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Phytoplankton acclimation and spectral penetration of UV irradiance off the central Chilean coast

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ABSTRACT: This study of surface and underwater UV irradiance and its effect on phytoplankton photosynthesis was carried out in autumn, winter and spring at coastal and oceanic stations off the coast of central Chile (30° and 33° S). At 30° S during autumn, 1% of surface UVB irradiance (308 nm) reached a minimum depth ($Z_{UV\,nm}$) of 11 m and a maximum depth of 15 m without a significant difference between coastal and oceanic areas. In winter, the $Z_{UV\,308\,nm}$ minimum was 15 m within 80 km offshore (coastal stations) and the $Z_{UV\,308\,nm}$ maximum was 17 m at the oceanic station, 200 km offshore. UVA ($Z_{UV\,380\,nm}$) reached a minimum of 24 m and a maximum of 42 m in autumn, also with no significant spatial trend. In winter, 1% of this spectral band reached a depth of 32 to 36 m at the coastal stations (within 80 km) and 50 m at the oceanic station. Photosynthesis (P) versus irradiance (I) experiments carried out on deck, with and without UV irradiance, showed no significant differences in maximum specific photosynthesis (PB_{max}). It was also found that on a scale of hours, the microalgae were able to increase the absorbance ratio 330–340/665 nm. *In vitro* during 2 h incubation under constant photosynthetically available radiation (PAR) plus 10 different levels of UVB, PB_{max} was significantly inhibited (>10%) at a 305 nm dosage rate of 1 µW cm^{-2} nm^{-1}. Nevertheless, this amount of UVB never reached deeper than 3 m into the water column during the period studied at 30° S. These results suggest that under severe ozone depletion only the upper fraction of the euphotic zone would be under higher UV irradiances and, given an appropriate time (hours) to acclimatize, phytoplankton will be able to cope with this environmental stress.

KEY WORDS: Upwelling · Chile-Peru Eastern Boundary Current · UV-absorbing compounds

INTRODUCTION

Solar ultraviolet B (UVB) irradiance has been a significant variable in the aquatic environment throughout evolution (Vincent & Roy 1993). Phytoplankton have developed defenses to protect their cells from its damaging effect. UV-absorbing compounds (absorbing in the range 310 to 360 nm) found in these microalgae (Carreto et al. 1990, Karentz et al. 1991b) act as a natural sunscreen. In addition to these protective mechanisms, phytoplankton are able to recover and repair some damage, e.g. through photorepair. This mechanism of repairing damaged portions of DNA by enzyme activation with blue-green light has been documented by Karentz et al. (1991a).

Subsurface phytoplankton in upwelling areas are suddenly exposed to higher PAR (photosynthetically available radiation) intensities, due to vertical mixing, in an environment where UV is also present (Kullenberg 1982). In this new radiation field, phytoplankton survival depends on their capacity to maintain an optimal photosynthetic rate. Because this key physiological process is affected by UV, phytoplankton must be able to acclimatize, even though surface UV is only 5% of PAR on a sunny day (Fleischmann 1989). In terms of energy content, UVA reaches an equivalent of about 4% of the PAR energy input and UVB is equivalent to 20% of the UVA and 0.8% of the PAR (Vincent & Roy 1993).

Photoacclimation has been shown to occur in response to variations in photon flux density and spectral distribution between 400 and 700 nm, and observed changes in primary productivity rates, or pigment concentrations, have been proposed to be related to complex processes in the photosynthetic apparatus (Falkowski & La Roche 1991). Fixed-depth *in situ*

measurements of primary productivity are influenced by UV at the water surface (Lorenzen 1979, Smith & Baker 1980, Cullen & Neale 1993), but this varies depending on latitude (Behrenfeld et al. 1993, Helbling et al. 1993). Long-term effects of UV are also mitigated by photoadaptation (Neori et al 1984, Samuelsson et al. 1985, Cullen & Lewis 1988). It is also known that UV tolerance varies according to species (Jokiel & York 1984, Karentz et al. 1991a, Vernet et al. 1994).

In order to characterize and assess the relevance of the UV climate in upwelling ecosystems in the Chile-Peru Eastern Boundary Current, primary production experiments (carbon fixation) with and without UV were performed. Quantification of photosynthetic pigments and the presence of UV-absorbing compounds (mycosporine-like amino acids, MAAs) was obtained through absorbance measurements from assemblages of phytoplankton.

The experiments were carried out at 2 locations, over a period of 2 yr. The first set of experiments was conducted during cruises off the coast of Chile in April, June and October 1992 and the second set of experiments was carried out in March and April 1993 using samples obtained offshore from Montemar (see Fig. 1).

