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# UV sensitivity of planktonic net community production in ocean surface waters

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**Abstract** The net plankton community metabolism of oceanic surface waters is particularly important as it more directly affects the partial pressure of  $CO_2$  in surface waters and thus the air-sea fluxes of  $CO_2$ . Plankton communities in surface waters are exposed to high irradiance that includes significant ultraviolet blue (UVB, 280–315 nm) radiation. UVB radiation affects both photosynthetic and respiration rates, increase plankton mortality rates, and other metabolic and chemical processes. Here we test the sensitivity of net community production (NCP) to UVB of planktonic communities in surface waters across contrasting regions of the ocean. We observed here that UVB radiation affects net plankton community production at the ocean surface, imposing a shift in NCP by, on average, 50% relative to the values measured when excluding partly UVB. Our results show that under full solar radiation, the metabolic balance shows the prevalence of net heterotrophic community production. The demonstration of an important effect of UVB radiation derived from the erosion of the stratospheric ozone layer. Our results encourage design future research to further our understanding of UVB effects on the metabolic balance of plankton communities.

## 1. Introduction

Net community production (NCP), the balance between gross primary production (GPP) and community respiration (CR), of planktonic communities is a key biological component of the carbon budget of the ocean, determining the role of oceanic plankton as sinks (NCP > 0) or sources (NCP < 0) of  $CO_2$  in the ocean [*del Giorgio and Williams*, 2005]. The NCP of plankton communities has been reported to be affected by multiple factors including light availability affecting photosynthetic rates [*Kirk*, 1994], nutrient availability, temperature and community biomass and structure acting on metabolic rates of both autotrophs and heterotrophs, and organic carbon availability altering respiration rates of heterotrophs [*Robinson and Williams*, 2005; *Regaudie-de-Gioux and Duarte*, 2012].

Planktonic communities in surface waters are exposed to high irradiance, including significant ultraviolet blue (UVB, 280-315 nm) radiation, which has increased since the stratospheric ozone layer was depleted by chlorofluorocarbons (CFCs), an impact from which it has not yet recovered [Butchart and Scaife, 2001; McKenzie et al., 2003; Weatherhead and Andersen, 2006]. Elevated UVB radiation affects marine biota, including planktonic organisms, greatly [Llabrés et al., 2013]. UVB radiation reduces plankton photosynthetic rates by 15% per unit biomass [Cullen and Neale, 1994] and reduces the photosynthetic biomass due to increased cell mortality rates of plankton in the presence of UVB radiation [Llabrés and Aqustí, 2006; Aqustí and Llabrés, 2007]. UVB radiation also impacts on microheterotrophs directly [Bertoni and Callieri, 1999; Davidson and van der Heijden, 2000] and indirectly, through photochemical effects on the availability of dissolved organic matter [Obernosterer et al., 1999] with consequences on bacterial production and community respiration [Herndl et al., 1993; Agustí et al., 2014]. Indeed, UVB may inhibit bacterial production and bacterial release of extracellular enzymes [Herndl et al., 1993] or may enhance bacterial production by affecting the availability of dissolved organic matter [Obernosterer et al., 1999]. In both cases, bacterial responses to ultraviolet radiation (UVR) will affect community respiration. Hence, UVB radiation may either increase NCP, if CR is suppressed relative to GPP, or decrease NCP if GPP is suppressed relative to CR. Furthermore, Aqustí et al. [2014] showed that NCP is directly affected by the bacterial response to UVR. Indeed, bacterial activity is inhibited in the presence of UVB, but may recover and even be enhanced in the dark following exposure to UVB, conducive to increased community respiration and reduced NCP when integrated over 24 h [Agustí et al., 2014].

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Figure 1. Areas where the experiments were conducted.

Despite the evidence that UVB radiation affects many relevant processes involved in determining NCP, the sensitivity of NCP to UVB exposure is poorly reported. There are still few studies on the impact of the UVB radiation on planktonic metabolism. *Godoy et al.* [2012] reported a tendency for NCP to decline in the presence of UVB, and *Agustí et al.* [2014] reported a series of experiments to explain how suppression of bacterial activity under UVR and subsequent recovery in the dark contributes to explain the effects of UVR on NCP. However, the number of experiments reported by these studies is limited [*Godoy et al.*, 2012; *Agustí et al.*, 2014] and whether their results apply to planktonic communities elsewhere in the ocean is unresolved. Indeed, all other estimates of NCP at specific depths in the ocean available to date were derived using borosilicate Winkler bottles, which partly remove UVR, to incubate the communities in the light.

