is reasonable to assume that UV radiation alters the DOM pool in the surface layer of the ocean by photochemically producing compounds that promote and inhibit the growth of bacterioplankton. Moreover, it has been shown that photolytic activity contributes significantly to the production of inorganic CO_2 in surface layers (26), thus converting a fraction of the dissolved organic carbon (DOC) pool into a form that is unavailable to bacteria.

Freshwater systems are usually characterized by a higher concentration of humic substances known to absorb UV light (21, 35, 40), while marine systems generally have lower concentrations of DOC and humic substances (22, 23); therefore, UV can penetrate much deeper into the water column (44).

UV radiation modifies not only the DOM pool in the surface layers of the ocean but also the organisms inhabiting these layers (42, 46). In order to shield themselves from UV, several phytoplankton species produce protective compounds, such as mycosporine-like amino acids (8), which absorb radiation in the UV range (14, 16). While the occurrence of UV-protective pigments is widespread among phytoplankton species, there is no evidence of such protective pigments in bacterioplankton (7). It has also been demonstrated that bacteria are affected by UV radiation more than other planktonic organisms are because of their small cell size (11) and because they are too small to be efficiently protected by pigments (7). These findings are in agreement with those of Herndl et al. (10) and Müller-Niklas et al. (36), who showed that bacterioplankton species from the surface layers of the sea are as sensitive as those from subpycnocline waters are to UV-B. Moreover, these authors and others showed that UV radiation greatly reduces the metabolic and ectoenzymatic activity of bacterioplankton from the surface layer of the sea (9, 10, 36).

UV radiation, particularly UV-B, leads to the formation of thymine dimers in bacterial cells (2, 15, 29, 30). DNA damage can be repaired by three different mechanisms, photoenzymatic repair (PER), nucleotide excision repair, and postreplication repair (5, 39). While the expression of the photolyase of PER is activated by the upper UV-A (370 to 400 nm) and lower photosynthetic active radiation (PAR; 400 to 450 nm), nucleotide excision repair and postreplication repair require ATP (14, 27). In the upper mixed layer, bacterioplankton are subjected to rapidly changing radiation conditions, receiving high doses of detrimental UV-B radiation near the surface for a certain period of time; if the bacterioplankton are mixed into deeper waters, where UV-B is largely attenuated, the UV-A radiation range prevails, potentially inducing repair of the damage caused by exposure to UV-B in the surface layer. This

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dynamic aspect of damage and repair has not yet been adequately addressed.

In this study we tried to evaluate (i) the potential of PER to restore bacterioplankton activity compared to that of other repair mechanisms and (ii) the role of changing levels of radiation on bacterioplankton activity in the upper mixed layer. We hypothesized that bacterioplankton efficiently repair UV-induced DNA damage if they are mixed into the deeper layers of the upper mixed water column. Furthermore, we assumed that DOM photolytically cleaved in the surface layers and mixed along with the bacterioplankton into deeper layers is taken up rapidly, leading to enhanced bacterial activity.

MATERIALS AND METHODS

In order to determine the influence of different ranges of wavelengths on the recovery of bacterioplankton activity following UV-B stress, both lab and field experiments were performed. To mimic the influence of the mixing of the water column on bacterial activity, field experiments were done in the northern Adriatic Sea (45°07′N, 14°05′E).

Importance of different wavelength ranges and nutrient conditions on the recovery of bacterial activity following UV-B stress. In order to test the role of different ranges of wavelengths and nutrient conditions on the recovery of bacterial activity from UV-B stress, we performed experiments in the lab with artificial radiation and experiments in the field with solar radiation. For lab experiments (described below), water collected in the northern Adriatic Sea was either used immediately as a model representing moderate nutrient conditions or aged for 3 weeks to mimic nutrient-depleted conditions. Before the experiments with seawater cultures were begun, 900 ml of filtered aged seawater (0.2-μm-pore-size filter) was inoculated with 100 ml of freshly collected water for 3 days. The DOC concentration of the freshly collected seawater ranged from 1.5 to 2.4 mg of C liter^{-1}, and that of the seawater culture (collected at a more oligotrophic site) at the beginning of the experiments (after freshly collected water was added) was 0.9 mg of C liter^{-1}. All the lab experiments were performed at 20°C.

