Role of ultraviolet radiation in aquatic systems: interaction between mixing processes, photochemistry and microbial activity

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ABSTRACT

In the surface layers of aquatic systems, ultraviolet (UV) radiation acts on dissolved organic matter (DOM) as well as on planktonic organisms. DOM is photolytically cleaved into low molecular weight compounds which are taken up efficiently by bacterioplankton. Bacterioplankton metabolism is significantly retarded in the presence of UV. Evidence is presented that originally labile DOM becomes more refractory upon exposure to UV while refractoy DOM becomes more labile. The development of a pronounced diurnal thermocline leads to extensive UV radiation exposure of DOM and the microorganisms entrappped in this layer. Only, when the diurnal thermocline breaks down in the late afternoon, and the upper water column is mixed again is the photolytically cleaved DOM then available for bacterioplankton uptake. Concurrrently, the bacterioplankton efficiently use UV-A and the lower PAR range to repair DNA damage.

Introduction

Ultraviolet radiation (UV) radiation in aquatic systems has received considerable attention over the past decade. Research on the impact of UV radiation on aquatic systems was initiated in response to the discovery of the ozone hole over Antarctica during the austral winter, and its spreading over vast areas of the southern hemisphere during austral spring [6]. This ozone depletion leads to increased penetration of UV-B (280-320 nm) through the atmosphere [6]. Increased UV-B radiation has been detected not only during the austral spring over the southern hemisphere, but is also evident in the northern hemisphere [5].

Early reports on the attenuation of UV in the water column of different systems indicated that UV is rapidly attenuated. Most earlier studies, therefore, concluded that its effect on aquatic organisms is minor. This view has been altered by using improved instrumentation to measure UV radiation in the water column [24]. It now appears that UV-B, although attenuated rapidly compared to UV-A (320-400 nm), penetrates to considerable depth. The 10 % radiation level of the 320 nm wavelength range is at < 25 m depth while the 10 % level of the 340 and 380 nm wavelengths is at 35 and 60 m depth, respectively (unpublished). Thus a considerable portion of the euphotic zone is exposed to UV radiation potentially harmful to planktonic organisms [26].

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Although in this paper particular attention is being paid to the direct and indirect impact of UV radiation on bacterioplankton and the bioavailability of the dissolved organic matter (DOM), the basic ecologically relevant questions to be answered are also valid for other planktonic organisms. The direct impact of UV radiation on organisms has to be evaluated under different nutrient conditions and (ideally) under natural radiation conditions. The exposure regime to solar radiation (i.e., dose and dose rate) of the planktonic organisms needs to be determined under the dominating turbulence regimes of the water column. Recovery rate from previous UV-stress needs to be determined under different nutrient regimes and radiation conditions. All of the points raised above address only the direct impact on bacterioplankton. DOM is also affected by solar radiation of different wavelength ranges depending on its molecular composition [21, 22]. Since DOM is the principal carbon and energy source for bacterioplankton, exposure of DOM to solar radiation will influence its bioavailability for bacterioplankton. Moreover, in natural systems bacterio- and phytoplankton live in close interaction with heterotrophic and mixotrophic protists which, in turn, may be affected in their activity by radiation in different ways. From this brief description of the potential interactions between bacterioplankton, UV radiation and DOM, it becomes clear that we are dealing with rather complex relations and interdependencies. From the insights obtained thus far, it is therefore premature to draw any firm conclusions on the impact of increased UV radiation on the overall functioning of marine and freshwater systems.

Effects of Acute Exposure of Bacterioplankton to Solar Radiation

Direct exposure of bacterioplankton to near-surface solar radiation levels results in a decline in bacterioplankton activity in marine and freshwater systems [11, 21]. The decrease in activity is related to the overall nutrient conditions [11]. High initial bacterial activity under high nutrient conditions results in higher inhibition than under limiting nutrient conditions [11]. In coastal waters, bacterial activity declined by about 40 % of the initial activity rate after exposure to near-surface solar radiation for 3 hr [11]. This tendency was found for thymidine as well as for leucine incorporation. Some authors found differences in the inhibition between leucine and thymidine uptake by bacteria in the presence of UV, however, these differences are not consistent [1, 11]. A similar decline as for bacterial activity measured by thymidine and leucine incorporation could be observed for bacterial ectoenzymatic activity [9]. Ectoenzymatic activity declined rapidly in the presence of solar radiation indicating that bacterial cells are not only inhibited at the uptake systems in the cell membrane, but the observed inhibition might also be due to the inactivation of the ectoenzymes by solar radiation, probably mainly in the UV range [19].