Here we test the response of NCP to the partial removal of ambient UVB in planktonic communities across surface waters in contrasting regions of the ocean (NW Mediterranean Sea, Antarctic Peninsula, eastern Pacific Ocean, and NE subtropical Atlantic).

## 2. Methods

We evaluated NCP incubated under full solar radiation exposure and when UV radiation was partly removed in planktonic communities in four different regions (Antarctic Peninsula, NW Mediterranean, NE subtropical Atlantic, and eastern Pacific; Figure 1) using two different materials for incubation: borosilicate (that partly remove UVB) and quartz (largely transparent to UV) bottles (Figure 2). A total of 59 experiments were conducted along these locations assessing the effect of different UVB exposure on the NCP of planktonic communities



(Table 1). The experiments in the northeastern subtropical Atlantic were conducted between the Canary Islands and the Cape Verde Islands during the RODA II cruise (3 February 2007 to 26 February 2007). The experiments in the Antarctic Peninsula were conducted during the Antarctic tourism opportunity spectrum (ATOS)-Antarctic cruise (26 January 2009 to 28 February 2009). The study conducted in the southeastern Pacific off Chile was along the Humboldt Current in the Patagonia channels during the Humboldt 2009 cruise (05 March 2009 to 15 March 2009). All three cruises were conducted aboard the Spanish Oceanography Research vessel Hesperidés. The experiments in the northwestern Mediterranean Sea were conducted at the

**Figure 2.** The spectral percentage of light transmitted in the UV radiation and PAR bands of the quartz and borosilicate Winkler bottles used during our studies.

Cap Salines lighthouse in Mallorca Island (39°16'N–3°32'E, from July 2008 to April 2010) and at Cabrera Island (39°19'N–21°56'E, September and October 2005).

The experiments involved incubating communities from surface (5 m depth samples for the NE subtropical Atlantic and eastern Pacific and 1 m depth samples for the Antarctic and NW Mediterranean). Water samples were collected using 12 L Niskin bottles attached to a Rosette sampler system or 30 L Niskin bottles for 1 m sampling used in the Antarctic cruise. Water samples were carefully siphoned into narrow-mouth borosilicate and quartz Winkler bottles. The water samples were taken during the early morning and were protected by a dark screen to avoid exposure to solar irradiance before the onset of the incubation. Replicated (n = 7) samples were immediately fixed to determine the initial oxygen concentration. Other set of seven replicated transparent borosilicate Winkler bottles and a set of five replicated transparent quartz Winkler bottles were suspended in seawater and incubated on deck for 24 h in a large 2000 L tank with continuous circulation of surface seawater to maintain the temperature of the surface waters and natural solar radiation.

Net community production (NCP) was estimated from changes in oxygen concentration along the incubation [*Carpenter*, 1965; *Carrit and Carpenter*, 1966]. Oxygen concentrations were analyzed by Winkler titration using a potentiometric electrode and automated endpoint detection allowing 0.1% precision in oxygen determination (Mettler Toledo, DL28 titrator) [*Oudot et al.*, 1988].

The depth-integrated NCP rates were calculated using a conventional trapezoid method, where rates were available for at least three depths within the euphotic layer. Considering that the NCP rates under full solar radiation (NCP<sub>FSR</sub>) were estimated only for the surface layer, the depth-integrated NCP<sub>FSR</sub> rates were calculated using the NCP<sub>FSR</sub> rates for the surface layer and the NCP rates when UV was partly removed (NCP<sub>-UV</sub>) for the deper depths when available.

Oceans	N	Date	Temperature (°C)	Chlorophyll <i>a</i> (mg m <sup>-3</sup> )	Maximum Daily UV Index	Solar Radiation (kJ m <sup><math>-2</math></sup> d <sup><math>-1</math></sup> )
Antarctic	13	28 January 2009–24 February 2009	$1.0 \pm 0.4$	$4.4 \pm 2.4$	$2.4 \pm 0.5$	8,716.39±1,834.68
			(-0.8-2.9)	(0.3–31.7)	(0.6–5.2)	(3,044–22,446)
Atlantic	20	21 August 2006–3 September 2009;	$20.9 \pm 0.3$	$0.4 \pm 0.1$	$6.7 \pm 0.2$	15,371.10±944.46
		05 February 2007–25 February 2007	(19.2–22.6)	(0.1–0.9)	(4.8-8.5)	(7,977–19,922)
Mediterranean Sea	21	30 September 2005–1 October 2005;	$20.2 \pm 1.4$	ND (not determined)	6±0.9	ND
		22 July 2008–16 April 2010	(12.0-28.0)	ND	(1–9.9)	ND
Pacifica	5	10 March 2009–14 March 2009	$16.6 \pm 0.6$	$1.3 \pm 0.5$	$7.2 \pm 1.0$	13,580.01 ± 2,760.20
			(14.9–18.4)	(0.5–3.3)	(3.8–9)	(4,528–21,102)

