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Role of ultraviolet radiation on phytoplankton extracellular release and its subsequent utilization by marine bacterioplankton

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ABSTRACT: The influence of ultraviolet (UV) radiation on the production rate and percentage of photosynthetic extracellular release (PER) to total production (PER + particulate) was investigated in the laboratory using the diatom species *Chaetoceros muelleri* grown under different nutrient and radiation conditions. Only when growing on higher nutrient concentrations (f/2 and f/4 media), were both specific particulate production and PER rates (production per unit chl *a*) were significantly lower in the presence of photosynthetic active radiation (PhAR) + UV as compared to the treatments receiving only PhAR. When growing on lower nutrient concentrations (f/16 medium), UV radiation had no significant effect on the production rates. The percentage of PER to the total amount of carbon fixed was similar for the PhAR + UV and the PhAR treatments. However, PER produced by *C. muelleri* during PhAR + UV exposure was taken up by bacterioplankton in the dark at significantly lower rates than PER produced in the absence of UV. This indicates that PER, considered as an important component of the dissolved organic carbon pool, becomes more resistant to bacterial utilization upon UV exposure. Whether this reduced PER-uptake by bacterioplankton is caused by changes in the macromolecular composition of the PER and/or is due to a subsequent photochemically induced alteration of the molecules during UV-exposure remains to be investigated.

KEY WORDS: Phytoplankton · Photosynthetic extracellular release · Dissolved organic matter · Ultraviolet radiation · Photolysis · Bacterial utilization

INTRODUCTION

Phytoplankton primary production is confined to the rather small layer of the water column where sufficient solar radiation penetrates to allow photosynthesis. Attenuation of solar radiation is wavelength dependent, allowing the blue region to penetrate deepest into the oceanic water column (Baker & Smith 1982). Although ultraviolet (UV) radiation is thought to be rapidly attenuated, the 10% radiation level in the oligotrophic, tropical Atlantic Ocean for the 305 nm wavelength is at ~15 m depth and for 320 nm at 25 m depth (Obernosterer unpubl. data). Thus a significant part of the euphotic zone is exposed to UV-B radiation (280 to 320 nm), which has been shown to have detrimental effects on phytoplankton (Smith et al. 1992).

Autotrophic organisms can produce pigments such as mycosporine-like amino acids that absorb harmful UV radiation (Karentz et al. 1991a,b). It has been shown that tropical and temperate phytoplankton are less sensitive to increased UV radiation than Antarctic phytoplankton (Helbling et al. 1992). Despite these adaptations to higher UV radiation levels in tropical and temperate phytoplankton, UV exposure certainly places stress on phytoplankton, leading to reduced photosynthetic rates even in temperate regions (for example Lorenzen 1979, Behrenfeld et al. 1995). This UV-induced stress might ultimately also lead to an alteration in the biosynthesis of intracellular material. It has been shown that soluble carbohydrate synthesis was reduced in UV-exposed phytoplankton while the synthesis of structural carbohydrates increased under UV radiation (Goes et al. 1996).

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Therefore, one might expect that UV radiation also changes the molecular composition of the photosynthetic extracellular release (PER) of phytoplankton. Numerous papers have shown that phytoplankton release copious amounts of PER (Lancelot 1979, Mague et al. 1980, Fogg 1983, Lignell & Lindqvist 1992). Especially under stress conditions, such as insufficient phosphorus supply, PER can make up to 80% of the total carbon fixed (Kaltenböck & Herndl 1992, Obernosterer & Herndl 1995). PER has been shown to be readily taken up by bacterioplankton, supplying from 5 to over 100% of the carbon and nitrogen requirements for bacteria (Lancelot 1979, Iturriaga & Zsolnay 1983, Kirchman et al. 1991, Lignell et al. 1993, Norman et al. 1995). Therefore, bacterioplankton metabolism is tightly coupled with phytoplankton activity, leading to distinct diel patterns in bacterioplankton production with higher production rates in the late afternoon when phytoplankton-derived dissolved organic carbon (DOC) tends to accumulate (Burney et al. 1982, Fuhrman et al. 1985, Herndl & Malacic 1987).

