Impact of UV radiation on plankton net community production: responses in Western Australian estuarine and coastal waters

Lara S. García-Corral[1,3,*], Carlos M. Duarte[2], Susana Agustí[2]

[1]The UWA Oceans Institute and School of Plant Biology, The University of Western Australia, Crawley, WA 6009, Australia
[2]King Abdullah University of Science and Technology (KAUST), Red Sea Research Center (RSRC), Thuwal, 23955-6900, Saudi Arabia

[3]*Present address:* Department of Biology, Geology, Physics and Inorganic Chemistry, King Juan Carlos University, C/ Tulipán s/n, 28933 Madrid, Spain

ABSTRACT: Net community production (NCP) is a relevant parameter informing on the role of plankton communities as sinks or sources of CO_2 in the ocean. We assessed the effect of ultraviolet (UV) radiation on NCP in different regions along the coast of Western Australia (WA). We compared 57 NCP measurements of surface communities receiving full-spectrum natural solar radiation, to communities with natural UVB radiation excluded (NCP_{-UV}). Very high values of incident UVB radiation were registered, especially during spring and summer (up to $75\,kJ\,m^{-2}\,d^{-1}$). Although a strong inhibitory effect of UVB on NCP was expected due to the high UVB levels, no significant differences between NCP and NCP_{-UV} were observed in any sampled region. However, we found a general trend of NCP inhibition by 33.4 % under UVB radiation along the WA coast. While NCP of autotrophic communities tended to slightly decrease under UVB radiation, no robust pattern was observed for heterotrophic communities. Experiments measuring the response of NCP exposed to a gradient of enhanced UVB doses exhibited a UV dose-dependent inhibition of NCP in estuarine communities (i.e. higher inhibition with higher UVB doses), and a UV dose-independent inhibition in coastal communities. Our *in situ* data showed that the net metabolism of surface plankton communities from the coast of WA was insignificantly affected by elevated environmental UVB radiation levels.

KEY WORDS: Plankton metabolism · Net community production · UVB radiation · Western Australia · Estuarine and coastal waters

1. INTRODUCTION

The stratospheric ozone concentration increases from the equator towards the poles, with an associated latitudinal and cloud cover variability of ultraviolet B (UVB) radiation (280–320 nm) incident on the sea surface (Sen Mandi 2016). The stratospheric ozone layer protects all living organisms from excess ultraviolet radiation (UVR); however, the destruction of this layer results in an increase in UVR levels (Molina & Rowland 1974, Weatherhead & Andersen 2006). The discovery of the ozone hole during the 1980s led to great research efforts to understand its consequences, and to assess the effects of enhanced UVR on marine organisms and processes (Smith & Baker 1989, Helbling & Zagarese 2003, Llabrés et al. 2013). The reduction of the ozone layer is asymmetrical between hemispheres, and the stratospheric ozone concentration in the Southern Hemisphere is lower than that in the Northern Hemisphere (Seckmeyer & McKenzie 1992, Agustí et al. 2015). Consequently, the southern part of the world has been receiving increased UVR for the past 3 decades, since the Antarctic ozone hole developed (Farman et al.

*Corresponding author: lara.silvia.g@gmail.com

1985, Herman 2010). Global evaluations of the effects of UVR on marine biota show that planktonic organisms are affected by UVB (280–320 nm) across different biomes including temperate, subtropical and polar waters (Llabrés et al. 2013). Indeed, there is a bias in studies analysing the effects of UVB on organisms from the Northern Hemisphere (two-thirds of studies) compared to the Southern Hemisphere (Agustí et al. 2015), and within the latter, most studies have been carried out in Antarctic waters, with fewer studies in mid-temperate regions (Agustí et al. 2015).