Table 1. Mean (±SE) and Range of Water Temperature, Chlorophyll *a* Concentration, Maximum Daily Incident Ultraviolet Radiation (UV Index), and Daily Doses of Solar Radiation for the Experiments Conducted in the Different Regions a *Godoy et al.* [2012]

Ocean	N	$\frac{\text{NCP}_{\text{FSR}}}{\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}}$	$\frac{\text{NCP}_{-\text{UV}}}{\text{mmol}\text{O}_2\text{m}^{-3}\text{d}^{-1}}$	$NCP_{FSR} - NCP_{-UV}$ mmol O <sub>2</sub> m <sup>-3</sup> d <sup>-1</sup>	Wilcoxon Sign Paired Test	NCP Response
		2.87±0.86 0.19	6.21 ± 0.32 2.26	$-3.34 \pm 0.94$ -2.55		increase = 10 (77%) <sup>b</sup> 0 = 1 (8%) <sup>c</sup>
Antarctic	13	(-5.14-24.29) -3.52±0.80 -2.6	(-0.43-38.68) -2.65 ± 1.48 -1.65	(14.39-1.49) 0.87 ± 1.20 0.69	P < 0.001	decrease = 2 $(15\%)^d$ increase = 11 $(52\%)^b$ $0 = 5 (24\%)^c$
Mediterranean	21	(-20.31-1.05) 1.32±0.04 0.35	(14.75-1.80) 1.26±0.04 1.24	(-5.57-3.32) 0.07±0.28 -0.45	P = 0.0091	decrease = 5 $(24\%)^{d}$ increase = 4 $(80\%)^{b}$ $0 = 0 (0\%)^{c}$
Pacific	5	(-1.68-6.76) 0.86±0.31 0.93	(-1.22-3.48) 1.06±0.31 1.41	(−1.59−3.27) −0.20±0.81 −0.11	<i>P</i> = 0.031	decrease = 1 (20%) <sup>d</sup> increase = 7 (35%) <sup>b</sup> $0 = 5 (25%)^{c}$
Subtropical Atlantic	20	(-3.13-6.07) $-0.22 \pm 0.68$ -0.47	(-2.93-4.27) 0.89±0.98 0.61	(-4.26-1.81) -1.11±0.35 -0.61	<i>P</i> = 0.42	decrease = 8 $(40\%)^{d}$ increase = 32 $(54\%)^{b}$ $0 = 11 (19\%)^{c}$
Overall	59	(-20.31-24.29)	(-14.75-38.68)	(-14.39-3.31)	P < 0.001	decrease = 16 (27%) <sup>d</sup>

#### Table 2. Number of Experiments Conducted in Each Region<sup>a</sup>

<sup>a</sup>Mean ( $\pm$ SE), median, and range of net community production measured under the full solar irradiance (NCP<sub>FSR</sub>) and when UVR was partly removed (NCP<sub>-UV</sub>). The mean ( $\pm$ SE), median, and range of the difference between these two and the probability of pairwise differences between both measurements of NCP (Wicoxon Ranked Sign Test).

<sup>b</sup>The number and proportion of experiments yielding a significant (*t* test, P < 0.05) increase in NCP when UVR was partly removed (NCP<sub>FSR</sub> – NCP<sub>-UV</sub> < 0, increase). <sup>c</sup>Those showing no statistically significant difference (NCP<sub>FSR</sub> NCP<sub>UV</sub> = 0, = 0).

<sup>d</sup>Those yielding a significant decline in NCP when UVR was partly removed (NCP<sub>FSR</sub> NCP<sub>UV</sub> > 0, decrease).