In the present study, we evaluated the influence of UV radiation on the production rate of PER by the diatom *Chaetoceros muelleri* and, subsequently, the utilization of this PER by marine bacterioplankton.

MATERIALS AND METHODS

Phytoplankton culture conditions. Batch cultures of the marine diatom *Chaetoceros muelleri* (obtained from the Culture Collection of Algae and Protozoa, Dunstaffnage Marine Research Laboratory, CCAP 1013) were grown and maintained xenically on a 16 h light:8 h dark cycle at 20°C in a light chamber. Illumination was provided by light bulbs with a photosynthetic active radiation (PhAR) of 180 µE m^{-2} s^{-1}. *C. muelleri* was chosen since it is common in temperate and subtropical regions of the Atlantic and the Pacific. Phytoplankton stock cultures were maintained in combusted (450°C for 4.5 h) 2 l Erlenmeyer flasks in f/2 medium (Guillard & Ryther 1962) using 0.2 µm filtered artificial seawater (Parsons et al. 1984). Cultures were kept in suspension by gentle stirring.

For the radiation experiments described below, *Chaetoceros muelleri* cultures were established with several different concentrations of the medium (f/2 [high nutrient concentration], f/4 [medium nutrient concentration], f/16 [low nutrient concentration]) and allowed to grow to the mid-exponential phase prior to exposure to different radiation regimes. The different nutrient concentrations were used in order to determine possible concentration-dependent effects in the response of *C. muelleri* to UV radiation but were not meant to cause nutrient limitation since all the cultures used for experiments were harvested in the mid-exponential phase. The stage of growth was determined daily by spectrophotometrically measuring the optical density (OD) of the cultures at 550 nm wavelength with a Hitachi 2000 spectrophotometer. Before starting the experiments, the chlorophyll *a* (chl *a*) concentration was determined by filtering 50 ml of the culture onto a Whatmann GF/F glass fiber filter, adding 10 ml of 90% acetone, storing the sample overnight at 4°C in the dark and determining the chl *a* concentration spectrophotometrically using the equation given in Parsons et al. (1984).

Primary production and PER under different radiation regimes. The role of different radiation regimes on biomass synthesis and PER was measured by transferring 100 ml of the exponentially growing *Chaetoceros muelleri* culture into 120 ml quartz Erlenmeyer flasks sealed with glass stoppers. Three different radiation regimes were established. One treatment received PhAR + UV, 1 only PhAR and 1 served as dark control. To shield off the UV range from the PhAR treatment, the quartz flasks were placed under an acrylic glass hood (XT 20013, 3 mm, Röhm, Germany). All the experiments were performed with 5 to 6 replicates. Details on the different radiation conditions are given below. Total carbon assimilation and the PER rates were measured by uptake of radiolabeled ^{14}C-sodium bicarbonate (Parsons et al. 1984). Two µCi $Na(H^{14}CO_3)_2$ (specific activity 55 µCi $mmol^{-1}$, Amersham) were added to each flask and incubated under the different radiation regimes for 8 to 14 h. Dark controls were wrapped in aluminum foil. Thereafter, the samples were filtered onto 0.45 µm pore size cellulose membrane filters (Millipore, 25 mm diameter) using a Millipore filtration manifold at a suction pressure not exceeding 20 mbar to prevent cell breakage. Radiolabeled dissolved inorganic carbon ($DI^{14}C$) was removed by exposing the filters to fumes of concentrated HCl under a fume hood for 1 h. Subsequently, the filters were placed in scintillation vials, dissolved in 1 ml of ethyl acetate (Riedel-de Haen) and 8 ml of liquid scintillation cocktail (Packard Insta-Gel plus) were added. The filtrate of each sample (100 ml) was acidified with 5 ml 6N H_2SO_4 and bubbled with filtered air to remove the $DI^{14}C$ for 18 h. This acidification also prevented decay of the PER (Chen & Wangersky 1996). One ml of the filtrate was transferred into a scintillation vial and 8 ml of scintillation cocktail were added. After 18 h, the radioactivity was measured in a liquid scintillation counter (Canberra Packard, TriCarb 2000).

