



Experimental assessment of the effect of UVB radiation on plankton community metabolism along the Southeastern Pacific off Chile

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Abstract. The potential effects of UV on community metabolism (NCP, GPP and *R*) were assessed along the Southeast Pacific off the Chilean coast during the Humboldt-2009 cruise (54.80° S–23.85° S) on board R/V *Hespérides* from 5 to 15 March 2009. Estimates of community metabolism were performed at eight stations, including three stations on Patagonian fjords and five stations on the Humboldt Current System. The effect of UVB radiation on net community production (NCP) was evaluated at the stations in the Humboldt Current system by comparing metabolic rates derived using quartz bottles, largely transparent to UVB, and borosilicate glass, which is opaque to UVB and part of UVA, incubated under the ambient solar radiation. Autotrophic planktonic communities with variable NCP prevailed along the area, with the highest NCP rates (7.1–11.1 mmol O₂ m⁻³ d⁻¹) observed in the Patagonian fjords and the northernmost station. All five experiments showed significantly different NCP rates between communities incubated under the full ambient radiation and those incubated under reduced UVB. One of the experiments showed elevated NCP when the community was exposed to the full solar radiation, while four experiments showed a significantly lower NCP in the presence of UVB. These results suggest that the intense UVB radiation in this area, partly inhibits NCP in the Southwest Pacific off Chile.

1 Introduction

UVB levels are particularly high in the Southern Hemisphere, due to the lower load of atmospheric aerosols (Solomon 1999, Son et al., 2009). Moreover, the erosion

of the ozone layer caused by the release of spell out CFC's into the atmosphere led to lower ozone levels, in the Southern Hemisphere, by up to 4 % decade⁻¹ between 1970 and 1995, than in the Northern hemisphere (Atkinson 1997, Weatherhead and Andersen, 2006). This decreased ozone levels caused an increase in the incident UVB irradiance at the surface (e.g. Madronich 1993). The increased UVB radiation has raised concern on the possible impacts on the South Pacific marine ecosystem (Villafañe et al., 2001; Helbling et al., 2005), suffering chronic exposure to UVB radiation (Hernández et al., 2012). 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). Thus the increased UV levels may continue to impact on marine biota for some decades.

The region affected includes the Chilean coastal region, including the Patagonian fjords and the Humboldt Current System (HCS), a highly productive Eastern Boundary Upwelling Ecosystem (e.g., Daneri et al., 2000; Montecinos et al., 2006; Montero et al., 2007), extending from southern Chile (45° S), where the West Wind Drift intersects the South American continent, to northern Peru and Ecuador (4° S) along the Chilean coast (Montecinos and Lange, 2009).

The high productivity of the marine ecosystem in the Southeastern Pacific off Chile (e.g. Daneri et al., 2000; Montecinos et al., 2006; Montero et al., 2007) is supported by upwelling, river runoff, mixing by Kelvin waves and topographic effects (Alheit and Bernal 1993; Quiñones and Montes 2001, Hormazabal et al., 2004; Jacob et al., 2011). Solar radiation may also play an important role in modulating plankton dynamics, both for autotrophs and heterotrophs in the region. Experiments conducted in productive waters in the upwelling zone (36° S) showed negative effects of ambient levels of UVB on production, size spectra and composition of bacterioplankton communities (Hernández et al., 2006, 2007). Planktonic species also invest significant resources in photoprotection against excessive UVB radiation (Häder et al., 2007), which may affect community metabolism.

However, evaluations of plankton net community metabolism are typically conducted in incubations using winkler glass borosilicate bottles (Robinson and Williams, 2005), which filters out most of the UVB radiation. 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), with an increase in UVB penetration from litoral waters (e.g. Hernández et al., 2012) to clear open ocean waters further offshore (Obernosterer et al., 1999). 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).

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 Heijden, 2000; Hilty and Merenlender, 2000), with a limited evaluation of UV impacts on ecosystem processes. Whereas the impact of UV radiation on planktonic photosynthesis (Cullen and Neale, 1994; Davidson, 1998) and bacterioplankton (Hernández et al., 2006, 2007) have been examined in the past, impacts on the net metabolism of plankton communities have not yet been tested. 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.