UV radiation leads to the formation of DNA damage as has been shown for the upper mixed water layers in the Gulf of Mexico [10]. There, a clear increase in DNA dimer formation has been found in the surface 5 m layer which was more pronounced for the <0.8 µm fraction (considered mainly bacteria) than for the > 0.8 µm fraction (mainly phytoplankton) [10]. This indicates that bacterioplankton are more sensitive to UV radiation than phytoplankton. Moreover, these authors showed that wind-induced mixing of the upper water layers significantly reduced dimer formation as compared to less turbulent conditions [10].

While there is information available on the general decline of bacterial activity in the presence of solar radiation, there is still uncertainty about the kinetic of the response. Current research in our laboratory focuses on these aspects of UV-mediated inhibition of freshwater and marine bacterioplankton under different nutrient regimes and refining our knowledge on the wavelength ranges responsible for the observed inhibition. Based on the few published measurements of bacterioplankton inhibition under different radiation ranges, it appears that UV-B is responsible only for about one third of the inhibition under surface solar radiation, another one third is caused by UV-A radiation, and the remaining inhibition by the high dose of photosynthetically active radiation (PAR, 400-700 nm) [13, 21]. However, inhibition of bacterial activity mediated by solar radiation does not affect all bacterial species to the same extent [3]. Large differences have been detected in the sensitivity of selected bacterial strains to solar radiation. At present, the factors causing these interspecific differences in the sensitivity of the bacterial strains are unclear, but it is unlikely to be caused by differences in pigmentation. It is more likely that the interspecific differerences in radiation-mediated inhibition are the result of differences in the efficiency of repairing the UV-mediated damage which can occur simultaneously.

Recovery of Bacterioplankton from UV-Stress

Bacterioplankton recovery from UV-stress is largely mediated by the photoenzymatic repair induced by UV-A and the lower PAR (400-450 nm) range [11, 21], while the dark excision repair requires ATP to be activated [12]. Only short exposure to UV-A led to a significantly higher bacterial activity as compared to bacteria kept in the dark [11]. In the dark, recovery of bacterioplankton was only modest [11]. As with UV-induced inhibition of bacterial activity, considerable interspecific differences were also detectable in the recovery of selected bacterial strains. This may indicate that UV radiation plays a role in bacterial community composition in upper layers of the water column. Using natural bacterioplankton communities exposed to different radiation ranges, it has been found that UV exposure leads to shifts in the bacterioplankton community (Winter and Herndl, unpublished). Results from humic-rich freshwater lakes indicate that recovery from UV-stress already takes place at 5-10 cm depth using photoenzymatic repair [21], while recovery in coastal areas was observed in the 5-10 m water layer [11]. Thus, depending on the attenuation rate of the UV-B and the UV-A range in different aquatic systems, mixing of water masses over a short distance might already lead to major alterations in the radiation field. Whether or not this mixing plays an important role in the exposure of bacterioplankton to solar radiation is discussed below.

Recovery of coastal bacterioplankton communities from previous UV-stress resulted in higher bacterial activity after the recovery than prior to the exposure to UV radiation [11], indicating an overall beneficial effect of solar radiation on bacterioplankton, most likely caused by the photochemical alteration of DOM.

Response of Bacterioplankton to DOM Exposed to Solar Radiation

Exposure of DOM to solar radiation leads to the formation of low molecular weight compounds [15, 16, 17, 18] which are, at least partly, utilized by bacterioplankton. Also, radicals are formed [15] inhibiting bacterioplankton growth. The balance between the formation of bioavailable low molecular weight compounds supporting bacterial activity and compounds inhibiting bacterial activity determines the net effect of the photochemically altered DOM for bacterioplankton [8]. The potential of photochemically altered DOM to support bacterioplankton growth has been investigated in a variety of different envrionments, including humic-rich and clear-water lakes and coastal marine environments. In these systems, DOM exposed to solar radiation led to increased bioavailability of DOM [11, 13, 14, 21].

Only very recently evidence has been presented that this is not a universal response [25]. Surface water DOM of the Gulf of Mexico and DOM collected above seagrass meadows in a shallow lagoon exhibited reduced bioavailability after exposure to solar radiation [4], Ziegler and Benner, (unpublished). In a recent study on phytoplankton-derived DOM, we consistently detected reduced bioavailability of the DOM after its exposure to solar radiation (Fig. 1) [20].