For the experiments, the initial bacterial activity (t_0) was measured, and the seawater was incubated in 1-liter quartz bottles and exposed to artificial UV-B radiation (wavelength range, 300 to 320 nm; 0.4 W m^{-2}; Philips TL 100 W/01 lamps) for either 2 h (freshly collected water) or 4 h (aged seawater). After exposure to UV-B, the sample was divided, bacterial activity was measured (described below), and the remaining subsamples were exposed to different ranges of radiation. UV-A was provided for various periods of time with Philips TL 100 W/10R lamps (wavelength range, 350 to 400 nm; 0.25 W m^{-2}). The lower intensity of UV-A was meant to simulate the lower radiation levels in the deeper layers of the upper water column. PAR was provided by cool white lamps (Philips TLD 58 W/84).

For the in situ experiments, water collected shortly after sunrise was brought to the lab and filtered through a 0.8-μm-pore-size filter (polycarbonate, 47-mm diameter; Millipore) to reduce the number of grazers and autotrophic organisms. After bacterial activity (t_0) was measured (as described below) in the 0.8-μm-pore-size filtrate, a 1-liter water sample was incubated in a quartz tube (stoppered at both ends with silicone) and exposed on a floating rack to surface solar radiation for 3 h around noon (experiments were done only on cloudless days, and radiation at 305 nm varied between 0.67 and 1.5 μW cm^{-2} nm^{-1} in August and between 0.6 and 0.91 μW cm^{-2} nm^{-1} in September). After bacterial activity was assessed again (incubation time, 30 min), the sample was divided and exposed either to the complete spectrum of solar radiation or to surface solar radiation from which UV-B was excluded by wrapping the quartz tube in Mylar D-foil or held in the dark. Measurements were performed five times each in August 1995 (between the 12th and the 24th) and September 1995 (between the 21st and the 27th). All surface solar radiation measurements were performed with a Biospherical PUV 510 radiometer.

Bacterial activity under changing radiation conditions. In order to mimic the role of changing radiation levels at different depths of the water column (caused by mixing), water from a depth of about 5 m was collected early in the morning. After the initial bacterial activity (t_0) was measured by the dual labeling technique (described below), filtered seawater (0.8-μm-pore-size filter) was incubated for 3 h in situ in 1-liter quartz tubes mounted on a floating rack exposed to surface solar radiation around noon. Thereafter, bacterial activity was again measured by the dual label technique, and the sample was divided and incubated for another 3 h in 50-ml quartz tubes at five different depths ranging from 0.5 to 10.5 m. One control (in darkness) was fixed at a depth of 5.5 m. After incubation, bacterial activity in the samples exposed to radiation at different depths, and therefore to different radiation conditions, was assessed.

Radiation throughout the water column (water depth, 15 to 20 m) was measured at four different UV wavelengths (305, 320, 340, and 380 nm) and at the PAR range (400 to 700 nm), together with temperature, with a Biospherical PUV 500 radiometer at the beginning and the end of the in situ incubation.

Bacterial production measurements. In the lab experiments, bacterial activity was measured in triplicate with two formalin-killed blanks (2% final concentration) by adding [^{3}H]thymidine (20 nM final concentration) to each of the 5-ml subsamples and incubating the samples in the dark at 20°C for 30 min (6). In preliminary experiments, [^{14}C]leucine was used to estimate the incorporation of leucine into bacterial protein (20); no significant difference was found between both measurements, similar to previous findings (10). For the in situ experiments, bacterial activity was measured by the dual labeling technique, with [^{3}H]thymidine and [^{14}C]leucine incorporated into bacterial macromolecules (13) and samples incubated in the dark at near-in situ temperature (20 to 23°C) for 20 min. After incubation, the samples were filtered onto cellulose nitrate filters (HAWP, 0.45-μm pore size, 25-mm diameter; Millipore) and rinsed with chilled 5% trichloroacetic acid. The filters were placed in scintillation vials with 1 ml of ethyl acetate and 7 ml of scintillation cocktail (Insta-Gel; Packard) added. Radioactivity was assessed with a liquid scintillation counter (Packard Tri-Carb 2000) by external standard ratio technique. For converting thymidine and leucine incorporation into bacterial production, the following factors were used: 1.1×10^{18} cells mol of thymidine consumed^{-1} (6) and 0.07×10^{18} cells mol of leucine^{-1} (3).