Plankton metabolism is a key biological component of the carbon cycle of the ocean, determining the role of plankton communities as sinks (gross primary production higher than community respiration, GPP > CR) or sources (GPP < CR) of CO_2 in the ocean (del Giorgio & Williams 2005). Therefore, the main metabolic processes of planktonic communities such as CR and GPP might be affected by UVB radiation, and consequently, the difference between GPP and CR, i.e. net community production (NCP), would also be affected. UVB radiation is a significant stressor in aquatic freshwater and marine environments, although its effects on NCP are not simple, possibly because NCP is an integrative property that brings together impacts at multiple levels. Studies have shown that UVB radiation inhibits surface NCP of the Atlantic, Southern and Pacific Oceans and the coastal Mediterranean Sea (Godoy et al. 2012, Agustí et al. 2014, Regaudie-de-Gioux et al. 2014, García-Corral et al. 2015). However, UV increased NCP of Arctic Ocean surface communities during summer (García-Corral et al. 2014), and also modified NCP of the upper global Subtropical oceans, depending on the metabolic status and the amount of UV irradiance received (García-Corral et al. 2017). In surface estuarine waters, primary production measured with ^{14}C showed an inhibition rate of 3–33% (Banaszak & Neale 2001) and 15–47% (Litchman & Neale 2005) in shallow, eutrophic and turbid temperate estuaries. However, no reduction in primary production was observed in a hypertrophic Baltic Sea estuary (Forster & Schubert 2001). Therefore, similar ecosystems responded differently to UVR, as many other factors (e.g. temperature, dissolved organic matter [DOM], community structure, nutrient status) can affect the diverse planktonic community responses to UVR.

The effect of UV on the NCP in the temperate coastal waters of the Southern Hemisphere, around Australia, has not been addressed to date. Here, we report the results of our studies on the effect of UVR on the net metabolism of plankton communities in coastal waters of Western Australia (WA), in which we examined the NCP of communities exposed to the ambient light environment and communities exposed to a light field where UVR was removed. To do so, we measured the incident irradiance and calculated UV doses received in the sampled areas and also experimentally tested the effects of artificially increasing daily UV doses on NCP. Our goal was to test whether UVR affects plankton net metabolism in surface waters of WA. Based on the previous literature, we expected that the strong UVR reaching WA coasts would affect and decrease the plankton net metabolic balance.

2. MATERIALS AND METHODS

2.1. Observational study

2.1.1. Sampling sites

We obtained 57 NCP measurements from surface waters (0.5–3 m) along the coast of WA in the Eastern Indian Ocean. Samples were subclassified into 4 different regions: (1) Ningaloo area (23°S; 2 stations), (2) Perth area (31.9–33.6°S) including 1 station at Rottnest Island, 1 at Busselton and a fortnightly sampled station at 32°S (March 2014 to March 2015) at Woodman Point beach (23 measurements), (3) a fortnightly sampled station at 32°S at the Swan River Estuary (28 measurements) and (4) at the Southernmost region in Albany at 35°S (2 stations) (Fig. 1).
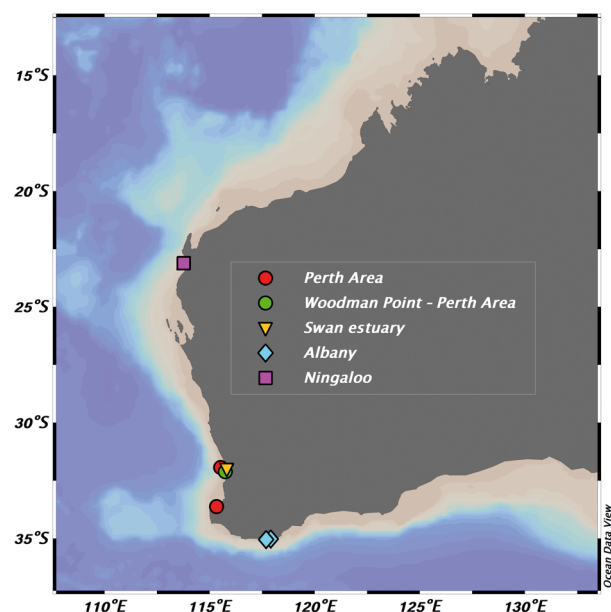