MATERIALS AND METHODS

This study was carried out off central Chile at 2 upwelling centers reported by Fonseca & Farías (1987), i.e. Coquimbo and Valparaíso. The upwelling center at 30° S, shown schematically in Fig. 1, spreads west over 30 to 50 km (Sergio Salinas pers. comm.) and includes Stns 8, 14 and 19.

Measurement of surface and subsurface UV irradiance was performed using PUV-510 and PUV-500 spectroradiometers (Biospherical Instruments, Inc., San Diego, CA, USA), respectively. Each sensor has 1 UVB mean spectral band (305 nm and 308 nm for the surface and underwater sensors, respectively), 3 UVA spectral bands with maxima at 320, 340, and 380 nm and 1 spectral band for PAR (400 to 700 nm). The sensors were interfaced with a portable computer that collected surface data every 30 s throughout the day, to obtain daily maximum values and daily integrals for each UV band and PAR. The underwater sensor also measured depth, temperature and natural fluorescence (not shown). Depth profiles were obtained by lowering the PUV-500 unit at a speed of 1 m s^{-1} and collecting data every second.

UV irradiance measurements (corrected following the calibration factors of the manufacturer) were performed at 30° S, during cruises sponsored by the Joint Global Ocean Flux Studies Project (JGOFS), in autumn (21 to 27 April), winter (22 to 25 June) and spring (24 to 26 October) 1992. Additional UV irradiance measurements were taken in the second set of experiments at 33° S at Montemar (Fig. 1) in early autumn 1993 (5 to 13 March and 22 April). The average daily maximum value for surface UV irradiance was obtained for each period at all sites. To analyse subsurface data, a mean irradiance extinction coefficient (k) for PAR and for each UV band (k_{UVnm}) was calculated from the depth gradient at each site. A 1% surface PAR penetration depth (Z_{eu}) and a 1% UV irradiance penetration depth per wavelength (Z_{UVnm}) were obtained. To compare profiles a test of equality among k regression coefficients was done and examined for significance (Sokal & Rohlf 1981, Zar 1984).

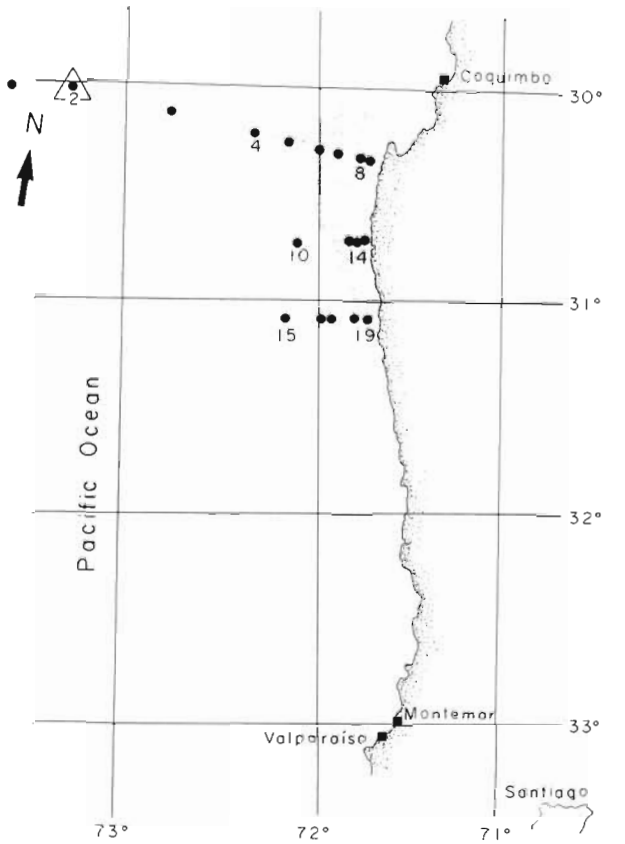

Fig. 1 Location of sampling sites off central Chile. Sampling Stns 2, 4, 8 and 19 are from JGOFS cruises in the 30° S upwelling area (shaded)

During the cruises, samples were collected with a Go flo bottle from 7 different depths, 100, 50, 25, 12, 6, 3, and 1% of surface irradiance. At Montemar, surface water samples were collected using a bucket. All of the samples were filtered in replicates (1 to 2 l) through glass fiber filters (Millipore AP47 or Whatman GF/F). Pigment extraction (chl *a*) using 90% acetone was performed on samples taken from all the sites. At some sites, additional samples were extracted in 80%

ethanol to test for UV-absorbing compounds (MAAs). After 24 h in the cold, both extracts were scanned for optical density (absorbance) measurements in a Shimadzu double beam Scanning Spectrophotometer 150-02. Acetone extracts were scanned only in the PAR range (Jeffrey & Humphrey 1975) and ethanol extracts were scanned for 250 to 700 nm (Yentsch & Phinney 1989, Carreto et al. 1990, Karentz et al. 1991a).