Statistical analysis. Statistical analyses were performed with the nonparametrical matched-pair rank test (Wilcoxon) and the multicomparison Friedman test with SYSTAT version 5.2 for Macintosh (Systat 1990–92, Inc.).

RESULTS

Importance of different wavelength ranges and nutrient conditions for the recovery of bacterial activity following UV-B stress. In the cultures with aged seawater inoculated with freshly collected bacterioplankton, the initial bacterial activity (t_0) measured by thymidine incorporation ranged from 1.33 to 41.18 μg of C liter^{-1} h^{-1} (n = 11). After the samples were exposed for 4 h to artificial UV-B radiation, bacterial activity declined significantly (Wilcoxon, $P = 0.004$; $n = 11$; on average by ≈20% compared to the initial activity) (Fig. 1A). Subsequent exposure to either continuous UV-A, PAR, or darkness for 4 h showed pronounced differences in bacterial activity (Fig. 1A). Bacterial activity in the dark treatment decreased further at approximately the same rate as that in the previous UV-B treatment (Fig. 1A), while in the PAR treatment the decline in bacterial activity was diminished. In the UV-A treatment, however, bacterial activity increased again (Fig. 1A) and was significantly higher than in the PAR and the dark treatments (Friedman, $P = 0.05$; $n = 4$); the PAR and the dark treatments were not significantly different from each other (Wilcoxon, $P = 0.113$; $n = 4$).

In freshly collected, filtered seawater (0.8-μm-pore-size filter), the initial bacterial activity (t_0) ranged from 0.83 to 17.70 μg of C liter^{-1} h^{-1} (n = 19). Bacterial activity decreased more rapidly than in the batch cultures with aged seawater (compare panels A and B in Fig. 1), declining by ≈35% within 2 h of UV-B exposure. Thereafter, the sample was divided and either exposed for various periods of time to UV-A or PAR or kept in the dark for 2 h (Fig. 1B). Similar to the results of the experiments with aged seawater, bacterial activity was lowest in the dark treatment following UV-B incubation; bacterial activity increased with increased exposure to UV-A (Fig. 1B). Exposure to UV-A for 0.5 h followed by incubation in the dark for 1.5 h led to a significantly higher bacterial activity than did continuous darkness (Wilcoxon, $P = 0.034$; $n = 4$) (Fig. 1B). Similar to the inhibition by UV-B, the recovery of bacterial activity following UV-B exposure was more pronounced in the freshly collected seawater than in the aged, probably more nutrient-depleted, seawater.

Experiments with surface solar radiation and filtered seawater (0.8-μm-pore-size filter) revealed the same tendency as the lab experiments. Bacterial activity (t_0) varied between 2.18 and 17.86 μg of C liter^{-1} h^{-1} for both leucine and thymidine incorporation in August and between 2.65 and 6.78 μg of C liter^{-1} h^{-1} in September. The experiments were performed only on cloudless days; during exposure, surface solar radiation at 305 nm varied between 0.67 and 1.5 μW cm^{-2} nm^{-1} in August and between 0.6 and 0.91 μW cm^{-2} nm^{-1} in Septem-

