**Biogeosciences
Discussions**

Impacts of UV radiation on plankton community metabolism along the Humboldt Current System

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Abstract

The Humbolt Current System along the Chilean coast is one of the most productive regions in the world, where UV levels are particularly high due to stratospheric ozone depletion. Research has shown that phytoplankton photosynthesis can be severely inhibited by surface radiation and there are concerns that this will reduce not only algal carbon fixation, but also the carbon supply for higher trophic level. Experimental estimates of community metabolism (NCP, GPP and R) and the impacts of UV on community metabolism were assessed at 8 stations along the meridional track by the Humbold-2009 cruise (54.80° S–23.85° S) on board RV Hespérides from 5 to 15 March 2009. The results showed an increase UVB penetration towards the Equator, along the Humboldt Current System, suggesting a more important impact of UVB radiation towards the north. The metabolic rates observed were within average values reported for the Ocean Pacific and did not show the water mass investigated to be exceptionally productive at the time of the study. Experimental evaluation of the effect of UVB radiation on surface waters, those most strongly affected by UVB, showed that UVB radiation suppressed net community production, resulting in a dominance of heterotrophic communities in surface waters, compared to the prevalence of autotrophic communities inferred when materials, excluding UVB radiation, are used for incubation. These results show that UVB radiation, which has increased greatly in the study area, may have suppressed net community production of the plankton communities, possibly driving plankton communities in the Southwest Pacific towards CO_2 sources.

1 Introduction

UV radiation has a negative effect on marine organisms through a range of processes, including inhibition of photosynthetic rates and other metabolic processes, and damage to essential cellular components, such as nucleic acids and proteins, among others (Banaszack, 2003; Häder et al., 2007). Earlier assessments considered impacts of

UVB radiation on marine biota to be low, as the underwater penetration of damaging UVB radiation was expected, on theoretical grounds, to be limited (Morel et al., 2007). Yet direct measurements of underwater UVB radiation showed it to penetrate deeper in the ocean than had been previously thought (Morel et al., 2007). For instance, UVB levels sufficient to cause mortality of photosynthetic plankton have been reported to penetrate as deep as 150 m in the "clearest" natural waters on the south pacific gyre (Morel et al., 2007), 60 m in the subtropical Atlantic (Llabrés and Agustí, 2006) and to 26 m in the Mediterranean Sea (Llabrés et al., 2010).

UV levels are particularly high in the Southern Hemisphere, due to the lower load of atmospheric aerosols therein (Solomon, 1999; Son et al., 2009). Moreover, the erosion of the ozone layer caused by the release of CFC's into the atmosphere, lead to reduced ozone levels, at rates higher in the Southern Hemisphere, up to 4% decade^{-1} between 1970 and 1995, than in the Northern Hemisphere (Weatherhead and Andersen, 2006), with a corresponding increase in the incident UV irradiance at surface. Whereas the Montreal Protocol led to reduced production and use of CFC's as of 1989, recovery of the stratospheric ozone levels is slow and may take decades (Weatherhead and Andersen, 2006), so that increased UV levels may continue to impact on marine biota for some decades.

Most assessments of UV impacts on marine biota have been conducted in laboratory experiments and focused on individual species or assemblages (e.g., Helbling et al., 1994; Davidson and van der Heijder, 2000; Hilty and Merenlender, 2000), with a limited evaluation of UV impacts on ecosystem processes. Whereas the impact of UV radiation on planktonic photosynthesis has been examined in the past (Cullen and Neale, 1994; Davidson, 1998), and impact on the net metabolism of plankton communities has not been reported. Net community production (NCP) represents the balance between gross photosynthetic production (GPP) and community respiration rates (R), and determines the role of planktonic communities as sources (GPP < R) or sinks (GPP > R) of CO_2. UV radiation can impact NCP through effects on both photosynthetic rates (Gala and Giesy, 1991; Holm-Hansen et al., 1993) and respiration rates (del Giorgio

and Duarte, 2002; Helbling et al., 2005) and can, therefore, affect the role of plankton communities on the carbon budget of pelagic ecosystems.