Fig. 1. Sampling sites along the coast of Western Australia

2.1.2. Plankton net community production

At each station, surface (0.5–3 m) seawater was carefully siphoned into 10 calibrated narrow-mouthed borosilicate glass Winkler bottles and 5 calibrated quartz bottles (100 cm^3) using a silicon tube. Five glass-bottle replicates were used to measure initial oxygen concentrations before incubation. The other 5 replicates of glass and 5 replicates of quartz bottles were incubated *in situ* at 0.5–1 m depth, except samples from Woodman Point beach and the Swan River Estuary that were incubated in outdoor temperature-controlled tanks at the UWA facilities. Both incubations received natural solar radiation underwater. The borosilicate glass bottles allowed 100% transmittance of photosynthetically active radiation (PAR; 400–700 nm) but removed almost all UVB, allowing the transmission of 0% at 280 nm up to 60% at 320 nm and a small part of UVA (320–400 nm), whereas quartz bottles allowed the transmittance of 100% PAR and 90% of UVB and UVA radiation (Godoy et al. 2012, Regaudie-de-Gioux et al. 2014). Hence, results derived from measurements conducted in quartz bottles were characteristic of the ambient light field, whereas those conducted in Winkler glass bottles tested the effect of reducing natural UVR.

Samples, both *in situ* and in the outdoor temperature-controlled tanks, were incubated for 24 h at the sampled water temperature and under natural solar radiation, to mimic the *in situ* conditions. After incubation, samples were fixed, and the final oxygen concentration was determined by automated high-precision Winkler titration (Carpenter 1965) with a Compact Titrator G20 (Mettler Toledo) based on a calibrated redox potentiometric end-point detection (Oudot et al. 1988). NCP rates, expressed as mmol O$_2$ m^{-3} d^{-1}, were determined under full solar radiation and when UVR was excluded (hereafter NCP and NCP$_{-UV}$, respectively); they were calculated from the difference between the oxygen concentrations measured in the incubated bottles for 24 h (glass or quartz), and concentrations measured in fixed samples at the beginning of the incubation period.

2.2. Experimental UV gradient study

We performed 6 experiments, 3 with Swan River Estuary surface waters on 1, 7 and 15 October 2015 and 3 with surface coastal waters from Woodman Point beach (Fig. 1) on 5, 12 and 20 October 2015 to test NCP responses to a gradient of increased UVB doses. NCP was determined under a gradient of UVB light

treatments. Samples were incubated at *in situ* temperature in a large controlled-temperature water bath inside a glass greenhouse located in the UWA plant growth facility. Inside the greenhouse, incident solar UVB radiation was filtered out by the glass structure. It is likely that most of the short wavelength UVA radiation was also filtered out, although we did not quantify this; however, solar PAR was received. UVB radiation was artificially added by using UVB lamps (312 nm, Vilber VL-8.M; Fisher biotec). The UVB lamps were hooked from a metal structure over the tank at different heights to create 3 underwater UVB dose treatments: low UVB (16.2 kJ m^{-2} d^{-1}, 0.09 mW cm^{-2}, 33 cm from the tank to the lamp), mid-low (34.2 kJ m^{-2} d^{-1}, 0.19 mW cm^{-2}, 17 cm), medium (50.4 kJ m^{-2} d^{-1}, 0.28 mW cm^{-2}, 11 cm) and high UVB (66.6 kJ m^{-2} d^{-1}, 0.37 mW cm^{-2}, 8 cm). The range of underwater UVB doses were based on the 25th, 50th, 75th and 90th percentiles of the incident solar UVB radiation doses measured in the field. The lamps were on for 5 h (from 10:30 to 15:30 h), and when the lamps were switched off, all samples received filtered solar radiation for the duration of the local photoperiod. Long-wavelength UVC emissions from the lamps were filtered out by the water bath. We tested NCP$_{-UV}$ treatments by incubating samples in glass borosilicate bottles and with no exposure to UVB radiation, and NCP$_{PAR+UVB}$ treatments by incubating the samples in quartz bottles at the different UVB treatments. Five replicate bottles for each light treatment were incubated for 24 h at *in situ* water temperature. The oxygen concentration in the light-treatment bottles was measured after the incubation, and the initial concentration of oxygen was measured in 5 replicates following the method described in Section 2.1.2.