Chl *a* concentration and MAAs absorbance values at different depths were integrated planimetrically for correlation analysis with k_{PAR} and k_{UVnm}. This was done for the cruises within the upper 30 m for chl *a* and within the upper 15 m for MAAs.

Primary production experiments, with and without UV, were performed during cruises and also at Montemar.

The first experiment was performed in winter near the coast (June 1992, Stn 19; Fig. 1). Samples (100 ml subsamples from a 10 l sample taken at 2 m depth) to which 20 µCi of $NaH^{14}CO_3$ had previously been added were incubated on deck in circulating surface water Replicate samples were exposed to 3 different treatments: total UV treatment in polyethylene bags (>257 nm), UVA treatment in polyethylene bags covered with Mylar (>340 nm) and without-UV treatment in glass bottles (50% transmission at 380 nm). Incubation (5.75 h) was done in a 5 level light gradient obtained with neutral-density filters: 100, 50, 22, 16, and 1% of surface irradiance. Total added radioactivity was determined storing aliquots of the inoculated sample with ethanolamine (Fluka). Dark controls were also included and all samples were filtered through GF/F filters. The filters were subsequently fumed with HCl, and a dioxane-based cockail was used for scintillation counting. As part of this first experiment, 500 ml of sample in polyethylene bags was also exposed to UV, uncovered, covered by Mylar or in glass bottles for pigments and MAAs analysis. At the start of the incubation, at least 1 l was filtered for each time zero value. The polyethylene bags used during incubation in this experiment were changed to open glass vials covered by the different filters in the autumn experiment, in consideration of the debate about the use of polyethylene bags as sample containers (Holm-Hansen & Helbling 1993, Prézelin & Smith 1993).

The following autumn (March and April 1993) a second set of experiments was performed with samples obtained from the Montemar bay (33° S). On March 9, subsamples of 10 ml, taken from a 20 l surface water sample, were inoculated with 0.5 µCi of $NaH^{14}CO_3$ and then exposed to natural irradiance in unstoppered 20 ml vials. These vials were arranged in rows in a tap water circulating incubator, and exposed for 4 h in a 5 level irradiance gradient: 100, 31, 19, 12, and 7% of surface irradiance, obtained using neutral-density screens. The rows of vials were covered with either polyethylene (with-UVB treatment), Mylar (with-UVA treatment) or Plexiglas (>383 nm) in the case of treatment without UV Total added activity was determined on aliquots as above. After exposure, each unfiltered 10 ml sample was fixed in the same incubation vial with 500 µl buffered formaline. These samples were then acidified with 250 µl HCl and shaken under a hood. Afterwards, 10 ml of Ready Gel (Beckmann) cocktail was added to each vial.

The experiment was repeated on 22 April using another surface sample from Montemar bay, in a light gradient of 10 intensities (100, 35, 25, 10, 6, 3, 1.4, 0.6, 0.4, and 0.3% of surface irradiance), but with 20 ml subsamples and adding 4 µCi of $NaH^{14}CO_3$ on each vial and incubating for 2 h. Then the 20 ml was filtered through GF/F filters that were thereafter exposed to HCl fumes and transferred to counting vials, adding 5 ml of Ecolume (ICN) cocktail.

Later, an experiment was carried out to measure the effect of UV on PB_{max} (specific photosynthesis at saturating light), using water from the surface sample taken on 22 April that had been stored in the cold and dark for 24 h. A UVB gradient with 10 intensity levels, from 100% to 1%, was simulated *in vitro* using a UVB lamp (Q Panel) and neutral-density screens placed on top of unstoppered 20 ml glass vials. Constant PAR (2614 µW cm^{-2}) was maintained using a fluorescent lamp placed sideways. A volume of 4 µCi $NaH^{14}CO_3$ was added to each sample, which were incubated at room temperature for 2 h. Then the samples were filtered using the same process of filtration treatment described above. After adding 10 ml of Ready Gel, radioactivity was measured in a liquid scintillation counter (Beckmann LS 5000 TD).

Photosynthetic parameters and their standard errors were obtained from the *P* (photosynthesis) versus *I* (irradiance) curves using the Systat program, fitting the model of Jassby & Platt (1976). These parameters were compared among treatments and dates using a nonparametric test (Kruskal-Wallis and Kolmogorov-Smirnov). Thereafter *PB* was normalized with the calculated PB_{max} for each curve.