Preparation of PER for photochemical DIC production. To 600 ml batch cultures grown in f/16 medium, 9 µCi $Na(H^{14}CO_3)_2$ (specific activity 55 µCi $mmol^{-1}$, Amersham) were added at the beginning of the exponential growth phase. After incubation under PhAR

conditions (180 µE m^{-2} s^{-1}, 16 h light : 8 h dark cycle) for 120 h, the culture (in stationary phase) was filtered onto a 0.8 µm polycarbonate filter (Millipore). The filtrate was then filtered through a 0.2 µm filter (Millipore, polycarbonate) to remove all the remaining particles, acidified with 30 ml of 6N H_2SO_4 and bubbled to remove the $DI^{14}C$ for 18 h. Subsequently, the pH was adjusted to the original pH with 6 N and 0.1 N NaOH. Fifty ml subsamples of the filtrate were filled into combusted quartz BOD bottles, stoppered and exposed to different radiation regimes as described above (PhAR+UV, PhAR, dark) for 16 h. Two experiments were performed, 1 with 4 replicates and 1 with 7 replicates. No significant differences were found between the 2 experiments; therefore, the data of the 2 experiments were pooled. After exposure, the bottles were capped with silicone stoppers to which wells were attached. In each well a filter wick (using Whatman # 1 filters) was placed, soaked with 100 µl phenethylamine. Then the filtrate was acidified again by adding 5 ml of 6N H_2SO_4 through the cap with a disposable syringe. The $DI^{14}C$ produced during exposure to the different radiation regimes was trapped in the phenethylamine-soaked filter wick. The filter wicks and 1 ml of the filtrate, respectively, were transferred into scintillation vials, 8 ml of scintillation cocktail added and counted as described above. Photochemical $DI^{14}C$ production was corrected for the small amount of dark $DI^{14}C$ production (generally less than 10% of the $DI^{14}C$ produced in the PhAR treatment).

Bacterial utilization of PER harvested under different radiation regimes. To estimate the role of different radiation regimes on the bioavailability of the PER, PER was harvested from *Chaetoceros muelleri* cultures exposed to different radiation levels (PhAR + UV, PhAR) as described above for 8 to 14 h. Aliquots of 45 ml radiolabeled PER were filled into BOD bottles sealed with glass stoppers, inoculated with 5 ml of 0.8 µm filtered (polycarbonate, Millipore) natural bacterial consortia and held in the dark at 20°C for 24 h. Thereafter bacterial incorporation and respiration of the radiolabeled material were measured. After replacing the glass stoppers by silicone stoppers, the sample was acidified by inserting the needle of a disposible syringe through the stopper and the bacterial-derived $DI^{14}C$ was captured in the phenethylamine-soaked filter wick as described above. After 18 h, the bacteria were filtered onto 0.45 µm filters (cellulose nitrate, Millipore). The radioactivity of the filter represents the radiolabeled PER incorporated into bacteria corrected for abiotic adsorption by subtracting formalin-fixed controls (2% v/v final conc.); the radioactivity measured in the filter wick represents respired PER. Additionally, the activity in 1 ml of the filtrate was also measured at the beginning and at the end of the experiment to determine the recover efficiency, which was generally >90%. Acidification of the PER to remove the $DI^{14}C$ might have caused some hydrolysis of the PER and thereby might have influenced the bioavailability of the PER to bacteria. Lignell (1992), however, found only small differences in the molecular weight distribution of acidified PER as compared to non-acidified PER. Therefore, we conclude that acidification of the PER and subsequent adjustment to the original pH did not significantly alter the molecular structure of the PER used for the utilization experiments.