Solar and UV radiation in the air were measured by a WeatherLink Vantage Pro. Davis Co. meteorological station located on board R/V *Hespérides* for each cruise except for the experiments conducted in the NW Mediterranean Sea. Photosynthetically active radiation (PAR) was measured using a solar radiation 6450 Davis sensor (from 400 to 1100 nm) every 1 or 10 min. In addition, Davis 6490 UV radiation sensor was used to detect UV radiation (290–390 nm) every 1 or 10 min. Its spectral response closely matches the Erythema action spectrum [*McKinlay and Diffey*, 1987]. Data of UV were 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+). UVB radiation for the experiments conducted in Mallorca (NW Mediterranean, Spain) was reported from the monitoring station at the Palma airport operated by AEMET (Spanish State Meteorological Agency), measuring erythemal irradiance as  $J m^{-2}$  each 30 min of a day (16.5 h of light in total per day). The maximum UV index was estimated using the maximum for any 30 min period of the day based on the measured  $J m^{-2}$  divided by the number of seconds in 30 min (1 J m<sup>-2</sup> s<sup>-1</sup>: 40 UV index). The solar and UV radiations presented here represent the radiation incident at the surface, which is higher than that received at depths from which plankton communities were sampled.

Temperature at 1 m depth was determined using a Sea-Bird conductivity-temperature-depth (CTD) 19 deployed from a Zodiac, and those at 5 m depths were determined from the Sea-Bird Electronics 25 CTD attached to the Rosette sampling system of the research vessel. Samples of 250 mL for chlorophyll *a* determinations were filtered through Millipore glass fiber filters (pressure < 0.3 kg cm<sup>-2</sup>), frozen and extracted for 24 h with 90% acetone. Chlorophyll *a* concentration was derived from the fluorescence of the extracts measured using a Shimadzu RF-5301 fluorometer [*Yentsch and Menzel*, 1963].

Literature data on net community metabolism under full solar radiation and UVR (eastern Pacific Ocean) [Godoy et al., 2012] were included in the analysis.

## 3. Results

The oceanic regions studied here ranged broadly in chlorophyll *a* concentration and temperature (Table 1). Among the regions investigated, the maximum daily UV index during the sampling studies was not significantly different between the NW Mediterranean Sea (6±0.9), the NE subtropical Atlantic (6.7±0.2), and the eastern Pacific (7.2±1.0) (Tukey Kramer honestly significant difference test, *P* > 0.05) (Table 1). The communities investigated span broad ranges of NCP (-20.3 to 24.3 mmol  $O_2$  m<sup>-3</sup> d<sup>-1</sup> and -14.8 to 38.7 mmol  $O_2$  m<sup>-3</sup> d<sup>-1</sup> for NCP<sub>FSR</sub> and NCP<sub>-UV</sub>, respectively), from highly heterotrophic to highly autotrophic communities (Table 2).</sub>



**Figure 3.** The relationship between the mean (±SE) net community production under full solar radiation exposure (NCP<sub>FSR</sub>) and that when UVR was partly removed (NCP<sub>-UV</sub>) for the individual experiments conducted in different oceans. The solid line indicates the orthogonal regression equation: NCP<sub>-UV</sub> = 1.17(±0.06) NCP<sub>FSR</sub> + 1.15(±0.34),  $R^2$  = 0.84, P < 0.05. The dotted line shows the 1:1 line.

A total of 26 experiments were conducted with heterotrophic communities (NCP < 0, *t* test, P < 0.05; supporting information), 20 with autotrophic ones (NCP > 0, *t* test, P < 0.05; supporting information) and 13 with communities in approximate metabolic balance (NCP = 0, *t* test, P > 0.05; supporting information).

Out of the 59 experiments conducted, 11 (19%) did not show significant differences (t test, P > 0.05) between the NCP measured under the full spectrum of solar radiation (NCP<sub>FSR</sub>) and when UVR was partly removed (NCP<sub>-UV</sub>; Table 2). A total of 48 experiments (81%) yielded significant differences (t test, P < 0.05) between the NCP<sub>FSR</sub> and NCP<sub>-UV</sub> (Table 2), with a prevalence of experiments where NCP was significantly enhanced when UV was partly removed (32 experiments, 54% of the total experiments; Table 2) compared to experiments showing a significant suppression of NCP when UVR was partially removed (16 experiments, 27% of the total experiments; Table 2). No significant relationship was observed between the difference between NCP<sub>-UV</sub> and NCP<sub>ESR</sub> and the incident UVR for each experiment (data not shown here).

The relationship between NCP<sub>FSR</sub> and NCP<sub>-UV</sub> (Figure 3) revealed a significant tendency for NCP<sub>-UV</sub> to be higher than NCP<sub>FSR</sub> as reflected in an intercept significantly greater than 0 (*F* test, P = 0.0015), whereas the slope did not differ significantly from 1 (*F* test, P = 0.2649).