RESULTS

Absolute mean maximum values of UVB and UVA at the surface are shown in Fig. 2a. At 30° S, mean maximum 305 nm irradiance was 3.06 ± 0.39 and 3.2 ± 0.59 µW cm^{-2} in spring (April 1992) and summer (January 1994), respectively. The minimum value was 0.63 ± 0.09 µW cm^{-2} in winter (June 1992). Between seasons, when 305, 320, 340, and 380 nm were normalized to PAR, a change in the spectral composition of

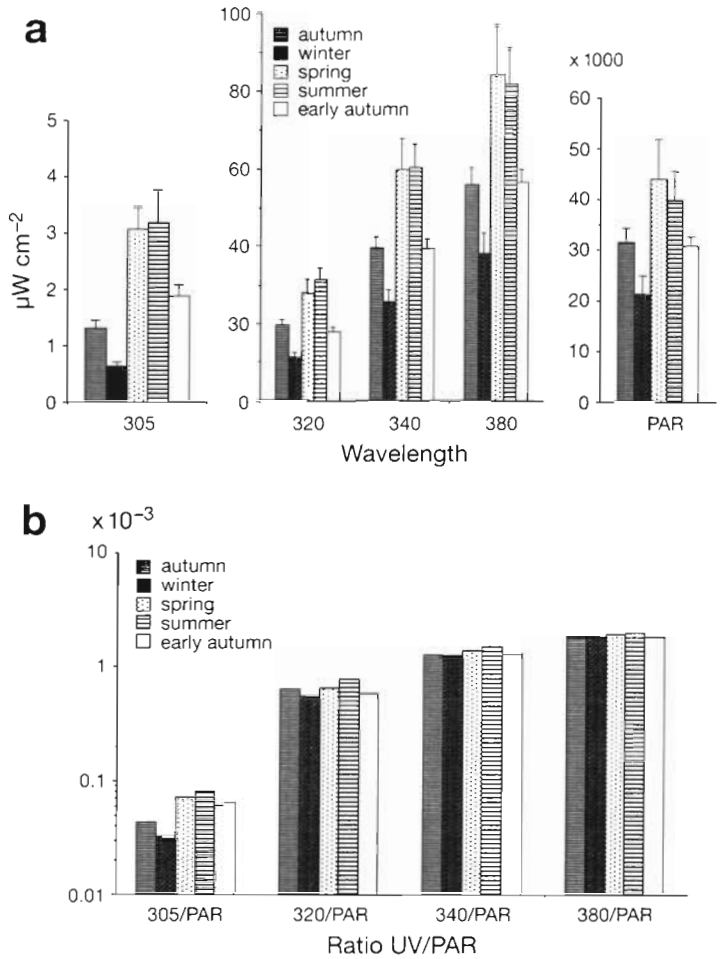

Fig. 2. (a) Mean (+ SE) maximum daily surface UV irradiance (305, 320, 340 and 380 nm) and PAR (400 to 700 nm) during 4 to 6 d in autumn (April), winter (June) and spring (October) 1992 cruises. Summer UV and PAR values are the mean maximum measured in January 1994, also at 30° S. Early autumn (March and April) 1993 values were measured at Montemar (33° S). (b) UV bands normalized to PAR of same measurements as above

UV irradiance was observed, especially for the proportion of UVB (Fig. 2b). After planimetrically integrating the UVA measured from 320 to 400 nm and the UVB measured from 305 to 320 nm, the UVB/PAR, UVA/PAR and UVB/UVA ratios were 0.42, 11.30 and 3.72, respectively.

Significance among extinction coefficients (k) measured at 30° S between 10.30 and 15.30 h (Table 1) indicates that in autumn there are no differences as a result of distance from the coast (mean $k_{308\,nm} = 0.349 \pm 0.012\ m^{-1}$). $Z_{UV\,308\,nm}$ reached a minimum of 11 m and a maximum of 15 m. In winter $k_{308\,nm}$ was significantly different according to the distance from the coast. The 1% depth minimum was 15 m within 80 km offshore coastal stations and the maximum was 17 m, 200 km offshore (oceanic station). UVA ($Z_{UV380\,nm}$) reached a minimum of 24 m and a maximum of 42 m in autumn, also with no significant difference in the spatial pattern. In winter $k_{380\,nm}$ was significantly different depending on distance from the coast. A total of 1% of this spectral band reached 32 to 36 m depth within 80 km offshore and 51 m depth at the oceanic station. $k_{308\,nm}$ was significantly higher in autumn than in winter. For PAR, Z_{eu} varied between 38 and 62 m in autumn and between 48 and 102 m in winter (Table 1).