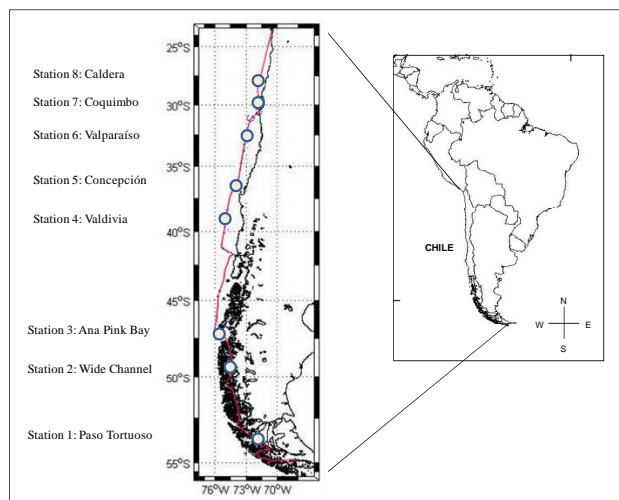


Fig. 1. Map of the study area showing the cruise track and the stations where submarine UV penetration and community metabolism were measured.

Because of the enhanced UV levels in the Southern Hemisphere, it is particularly important to assess the impact of UV radiation on the NCP of plankton communities in the Southern Hemisphere. The assessment of UV impacts on 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, which may be possible for specially-adapted organisms present in the region (e.g. González and Quiñones, 2002). 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 fish yield of this important region for the world fisheries.

Here we report the plankton metabolism community, underwater UV penetration and absorption and the impact of UVB radiation on NCP along the Southeast Pacific off the Chilean coast. We do so on the basis of measurements and experiments conducted by a meridional cruise off the Chilean coast in March 2009 from the Patagonian channels to 23.85° S (Antofagasta, Chile) on board R/V *Hespérides*.

2 Methods

The study was conducted on the Humboldt-2009 cruise on board R/V *Hespérides* from 5 to 15 March 2009. The cruise track followed the South eastern Pacific off Chile, starting in the Patagonia channels (54.80° S) proceeding North offshore along the Humboldt Current until the proximity of Antofagasta (Chile, 23.85° S; Fig. 1).

Table 1. Location of the fjord stations, and values at the surface on net community metabolism (NCP \pm SE) excluding UVB radiation (glass incubations), and the total incident solar radiation, average wind speed, dissolved oxygen concentration and salinity, and the depth of the station.

Sampling Fjord Station	NCP (mmol O ₂ m ⁻³ d ⁻¹)	Solar radiation (W m ⁻²)	Wind Speed (m s ⁻¹)	Dissolved oxygen concentration (mmol O ₂ m ⁻³)	Salinity	Bottom deep (m)
	Glass					
Strait of Magellan (Paso Tortuoso) 53°S–72° W	0.08 \pm 0.02	173.19	10 \pm 1.54	8.13 \pm 0.05	28.41	239
Wide Patagonian Channel 49° S–74° W	9.36 \pm 0.02	46.8	6.94 \pm 2.1	8.37 \pm 0.01	25.36	957
Gulf of Pena Ana Pink Bay 46° S–75° W	3.90 \pm 0.02	205.96	10.39 \pm 2.36	8.15 \pm 0.03	33.49	1680

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: (1) Strait of Magellan (Paso Tortuoso; 53°33' S–72°31' W); (2) Wide Patagonian Channel (49°58' S–74°27' W); and (3) Ana Pink Bay on Gulf of Pena (46° 02' S–75°04' W), where metabolic rates were measured at surface (5 m depth) waters only (Table 1). Five stations were sampled in the open Pacific Ocean, off Valdivia, Concepción, Valparaíso, Coquimbo and Caldera, Chile (Table 2), 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 surface by using the teflon 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.

Incident solar radiation was 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 by the meteorological station as UV Index, an irradiance scale adopted by the World Health Organization where UV intensity is described in terms of ranges running from low values (0–2) to medium (3–5), high (6–7), very high (8–10) and extreme (11+).

Underwater UVR and PAR profiles were obtained at the 5 oceanic stations around noon using a calibrated 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 PUV-2500 detectors incorporate interference filters that, in combination with UV-passing/light-blocking filters and sensitive silicon photodiodes, minimize errors associated with spectral leakage, resulting in an error of the irradiance measurements of 10^{-5} μ W cm⁻² nm⁻¹. The instrument

is also fitted with a PAR (400–700 nm) sensor, and a pressure sensor. The integration of UV radiation across the UVB 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 was determined from linear regressions of the natural logarithmic downwelling irradiance against depth.