Furthermore, for the different sampling regions, NCP<sub>-UV</sub> rates were significantly higher than NCP<sub>FSR</sub> rates for planktonic communities sampled at the Antarctic Ocean and the Mediterranean Sea (Wilcoxon ranked sign test, P < 0.05). For planktonic communities sampled at the subtropical Atlantic and at the Pacific, no overall significant difference was observed between NCP<sub>FSR</sub> and NCP<sub>-UV</sub> rates (Wilcoxon



**Figure 4.** Box plot representing the distribution of the mean difference (NCP<sub>FSR</sub> - NCP<sub>-UV</sub>) (mmol O<sub>2</sub> m<sup>-3</sup> d<sup>-1</sup>) for each cruise.

ranked sign test, P > 0.05), although experiments with individual communities often revealed significant responses (Table 2).

Full solar radiation exposure may also change the metabolic status of planktonic communities. Indeed, the communities in seven of the experiments reverted from heterotrophic to net autotrophic, and the communities of only one experiment reverted from autotrophic to heterotrophic when UV was partially removed. As 54% of the experiments here showed NCP<sub>-UV</sub> to be higher than its corresponding NCP<sub>FSR</sub> (Table 2), full solar radiation exposure appears to be conducive to more heterotrophic planktonic metabolism. The magnitude of change in NCP when UV was partly removed ranged  $-1.11 \pm 0.35 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$  (Table 2), significantly lower than 0 (*t* test, *P* < 0.05). The magnitude of the response of NCP to partial UV removal was strongly dependent on latitude, with the magnitude of the response increasing from subtropical to Antarctic communities (Figure 4).

## 4. Discussion

The results presented, based on a large number of experiments conducted across broadly different regions of the ocean, conclusively show that UV radiation affects net plankton community production in ocean surface waters, imposing a shift in NCP by, on average, 50% relative to the values measured when UV was partly removed. This difference increased, on average, fourfold from subtropical communities, where the impact was quantified at about 1 mmol  $O_2 m^{-3} d^{-1}$ , to Antarctic latitudes, where plankton communities showed the greatest response to partial UV removal, quantified at about 4 mmol  $O_2 m^{-3} d^{-1}$ .

Our results show that the prevalent response to partial removal of UV radiation is a decline in NCP. These results confirm the findings of *Godoy et al.* [2012], who reported, on the basis of a limited data set, a tendency toward an increase in NCP when UV radiation was partly removed for plankton communities in the Pacific along the Chilean Coast. Furthermore, *Agustí et al.* [2014] showed experimentally how responses of NCP to UVB radiation are complex and can lead to either reduced or increased NCP. In particular, *Agustí et al.* [2014] showed that heterotrophic activity is suppressed in the presence of ambient levels of UVB radiation, but that heterotrophic activity can increase in the night, following exposure to UVB radiation, to overcompensate the decline in the light, thereby leading to a decline in NCP when the light and dark periods are integrated. Indeed, most (54%; Table 2) of the experiments conducted here resulted in a significant increase in NCP when UVB radiation was excluded.

UVB effects on gross primary production are expected to be negative, as exposure to UVB causes phytoplankton cell death [Llabrés and Agustí, 2006; Agustí and Llabrés, 2007] and reduces specific photosynthetic rates through pigment destruction and photoinhibitory processes [Cullen and Neale, 1994]. In contrast, respiration rates may be either suppressed or enhanced by UVB radiation. Heterotrophic microorganisms have been reported to exhibit mortality when exposed to UVB [Llabrés et al., 2013], which would tend to reduce community respiration rates. On the other hand, UVB can also enhance respiratory mechanisms through a number of processes including the improvement of energetic demands to repair cellular and molecular damage [Vincent and Neale, 2000], increasing the flow of dissolved organic carbon from damaged phytoplankton cells [Llabrés et al., 2013] and increasing the lability of dissolved organic matter (DOM) through photochemical reactions [Zepp et al., 1995; Zepp, 2003]. Under UV exposure, heterotrophic and bacterial production may be suppressed by damaging deoxyribonucleic acid, proteins, and cell membranes [Herndl et al., 1993; Arrieta et al., 2000] or enhanced by the photochemical processes making available DOM for bacterial consumption [Kaiser and Herndl, 1997; Arrieta et al., 2000; Agustí et al., 2014]. The complexity of the responses of NCP to UVR, which integrated responses at multiple levels by autotrophs and microheterotrophs, explains that there is no simple relationship between the NCP<sub>FSR</sub> – NCP<sub>-UV</sub> and UVR in our experiments. The effects of full solar radiation exposure on net community production shown here reflects the balance between these processes, which may yield enhanced NCP, when respiration rates are more suppressed by UV than gross primary production, or reduced NCP, when the opposite holds.