Because of the enhanced UV levels in the Southern Hemisphere, it is particularly important to assess impacts of UV radiation on the NCP of plankton communities in the Southern Hemisphere. However, estimates of community metabolism in the Southern Hemisphere are few, mostly concentrated in the Atlantic and the Southern Ocean (Robinson and Williams, 2005), and there are, as yet, no reports on plankton community metabolism in the South Pacific Ocean, where the most transparent waters to UV penetration have been reported (Morel et al., 2007). The assessment of UV impacts of community metabolism may be particularly relevant for the Humboldt Current System, along the Chilean coast, one of the most productive regions in the world (Thiel et al., 2009), where the presence of a shallow oxygen minimum zone limits the capacity of marine biota to find refuge from UV at depth. Impacts of UV radiation on NCP along the Humboldt Current System could affect the net supply of organic carbon to the food web, thereby affecting the fisheries yield of this important region for the world fisheries catch.

Here we experimentally evaluate underwater UV penetration and absorption and the impact of UV radiation on NCP along the Humboldt Current System. We do so on the basis of measurements and experiments conducted by a meridional cruise along the Chilean coast in March 2009 from the Patagonian channels to 23.85° S (Antofagasta, Chile) on board R/V Hespérides.

2 Methods

2.1 Study site

The study was conducted on the Humbold-2009 cruise on board RV Hespérides from 5 to 15 March 2009. The cruise track followed the Chilean coast, starting in the Patagonia channels (54.80° S) proceeding North along the Humboldt Current until the proximity of Antofagasta (Chile, 23.85° S; Fig. 1).

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2.2 Sampling metabolism

Estimates of community metabolism (NCP, GPP and R) were obtained at 8 stations along the meridional track. Three of the stations were sampled in the Patagonian channels, where metabolic rates were measured at surface (5 m depth) waters only, and five stations were sampled in the open Pacific Ocean, at about 50 miles away from land (Table 1), where metabolic rates were resolved at three depths (5 m, 15 m and 30 m). Seawater samples for community metabolism measurements were collected from the underway pumping system of the vessel in the Patagonian Channels stations, and from 12 l Niskin bottles operated from a Rosette sampling system mounted on a Seabird 9 CTD probe at the open ocean stations.

2.3 Solar radiation measurement

Incidence solar and ultraviolet (UV) radiations were automatically measured by a Weatherlink Vantage Pro. Davis Co. meteorological station located on board the R/V Hespérides. Photosynthetically Active Radiation (PAR) was measured with the solar radiation 6450 Davis sensor (from 400–1100 nm) every 5 min. In addition, integrated UV (290–390 nm) values in all the wavelengths were obtained every 5 min with the UV Davis 6490 sensor. Data of UV was provided as UV Index.

Underwater UVR and PAR profiles were obtained at the 5 oceanic stations around noon using a PUV-2500 profiling radiometer (Biospherical Instruments) which measures UVR at 6 wavelengths: 305, 313, 320, 340, 380, 395 nm, with 10 nm Full-Width Half-Maximum (FWHM) standard, except 305 (controlled by atmospheric ozone cut off). The instrument is also fitted with a PAR (400–700 nm) sensor. The integration of UV radiation across the UV-B range from measurements at discrete wavelengths followed the trapezoidal Riemann sum (Keisler, 1986). The diffuse attenuation coefficient (K_d, m^{-1}) for each UVB wavelength and PAR were determined from linear regressions of the natural logarithmic downwelling irradiance against depth.

2.4 Light absorption estimates

Light absorption properties of seston were measured on seawater particles concentrated on filters (Agustí and Cruzado, 1992; Lieselotte and Dale, 1997; Varela et al., 1998). Water samples were collected from the surface (5 m) at the stations where UVR profiles were taken. The seston samples where obtained after filtering a variable volume of water with Whatman GF/F filters. Filters were kept wet on petri disks and conserved, refrigerated in the dark, until spectrophotometric measurements. The optical density of the filters (OD_f) was measured in a spectrophotometer (Shimadzu) using a clean-water saturated Whatman GF/F filter as a blank (Agustí and Cruzado, 1992). ODf was measured at several wavelengths covering the UV-A, B and PAR spectra. Absorption coefficient (a) was calculated using:

$$a_{(\lambda)} = 2.3OD_{f(\lambda)}C/V\beta_{(\lambda)} \tag{1}$$

where λ = wavelength (nm); 2.3 is the factor to convert base 10 logarithms to natural logarithms; C = clearance area of the filter (m^2); V = volume of seawater filtered (m^3); and β = wavelength-dependent pathlength amplification factor of the filters, following (Bricaud and Stramski, 1990).