During an extensive survey in the Mediterranean Sea we consistently found reduced bacterial activity on DOM collected from the upper mixed layer as compared to bacterial activity on DOM held in the dark. Exposure of deep water (>200 m) DOM to solar radiation always resulted in higher bacterial activity in the radiation-exposed treatments as compared to the dark controls. Addition of the protein bovine serum albumine (BSA, 5 mg C l^{-1}), to deep water samples, however, reversed the trend. [Radiation-exposed, BSA-amended DOM from the deep water supported significantly lower bacterial activity than the BSA-amended DOM held in the dark. The bacterial activity in the radiation-exposed, BSA-amended deep water DOM was similar to that in the unamended radiation-exposed deep water DOM. This indicates that originally labile proteins are photochemically altered into a semi-labile or refractory state by solar radiation. This alteration is not simply caused by photo-oxidation since measured photo-oxidation rates are too low to convert 5 mg BSA-C l^{-1} into CO_2 within an exposure period of 5 hr. There is evidence that the bioavailability of DOM to bacterioplankton determines the subsequent response of the bacteria to the radiation-exposed DOM. If the bioavailability of the original DOM is high, as indicated by a high ratio of bacterial production:DOC concentration, exposure of DOM to solar radiation leads to a reduced bacterial production in the radiation-exposed treatment compared to the dark control.

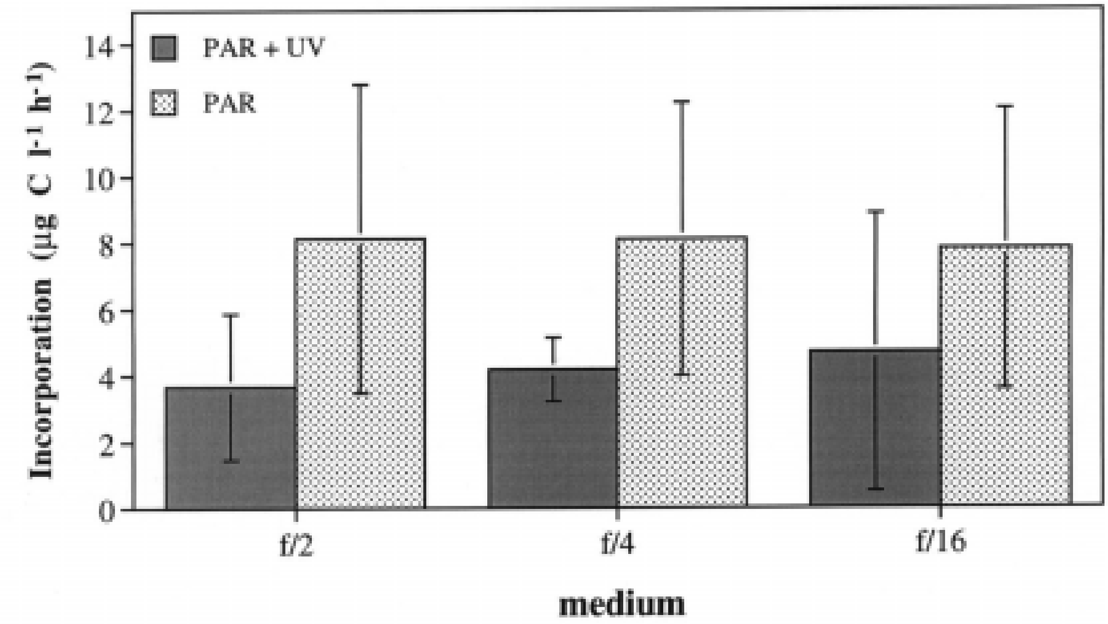

Fig. 1. Bacterial incorporation of radiolabeled DOM derived from *Chaetoceros muelleri* grown in different media (f/2, f/4, f/16) and under PAR+UV and PAR radiation, respectively. Bars indicate means ± 1 SD of 6 experiments with DOM derived from *C. muelleri* cultures grown in f/2, 2 experiments in the f/4, and 10 experiments in the f/16 medium. Each experiment consisted of 5-6 replicates. (From [20]).