Light absorption properties of phytoplankton from the surface waters were measured in samples from the Niskin bottles in the oceanic stations. Seston was concentrated by filtering a variable volume of water (0.5 to 2.5 l, depending on particles concentration) through 2.5 cm Whatman GF/F filters. Light absorption by particles concentrated on the filters was measured immediately after collection. The optical density of the filters (OD_f) was measured in a dual beam scanning spectrophotometer (Shimadzu UV-2100) using a clean, water saturated Whatman GF/F filter as a blank.

The wet filters are placed in front of the photomultiplier and the clean, water-saturated filter used as a reference blank through baseline corrections. OD_f was measured at 1 nm intervals between 280 and 750 nm, covering the UV-B, A and PAR spectra. Absorption coefficients (m⁻¹, a) was calculated using the equation:

$$a_{(\lambda)} = 2.3 \text{ OD}_{f(\lambda)} C / V \beta_{(\lambda)} \quad (1)$$

Where λ = wavelength (nm); 2.3 is the factor to convert base 10 logarithms to natural logarithms; C = clearance area of the filter (m²); V = volume of seawater filtered (m³); and β = wavelength-dependent pathlength amplification factor of the filters, following Bricaud and Stramski (1990).

$$\beta_{(\lambda)} = 1.63 \text{ OD}_{f(\lambda)}^{-0.22} \quad (2)$$

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), following:

$$a_{d(\lambda)} = A \text{ EXP}(-S\lambda) + a_p(750) - A \text{ EXP}(-750S) \quad (3)$$

Where A and S were obtained from the following systems of equations, using a quasi-Newton estimation technique

Table 2. Location of the open ocean sampling stations, and net community metabolism (\pm SE) in surface waters under the full irradiance (quartz incubations) and after excluding UVB radiation (glass incubations), the mean $p\text{CO}_2$ (\pm SE) and air sea CO_2 flux (\pm SE), UV index and maximum incident surface UV during the metabolism experiments, the extinction coefficients (K_d) and the depth of 1% of surface irradiance for UVB, UVA and PAR; average wind speed, dissolved oxygen concentration and salinity at the surface, and the depth of the station.

Oceanic Stations	NCP ($\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$) at 5 m		$p\text{CO}_2$ at (ppm) 5 m	CO_2 flux ($\text{mmol C m}^{-2} \text{ d}^{-1}$)	UV index	Wavelength (nm)	Maximum surface UV ($\mu\text{W cm}^{-2} \text{ nm}^{-1}$)	K_d (m^{-1})	Depth 1% (m)	Wind Speed (m s^{-1})	Dissolved oxygen (mmol m^{-3}) Salinity			Depth (m)
	Quartz	Glass									5 m	15 m	30 m	
Valdivia 39° S–75° W	0.35* \pm 0.04	1.94 \pm 0.04	367.4 \pm 0.4	–3.58 \pm 0.12	6	UVB (305–320)	16.21	0.47	9.74	7.46 \pm 1.06	7.27 \pm 0.01	7.28 \pm 0.01	7.26 \pm 0.04	4383
						UVA	13.39	0.35	12.98					
						340	17.56	0.23	19.43					
						380	18.09	0.21	21.22					
						395	0.04	0.13	34.11					
PAR (400–700)	0.04	0.13	34.11											
Concepcion 36° S–74° W	0.25* \pm 0.04	0.84 \pm 0.04	428.9 \pm 1.0	2.87 \pm 0.08	8	UVB (305–320)	73.00	0.33	13.62	6.64 \pm 0.92	7.51 \pm 0.04	7.4 \pm 0.03	6.92 \pm 0.03	3316
						UVA	44.27	0.24	18.64					
						340	65.85	0.16	27.25					
						380	69.67	0.15	29.71					
						395	0.17	0.11	41.49					
PAR (400–700)	0.17	0.11	41.49											
Valparaíso 33° S–73° W	0.93* \pm 0.009	1.24 \pm 0.01	397.6 \pm 0.6	0.82 \pm 0.14	9	UVB (305–320)	24.72	0.26	17.44	9.48 \pm 1.6	7.12 \pm 0.02	7.13 \pm 0.04	6.95 \pm 0.02	5234
						UVA	15.62	0.17	25.73					
						340	18.45	0.11	39.03					
						380	17.13	0.09	56.16					
						395	0.03	0.08	57.56					
PAR (400–700)	0.03	0.08	57.56											
Coquimbo 30° S–72° W	–1.67* \pm 0.02	–1.22 \pm 0.03	405.4 \pm 0.7	1.64 \pm 0.07	9	UVB (305–320)	36.80	0.27	16.87	4.70 \pm 1.06	7.22 \pm 0.06	7.17 \pm 0.04	6.22 \pm 0.02	3368
						UVA	27.40	0.18	24.50					
						340	34.57	0.11	41.12					
						380	35.27	0.15	46.99					
						395	0.07	0.07	58.29					
PAR (400–700)	0.07	0.07	58.29											
Caldera 28° S–71° W	6.76* \pm 0.03	3.48 \pm 0.02	407.3 \pm 0.8	1.46 \pm 0.07	11	UVB (305–320)	94.37	0.29	15.6	2.97 \pm 1.64	6.93 \pm 0.05	7.11 \pm 0.04	7.3 \pm 0.07	4624
						UVA	51.23	0.24	19.43					
						340	74.9	0.17	27.41					
						380	80.28	0.16	29.33					
						395	0.21	0.1	44.71					
PAR (400–700)	0.21	0.1	44.71											