$$\beta_{(\lambda)} = 1.63OD_{f(\lambda)}^{-0.22} \tag{2}$$

The absorption coefficient for total particles (a_p) was corrected by subtracting the absorption at 750 nm (Varela et al., 1998) for all wavelength range. In order to obtain the absorption coefficient of non algal particles (a_d), an indirect method was used (Bricaud and Stramski, 1990; Lieselotte and Dale, 1997), following:

$$a_{d(\lambda)} = AEXP(-S\lambda) + a_p(750) - AEXP(-750S) \tag{3}$$

where A and S were obtained from the following systems of equations, using a quasi-Newton estimation technique (Varela et al., 1998):

$$0.99AEXP(-380S) - AEXP(-505S) = 0.99a_p(380) - a_p(505) \tag{4}$$

$$AEXP(-580S) - 0.92AEXP(-692.5S) = a_p(580) - 0.92a_p(692.5) \tag{5}$$

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Finally to calculate the light absorption coefficient for phytoplankton (a_{ph}) the following relation was used:

$$a_{ph} = a_p - a_d \qquad (6)$$

2.5 p_{CO_2} measurement

Determination of water surface p_{CO_2} ($p_{CO_{2w}}$) and atmospheric p_{CO_2} ($p_{CO_{2a}}$) were performed using two high-precision (± 1 ppm) non-dispersive infrared gas analyzer (EGM-4, PP-systems) at 1 min recording interval. Before entering the gas analyzer, the gas stream was circulated through a calcium sulfate column to avoid interference from water vapor. The instrument recording $p_{CO_{2w}}$ was connected to the flow-through port of the vessel's system and interfaced with a gas exchange column (Mini-Module 1.25×9 Membrane Contactor, Celgard) with an effective surface area of $0.5\,m^2$, a total volume of 52 ml and a water flow of about 300 ml min^{-1} for air-surface sea-water equilibration, resulting in a residence time of only 10 s and no temperature difference between in situ seawater and water in the equilibrator. The gas phase was continuously circulated through the equilibrator and the infrared gas analyzer. The Gas analyzer was calibrated using two dry standards: pure nitrogen (0.0 ppm) and a gas mixture of p_{CO_2} and N$_2$ containing a CO$_2$ molar fraction of 541 ppm, which gave an accuracy of ± 1 ppm in the determinations of p_{CO_2}. All p_{CO_2} measurements were corrected for water vapor pressure and temperature, and final results reflected p_{CO_2} at 1 atmospheric pressure with 100 % saturation of water vapor and in situ temperature.

2.6 Meteorological measurements

Pressure, wind speed, air temperature (Aanderaa meteorological station) and sea-surface (4 m depth) salinity and water temperature (Seabird SBE 21 Thermo-salinographer) were measured at 1 min intervals. Pitch, roll and heading of the research vessel were also recorded at 1 min intervals and used in a routine, embedded in the software, integrating navigation and meteorological data, to correct wind speed for

ship movement and flow distortion. The corrected wind velocities were then converted to wind at 10 m (U_{10}) using the logarithmic correction $U_{10} = U_z[0.097\ln(z/10) + 1]^{-1}$ where z is the height of the wind sensor position (Hartman and Hammond, 1985).

2.7 Air-water exchange

Diffusive air-water exchange was estimated using the wind speed dependence of the mass transfer velocity ($k600$) from instantaneous wind speeds (U_{10}, m s^{-1}) following the equation $k600 = 0.24U_{10}^2 + 0.061U_{10}$ (Nightingale et al., 2000). The calculation of air-sea CO_2 flux (F_{CO_2}) used the expression:

$$F_{CO_2} = k \times S \times \Delta p_{CO_2} \tag{7}$$

where Δp_{CO_2} is the difference between CO_2 partial pressure in the surface ocean and that in the lower atmosphere ($\Delta p_{CO_2} = p_{CO_{2w}} - p_{CO_{2a}}$) and S is the CO_2 solubility term, calculated from water temperature and salinity (Weiss, 1974).