Integrated chl a values ($\int_0^{30}$) were highest in autumn in the coastal zone, 45.9 to 50.6 mg chl a m^{-2} (Table 1), with $\int_0^{30}$ 665 nm absorbance units of the extracts of 3.23 and 3.93 respectively. The lowest $\int_0^{30}$ chl a values were found at the oceanic station in June (6.9 mg chl a m^{-2}) and in the coastal zone in October (8.1 mg chl a m^{-2}) (Table 1); the $\int_0^{30}$ 665 nm absorbance in these extracts was 0.34 and 1.77 OD m^{-2} respectively.

Correlations between $\int_0^{30}$ chl a and $\int_0^{15}$ chl a with $k_{308\,nm}$ were significant ($r^2 = 0.717$, $p < 0.004$; $r^2 = 0.928$, $p < 0.0001$, respectively). This was not the case for the relationship between $\int_0^{30}$ chl a and the k of the other UV bands nor with the k for PAR. Also, a significant correlation was obtained between UV absorbance peaks found between 330 and 340 nm (MAAs) in the samples from 0 to 15 m with $k_{308\,nm}$ ($r^2 = 0.963$, $p < 0.018$) and also with k_{PAR} ($r^2 = 0.921$, $p < 0.04$) (calculated from Table 1).

Fig. 3 shows a higher amount of MAAs in an autumn sample of 1 m depth than in a sample from 20 m depth from the same cast at Stn 19 (27 April), with a difference in the absorbance ratio 330–340/665 nm of 42%. The difference is more remarkable since chl a was higher in the 20 m sample. This absorbance ratio difference was also obtained experimentally at a coastal station with a 4 m depth sample, incubated on deck during the cruise of June 1992, and also in April 1993 with a surface sample from Montemar. The exposure period under solar irradiance was 5.75 h in winter (June) and 2 h in autumn (April). The total UV was calculated by integrating the 305 nm radiation dosage rate received during the incubation time (6394 and 1770 µW cm^{-2} respectively). The increase in MAAs was 20 to 44% in the June experiment and 118% in the April experiment, with a decrease in chl a of 44 and 25% in June and April respectively. The highest $\int_0^{15}$ absorbance ratio 330–340/665 nm was found in October. The highest ratio $UV_{305\,nm}$/PAR was also found in October (Fig. 2b).

Table 1. Extinction coefficients of UV and PAR; integrated chlorophyll a $\int_0^{30}$ and UV absorbance between 330 and 340 nm integrated in the upper 15 m from samples of 3 to 5 different depths at different stations at 30° S. n: number of samples

Date (1992)	Stn	Wavelength (nm)	k (m^{-1})	± SE	Chl a $\int_0^{30}$ (mg m^{-2})	n	UV absorbance units $\int_0^{15}$
April							
21	8	308	0.306	0.004	19.38	4	
		320	0.242	0.001			
		340	0.178	0.001			
		380	0.112	0.001			
		PAR	0.090	0.001			
24	2	308	0.309	0.013	16.85	3	
		320	0.286	0.006			
		340	0.254	0.006			
		380	0.168	0.004			
		PAR	0.122	0.002			
26	8	308	0.420	0.013	45.90	5	3.31
		320	0.293	0.005			
		340	0.231	0.001			
		380	0.168	0.001			
		PAR	0.102	0.001			
26	14	308	0.421	0.013	36.48	5	
		320	0.324	0.003			
		340	0.205	0.004			
		380	0.109	0.001			
		PAR	0.074	0.001			
27	19	308	0.363	0.014	50.57	5	2.70
		320	0.321	0.006			
		340	0.264	0.003			
		380	0.192	0.001			
		PAR	0.102	0.002			
June							
22	2	308	0.272	0.007	6.85	4	0.40
		320	0.240	0.003			
		340	0.180	0.001			
		380	0.091	0.001			
		PAR	0.045	0.001			
23	4	308	0.304	0.005	18.98	5	
		320	0.280	0.002			
		340	0.217	0.001			
		380	0.144	0.000			
		PAR	0.096	0.002			
24	8	308	0.306	0.021	12.22	5	
		320	0.268	0.003			
		340	0.218	0.001			
		380	0.128	0.001			
		PAR	0.070	0.001			
October							
27	8	308	0.318	0.012	8.10	3	1.29
		320	0.272	0.003			
		340	0.220	0.003			
		380	0.150	0.003			
		PAR	0.077	0.001			

Despite differences in the experimental settings (polyethylene bags or vials) in the 3 *P-I* experiments with different UV screening, no significant differences were found in PB_{max} in June, March and April. The lowest PB_{max} values for all the UV treatments were found in June, off Coquimbo (Table 2).

Nonetheless normalized *PB* (with the calculated PB_{max} for each curve), showed a difference between treatments in June (Fig. 4) where a reduction of 22 to 29% was found at higher intensities in the experiment with UV, at PAR irradiance higher than 6000 μW cm^{-2} (Fig. 4a).