2.3. Biogeochemical and physical parameters

Environmental surface incident PAR and UVB measurements were obtained with a company-calibrated Solar Light radiometer (Model PMA2100), coupled to pre-calibrated digital sensors measuring the electromagnetic spectrum of PAR (PMA2132; 400–700 nm) and a UVB band (PMA2106; 280–320 nm). Sensors were located at the same height and close to the incubation point without shading. PAR and UVB daily doses (kJ m^{-2} d^{-1}) were calculated as the sum of the surface radiation received during the incubation period. UV index values measured in air were obtained from the Australian Radiation Protection and Nuclear Safety Agency website (https://www.arpansa.gov.au) for each sampled day and location.

Chlorophyll *a* (chl *a*) concentration was determined by filtering a 100–300 ml water sample through a 25 mm GF/F glass microfibre filter (Whatman®; nominal pore size of 0.7 µm) and extracting chl *a* for 24 h within 90% acetone. Chl *a* concentration (mg m^{-3}) was derived from the fluorescence of the extracts measured using a pre-calibrated non-acidification module in a Trilogy fluorometer (Turner Designs). Water temperature, salinity, dissolved oxygen, conductivity and pH were recorded with a calibrated YSI EXO1 Multi-parameter Water Quality Sonde (Agusti et al. 2018).

2.4. Data analysis and statistics

All data were recorded in Microsoft Excel and analysed with the statistical package program JMP version 9.0.1. A Shapiro-Wilk test was conducted to assess the normal distribution of each set of data; in all cases, the p-value was found to be less than 0.05. Nonparametric tests, including all-pairs Steel-Dwass tests, Wilcoxon paired-sample tests and Kruskal-Wallis tests, were performed to reveal any signifi-

cant differences between treatments and to test our initial hypothesis. A Model II regression was fitted to evaluate the linear relationship between variables. The software Ocean Data View version 4.6.3 (Schlitzer 2013) was used to create the map of the sampled areas. Means ± SEM are reported.

3. RESULTS

3.1. Environmental parameters

The sampled areas showed higher temperatures in the tropical northwest region of Ningaloo (23.4 ± 0.44°C), and lower and similar temperatures in the southwest regions: Swan Estuary (20.67 ± 0.62°C), Perth area (20.5 ± 0.55°C) and Albany (20.5 ± 0.50°C) (Fig. 1, Table 1). Salinity was uniform for marine regions (~35) but varied widely at the Swan Estuary, exhibiting low salinity (22) after winter rains, and high salinities (37) during summer, because of the strong evaporation (Table 1). The maximum UV index registered was high across the sampling areas, ranging from 10 to 12, with the lowest

Table 1. Sampled areas in Western Australia: number of measurements (N), latitude and longitude range, sampling dates, water temperature, salinity, UV index, UVB doses and chlorophyll *a* concentration

Variable		Albany	Perth area	Swan River Estuary	Ningaloo
N		2	25	28	2
Latitude (° S)	Min	35.07	33.63	31.99	23.16
	Max	35.03	31.94	31.99	23.11
Longitude (° E)	Min	117.69	115.34	115.82	113.76
	Max	117.92	115.75	115.82	114.1
Dates		November 2014	March 2014 to March 2015	March 2014 to March 2015	October 2014
Temperature (°C)	Mean ± SEM	20.50	20.50 ± 0.55	20.67 ± 0.62	23.40
	Min	20.00	15.10	14.30	23.00
	Max	21.00	25.00	25.50	23.80
	Median	20.50	21.20	20.65	23.40
Salinity	Mean ± SEM	35.14	35.15 ± 0.29	32.12 ± 0.97	35.44
	Min	35.14	31.62	22.03	35.44
	Max	35.14	36.88	36.97	35.44
	Median	35.14	35.02	34.35	35.44
UV index	Max	10.00	12.00	12.00	11.00
UVB dose (kJ m^{-2} d^{-1})	Mean ± SEM	51.38	37.78 ± 4.43	41.41 ± 3.67	70.48
	Min	51.38	7.63	7.74	70.48
	Max	51.38	72.37	75.05	70.48
	Median	51.38	35.07	39.25	70.48
Chlorophyll *a* (mg m^{-3})	Mean ± SEM	0.35	1.52 ± 0.15	3.69 ± 0.33	0.19
	Min	0.13	0.28	1.29	0.16
	Max	0.58	3.40	8.47	0.22
	Median	0.35	1.55	3.21	0.19