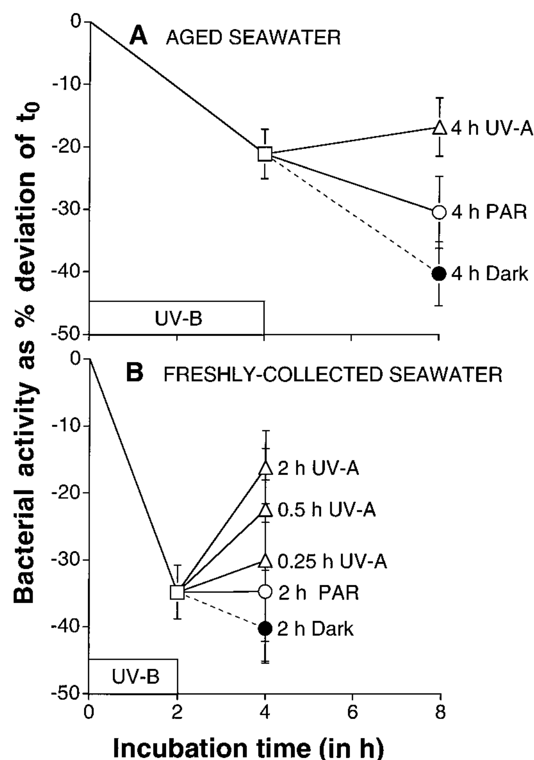

FIG. 1. Development of bacterial activity after exposure to artificial sources of UV-B and subsequent exposure to the following radiation conditions: UV-A, PAR, and darkness in aged seawater (for 3 weeks; thereafter, freshly collected bacteria were inoculated and incubated for 3 days before starting the experiment) (A) and freshly collected filtered seawater (0.8-μm-pore-size filter) from the northern Adriatic Sea (45°07′N, 14°05′E) (B). Bacterial activity is given as percentage deviation of thymidine incorporation prior to UV-B exposure; symbols indicate means, and vertical bars represent standard errors (n ranged from 4 to 18). The duration of the treatments as well as the radiation range are given. Samples exposed for 0.25 and 0.5 h to UV-A were kept in the dark for the rest of the incubation period. The total incubation period after exposure to UV-B was 2 h.

ber. Bacterial activity after 3 h of exposure to surface solar radiation decreased by ≈40% for both thymidine and leucine incorporation in August and September (Fig. 2). Subsequent exposure to different radiation conditions indicated that exposure to continuous full-range solar radiation led to a further reduction in bacterial activity (Fig. 2), while the dark treatment either increased bacterial activity (Fig. 2A) or caused it to remain at the level that was reached after exposure to solar radiation (Fig. 2B). For both months, the exclusion of the UV-B range from the solar spectrum caused bacterial activity to become higher than the initial level (t_0). Bacterial activity was significantly higher as a result of the treatment from which UV-B was excluded (UV-A plus PAR treatment) than it was after the dark treatment (Wilcoxon, $P = 0.022$; $n = 4$) in September, while no significant difference between the UV-A plus PAR and the dark treatments was detectable in August (Fig. 2A) (Wilcoxon, $P = 0.07$; $n = 4$).

Bacterial activity under changing radiation conditions. Bacterial activity (t_0) of water samples collected in the morning and filtered through 0.8-μm-pore-size filters was measured (by thymidine and leucine incorporation). The water samples were subsequently exposed to surface solar radiation around noon for 3 h, and bacterial activity was measured again immediately thereafter. In order to mimic the mixing of the upper layers of the water column, the sample exposed to solar radiation was divided and incubated in situ at different depths.

On the basis of temperature profiles (with the Biospherical PUV 500), the water column was well mixed to depths of 6 to 8 m in August and 17 m in September. A strong pycnocline was developed in both months, with temperature decreases of 1.2°C in August and 1.4°C in September over a distance of 1 m. During August, the 1% radiation level for a 305-nm wavelength ranged from 5.15 to 5.84 m (mean ± standard deviation [SD], 5.5 ± 0.28 m; $n = 5$); in September, the 1% level for a 305-nm wavelength was between 5.69 and 6.07 m (mean ± SD, 5.82 ± 0.22; $n = 4$). The 1% radiation level at 305 nm corresponds roughly to the 3.5% radiation level at 320 nm, the 10% level at 340 nm, and the 30% level at 380 nm, and 40% of PAR penetrates to this depth, reflecting the differential attenuation. The mean attenuation coefficients (K_d) of the different wavelengths are shown in Table 1. For all wavelength ranges, K_d was higher in August than in September.