2.8 Metabolism measurement

Community metabolism (GPP, CR and NCP) was determined from changes in oxygen in samples incubated for 24 h. Water samples were carefully siphoned from the Niskin bottles, into 100 ml narrow mouth Winkler bottles. Seven replicates were used to determine the initial oxygen concentration, and seven replicated bottles were incubated for 24 h in the "dark" and in the "light". The bottles for "light" were incubated on deck at in situ temperature, adjusting the natural irradiance to that received in situ, using neutral density screens, or in the dark, in the case of the seven replicate "dark" bottles. NCP and CR were measured by monitoring changes in oxygen concentration in the light and dark bottles during the incubation (Carpenter, 1965; Carritt and Carpenter, 1966). Oxygen concentrations were analysed by Winkler titration using a potentiometric electrode and automated endpoint detection (Mettler Toledo, DL28 titrator) (Oudot et al., 1988). CR and NCP were calculated from changes in dissolved oxygen concentration

after incubation of samples under "dark" and "light" conditions, respectively, and GPP was calculated by solving the mass balance equation GPP = NCP – CR.

2.9 UV impacts on community metabolism

The impact of UV on community metabolism was assessed, for the 5 m community only, at the five open water stations. This was done by pairing five 125 ml gas-tight quartz bottles, transparent to UVB, with the "clear" Winkler bottles. The quartz bottles were covered by a neutral screen to simulate the irradiance at 5 m depth, and were incubated for 24 h in an on-deck incubator at in situ temperature. The Winkler bottles used were made of borosilicate, which is opaque to UVB and part of UVA, they are, therefore, excluded. In contrast, the quartz bottles allow the entire light spectrum to reach the sample. Hence, the difference in oxygen evolution between the quartz and borosilicate bottles represents the effect of UV radiation on NCP (i.e. the net result of impacts on both GPP and R).

3 Results

3.1 UVB absorption peaks

Incident UV levels ranged broadly, from 1 to 11 UV index values, during the study, depending on weather conditions, and tended to increase toward the Equator, depending on cloud cover. UVB-extinction coefficients values ranged between $0.26\,\mathrm{m}^{-1}$ and $0.47\,\mathrm{m}^{-1}$ and decreased toward the Equator, such that the 1 % level reached deeper toward the Equator (Table 1). The depth to which 1 % of the UVB incident on the surface penetrated, increased from 9.7 m in the southernmost open-ocean station to 15.6 m at the northernmost station (Table 1). Absorption spectra of particulate material showed the presence of two absorption peaks around 440 nm and around 675 nm, corresponding to the peaks of chlorophyll-*a* (Fig. 2), although for stations 1 and 2, those

peaks were minor indications of the presence of a large amount of non-phytoplankton particles. For station 1 and 2 no evidence of absorption peaks at the UVB range was observed, however station 3, 4 and 5 showed soft peaks at the range of 330–340 nm, indicative of the presence of UV photoprotection pigments (Fig. 2).

3.2 NCP values associated to UVB intensity

Incubation of surface samples, those receiving the highest UVB radiation levels, in quartz, lead to significantly lower NCP values (*t*-test, $P < 0.05$), than those in glass bottles in four out of the five experiments conducted (Fig. 3). Indeed, NCP in the presence of UVB was negative in all but two experiments, indicative of an excess respiration, relative to production in the presence of UVB (Fig. 4), with a median decrease in NCP by 2.17 mmol O_2 m^{-2} d^{-1}. NCP increased when plankton communities were exposed to ambient UVB levels in only one station, that at the northernmost station sampled, where NCP increased to 6.75 ± 0.03 mmol O_2 m^{-2} d^{-1} compared to 3.48 ± 0.02 mmol O_2 m^{-2} d^{-1} when UVB was removed (Table 1).