In relation to the effect of different intensities of UV on PB_{max}, it was found that with a 305 nm dosage rate of 1 μW cm^{-2}, *PB* decreased significantly (>15%) after 2 h of incubation (Fig. 5). Above this irradiance a *PB* relative decrease of 45% was observed (Fig. 5).

DISCUSSION

It is extremely difficult to assess the potential impact of UV irradiance on organisms like phytoplankton that not only thrive in a dynamic medium like the ocean, but also possess great physiological plasticity. Throughout evolution, microalgae have coped with UV irradiance by inducing mechanisms to protect against or recover from damage (Vincent & Roy 1993). Difficulties in quantifying UV effects experimentally are mainly related to the time dependence of photoinhibition and determining the dosage rates or the dose to be used in order to mimic the effect of vertical mixing (Cullen & Lewis 1988, Cullen & Lesser 1991). They are also related to the differing sensitivity of phytoplankton taxa (Vernet et al. 1993).

High UV irradiance affects primary productivity (PP) of natural phytoplankton assemblages differently depending on latitude. There is little effect on photosynthetic capacity at low latitudes where UV irradiance is high (Helbling et al. 1992). This situation is reversed at high latitudes, especially during ozone depletion (Vernet et al. 1994). The question of the impact of UV irradiation on phytoplankton carbon fixation could be relevant to international programs related to ocean flux studies and is

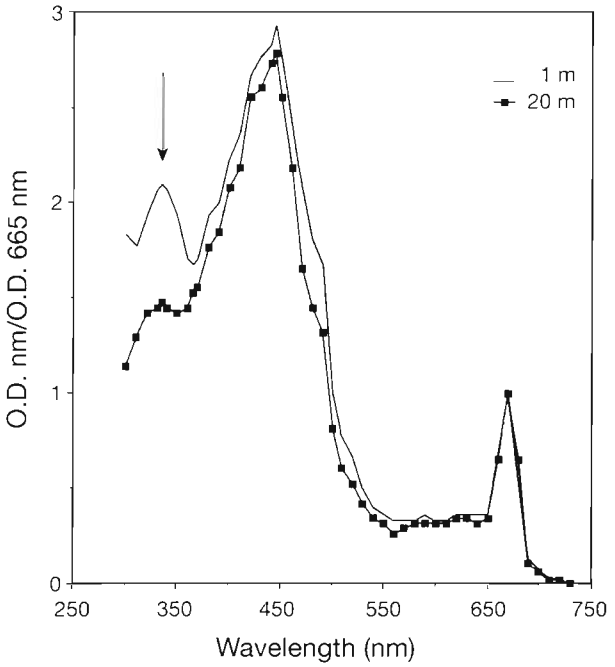

Fig. 3. Relative absorption spectra of ethanol extracts, normalized at 665 nm, from a 1 m and a 20 m water sample from the same cast at Stn 19 (27 April 1992). Arrow indicates 42% difference in the 330–340/665 ratio

crucial when considering methodological protocols, including long-term *in situ* exposures (i.e. JGOFS) that may well overestimate the PP results at intermediate latitudes.

To mimic ecologically significant UV intensities for PP measurements, this study was carried out mainly under environmental radiation levels and used incubation times that were similar to time periods of exposure to UV due to vertical mixing. In upwelling zones, in which phytoplankton are exposed to high PAR for short periods of time, the expected response in PP, of rapid inhibition (mainly by oversaturation of the photosynthetic apparatus and photooxidation, reduction in its carbon fixation capacity or photorespiration processes) and slower repair (Samuelsson et al. 1985), was not significant in autumn or in winter (see below). According to Behrenfeld et al. (1993), because of the difficulty in extrapolating laboratory results, the importance of UVB in photosynthesis is confounded. The effects of PAR and UV that occur simultaneously (Cullen & Neale 1993) and the mitigation of long-term effects by photoadaptation and photorepair (Karentz et al. 1991a) should be clearly distinguished.

Table 2. Photosynthetic parameters (± SE) of *P-I* curves of the different incubation treatments. PB_{max}: maximum specific photosynthesis at saturating light (mg C mg^{-1} chl *a* h^{-1}); I_k: photoadaptation (μW cm^{-2}); α: initial slope [(mg C mg^{-1} chl *a* h^{-1})/(μW cm^{-2})]