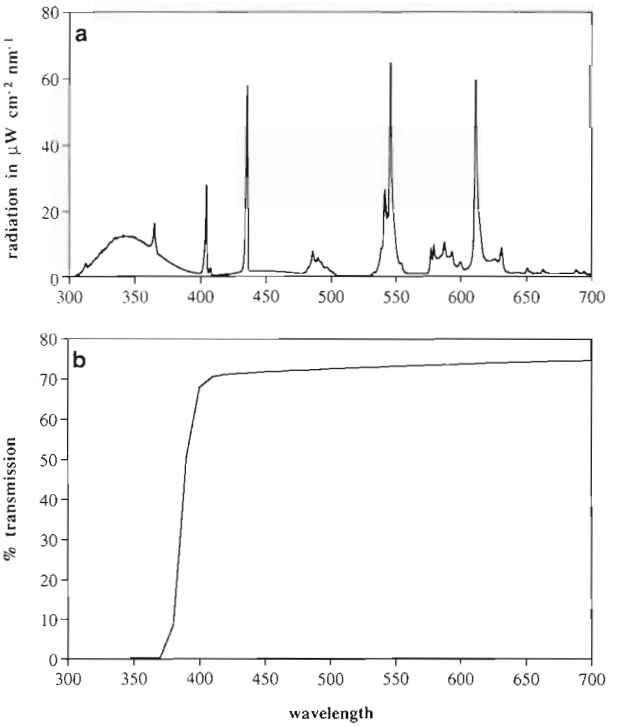

Fig. 1 Radiation spectrum used in the experiments to determine (a) the influence of UV radiation on particulate and PER production of *Chaetoceros muelleri* and (b) the % transmission of the acrylic glass used to shield off the UV range from the PhAR treatments. The spectrum was measured with an Oriel Instaspec system. Further details concerning the light sources and the specifics of the acrylic glass are given in the text

Bacterioplankton sampling and enumeration. Water samples were collected from the Adriatic Sea off Rovinj (Croatia) from a depth of about 2 to 5 m and filtered through 0.8 µm polycarbonate filters (Millipore) immediately before starting the experiment. Bacterial abundance was determined by acridine orange staining and epifluorescence microscopy (Hobbie et al. 1977).

Radiation conditions. Artificial light sources were used throughout the experiments. UV-B was provided by 2 Q-panel bulbs which closely resemble solar radiation from 300 to 340 nm (Fig. 1a). Additional UV-A was provided using Philips TL 100 W/10R lamps (wave-

Table 1. Summary of total and particulate production of *Chaetoceros muelleri* cultures grown under different nutrient and radiation regimes (PhAR + UV and only PhAR). Production rates are normalized to the chlorophyll *a* (chl *a*) concentrations. Means ±1 SD are also given; n: total number of replicates. Test for significant differences between the PhAR + UV and the PhAR treatment was performed by ANOVA

Medium	Initial chl *a* concentration (µg chl *a* l^{-1})	PhAR + UV		PhAR		Sign. diff. Total production (p)	n
		Total production (µg C µg^{-1} chl *a* h^{-1})	Particulate production (%)	Total production (µg C µg^{-1} chl *a* h^{-1})	Particulate production (%)		
f/2	55.3 ± 26.8	2.71 ± 0.59	89.92 ± 5.38	4.86 ± 1.32	91.4 ± 5.0	0.001	32
f/4	20.7 ± 4.5	6.97 ± 2.26	79.98 ± 0.09	9.80 ± 4.97	79.5 ± 1.0	0.001	12
f/16	44.4 ± 9.6	4.27 ± 1.67	71.57 ± 3.88	4.48 ± 1.36	74.7 ± 10.4	0.367	53

length range: 350 to 400 nm, 5.45 W m^{-2}). PhAR was provided by white cool lamps (Philips TLD 58 W/84, 9.11 W m^{-2}). The spectrum of light used for the experiments is given in Fig. 1a, the transmission of the acrylic glass (Röhm, Plexiglas XT 20013, 3 mm thick) used to cut off the UV radiation in the PhAR treatments in Fig. 1b. Measurements of the spectrum were performed with an Oriel Instaspec system. For maintainance of the phytoplankton cultures only PhAR was used.

Statistical analysis. All the replicates of the different experiments were treated as separate experimental units with the experiments as blocking factors and subjected to ANOVA and the normality of the data was tested on the residuals. Thus, the n given for each test refers to the total number of replicates.