3.3 GPP, R and NCP variability in the studied water column

GPP and R were relatively uniform in depth, with a tendency for higher GPP rates in surface waters at some stations and R increasing with depth at other stations (Fig. 4). Accordingly, NCP rates tended to decline with depth and tended to be negative, indicative of excess respiration relative to net community production, at 30 m depth (Fig. 4). The UVB incident at 5 m depth corresponded, on average, to 20.02 ± 7.97 % of that incident just below the surface, decreasing to 1.07 ± 0.86 % and 0.01 ± 0.02 % at a depth of 15 and 30 m, respectively (Fig. 4). GPP rates in surface water (5 m) were highly variable across the stations' samples, ranging from 1,45 mmol O_2 m^{-3} d^{-1} to 11,14 mmol O_2 m^{-3} d^{-1} (Fig. 5). Respiration rates at surface were generally lower and more uniform across stations, resulting in a prevalence of net autotrophic communities (GPP > R) throughout the entire section (Fig. 5). In contrast, the surface waters

were supersaturated with CO_2 at all open-ocean stations, supporting, therefore, a net efflux of CO_2 into the atmosphere (Table 1).

4 Discussion

The results presented showed increased UVB penetration towards the Equator along the Humboldt Current System. The waters sampled were not particularly transparent to UVB compared to the ultraoligotrophic waters in the South Pacific Gyre, where UVB was reported to penetrate down to 150 m (Morel et al., 2007). Indeed, the waters along the Humboldt Current System are highly productive, especially on more southern station (1 and 2 station), were the plankton community and particles in suspension are responsible for most of the absorption of light underwater. The contribution of particles to the light extinction diminished towards low latitude or northern stations. Examination of absorption spectra by the plankton communities revealed evidence of the presence of UVB photoprotecting pigments showing the peaks of absorption of micosporine-like aminoacids , as observed in plankton at areas exposed to high UVB as reported from the Southern Ocean (Karentz et al., 1991; Helbling et al., 1996; Moisan and Mitchell, 2001; Ingalls et al., 2010).

The metabolic rates observed were within average values reported for the ocean (Robinson and Williams, 2005), and indicated that the area sampled was not exceptionally productive at the time of the study. All stations occupied had autotrophic plankton communities when incubated in glass, as has been done in the past. However, plankton communities are exposed to UVB in nature, so that assessments of metabolic rates in glass material overlook the effect of in situ UVB levels on metabolic rates. Indeed incubation in glass material removes the incidence of in the water column, whereas the results derived from incubation of the community in quartz better represents the metabolic rates under the light field in situ, which includes significant UVB levels. Exposure of surface (5 m) communities to UVB radiation, greatly reduced NCP in all but one community and rendered all, except one of the communities investigated heterotrophic.

Our experiments did not allow evaluate the effect of UVB on respiration vs. that on GPP, as R was measured in the dark, although there is evidence that UV radiation enhances R (Ekelund, 2000; Pringault et al., 2009) and suppresses GPP (Holm-Hansen et al., 1993). Plankton metabolic rates derived after excluding UVB radiation were generally positive (NCP > 0), indicative of autotrophic communities acting as a CO_2 sink, which is inconsistent with the supersaturation of surface waters in CO_2 (Table 1). However, when community metabolism was assessed using the full irradiance spectrum, including the UVB doses reaching to 5 m depth, the communities in surface waters resulted to be, in general, strongly heterotrophic, thereby acting as a CO_2 source, consistent with the supersaturation in p_{CO_2} in surface waters driving a CO_2 efflux to the atmosphere (Table 1).

Our results show, therefore, that the penetration of UVB radiation increases towards the Equator along the Humboldt Current System, affects the communities located in the upper layers of the water column. In experimental evaluation of the effect of UVB radiation in surface waters, those most strongly affected by UVB, showed that UVB radiation strongly suppressed net community production in most communities, resulting in a dominance of heterotrophic communities in surface waters, compared to the prevalence of autotrophic communities inferred when materials excluding UVB radiation are used for the incubation. To the best of our knowledge, all previous assessments of planktonic metabolism (reviewed in Robinson and Williams, 2005; Duarte and Regaudie-de-Gioux, 2009) used glass bottles, thereby removing the UVB from the solar radiation in incubation. Our results show that, for the communities studied along the Humboldt Current System, removal of UVB increases net community production, by suppressing respiration and possibly increasing gross primary production. Moreover, the exclusion of UVB from the solar radiation not only inflates NCP rates, but may even alter the NCP, in our case shifting the communities from net heterotrophic to autotrophic. The use of quartz bottles to allow the UVB component of the irradiance field yields net heterotrophic communities in surface waters, consistent with the supersaturation in p_{CO_2} in surface waters observed along the cruise. Whereas UVB

radiation is expected to impact only on the surface waters, it is the metabolism of the communities therein that most directly affects surface p_{CO_2}. These results show that UVB radiation, which has been increased greatly in the study area due to trophosperic ozone destruction, may have suppressed net community production of the plankton communities in the study area, possibly driving plankton communities in the Southwest Pacific toward CO_2 sources.