The demonstration of the effect of UV radiation on net plankton community production in surface waters presented here is of particular relevance in relation to the increased in UVB radiation derived from the erosion of the stratospheric ozone layer. Those effects could not be revealed by measurements of net community production in the ocean conducted to date, as most of these measurements have always been conducted using material partly removing UVB radiation. The erosion of the stratospheric ozone layer led to a global increase in UVB, with the increased rates declining toward the equator and higher, for any given latitude, in the Southern compared to the Northern Hemisphere [*Armstrong*, 1994]. Despite the success of the Montreal Protocol, banning the use and emissions of CFCs in 1987, there is as yet no clear evidence of the recovery of the stratospheric ozone layer, and UVB radiation remains elevated and will likely continue to do so over the coming decades [*Pyle*, 2000; *Bernath*, 2005; *Weatherhead and Andersen*, 2006]. Our experiments suggest that net community production in the ocean surface waters may have changed, with a tendency for plankton communities in surface waters to become more heterotrophic, in response to elevated UVB radiation. This

effect is likely to be highest in the southern Ocean, where UVB has increased most [*Armstrong*, 1994]. Indeed, the experimental assessment of impacts of UV removal on net plankton community production showed the magnitude of these effects to increase with latitude, being highest for the experiments conducted in the Antarctic Peninsula (Figure 4 and Table 2). Furthermore, the metabolic balance integrated into the mixed layer column may have been biased and overestimated or underestimated. Indeed, the impacts of UV radiation on NCP are significant at the ecosystem level, as where integrated rates could have been calculated, the estimated calculated NCP rates increased by 46% and 89% when UV was partly removed in the Antarctic (NCP<sub>-UV</sub> = 63.4 mmol  $O_2$  m<sup>-2</sup> d<sup>-1</sup> and NCP<sub>FSR</sub> = 43.3 mmol  $O_2$  m<sup>-2</sup> d<sup>-1</sup>, *t* test, *P* = 0.02) and the Pacific (NCP<sub>-UV</sub> = 18.7 mmol  $O_2$  m<sup>-2</sup> d<sup>-1</sup> and NCP<sub>FSR</sub> = 9.9 mmol  $O_2$  m<sup>-2</sup> d<sup>-1</sup>, *t* test, *P* = 0.23; supporting information). These values provide a crude approximation, as the integrated rates were based on three levels only and include therefore considerable uncertainty.

The results focus on impacts of removing UVB radiation on NCP in surface waters. The NCP in surface waters is of particular importance as it plays a determinant role of controlling the partial pressure of metabolic gases, such as CO<sub>2</sub> and O<sub>2</sub>, and therefore the corresponding air-sea fluxes [*Calleja et al.*, 2005]. Moreover, UVB radiation penetrates down to considerable depths, with 10% of subsurface UVB radiation penetrating down to 40 m in the South Pacific [*Tedetti et al.*, 2007] and lethal doses sufficient to remove 50% of the dominant *Prochoroccocus* population per day penetrating down to 60 m in the subtropical Atlantic [*Llabrés and Agustí*, 2006]. Hence, UVB radiation is a component of the light field experienced in situ by planktonic communities. However, experiments to resolve metabolic rates, whether using oxygen or carbon evolution of tracer (<sup>14</sup>C, <sup>18</sup>O) additions typically, use borosilicate glass or polycarbonate bottles to incubate the community [*Steeman Nielsen*, 1952; *Grande et al.*, 1982; *Bender et al.*, 1987]. Although borosilicate and polycarbonate have different optical properties, both remove much of UV radiation. The impacts of UVB on NCP in the upper layers of the photic layer may affect the integrated NCP rates. In particular, NCP in the oligotrophic ocean has been reported to be positive, on average, only in surface waters [*Duarte et al.*, 2013]. However, consideration of bias in NCP derived from exclusion of UVB radiation suggests that NCP may have been overestimated in the past in the oligotrophic ocean.

We believe that the estimates presented here on the magnitude of NCP measurements associated with the exposure to full solar radiation are conservative ones. The cruise conducted here in the Antarctic Peninsula waters was characterized by low UV radiation associated with overcast and foggy conditions, so that effects would have been possibly much larger under clear-sky conditions. Moreover, the cruises were conducted in the late summer (southern Ocean), while UV radiation is highest in spring [*Madronich et al.*, 1998].