* denote NCP rates in quartz to be significantly different from those in glass (t-test, $P < 0.001$).

(Varela et al., 1998):

$$0.99 \text{ A EXP}(-380 \text{ S}) - \text{A EXP}(-505 \text{ S}) = 0.99 a_p(380) - a_p(505) \quad (4)$$

$$\text{A EXP}(-580 \text{ S}) - 0.92 \text{ A EXP}(-692.5 \text{ S}) = a_p(580) - 0.92 a_p(692.5) \quad (5)$$

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

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

The light absorption coefficients spectra of the phytoplanktonic component was examined in the UVR bands to detect peaks of photoprotective substances, indicative of UVB stress.

Determination of water surface $p\text{CO}_2$ ($p\text{CO}_{2w}$) and atmospheric $p\text{CO}_2$ ($p\text{CO}_{2a}$) 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 $p\text{CO}_{2w}$ was connected to the flowthrough port of the vessel's system and interfaced with a gas exchange column (Mini-Module 1.25 \times 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 $p\text{CO}_2$ and N_2 containing a CO_2 molar fraction of 541 ppm, which gave an accuracy of ± 1 ppm in the determinations of $p\text{CO}_2$. All $p\text{CO}_2$ measurements were corrected for water vapor pressure and temperature, and final results reflected $p\text{CO}_2$ at 1 atmospheric pressure with 100 % saturation of water vapor and in situ temperature.

Pressure, wind speed, air temperature (Aanderaa meteorological station) and seasurface (4 m depth) salinity and water temperature (Seabird SBE 21 Thermosalinographer) 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).

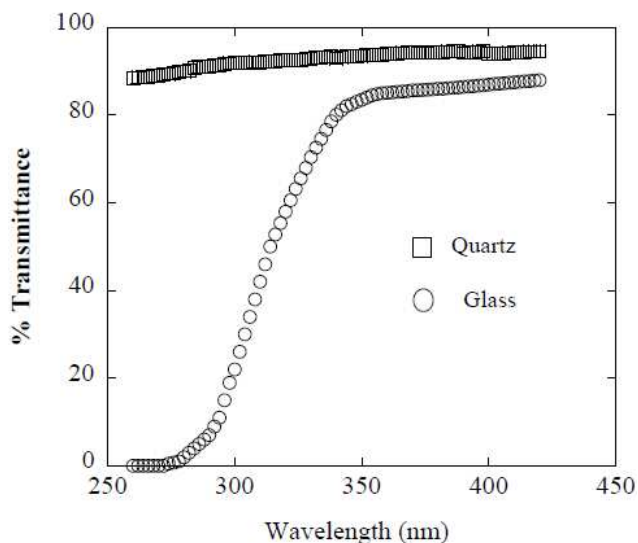


Fig. 2. The spectral percentage of light transmitted in the UVB, UVA and PAR bands of the quartz and borosilicate bottles used in the metabolism measurements.