The exact nature of the photochemical conversion of labile DOM into semi-labile or refractory DOM is unknown at present, and deserves more attention since it further complicates the scenarios on the impact of UV on aquatic ecosystems. To summarize emerging evidence: refractory to semi-labile DOM becomes more labile upon exposure to solar radiation while originally labile DOM becomes more refractory.

Synthesis

The ultimate question when evaluating the ecological role of UV radiation on bacterioplankton activity and DOM is how long the organisms and DOM of the uppermost layers of aquatic systems are exposed to high radiation levels. One would tentatively assume that open ocean waters are subjected to constant wind-induced mixing of the upper water column. There is evidence, however, that diurnal stratification is a common phenomenon [7]. In the subtropical North Atlantic, for example, , Obernosterer, Reitner and Herndl (unpublished) used hydrogen peroxide as a tracer for vertical mixing. The advantage of using H_2O_2 as a tracer of vertical mixing in studies of the impact of UV radiation is that H_2O_2 is mainly formed by UV acting on DOM [23]. Throughout the subtropical North Atlantic, diurnal stratification has been detected. The diurnally stratified layers are mixed with the underlying water shortly before dusk due to surface cooling (Fig. 2).

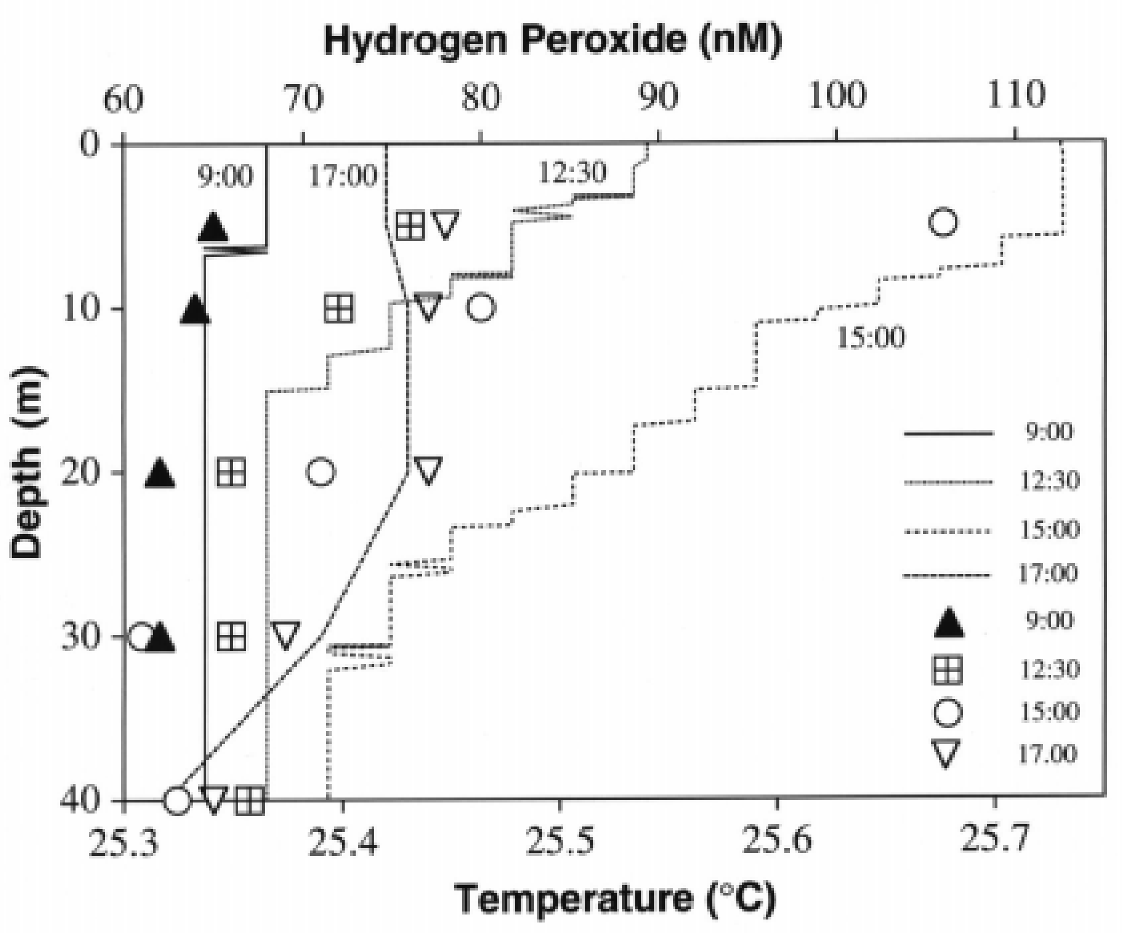

Fig. 2. Typical example of diurnal dynamics in the concentration of hydrogen peroxide (H_2O_2) and temperature in the upper layers in the subtropical North Atlantic (22°N 38°W) measured in July 96.