The persistence of elevated UVB levels in the biosphere due to the poor resilience of the ozone layer [*Pyle*, 2000; *Bernath*, 2005; *Weatherhead and Andersen*, 2006] implies that the role of UVB in modulating biogeochemical processes in the ocean has been enhanced, with UVB radiation affecting phytoplankton cell mortality [*Llabrés and Agustí*, 2006; *Agustí and Llabrés*, 2007] and net community production, as shown here, among other processes. The response of NCP to UV exposure is complex considering that it depends on the response of CR and so of bacteria activity to UVR. Whereas UVR may enhance CR as bacterial production may be enhanced [*Agustí et al.*, 2014] by UVB, it could be as well suppressed by UVB [*Herndl et al.*, 1993]. Because UVB radiation may continue to change in the future, as the recent ozone depletion over the Arctic suggests [*Manney et al.*, 2011], efforts to further our understanding on UVB effects on plankton metabolism must be sustained.

## References

- Agustí, S., and M. Llabrés (2007), Solar radiation-induced mortality of marine pico-phytoplankton in the oligotrophic ocean, *Photochem. Photobiol.*, 83, 793–801.
- Agustí, S., A. Regaudie-de-Gioux, J. M. Arrieta, and C. M. Duarte (2014), Consequences of UV-enhanced community respiration for planktonic metabolic balance, *Limnol. Oceanogr.*, 59, 223–232.
- Armstrong, B. K. (1994), Stratospheric ozone and health, Int. J. Epidemiol., 23(5), 873–88.
- Arrieta, J. M., M. G. Weinbauer, and G. J. Herndl (2000), Interspecific variability in sensitivity to UV radiation and subsequent recovery in selected isolates of marine bacteria, *Appl. Environ. Microbiol.*, *66*, 1468–1473.
- Bender, M. L., et al. (1987), A comparison of four methods for determining planktonic community production, *Limnol. Oceanogr.*, 32, 1085–1098.
- Bernath, P. F. (2005), Atmospheric chemistry experiment (ACE): Mission overview, *Geophys. Res. Lett.*, *32*, L15S01, doi:10.1029/2005GL022386. Bertoni, R., and C. Callieri (1999), Effects of UVB radiation on freshwater autotrophic and heterotrophic picoplankton in a subalpine lake, *J. Plankton Res.*, *21*, 1373–1388.

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Calleja, M. L., C. M. Duarte, N. Navarro, and S. Agustí (2005), Control of air-sea CO<sub>2</sub> disequilibria in the subtropical NE Atlantic by planktonic metabolism under the ocean skin, *Geophys. Res. Lett.*, 32, L08606, doi:10.1029/2004GL022120.

Carpenter, J. H. (1965), The accuracy of the Winkler method for dissolved oxygen analysis, Limnol. Oceanogr., 10, 135-140.

Carrit, D. E., and J. H. Carpenter (1966), Comparison and evaluation of currently employed modifications of the Winkler method for determining dissolved oxygen in sea-water, J. Mar. Res., 24, 286–318.

Cullen, J. J., and P. J. Neale (1994), Ultraviolet radiation, ozone depletion, and marine photosynthesis, Photosynth. Res., 39, 303-320.

Davidson, A. T., and A. van der Heijden (2000), Exposure of natural Antarctic marine microbial assemblages to ambient UV radiation: Effects on bacterioplankton, Aquat. Micr'ob. Ecol., 21, 257–264.

del Giorgio, P. A., and P. J. I. B. Williams (2005), Respiration in Aquatic Ecosystems, Oxford Univ. Press, New York.

Duarte, C. M., A. Regaudie-de-Gioux, J. M. Arrieta, A. Delgado-Huertas, and S. Agustí (2013), The oligotrophic ocean is heterotrophic, Annu. Rev. Mar. Sci., 5, 551–569.

Godoy, N., A. Canepa, S. Lasternas, E. Mayol, S. Ruíz-Halpern, S. Agustí, J. C. Castilla, and C. M. Duarte (2012), Impacts of UV radiation on plankton community metabolism along the Humboldt Current System, *Biogeosciences*, *8*, 5827–5848.
Grande, K. D., P. Kroopnick, D. Burns, and M. L. Bender (1982), <sup>18</sup>O as a tracer for measuring gross primary production in bottle experiment,

Grande, K. D., P. Kroopnick, D. Burns, and M. L. Bender (1982), <sup>1o</sup>O as a tracer for measuring gross primary production in bottle experiment *Eos Trans. AGU*, *63*, 107.

Herndl, G. J., G. Müller-Niklas, and J. Frick (1993), Major role of ultraviolet-B in controlling bacterioplankton growth in the surface layer of the ocean, *Nature*, 361, 717–719.