Diffusive air-water exchange was estimated using the wind speed dependence of the mass transfer velocity (k_{600}) from instantaneous wind speeds (U_{10} , m s^{-1}) following the equation $k_{600} = 0.24 U_{10}^2 + 0.061 U_{10}$ (Nightingale et al., 2000). The calculation of air-sea CO_2 flux (F_{CO_2}) used the expression:

$$F_{\text{CO}_2} = k \times S \times \Delta p_{\text{CO}_2} \quad (7)$$

Where Δp_{CO_2} is the difference between CO_2 partial pressure in the surface ocean and that in the lower atmosphere ($\Delta p_{\text{CO}_2} = p_{\text{CO}_2w} - p_{\text{CO}_2a}$) and S is the CO_2 solubility term calculated from water temperature and salinity (Weiss, 1974).

Oxygen concentration was analysed in seven replicate samples, carefully siphoned into Winkler bottles using Winkler titration and potentiometric electrode with automated endpoint detection (Mettler Toledo, DL28 titrator) (Oudot et al. 1988). 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 borosilicate Winkler bottles. Seven replicates were used to determine the initial oxygen concentration, and seven replicate 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 $\pm 1^\circ\text{C}$, adjusting the natural irradiance to that received in situ using neutral density screens or held in the dark. NCP and CR were measured by monitoring changes in oxygen concentration in the light and dark bottles during the incubation period (Carpenter, 1965, Carritt and Carpenter, 1966). CR and NCP were calculated from changes in dissolved oxygen concentration after incubating the samples under “dark” and “light”

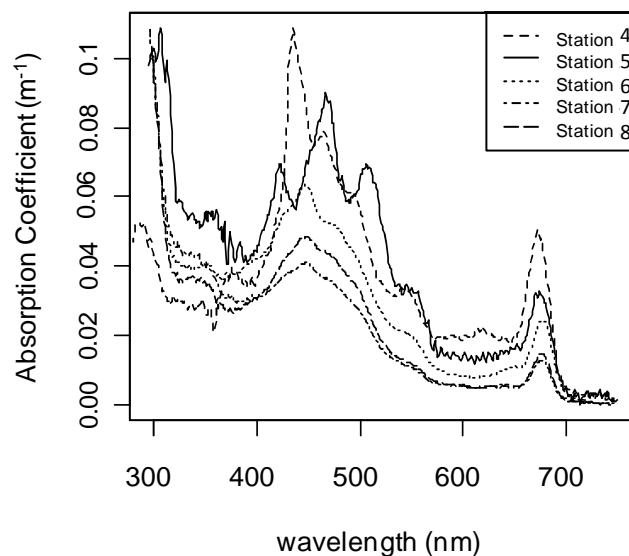


Fig. 3. Absorption spectra coefficients for the phytoplanktonic component of particles observed at the surface water (5 m) along the stations sampled.

conditions, respectively. GPP was calculated by solving the mass balance equation $\text{GPP} = \text{NCP} - \text{CR}$.

The impact of UVB 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 borosilicate 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

In contrast, the quartz bottles allow the entire light spectrum to reach the sample (Fig. 2). Evaluation in a dual beam spectrophotometer of the transmittance of the materials involved showed that borosilicate bottles removed 15 % of the solar radiation in the wavelength range, with the transmittance decreasing sharply with decreasing wavelength to remove all of the radiation at wavelengths shorter than 280 nm, while quartz bottles removed about 10 % of radiation in the visible spectra with only a slight decrease in transmittance ($<3\%$) with decreasing wavelength (Fig. 2). 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

Incident UV levels ranged broadly, from 1 to 11 UV index values, along the study, depending on weather conditions, and tended to increase toward the Equator, depending on cloud cover during the cruise. UVB-extinction coefficients

values ranged between 0.26 m^{-1} and 0.47 m^{-1} and decreased toward the Equator, such that the 1 % level reached deeper into the water column toward the Equator (Table 2). The depth to which 1 % of the surface UVB penetrated, increased from 9.7 m in the southernmost open-ocean station to 15.6 m at the northernmost station (Table 2). Absorption spectra of particulate material showed the presence of two absorption peaks at around 440 nm and around 675 nm, corresponding to the peaks of chlorophyll *a* (Fig. 3), although for stations 4 and 5, those peaks were minor indications of the presence of a large amount of non-phytoplankton particles. For station 4 and 5 no evidence of absorption peaks at the UVB range was observed. However station 6, 7 and 8 showed peaks at the range of 330–340 nm, indicative of the presence of UV photoprotection pigments (Fig. 3). The UVB radiation at 5 m depth corresponded, on average, to $20.02 \pm 7.97 \%$ of that at the surface, decreasing to $1.07 \pm 0.86 \%$ and $0.01 \pm 0.02 \%$ at a depth of 15 and 30 m respectively (Fig. 4).