After in situ incubation of the samples, bacterial activity was assessed again (Fig. 3). At a depth of 0.5 m, bacterial activity (measured by thymidine and leucine incorporation) was reduced compared to the initial activity in August but not in September (Fig. 3). In deeper layers, bacterial activity was always higher than the activity measured prior to exposure to surface solar radiation. The highest bacterial activity was between 5.5 and 10.5 m (Fig. 3). Dark controls exhibited bacterial activity that was lower than that prior to exposure to surface solar radiation except when thymidine was incorporated in August, resulting in a slight increase in bacterial activity under dark conditions (Fig. 3). Maximum enhancement of bacterial

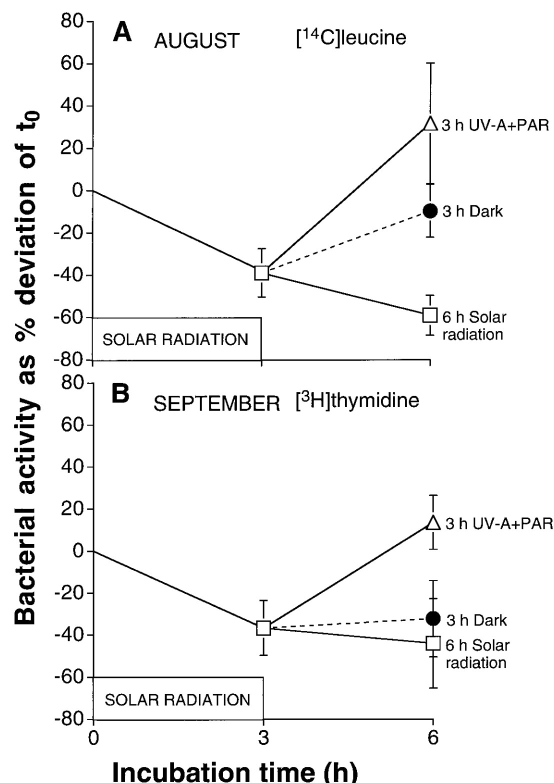

FIG. 2. Development of bacterial activity in filtered (0.8-μm-pore-size filter) seawater at different solar wavelength ranges compared to activity prior to exposure to solar radiation in August (measured by [^{14}C]leucine incorporation) (A) and September (measured by [^{3}H]thymidine incorporation) (B). Measurements were performed five times in August (between the 12th and the 24th) and five times in September (between the 21st and the 27th). Data points represent the means of five experiments; vertical bars indicate standard errors.

TABLE 1. Attenuation coefficient (K_d) of different UV wavelengths and PAR range in the water column of the northern Adriatic Sea in August and September 1995

Wavelength (nm)	Mean K_d ± SD[a]	
	August	September
305	0.912 ± 0.132	0.877 ± 0.071
320	0.539 ± 0.032	0.478 ± 0.029
340	0.386 ± 0.027	0.353 ± 0.023
380	0.217 ± 0.022	0.206 ± 0.023
PAR	0.169 ± 0.056	0.141 ± 0.023

[a] Mean K_ds ± SDs were determined based on profiles done throughout the water column (10 for August and 4 for September).

activity coincided with a wavelength ratio (320_S:[320_D:380_D]) ranging from 215 to 2,355 (Fig. 3). The wavelength of 320 nm represents the detrimental UV-B to lower UV-A range; 380 nm represents the wavelength range inducing the PER mechanism; 320_S represents irradiance at 320 nm at the surface, responsible for the UV stress in bacteria; and the 320_D:380_D ratio represents irradiance at the respective wavelength in the deeper layers where bacteria were incubated and stands for the relation between the damaging wavelengths and those responsible for recovery. The ratio between the radiation at 320_D:380_D nm, averaged over the 2 months, declined from 0.356 ± 0.032 (mean ± SD; n = 13) at a depth of 10 cm to 0.069 ± 0.015 at a depth of 5 m.

DISCUSSION

In this study we used artificial and natural solar radiation to investigate the role of UV radiation in inhibiting bacterial activity and to determine the importance of different repair mechanisms. Similar to the results of earlier studies (10, 36, 41), UV-B and natural solar radiation were found to significantly reduce bacterial activity. In this study and a former study, reduction in bacterial activity was determined by thymidine incorporation as well as by leucine incorporation (Fig. 2) (10). Exposure to UV-B radiation is known to damage DNA (14, 16) and to reduce bacterial ectoenzymatic activity (36). Recently, it has been shown that bacterioplankton are affected more by UV radiation than other planktonic organisms are (11), probably because of their large surface:volume ratio and an obvious lack of protective pigments (7), which are widespread among phytoplankton (14, 16, 38).