Kaiser, E., and G. J. Herndl (1997), Rapid recovery of marine bacterioplankton activity after inhibition by UV radiation in coastal waters, *Appl. Environ. Microbiol.*, 63, 4026–4031.

Kirk, J. T. O. (1994), Light and Photosynthesis in Aquatic Ecosystems, Cambridge Univ. Press, New York.

Llabrés, M., and S. Agustí (2006), Picoplankton cell death induced by UV radiation: Evidence for oceanic Atlantic communities, *Limnol. Oceanogr.*, *51*, 21–29.

Llabrés, M., S. Agustí, M. Fernández, A. Canepa, F. Maurin, F. Vidal, and C. M. Duarte (2013), Impact of elevated UVB radiation on marine biota: A meta-analysis, *Global Ecol. Biogeogr.*, 22, 131–144.

Madronich, S., R. L. McKenzie, L. O. Björn, and M. M. Caldwell (1998), Changes in biologically active ultraviolet radiation reaching the Earth's surface, J. Photochem. Photobiol., B, 46, 5–19.

Manney, G. L., et al. (2011), Unprecendented Arctic ozone loss in 2011, Nature, 478, 469-475.

McKenzie, R. L., L. O. Björn, A. Bais, and M. Ilyasd (2003), Changes in biologically active ultraviolet radiation reaching the Earth's surface, *Photochem. Photobiol. Sci.*, 2, 5–15.

McKinlay, A. F., and B. L. Diffey (1987), A reference action spectrum for ultraviolet inducted erythema in human skin, CIE J., 6, 17–22.

Obernosterer, I., B. Reitner, and G. J. Herndl (1999), Effects of solar radiation on dissolved organic matter and its bioavailability to marine bacterioplankton, *Limnol. Oceanogr.*, 44, 1645–1654.

Oudot, C., R. Gerard, P. Morin, and I. Gningue (1988), Precise shipboard determination of dissolved-oxygen (Winkler Procedure) for productivity studies with a commercial system, *Limnol. Oceanogr.*, 33, 146–150.

Pyle, J. A. (2000), Statospheric ozone depletion: A discussion of our present understanding, in *Causes and Environmental Implications of Increased UV-B Radiation*, edited by R. E. Hester and R. M. Harrison, pp. 1–16, The Royal Society of Chemistry, Cambridge, U. K.

Regaudie-de-Gioux, A., and C. M. Duarte (2012), Temperature dependence of planktonic metabolism in the ocean, *Global Biochem. Cycles*, 26, GB1015, doi:10.1029/2010GB003907.

Robinson, C. and P. J. I B. Williams (2005), Respiration and its measurement in surface marine waters, in *Respiration in Aquatic Ecosystems*, edited by P. del Giorgio and P. J. I B. Williams, pp. 148–181, Oxford Univ. Press, New York.

Steeman Nielsen, E. (1952), The use of radioactive carbon (<sup>14</sup>C) for measuring production in the sea, *J. Cons. Perm. Int. Explor. Mer.*, 18, 117–140.

Tedetti, M., R. Sempéré, A. Vasilkov, B. Charrière, D. Nérini, W. L. Miller, K. Kawamura, and P. Raimbault (2007), High penetration of ultraviolet radiation in the south east Pacific waters, *Geophys. Res. Lett.*, *34*, L12610, doi:10.1029/2007GL029823.

Vincent, W. F., and P. J. Neale (2000), Mechanisms of UV damage to aquatic organisms, in *The Effects of UV Radiation in the Marine Environment*, edited by S. de Mora et al., pp. 149–176, Cambridge Univ. Press, Cambridge, U. K.

Weatherhead, E. C., and S. B. Andersen (2006), The search for signs of recovery of the ozone layer, *Nature*, 441, doi:10.1038/nature04746. Yentsch, C. S., and D. W. Menzel (1963), A method for determination of chlorophyll and phaeophytin by fluorescence, *Deep-Sea Res.*, 10, 221–231.

Zepp, R. G. (2003), Solar UVR and aquatic carbon, nitrogen, sulfur and metals cycles, in UV effects in Aquatic Organisms and Ecosystems, edited by E. W. Helbling and H. Zagarese, pp. 137–183, The Royal Society of Chemistry, Cambridge, U. K.

Zepp, R. G., T. V. Callaghan, and D. J. Erickson (1995), Effects of increased solar ultraviolet radiation on biogeochemical cycles, Ambio, 24, 1995.