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UV radiation on plankton metabolism

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Table 1. Location of the open ocean sampling stations, net community metabolism ($\pm$ SE) in surface waters under the full irradiance spectra (quartz incubations) and after excluding UVB radiation (glass incubations), and the mean p_{CO_2} ($\pm$ SE) and air-sea CO_2 flux ($\pm$ SE) at the sampling stations, UV index and maximum surface UV during the metabolism experiments, the extinction coefficients (K_d) and the depth of 1 % of surface irradiance for UVB, UVA and PAR.

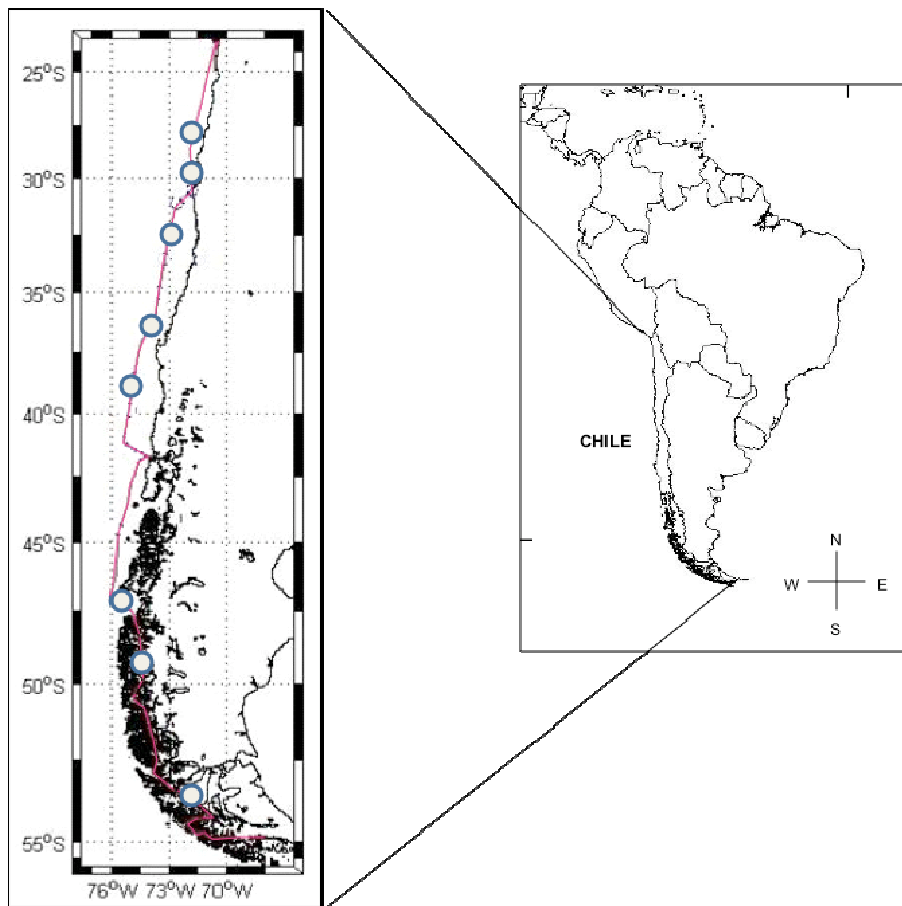| Sampling stations	NCP (mmol O_2 m^{-3} d^{-1}) Quartz	NCP Glass	p_{CO_2} (ppm) at 5 m	CO_2 flux (mmol C m^{-2} d^{-1})	UV index	Wave length (nm)	Maximum surface UV (μW cm^{-2} nm^{-1})	Kd (m^{-1})	Depth 1 % (m)
39° S–75° W	0.35 (0.04)	1.94 (0.04)	367.4 (0.4)	−3.58 (0.12)	6	UVB (305–320)	16.21	0.47	9.74
						UVA			
						340	13.39	0.35	12.98
						380	17.56	0.23	19.43
						395	18.09	0.21	21.22
						PAR (400–700)	0.04	0.13	34.11
36° S–74° W	0.25 (0.04)	0.84 (0.04)	428.9 (1.0)	2.87 (0.08)	8	UVB (305–320)	73.00	0.33	13.62
						UVA			
						340	44.27	0.24	18.64
						380	65.85	0.16	27.25
						395	69.67	0.15	29.71
						PAR (400–700)	0.17	0.11	41.49
33° S–73° W	0.93 (0.009)	1.24 (0.01)	397.6 (0.6)	0.82 (0.14)	9	UVB (305–320)	24.72	0.26	17.44
						UVA			
						340	15.62	0.17	25.73
						380	18.45	0.11	39.03
						395	17.13	0.09	56.16
						PAR (400–700)	0.03	0.08	57.56
30° S–72° W	−1.67 (0.02)	−1.22 (0.03)	405.4 (0.7)	1.64 (0.07)	9	UVB (305–320)	36.80	0.27	16.87
						UVA			
						340	27.40	0.18	24.50
						380	34.57	0.11	41.12
						395	35.27	0.15	46.99
						PAR (400–700)	0.07	0.07	58.29
28° S–71° W	6.76 (0.03)	3.48 (0.02)	407.3 (0.8)	1.46 (0.07)	11	UVB (305–320)	94.37	0.29	15.6
						UVA			
						340	51.23	0.24	19.43
						380	74.9	0.17	27.41
						395	80.28	0.16	29.33
						PAR (400–700)	0.21	0.1	44.71