maximum value (10) registered at Albany and the highest at the Swan Estuary and in the Perth area (12). Overall, UV daily doses ranged from the lowest winter measurements of 7.63 kJ m^{-2} d^{-1} in the Perth area, to the high levels of 75.05 kJ m^{-2} d^{-1} registered at the Swan Estuary during summer. An analysis of the entire dataset showed that spring and summer registered significantly higher (Steel-Dwass test, p < 0.05) UV daily doses, compared to autumn and winter (Table 1, Fig. 2).

Chl *a* values were significantly higher (p < 0.05) at the Swan Estuary (ranging from 1.29 to 8.47 mg m^{-3}), whereas the lowest concentrations were registered at Ningaloo (0.16–0.22 mg m^{-3}) (Table 1).

3.2. Observational study results

Mean surface NCP$_{-UV}$ was higher and net autotrophic at the Swan Estuary (6.81 ± 1.06 mmol O$_2$ m^{-3} d^{-1}), followed by the open coast of the Perth area (1.79 ± 0.66 mmol O$_2$ m^{-3} d^{-1}) and Ningaloo (1.29 ± 4.48 mmol O$_2$ m^{-3} d^{-1}), and lower and net heterotrophic at Albany (−0.67 ± 4.08 mmol O$_2$ m^{-3} d^{-1}). Surface NCP under full solar radiation followed a similar pattern as NCP$_{-UV}$, with higher values measured at the Swan Estuary (5.62 ± 0.93 mmol O$_2$ m^{-3} d^{-1}) in comparison with the Perth area (1.86 ± 0.57 mmol O$_2$ m^{-3} d^{-1}), Ningaloo (1.03 ± 4.81 mmol O$_2$ m^{-3} d^{-1}) and the heterotrophic region of Albany (−1.79 ± 1.82 mmol O$_2$ m^{-3} d^{-1}) (Fig. 3). However, within each sampled area, the surface NCP and NCP$_{-UV}$ rates (mmol O$_2$ m^{-3} d^{-1}) were not significantly different (Fig. 3).

Although no significant differences were observed between NCP and NCP$_{-UV}$ in any of the sampled regions, there was a general linear relationship between NCP$_{-UV}$ and NCP (Fig. 4), with a significant tendency for NCP$_{-UV}$ to be higher than NCP (Wilcoxon paired *t*-test, $t = -2.18$, df = 56, p < 0.05), as also confirmed by the fitted regression equation, NCP = 0.79 (± 0.04) × NCP$_{-UV}$ + 0.25 (± 0.30) (R^2 = 0.85, p < 0.0001, n = 57, Fig. 4). NCP declined on average by 33.4 % under UVB radiation, compared with NCP$_{-UV}$, with a mean difference between NCP and NCP$_{-UV}$ across regions of −0.6 ± 0.27 mmol O$_2$ m^{-3} d^{-1}.

No significant differences were observed between the effect size (i.e. [NCP$_{-UV}$ − NCP]/NCP$_{-UV}$) and the differences (NCP − NCP$_{-UV}$ vs. NCP) with the community trophic status (*t*-test, p > 0.05). However, a closer inspection of the linear regression showed that NCP under full solar radiation tended to be lower than NCP$_{-UV}$ when the plankton community was net autotrophic (NCP > 0), whereas NCP tended to be
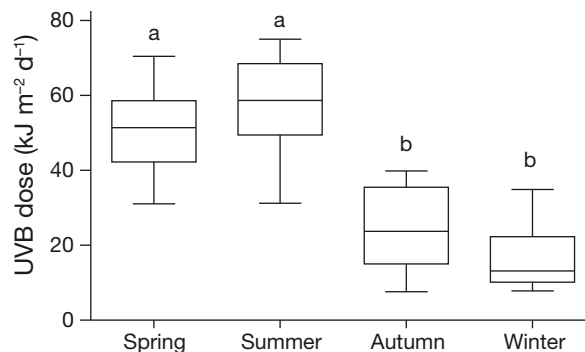