GPP and *R* were relatively uniform with 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). GPP rates in surface waters (5 m) were highly variable across the stations ranging from $1.45 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ to $11.14 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ (Fig. 5). Respiration rates in surface waters were generally lower and more uniform across stations, resulting in a prevalence of net autotrophic communities ($\text{GPP} > \text{R}$) throughout most of the section (Tables 1, 2, 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 (Tables 1 and 2).

All five experiments comparing NCP rates derived from incubations in glass and quartz bottles showed significantly different NCP rates between samples incubated under the full in situ solar radiation and those incubated under reduced UVB (t-test, $P < 0.001$, Table 2). The probability that the difference in NCP between quartz and glass bottles was obtained by chance was, for each individual experiment, less than 0.0001 (t-test, Table 2), and the combined probability that the difference was obtained by chance was, when the experiments were taken in concert, less than 10^{-6} (Fisher's χ^2 test, Fisher 1925). Four of the experiments conducted showed a significant decrease in NCP in the presence of UVB radiation (t-test, $P < 0.001$). However, one of five experiments, that was conducted at the northernmost station, yielded an increase in NCP to $6.75 \pm 0.03 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ in the presence of UVB radiation compared to $3.48 \pm 0.02 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ when UVB was removed (Fig. 6, Table 2). Yet, there was a strong, statistically significant overall combined probability for NCP to decline significantly in the presence of UVB (Fisher's χ^2 test, $p < 10^{-6}$, Fisher 1925) with a median reduction of NCP by $0.45 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$.

4 Discussion

UVB penetration into the water column increased towards the Equator along the Humboldt Current System. The penetration of UVB in the waters sampled was, as expected, intermediate between the extreme transparency to UVB of the ultraoligotrophic waters in the South Pacific Gyre, where UVB was reported to penetrate down to 150 m (Morel et al., 2007), and the turbid waters of the Chilean littoral (Huovinen and Gomez, 2011). The exhibited extinction coefficients in the UVB range between 1.71 and 1.31 m^{-1} (Huovinen and Gomez, 2011), well above the values we observed (0.47 – 0.23 m^{-1}). The waters along the Humboldt Current System studied were more productive at the southern stations (4 and 5 station), where the plankton community and suspended particles are responsible for most of the absorption of light underwater. The contribution of particles to the light attenuation decreased towards low latitude at the northernmost stations. The absorption spectra of the phytoplankton indicated the presence of UVB photoprotecting pigments with peaks of absorption of micosporine-like amino acids, 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 the range of values reported for the global ocean (Robinson and Williams, 2005) and the Southeast Pacific off Chile (e.g. Daneri et al., 2011; Jacobs et al., 2011), indicating that the area sampled was not exceptionally productive at the time of the study. One of the stations (Station 7, Fig. 1) supported a heterotrophic community, while all other communities supported autotrophic ones, irrespective of whether or not the communities were exposed to the full solar radiation spectra. Indeed, communities towards the northern region of the area have been reported to oscillate between autotrophic and heterotrophic phases (Jacobs et al., 2011). Whereas the plankton system was generally net autotrophic ($\text{NCP} > 0$), and should act as CO_2 sink, there was a prevalence of $p\text{CO}_2$ supersaturation of surface waters (Table 1). This suggests that CO_2 fluxes were driven by physical and thermodynamic factors, rather than biological processes (cf. Torres et al., 2011).