	Treatment		
	UVB >308 nm	UVA >327 nm	PAR >380 nm
25 June 1992			
PB_{max}	6.4 ± 0.5	6.2 ± 0.5	7.4 ± 0.4
I_K	676 ± 369	716 ± 280	2092 ± 270
α	0.206 ± 0.106	0.189 ± 0.068	0.077 ± 0.008
9 March 1993			
PB_{max}	11.8 ± 0.6	13.5 ± 0.2	11.423 ± 0.2
I_K	972 ± 201	1064 ± 46	1224 ± 124
α	0.263 ± 0.047	0.277 ± 0.010	0.203 ± 0.018
22 April 1993			
PB_{max}	10.2 ± 0.6	11.3 ± 0.6	10.3 ± 0.6
I_K	2075 ± 238	2592 ± 304	2648 ± 318
α	0.107 ± 0.009	0.095 ± 0.008	0.085 ± 0.008

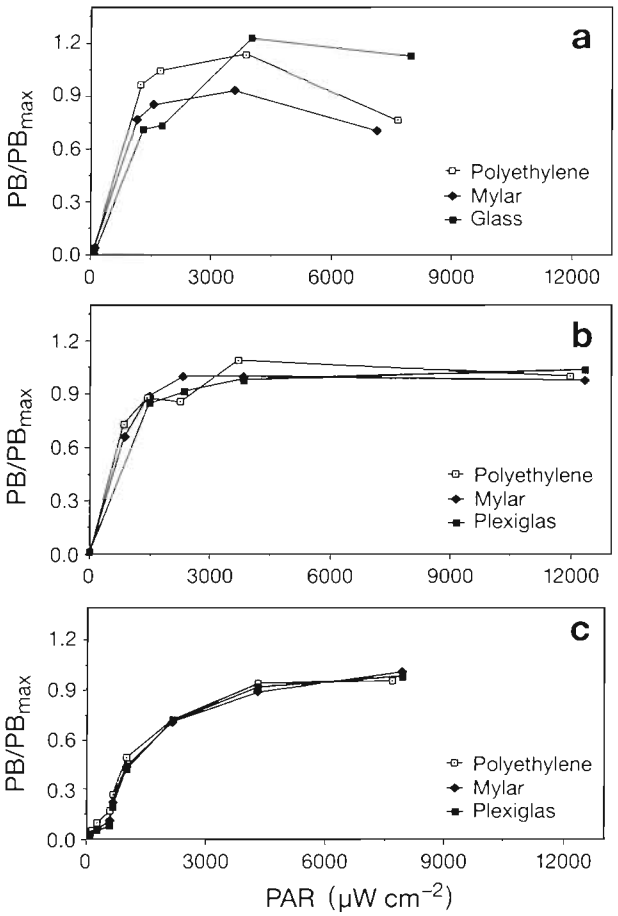

Fig. 4. Relative *PB* normalized by calculated PB_{max}, from photosynthesis vs irradiance (*P-I*) experiments performed on deck with different filters (Polyethylene, >257 nm; Mylar, >340 nm; glass, >380 nm; Plexiglas, >383 nm) for UV. (a) 25 June 1992, 2 m water sample from Stn 19. (b) 9 March 1993, surface sample obtained off Montemar. (c) 22 April 1993, surface sample obtained off Montemar

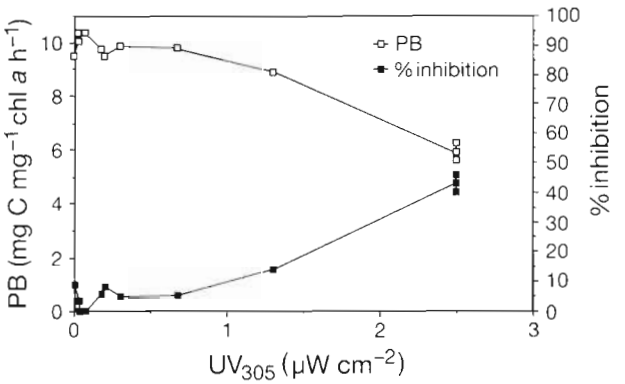

Fig. 5. *PB* of the April 1993 surface sample exposed to constant PAR (2614 μW cm^{-2}) in an UV gradient of 10 intensities provided by a fluorescent UV lamp centered in 313 nm. Percentage inhibition is with respect to control values (zero UV) of the same data

Surface and subsurface spectral UV changes

From this survey of different UV bands, it can be seen that at 30° S there was not only an increase in the surface irradiance, but also a shift in the spectral composition of UV in the spring, when UVB showed the greatest increase. Use of the 305 nm band as an indicator of UVB is supported by measurements made in Antarctica, where a significant correlation was found between absolute values of 305 nm and total UV measurements using YESDAS equipment (Cabrera & Pizarro 1994). Comparing the mean of 305 nm (normalized to PAR) in June with those found in April and October, there was an increase of 34 and 130% respectively (Fig. 2b). Changes at 340 nm during the year were not more than 19%. In comparison to Vincent & Roy (1993), who found UVB be to 0.8% and UVA to be 8% of PAR, in our study UVB was 0.4% and UVA was 11% of PAR. Only one major discrepancy was found, related to the percentage of UVB from UVA: 3.7% compared with 20% in Vincent & Roy (1993).