Fig. 2. Calculated UVB doses (kJ m^{-2} d^{-1}) by austral season along the sampled Western Australian coastal areas. The boxes show the central horizontal line which represents the median UVB dose, and the lower and upper edges represent the 25th and 75th percentiles, respectively. Whiskers indicate 1.5 times the Interquartile Range (IQR). Lower case letters indicate the Tukey HSD test, where seasons not connected by the same letter are significantly different
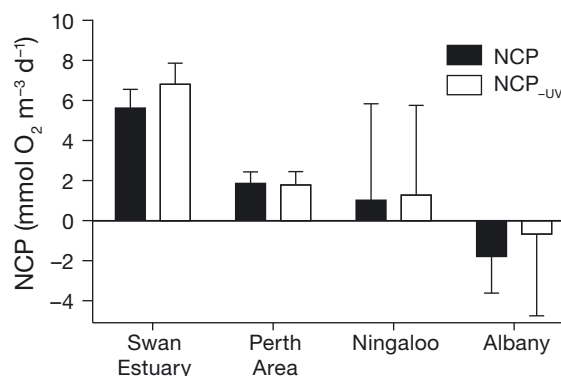

Fig. 3. Mean (± SEM) of net community production under full solar radiation (NCP) and when UVB was excluded (NCP$_{-UV}$) at the sampled areas
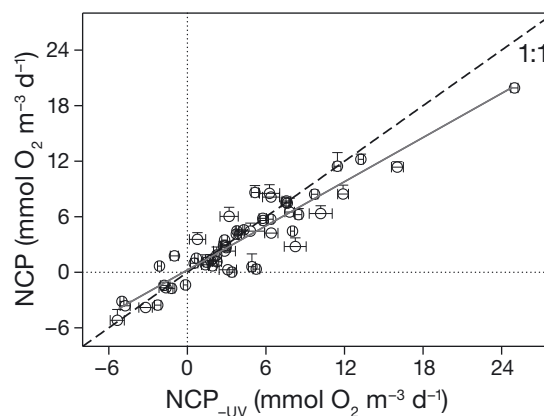

Fig. 4. Relationship for all sampled communities between net community production under natural full solar radiation (NCP) and NCP when UVB radiation was excluded (NCP$_{-UV}$). The solid line represents the fitted Type II regression equation: NCP = 0.79 (± 0.04) × NCP$_{-UV}$ + 0.25 (± 0.30) (R^2 = 0.85, p < 0.0001, n = 57). The dashed line indicates the 1:1 line and dotted lines mark the thresholds where NCP and NCP$_{-UV}$ are equal to zero. Means ± SEM are shown

equal or slightly higher than NCP_{-UV} when the community was net heterotrophic (NCP < 0) (Fig. 4). NCP of heterotrophic communities was close to zero and only found at 9 stations compared to the 48 autotrophic communities, and therefore the results are not robust enough to confirm a pattern.

3.3. Experimental UVB gradient results

The experiments tested the responses of surface NCP to the supplemented gradient of artificial UVB radiation (Fig. A1 in Appendix 1). PAR daily doses (kJ m^{-2}) received during the experiments by the Swan Estuary communities were 7810, 7541 and 6865 kJ m^{-2} on the first, second and third experimental day, respectively. For the coastal Woodman Point communities, PAR doses were 8491, 6685 and 12798 kJ m^{-2}, respectively. The communities tested showed similar initial exposure conditions: the UV index was 8 at both sites at the sampling time in all experiments, except the last sample (3rd experiment) from Woodman Point, in which the UV index was 9.

In general, the communities tested showed a tendency for NCP to decrease as underwater UVB doses increased. Four of the 6 experiments showed a lower NCP, as a result of an increase in UVB doses; in 2 of them, NCP changed from autotrophic (NCP > 0) to heterotrophic (NCP < 0) when UVB increased (Fig. A1). The 3 experiments with the Swan Estuary communities exposed to a gradient of artificial UVB doses showed a strong pattern of decreasing NCP as UVB doses increased. The other set of experimental incubations with the Woodman Point communities showed larger variability in NCP responses to increased UVB levels (Fig. A1). The third experiment (20 October) with Woodman Point communities showed a similar pattern to that obtained for the Swan Estuary communities, i.e. a linear decrease of NCP with elevated UVB doses. However, the previous 2 experiments (on 5 and 12 October) showed opposite trends.