Several mechanisms are responsible for repairing DNA damage caused by UV radiation. In this study we performed lab as well as field experiments, using natural solar radiation to determine the potential importance of the PER of DNA damage. The UV-B radiation level of 0.4 W m^{-2} used in our laboratory experiments is similar to radiation levels detected in the field on sunny days (10). The UV-A radiation level used for the lab experiments was similar to that detectable at depths of 5 to 10 m in the northern Adriatic Sea (9a). PER is the only mechanism that repairs DNA damage with the longer UV-A and the shorter PAR range (370 to 450 nm) and does not require ATP (5, 14); radiation of this wavelength induces the expression of the photolyase to repair damaged DNA (5). Both lab and field experiments showed that after exposure to UV-B, UV-A and PAR significantly increased bacterial activity (Fig. 1 and 2). Remarkably, a period of exposure as short as 30 min, followed by incubation in the dark, led to a bacterial activity significantly higher than that obtained under conditions of continuous darkness (Fig. 1B). This indicates that radiation in the range of UV-A and PAR is efficiently used by bacterioplankton to recover from UV stress. Although we did not directly measure the amount of UV-induced damage and its subsequent repair, the incorporation of thymidine and leucine into bacterioplankton as an integrated measure of bacterial activity seems useful for evaluating the role of UV on bacterioplankton in an ecological context.

In view of the wavelength-dependent attenuation of irradiance in the water column (Table 1), it is obvious that bacterioplankton in the upper mixed layer are exposed to radiation

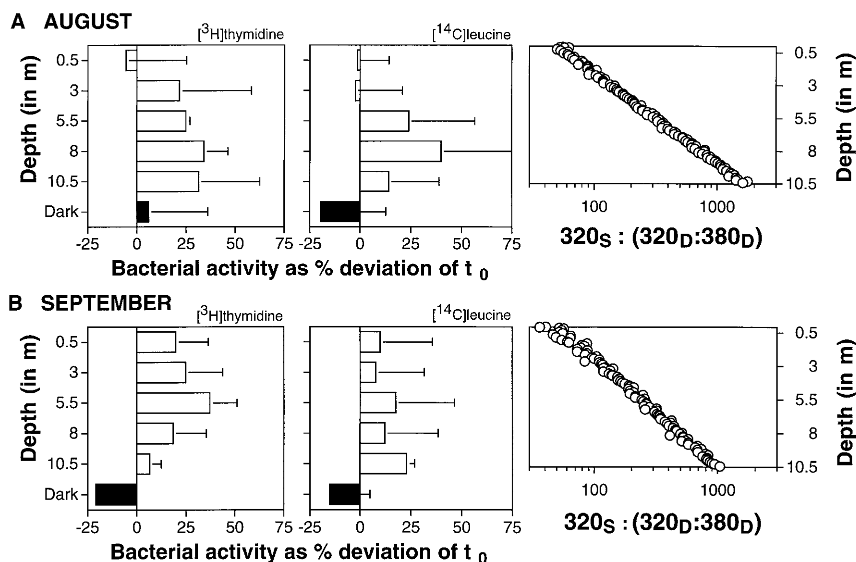

FIG. 3. Pattern of bacterial activity after 3 h of exposure to surface solar radiation levels and subsequent incubation at different depths. Bacterial activity is expressed as the percentage of deviation from the incorporation of thymidine and leucine prior to exposure to surface solar radiation (t_0). Bacterial activity of a sample kept in the dark after exposure to surface solar radiation is given for comparison. Columns represent the means of five measurements in August and five in September; horizontal bars indicate standard errors. The highest bacterial activity is at the wavelength ratio 320_S:(320_D:380_D), ranging from 215 to 2,355 (right panels). Data shown are the means of nine measurements in August (A) and four measurements in September (B).

conditions that are constantly changing. While detrimental radiation levels of UV-B and UV-A dominate close to the surface, long wavelength UV-A and PAR ranges prevail deeper in the upper mixed water column. These wavelength ranges are obviously used efficiently to repair the UV-induced damage, leading to a rapid recovery of bacterioplankton activity. As shown in Fig. 1, recovery from UV stress likely depends on nutrient conditions. In aged seawater, assumed to represent nutrient-depleted conditions (Fig. 1A), both inhibition and recovery were lower than in freshly collected seawater (Fig. 1B).