RESULTS

Role of UV on primary production and PER

Chaetoceros muelleri cultures grown under PhAR to the exponential growth phase and subsequently exposed to PhAR + UV exhibited significantly lower total primary production (particulate + PER) than under PhAR radiation in the f/2 and f/4 media (Table 1). For the lower nutrient concentration of the f/16 medium, no significant differences in total primary production were observed between the PhAR + UV and the PhAR treatments (Table 1). The percentage of particulate primary production decreased with decreasing nutrient concentrations (from f/2 to f/16 media) under both radiation regimes (Table 1) and, consequently, the percentage of PER to total primary production increased with decreasing nutrient concentrations in the media. Particulate production was significantly lower in the f/2 and f/4 media under PhAR + UV than under PhAR conditions (ANOVA, $p < 0.001$, $n = 32$ and 12, respectively) while no significant differences between the PhAR + UV and the PhAR treatment were found in particulate production in the f/16 medium (Fig. 2a). Also, significantly lower PER production in the PhAR + UV regime was detected for *C. muelleri* grown in the f/2 and f/4 media as compared to the PhAR treatment (ANOVA for f/2 medium, $p = 0.032$, $n = 32$, for f/4 medium, $p < 0.001$, $n = 12$) (Fig. 2b).

Photochemical DI^{14}C production from PER

Exposure of the 0.2 µm filtered radiolabeled PER produced by *Chaetoceras muelleri* in the f/16 medium under PhAR conditions to the 2 different radiation regimes (PhAR + UV and PhAR) resulted in photochemical production of DI^{14}C (Table 2). The photochemical DI^{14}C production under PhAR + UV radiation amounted to 1.27 ± 0.31 µg C l^{-1} h^{-1}; the DI^{14}C production under PhAR conditions was about one third of the DI^{14}C production in the PhAR + UV treatment (Table 2).

Bacterial utilization of PER produced under different radiation conditions

Inoculation of bacterioplankton to PER produced under different radiation regimes always resulted in

Table 2. Photochemical production of radiolabeled dissolved inorganic carbon (DI^{14}C) from labeled PER derived from *Chaetoceros muelleri* cultures grown in f/16 medium under PhAR conditions. Radiolabeled PER was harvested by 0.2 µm filtration and exposed to different wavelength ranges (PhAR + UV and PhAR) using artificial light sources; the initial concentration of the PER (PER-DO^{14}C) is also given; means ±1 SD are given of the total number (n) of replicates

Treatment	PER-DO^{14}C (µg C l^{-1})	DI^{14}C produced h^{-1} (µg C l^{-1} h^{-1})	n
PhAR+UV	5080 ± 556	1.27 ± 0.31	11
PhAR	5093 ± 559	0.46 ± 0.09	11

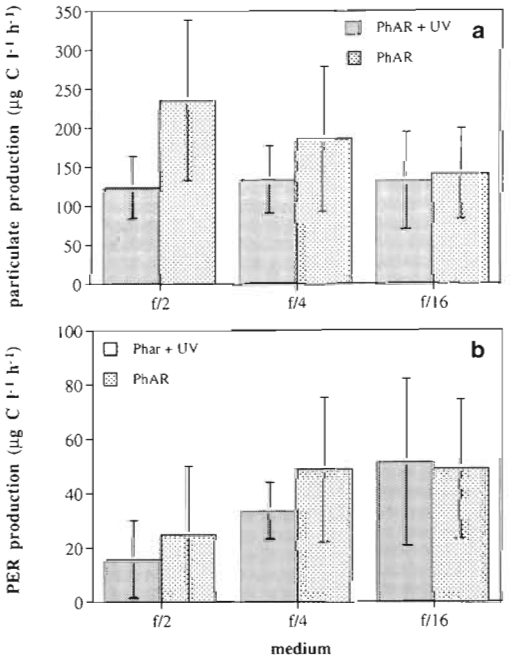

Fig. 2. (a) Particulate and (b) PER production of *Chaetoceros muelleri* under different nutrient and radiation conditions. Bars represent means of 6 experiments (each consisting of 5 to 6 replicates) in the f/2 medium, 2 in f/4, and 10 in the f/16 medium. Vertical lines indicate ±1 SD