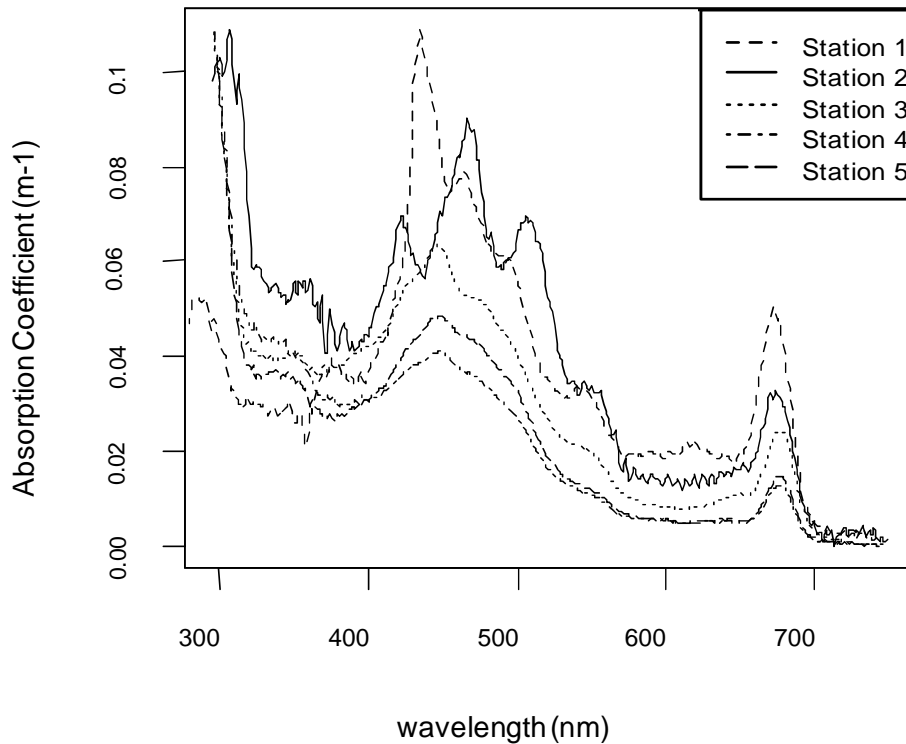**Fig. 1.** Map of the study area showing the cruise track and the stations where submarine UV penetration and community metabolism were measured.