Bacterioplankton activity following exposure to surface levels of solar radiation and subsequently to UV-A plus PAR was always higher than it was prior to the exposure (Fig. 2), indicating that overall, solar radiation has some beneficial effects on bacterial activity. This issue was further investigated in in situ-mimicking mixing processes in the upper water column with the accompanying changes in radiation conditions (Fig. 3).

The attenuation in the water column of the northern Adriatic Sea (Table 1) is similar to that in other marine meso- to oligotrophic coastal waters (31, 43) and is within the range recently reported for oligotrophic freshwater systems (35).

Incubation of filtered water (0.8-μm-pore-size filter) at different depths of the water column following exposure to surface solar radiation levels for 3 h led to an elevated bacterial activity compared to the level prior to exposure (Fig. 3). Bacterial activity was highest at depths between 5.5 and 10.5 m. In this depth range, UV-B is almost completely attenuated (the 1% radiation depth at 320 nm was between 7.64 and 9.21 m during the investigation period), while between 10 and 20% of the surface radiation at 380 nm and in the PAR range is still present at this depth range. This depth-dependent pattern in bacterial activity points to the dominant role of the range of longer UV-A and PAR wavelengths in the recovery of bacterioplankton from solar radiation stress, which can be expressed by the wavelength ratio 320_S:(320_D:380_D) (Fig. 3). The highest bacterial activity following exposure to surface solar radiation was observed at a ratio of 320_S:(320_D:380_D), ranging from 215 to 2,355 (Fig. 3).

The elevated bacterial activity in the deeper layers of the upper water column is a consequence of rapid recovery from solar radiation stress experienced near the surface and probably of the photolysis of DOM. Although we did not measure directly photolytic activity in the DOM pool, it has been reported that solar radiation, especially in the UV-B and the UV-A ranges, photochemically cleaves DOM to produce labile, low-molecular-weight compounds which might be utilized by bacterioplankton. UV-mediated cleavage of DOM produces low-molecular-weight carbonyl compounds (17–19, 32, 33). Recently, Lindell et al. (24) and Wetzel et al. (45) showed that UV-exposed DOM is more accessible to bacterioplankton than untreated DOM. This increased availability of growth-supporting DOM might be at least partly compensated for the concurrent UV-mediated production of growth-inhibiting substances such as free radicals (37, 47). Thus, the observed effects on bacterioplankton activity in our study and others (24, 45) are actually net effects.

To our knowledge, previous experiments on the effects of UV on DOM and bacterioplankton have been conducted under conditions of constant radiation, whereas the upper layer of the water column is characterized by mixing processes and therefore by an environment in which radiation conditions are rapidly changing. As indicated in our experiments (Fig. 3), the combined effects of the photolysis of DOM and solar radiation on bacterioplankton and the mixing processes determine the turnover of DOM in the upper layers of the ocean. While close to the surface, high radiation levels photolytically cleave DOM, producing low-molecular-weight compounds which are easily available for bacterial uptake. At the same time, however, this high radiation level inhibits the uptake of substrate by bacterioplankton due to the damage of macromolecules such as DNA and ectoenzymes. Only if mixed into deeper layers of the ocean can bacteria efficiently repair damage by using the longer UV-A radiation and the short PAR range to repair DNA damage. The compounds which were photolytically cleaved in the surface layers are then efficiently taken up by the bacterioplankton, leading, overall, to a rapid recovery from UV stress. Thus, in the evaluation of the role of UV on the dynamics of DOM and its uptake by bacterioplankton, more attention should be paid to the rapidly changing radiation conditions in the surface layers of the ocean.

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