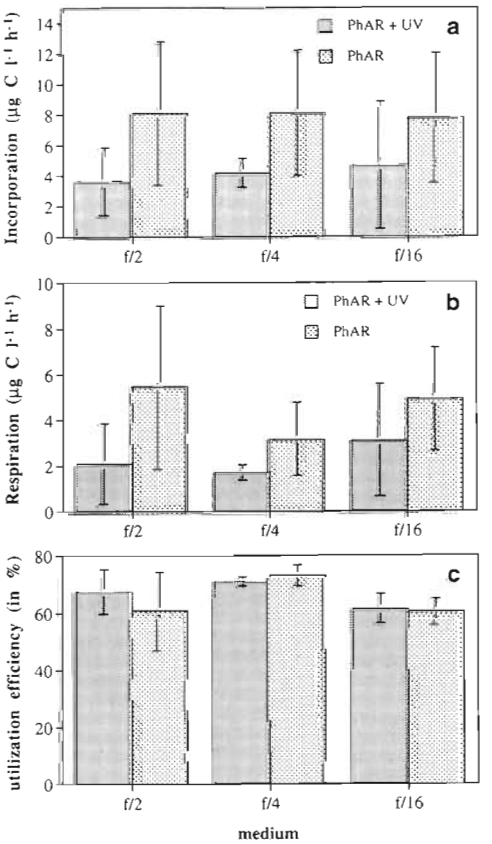

Fig. 3. (a) Bacterial incorporation and (b) respiration of radiolabeled PER derived from *Chaetoceros muelleri* grown in different media and under PhAR+UV and PhAR radiation, respectively. The utilization eficiency in % (incorporation/[incorporation + respiration] × 100) is also given (c). Bars indicate means ±1 SD of 6 experiments with PER 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 to 6 replicates

significantly lower bacterial utilization of PER produced by *Chaetoceras muelleri* under PhAR + UV conditions as compared to PER produced under PhAR radiation (Table 3, Fig. 3a,b). Bacterial incorporation as well as respiration of PER produced under PhAR + UV radiation were significantly lower than of PER produced under PhAR (for the f/2- and f/4-derived PER: ANOVA, $p < 0.001$, $n = 20$ and $n = 10$, respectively; for the f/16 derived PER: ANOVA, $p = 0.041$, $p = 0.027$, $n = 17$, for incorporation and respiration, respectively) (Fig. 3a,b). Both, bacterial incorporation and respiration of PER produced under PhAR + UV conditions were reduced at similar rates (Fig. 3a,b). Thus, there is no significant difference detectable in the utilization efficiency (incorporation/incorporation + respiration) of bacterioplankton growing on PER between the PhAR + UV- and the PhAR-derived PER (Fig. 3c).

Table 3. Total bacterial uptake (incorporation + respiration) of radiolabeled PER produced by *Chaetoceros muelleri* under different nutrient (f/2, f/4, f/16 medium) and radiation regimes (PhAR +UV, PhAR) and the $DO^{14}C$ taken up h^{-1} as percentage of the original PER concentration. The significance levels (tested by ANOVA) between the PhAR+UV and the PhAR treatment of the % taken up h^{-1} of the initial PER present are also given; n: total number of replicates

Medium	PhAR + UV			PhAR			Difference uptake h^{-1}	n
	Initial PER conc. (µg C l^{-1})	Total bacterial uptake (µg C l^{-1} h^{-1})	Bacterial uptake h^{-1} (%)	Initial PER conc. (µg C l^{-1})	Total bacterial uptake (µg C l^{-1} h^{-1})	Bacterial uptake h^{-1} (%)	(p)	
f/2	371.2±285.8	5.7±3.6	1.7±0.5	642.7±413.6	14.3±9.1	2.2±0.3	0.001	20
f/4	448.3± 94.1	5.8±1.6	1.3±0.1	669.7±329.9	11.6±7.5	1.7±0.3	0.001	10
f/16	473.0±346.5	6.6±5.6	1.4±0.7	515.5±249.5	11.3±5.4	2.3±0.4	0.034	17

One has to take into account, however, that the concentrations of the radiolabeled PER used in the experiments were different among the different nutrient and light treatments. Normalizing the assimilation rate to the substrate potentially available (Table 3), it is evident that, even though PER production and consequently also the PER concentrations were higher in the experiments using PER derived from cultures grown under PhAR conditions, PER from PhAR + UV treatments were utilized by bacteria at a significantly lower rate than PER produced under PhAR.