The effect size of UVB on NCP, i.e. $(NCP_{-UV} - NCP)/(NCP_{-UV})$, was strongly dependent on the UVB dose received for the Swan Estuary communities (R^2 = 0.98, p = 0.008), with the magnitude of the effect size of NCP increasing at higher daily UVB doses (Fig. 5). However, this was not observed in the communities from Woodman Point, where the effect size was independent from the doses (p > 0.05) (Fig. 5).

4. DISCUSSION

The results presented here show that net community metabolism in coastal surface waters of WA tended to be net autotrophic. In our study, the surface waters of the Eastern Indian Ocean coast showed that NCP was generally higher when UV radiation was removed (i.e. NCP ≤ NCP_{-UV}) and therefore our hypothesis is supported. Nevertheless, the inhibitory effect of UV on NCP was only observed for those communities with a net autotrophic balance (NCP > 0).

This effect has also been described for the Mediterranean Sea (Regaudie-de-Gioux et al. 2014, García-Corral et al. 2015), Atlantic, Pacific and Antarctic plankton communities (Godoy et al. 2012, Agustí et al. 2014, Regaudie-de-Gioux et al. 2014) and for the global subtropical regions of the Indian, Pacific and Atlantic Oceans (García-Corral et al. 2017). The mean difference of NCP – NCP_{-UV} at the WA coast was −0.6 ± 0.27 mmol O_2 m^{-3} d^{-1}, not significantly different from the mean values reported for Subtropical Indian, Atlantic and Pacific communities exposed to lower UVB doses (Table 1 in García-Corral et al. 2017). Indeed, the ultraoligotrophic nature of the subtropical waters might explain the lower values found for both NCP and NCP_{-UV}, compared to the more productive waters of the WA coast sampled in this study.

The relationship between NCP and NCP_{-UV} had a slope of 0.79 ± 0.04 (SE) (Fig. 4), not significantly different (ANCOVA F-test p > 0.05) from the slope described for the surface Indian Ocean of 0.88 ± 0.08 (García-Corral et al. 2017) and 0.61 ± 0.18 (SE) found for the global tropical and subtropical surface communities (García-Corral et al. 2017). In our study, NCP of autotrophic communities clearly tended to decrease under natural UVB radiation (i.e. NCP <
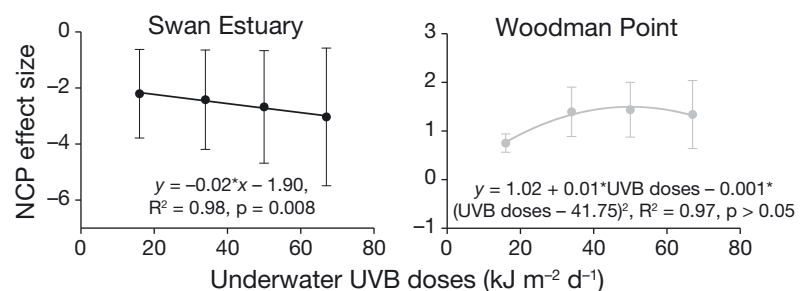

Fig. 5. Mean (± SEM) effect size ([NCP_{-UV} − NCP]/NCP_{-UV}, where NCP is net community production under UVB and photosynthetically active radiation [PAR] and NCP_{-UV} is NCP of communities exposed only to PAR) in response to the experimental gradient of increasing daily doses of UVB (from lamps) received underwater, tested on plankton communities from the Swan River Estuary and Woodman Point

NCP$_{-UV}$), whereas the NCP of heterotrophic communities tended to stay equal or a slightly higher (i.e. NCP ≥ NCP$_{-UV}$).