Fig. 2. Absorption spectra coefficients of sestonic particles at the surface water (5 m) along the stations sampled.
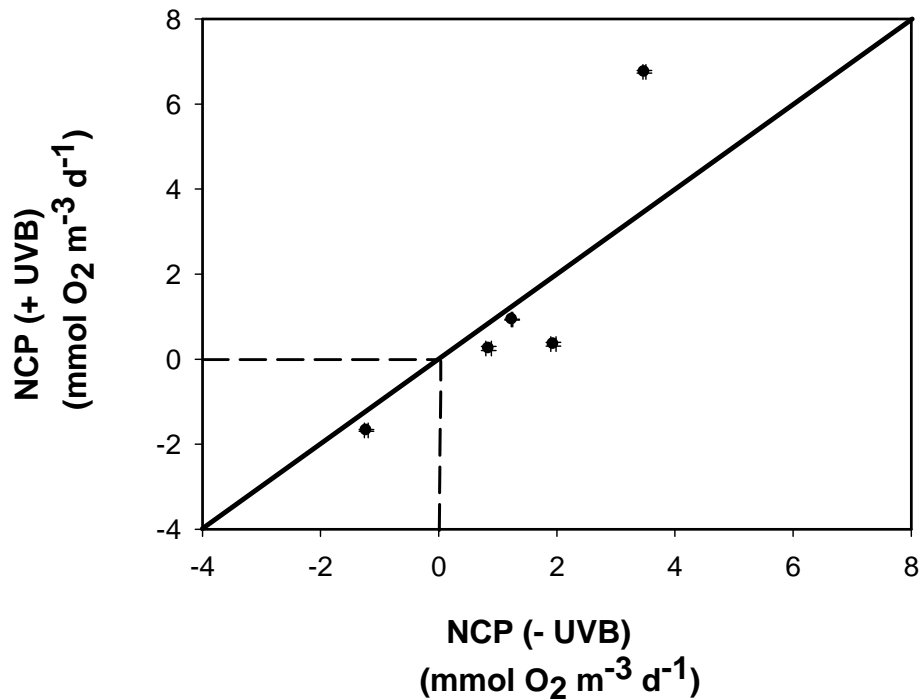
Fig. 3. The relationship between the net community production (NCP) measured in the presence (quartz bottles) and absence (glass bottles) of solar UVB radiation.
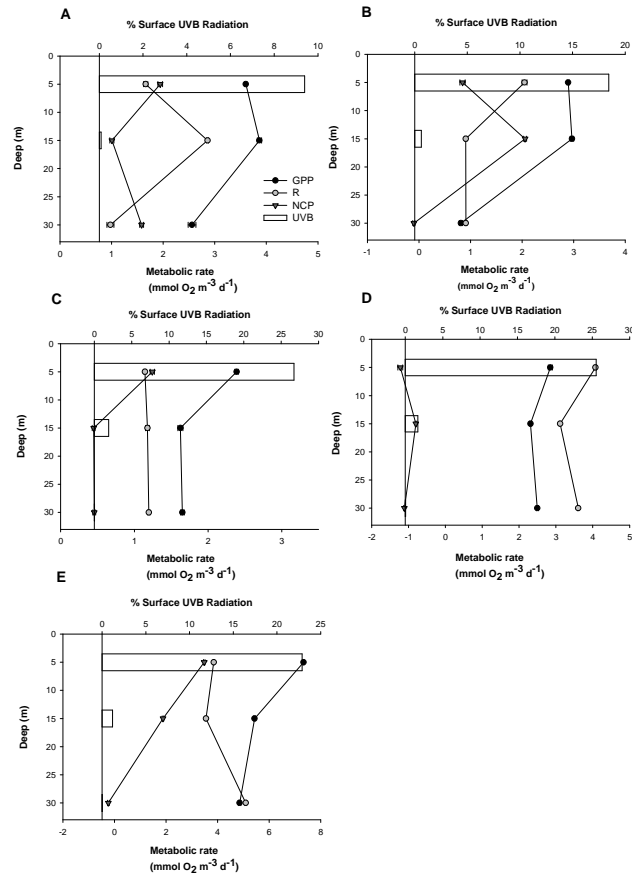
Fig. 4. Vertical profiles of planktonic metabolic rates (mean ± SE for GPP, R and NCP) and the percent UVB irradiance reaching to the sampling depths at each of the open ocean stations investigated **(A)** 39° S–75° W; **(B)** 36° S–74° W; **(C)** 33° S–73° W; **(D)** 30° S–72° W; **(E)** 28° S–71° W.

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Fig. 5. Averaged plankton metabolic rates (mean ± SE for GPP, R and NCP) at the surface water (5 m) along the Chilean coast.