DISCUSSION

UV radiation penetrates to considerable depth in the open ocean especially under oligotrophic conditions (Fleischmann 1989, Smith 1989). In the tropical Atlantic, the 10% radiation level of 320 nm wavelength is at about 25 m depth, indicating that a large portion of the water column primary production is affected by energy-rich UV-B radiation (Obernosterer unpubl. data). A number of studies have shown that phytoplankton production is reduced in the presence of UV radiation (Cullen & Lesser 1991, Smith et al. 1992, Cullen & Neale 1994, Davidson et al. 1994). This reduced primary production is accompanied by a change in the intracellular composition of phytoplankton (Goes et al. 1994, 1995, 1996, Buma et al. 1996). Thus alterations can also be expected in the molecular composition of the PER released by phytoplankton under UV stress. PER has been shown to be readily taken up by bacterioplankton (Chrost 1983, Chrost & Faust 1983, Fogg 1983, Bjørnsen 1988, Lignell 1990, Kirchman et al. 1991), leading to distinct diel patterns in bacterioplankton growth (Johnson et al. 1981, Jørgensen et al. 1983, Carlucci et al. 1984, Herndl & Malacic 1987). This tight coupling between primary production and bacterial activity might be altered by UV radiation.

In this study we used artificial light sources to determine possible changes in the percentage of PER released under UV stress. The light sources used mimicked natural solar radiation only adequately in the UV-B range and the lower UV-A (up to 340 nm) (Fig. 1a). The higher wavelength ranges were characterized by single peaks not representative for the more continuous solar wavelength spectrum. Also, the ratio PhAR:UV (~2) was considerably lower than the ratio for the solar spectrum (PhAR : UV ~ 10, Frederick et al. 1989). The availability of UV-A to induce repair mechanisms (Karentz 1994) was lower in our experiments than in nature. Nevertheless, the general tendencies observed in this study should also be detectable in the water column under natural conditions. Under natural conditions, phytoplankton might be confined to the upper layer of the water column for most of the day due to the development of diurnal thermoclines when solar radiation is strong enough (Doney et al. 1995). Thus, under natural conditions, phytoplankton might receive not only high levels of PhAR (which also exerts stress on the phytoplankton) but also a high dose of UV.

Chaetoceros muelleri used in this study is widely distributed over the world's oceans. We have shown that phytoplankton production is significantly reduced in the presence of UV radiation when grown in f/2 and f/4 media (Table 1, Fig. 2). PER production was reduced to a similar extent as particulate production under UV radiation for the higher nutrient concentrations (f/2 and f/4 media) used in this study (Table 1). No significant differences, however, were detectable for the lower nutrient concentrations used (f/16 medium) (Fig. 2). The lack of a significant difference between the PhAR + UV treatment and the PhAR treatment for *C. muelleri* growing in f/16 medium is in contrast to the finding of Cullen & Lesser (1991), who found higher sensitivity against UV radiation under low nutrient conditions. The percentage of PER to total production did not change significantly in the presence of UV radiation, indicating that UV stress does not result in elevated PER production.