In the water column in these upwelling areas, $Z_{UV\,308\,nm}$ varied only 2.8 m between autumn and winter. This was the case even when considering the variability of $\int_0^{30}$ chl *a* (6.9 to 50.6 mg m^{-2}) and absorbing compounds within the upper 15 m (0.40 to 3.31 absorbance units) (Table 1). The mean $k_{308\,nm}$ was 0.349 m^{-1} in autumn and 0.289 m^{-1} in winter. Jerlov (1950) reported that UV at 310 nm was reduced by only 14% per 1 m depth (k = 0.15 m^{-1}) in clear waters in the eastern Mediterranean. Armstrong & Boalch (1961) found regional and seasonal differences similar to those we suggest for the study area. Smith & Baker (1978) showed k values at 310 nm that varied between 0.10 m^{-1} for open ocean waters and 0.38 m^{-1} for moderately productive waters (0.5 mg chl *a* m^{-3}). This is also similar to the values higher than 0.30 m^{-1} for 308 nm which are reported here (see Table 1).

Under severe ozone depletion, UVB levels would be higher only in the upper fraction of the euphotic zone. Nonetheless turbulence in the mixed layer has to be taken into account, especially in upwelling areas where the radiation field regime for displaced phytoplankton is constantly changing.

UV absorption

Sufficient evidence exists about microalgae synthesising UV-absorbing compounds (Carreto et al. 1990, García-Pichel & Castenholz 1993, Vincent & Roy 1993). In this study, it was found that in 2 to 6 h, medium latitudinal phytoplankton changed the 330–340/665 absorbance ratio 4-fold. *In situ*, this ratio was 1.4 times higher in surface water compared with the 12% light intensity depth (Fig. 3). The same was shown by Yentsch & Phinney (1989) for water columns with 2 different dynamics, one stratified and sunny weather and the other mixed and cloudy skies. These authors attributed large increases in the short-wave attenuation to the presence of UV-absorbing compounds.

The analysis of the spectral penetration of UV showed that 330–340/665 absorbance ratios were correlated to $k_{308\,nm}$, indicating the presence of UV-absorbing compounds. It is surprising that these types of protecting compound absorb at wavelengths at which the relative DNA damage per quantum is small (Vincent & Roy 1993). Not dismissing its relevance for other targets, this mechanism should be sufficient to cope with mean environmental stress.

The strong nonlinear correlation between absorbance and chlorophyll found by Yentsch & Phinney (1989) speaks for the inclusion of ecological factors in ocean physics. In the present work, short-wavelength attenuation was found to be correlated with chlorophyll and other absorbing substances. Nevertheless, phytoplankton composition and cell geometry, gelbstoff and detritus may cause variability in the correlation of k_{UVnm} with phytoplankton biomass and therefore caution is advisable when using $k_{308\,nm}$ as an indicator of biomass concentration.

Photosynthesis

The nonsignificant difference of PB_{max} between treatments (on-deck *P-I* experiments), while screening UV irradiance in autumn and winter, suggests either that environmental stress was not sufficiently high or that microalgae can cope with it. Helbling et al. (1993), by means of *in situ* measurements with the same autumn

sample from Montemar (9 March 1993), concluded that the effect of UV on integrated PP in a euphotic zone of 14 m was less than 3%. Prézelin et al. (1993) proposed that lower sensitivity to UV inhibition during parts of the day is related, among other factors, to a diurnal increase in photoprotective screening.

In winter, at a mean dosage rate of PAR during 4 h higher than 6000 $\mu W\ cm^{-2}$ in the <380 nm treatment (glass bottles), a relative decrease of 22 to 29% was observed when PB was normalized by PB_{max} (Fig. 4). This is probably consistent with different sensitivities due to species composition, adaptation to low mean PAR values in winter (June), or the need for different time periods to acclimatize. This low light adaptation agrees with the fact that the lowest PB_{max} were recorded in June (Table 2).

Differential response to simultaneously occurring PAR and UV should be evaluated in further extensive studies of upwelling events, using more sophisticated incubators (see Cullen et al 1992).

Since the amount of UVB irradiance in the light limited portion of the water column is insignificant, it may be enlightening to focus on diminution of PB_{max}. Under an experimental UV gradient and saturating PAR, maximum photosynthesis (PB_{max}) was inhibited only at a dosage rate that was measured *in situ* at less than 3 m depth at 30° S and less than 1 m depth at 33° S (data not shown), and because we didn't take the reflection into account, even this shallow depth may be an overestimation.

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