Our results show that, for the communities studied along the Humboldt Current System, removal of UVB affects net community production, with a prevalence of a tendency for net community metabolism to decline. The northernmost experimental station showed opposite results to the general pattern obtained on the remaining stations. Whereas this community also received the highest UVB, the community was also the one growing in the warmest waters and receiving the highest PAR irradiance. Indeed, this anomaly suggests that the response of NCP to UVB is not a simple function of the UVB level, and that communities receiving high UVB do not necessarily show reduced NCP in the presence of UVB relative to that when UVB is excluded. Further research is required to identify the traits that can render some plankton

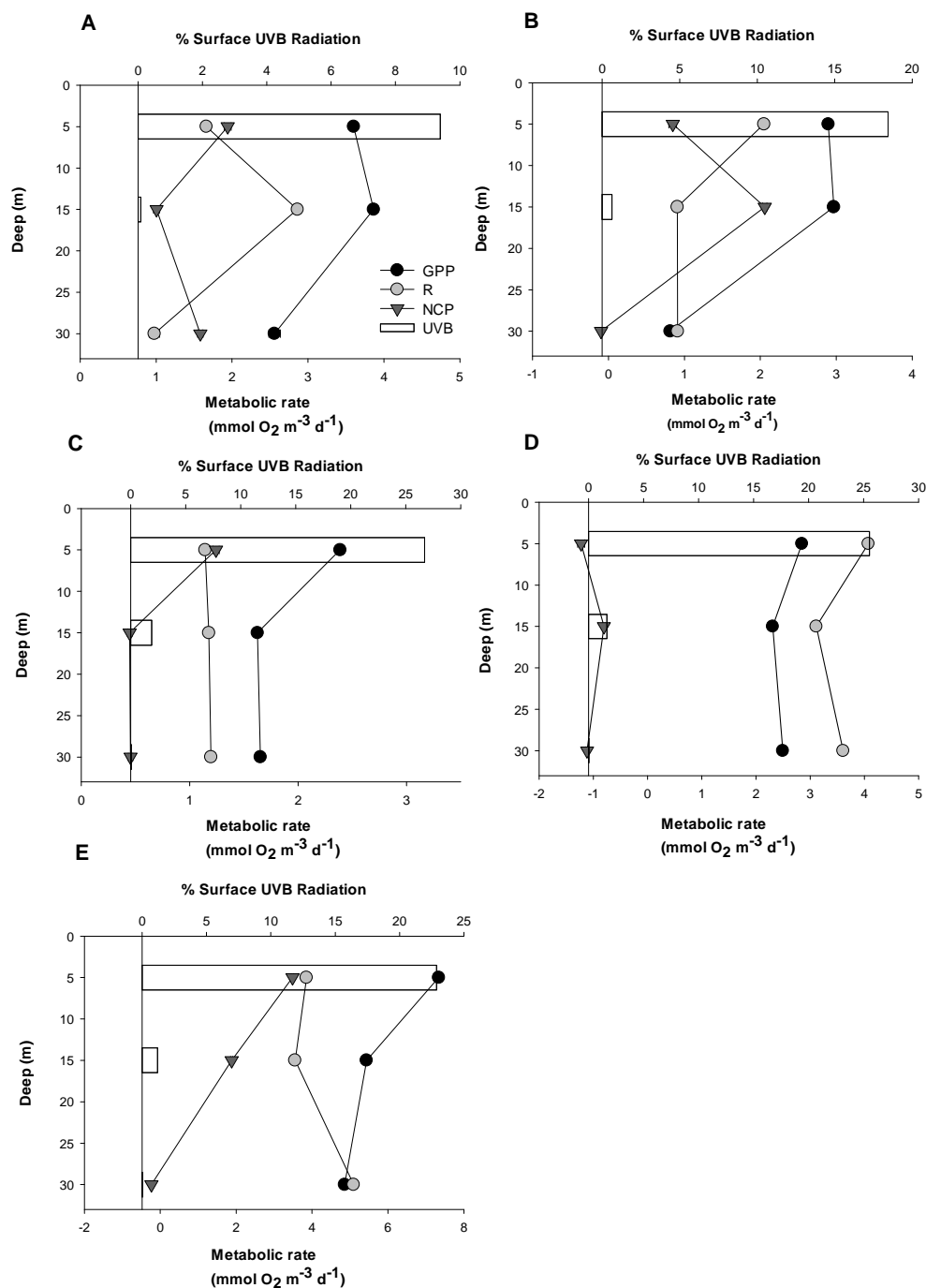


Fig. 4. Vertical profile of planktonic metabolic rates (mean \pm SE for GPP, R and NCP) and the percent UVB irradiance reaching to the sampling depth at each of the open ocean stations investigated (A: Valdivia; B: Concepcion; C: Valparaiso; D: Coquimbo; E: Caldera).

communities to enhanced NCP in response to UVB, which may involve changes in resource supply, community structure or effects of UVB on micrograzers, among other factors.