This PER is, at least partially, photochemically oxidized as indicated by the $DI^{14}C$ production from the radiolabeled PER upon exposure to radiation. Our mean $DI^{14}C$ production rate of 1.27 µg C l^{-1} h^{-1} for the PhAR + UV exposure (Table 2) is in the range of carbon-specific rates given in Granéli et al. (1996). It has been shown that UV-A and the lower PhAR range account for about two-thirds of the photochemical DIC production or O_2 consumption under natural solar radiation (Granéli et al. 1996, Reitner et al. 1997). The photochemical $DI^{14}C$ production in the PhAR exposure is rather low (Table 2), reflecting the low radiation levels used in this wavelength range in our study. Thus, the photochemical oxidation and, consequently, the photochemical alterations of PER due to exposure to radiation might be underestimated in our study as compared to natural conditions. Our intention, however, was not to estimate *in situ* photolysis rates but to test whether UV radiation has the potential to alter the molecular composition of the PER.

Although the radiation levels mainly responsible for photochemical alterations of organic molecules were lower in our experiments than under natural surface-level solar radiation, PER produced by phytoplankton under PhAR + UV radiation was taken up at significantly lower rates than PER produced under PhAR (Fig. 3, Table 3). This is contrary to numerous recently published papers on freshwater and marine systems showing that UV-exposed DOM is more readily avail-

able for subsequent bacterial growth (Geller 1985, Amador et al. 1989, Mopper et al. 1991, Amon & Benner 1996, Bushaw et al. 1996, Lindell et al. 1996, Kaiser & Herndl 1997, Reitner et al. 1997).

The vast majority of the bulk DOC in seawater is rather refractory with turnover times ranging from less than 40 d under phytoplankton bloom conditions (Kirchman et al. 1991) to more than 1000 yr (Hedges 1992). Moreover, most of the above-mentioned studies have been performed in humic-rich waters (Amon & Benner 1996, Bushaw et al. 1996, Lindell et al. 1996, Reitner et al. 1997) and humic substances are known to be rather refractory against microbial degradation. There is evidence that refractory DOC becomes more labile to bacterioplankton mainly due to the formation of low molecular weight organic acids (Mopper & Stahovec 1986, Kieber & Mopper 1987, Kieber et al. 1989, 1990, Mopper et al. 1991, Kulovaara 1996). The consistantly lower bacterial utilization of freshly produced, UV-exposed PER as compared to PhAR-exposed PER obtained in our study is in agreement with the few observations available that labile DOC becomes more refractory upon UV-exposure (Thomas & Lara 1995, Naganuma et al. 1996). Also using phytoplankton-derived PER, Thomas & Lara (1995) found no evidence for a decrease in DOC concentration upon exposure to radiation. Naganuma et al. (1996) detected lower bacterial growth on UV-radiated as compared to non-radiated peptone. Moreover, in a recent investigation, Tranvik & Kokalj (1998) showed that phytoplankton-derived PER interacts with humic substances upon UV radiation, making the PER less available for bacterioplankton.

Thus, there is evidence now that labile, algal-derived DOC becomes more refractory upon UV exposure (Tranvik & Kokalj 1998, present study) while refractory DOC becomes more labile for bacterial utilization (Amon & Benner 1996, Bushaw et al. 1996, Lindell et al. 1996, Kaiser & Herndl 1997, Reitner et al. 1997). The interaction between UV radiation, DOC and its bacterioplankton utilization is therefore more complex than hitherto assumed. The reduced availability of the PER released by phytoplankton under UV stress might be responsible for the net accumulation of DOC frequently detectable in the oceanic water column in the afternoon (Sieburth et al. 1977, Burney et al. 1982). Reduced availability of photochemically altered PER coincides under such conditions with direct UV-mediated inhibition of bacterial activity (Herndl et al. 1993, Aas et al. 1996, Jeffrey et al. 1996, Herndl 1997, Herndl et al. 1997).

In summary, we have shown that phytoplankton PER production under UV is reduced to a similar extent as particulate production. This PER is sensitive to UV radiation as indicated by the production of $DI^{14}C$ in the presence of UV. PER produced by phytoplankton in the presence of UV is utilized by bacterioplankton at significantly lower rates than PER produced in the absence of UV. This UV-mediated lower availability of PER might be at least partially responsible for the observed diurnal accumulation of DOC in the water column. Considering the deep penetration depth of chemically and biologically effective radiation in the open ocean, the reduced availability of PER for bacterioplankton might considerably affect the microbial interactions in the upper layer of the euphotic zone.

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