It is therefore reasonable to assume that DOM and planktonic organisms are confined in the highly-irradiated surface water layers during most of the day and receive considerable dose of high-energy radiation. Bacterioplankton are then signifcantly retarded in their activity and photoproducts are formed from the parent DOM (Fig. 3). Before dusk these waters are mixed into deeper layers where bacterioplankton use UV-A and the lower PAR range to repair damage and take up parts of the photoproducts formed in the surface layers during the period of intense solar radiation. Whether or not bacterioplankton activity is significantly enhanced or reduced by the photochemical alteration of the DOM is dependent on the overall availability of the DOM. If the DOM consists mainly of phytoplankton-derived, young DOM, then the photoproducts formed are likely to lead to reduced bacterial activity [20], while originally refractory DOM stimulates bacterioplankton leading to enhanced bacterial activity in surface waters [14]. Such areas of greatly enhanced bacterial activity due to photochemically altered DOM should be upwelling areas (coastal and offshore) where deep water is transported into the sunlit surface layers.

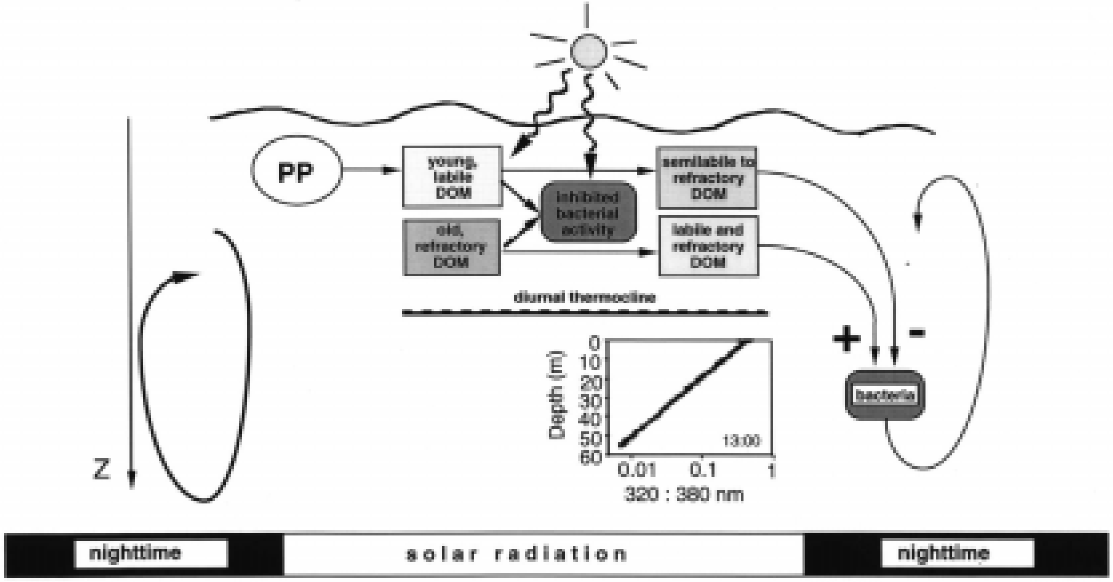

Fig. 3. Scheme of the interaction between diurnal stratification and the action of solar radiation on the DOM pool and on bacterioplankton in stratified surface layers. The inset indicates the relation between depth and the irradiance-ratio of 320:380 nm wavelength. The 320 nm wavelength represents the damaging radiation range and the 380 nm wavelength represents the radiation range used for the photoenzymatic repair by bacterioplankton. The rapid decline of the damaging radiation range with depth is obvious. See text for details.

The above scenario is based on findings gathered over the last few years. The response of bacterioplankton to photochemically altered DOM is still poorly investigated and largely restricted to coastal areas and freshwaters. Oceanic conditions might differ significantly, however, in the nature and molecular composition of the DOM pool [2]. The molecular processes leading to alteration in the bioavailability of DOM (labile DOM becoming more refractory and refractory DOM becoming more labile upon exposure to solar radiation) is not understood at present.

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