Our experiments did not allow the partitioning of the effects of UVB on NCP between the effects on respiration and GPP, since R was measured in the dark. However, there is evidence that UV radiation enhances R (Ekelund 2000)

and suppresses GPP (Holm-Hansen et al., 1993). UVB radiation affects planktonic production by reducing planktonic photosynthetic rates by 15 % per unit biomass (Cullen and Neale, 1994) and by reducing the biomass of photosynthetic plankton due to increased cell mortality rates in the presence of UVB radiation (Llabrés and Agustí, 2006, Llabrés et al., 2010; Agustí and Llabrés, 2007). UVB radiation also affects

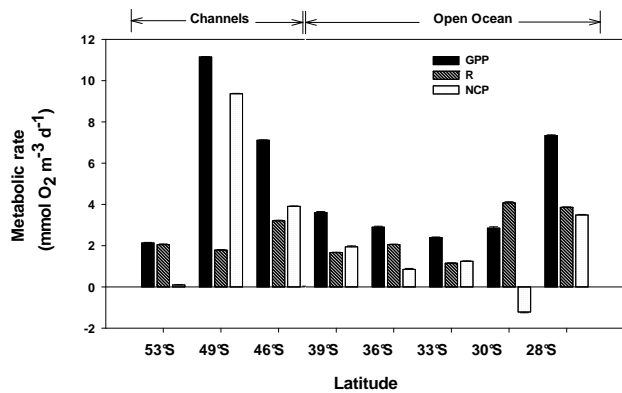


Fig. 5. Average plankton metabolic rates (mean \pm SE for GPP, R and NCP) at the surface water (5 m) along the Chilean coast.

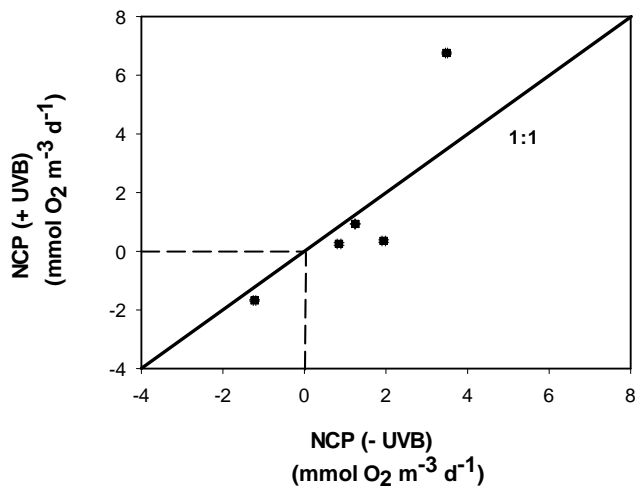


Fig. 6. The relationship between the net community production (NCP) measured in the presence (quartz bottles) and absence (glass bottles) of solar UVB radiation.

planktonic respiration by impacting on microheterotrophic processes (Hernández et al., 2006, 2007) and through photochemical reactions leading to changes in the availability of dissolved organic matter (Obernosterer et al., 1999). Hence, UVB radiation may either increase NCP, if CR is suppressed relative to GPP, or decrease NCP if GPP is suppressed relative to CR. In the experiments conducted here, the effect of UVB in suppressing GPP prevailed over the possible suppression of community respiration. Our results show, therefore, that the penetration of UVB radiation increases towards the Equator along the Humboldt Current System, affecting the communities located in the upper layers of the water column. Those surface waters affected by UVB, most showed that UVB radiation strongly suppressed net community production in most communities. To the best of our knowledge, all previous assessments of planktonic metabolism (reviewed in Robinson and Williams 2005 and Duarte and Regaudie-

de-Gioux 2009), including previous studies in the studied region (e.g. Daneri et al., 2011, Jacobs et al., 2011), used glass bottles, thereby removing the existing UVB from the incubations. Our results show that, for the communities studied along the Humboldt Current System, removal of UVB tends to suppress net community production. Hence, the exclusion of UVB from the solar radiation may bias NCP estimated. The use of quartz bottles to allow the UVB component of the irradiance field should be used in future assessment of net community production. This is particularly important in the studied region, where UVB radiation has increased greatly due to tropospheric ozone destruction, with potentially important consequences for carbon flow and biological production in this region.

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