Overall, *in situ* communities showed, on average, a decrease of NCP by 33.4% compared to NCP$_{-UV}$. On the one hand, a decline in NCP under natural UV and autotrophic conditions could be due to a reduction in phytoplankton growth rates and biomass of UV-sensitive species (Villafañe et al. 2003), as well as changes in the abundance and community taxonomic composition (Helbling et al. 1992, Behrenfeld et al. 1993a,b, Weinbauer et al. 1997, Keller et al. 1997, Wängberg et al. 1999, Garde & Cailliau 2000, Barbieri et al. 2002, Villafañe et al. 2004, Litchman & Neale 2005). UV-induced inhibition of primary production varied from 10–30% in coastal waters (Helbling & Zagarese 2003), 5–44% in Antarctic phytoplankton assemblages (Holm-Hansen et al. 1993, Boucher & Prézelin 1996), 15–55% in the open ocean (Helbling et al. 1992, Conan et al. 2008, Li et al. 2011, Fuentes-Lema et al. 2015) and about 32–42% in the oligotrophic Mediterranean Sea (Bertoni et al. 2011). Indeed, the UV-induced inhibition of primary production might also be explainable by the cellular damage caused to the oxygen-electron transport components of photosystem II, such as D1/D2 proteins (Vass et al. 1996, Sass et al. 1997, Kataria et al. 2014) that cannot be counteracted by cellular repair (Neale et al. 2014).

On the other hand, NCP can decrease if UVR increases CR. Respiration can be enhanced through the photolysis of DOM and dissolved organic carbon, providing more bioavailable and labile carbon and nutrients for heterotrophic organisms (Moran & Zepp 1997, Zepp et al. 2007, Carrillo et al. 2015, Fuentes-Lema et al. 2015). UV exposure enhances plankton community respiration during dark hours (Agustí et al. 2014). Thus, during the night, bacterioplankton activity and growth increased, using DOM released by phytoplankton mortality induced by UVR during the day (Llabrés & Agustí 2006, Llabrés et al. 2010).

Finally, UV exposure can also reduce NCP when both processes (GPP and CR) are inhibited, albeit at a different rate, if inhibition of phytoplankton production is proportionally higher than the inhibition of bacterioplankton activity (Kaiser & Herndl 1997, Ogbebo & Ochs 2008). UVB can also reduce community respiration, as it affects the activity and functions of heterotrophic organisms such as bacterioplankton and viruses (Jeffrey et al. 1996, Huot et al. 2000, Wilhelm et al. 2003). UV can induce cellular and molecular damage (Mora et al. 2000, Sobrino et al. 2004, Llabrés & Agustí 2006, Llabrés et al. 2010),

changes in the bacterioplankton community composition (Arrieta et al. 2000), decreases in bacterial abundance and inhibition of bacterial production and respiration (Herndl et al. 1993, Müller-Niklas et al. 1995, Kaiser & Herndl 1997, Ogbebo & Ochs 2008, Bertoni et al. 2011), and generally increases mortality rates in heterotrophic marine microorganisms (Llabrés et al. 2013).

Regarding the experiments involving exposure to a UVB gradient, we observed some differences between days and places. At Woodman Point, during the first experiment (5 October), the weather was completely different from the other 2 sampled days. Therefore, the strong wind, high turbidity and vertical mixing water may have influenced the observed lower inhibition effect of UVB on NCP (Bertoni et al. 2011). On the second sampling date (12 October), the NCP showed a typical photoinhibition response curve (Jokiel & York 1984, Yamamoto 2016), where NCP increased with UVB; however, above the optimal threshold, NCP decreased. This is consistent with the repair rate of phytoplankton, which increases gradually with irradiance until a maximum is reached, and above this maximum, the chronic damage due to high irradiance cannot be counteracted by the repair rate (Neale et al. 2014). At this stage, negative effects accumulate, leading to the breakdown of cellular metabolism.

Moreover, the observed different responses between coastal and estuarine communities with respect to UVB doses are difficult to elucidate, although several effects may partially explain the differences. Firstly, differences in water turbidity or transparency are key in determining the attenuation and penetration of the radiation into the water and therefore the potential sensitivity and impact of UVB on the communities (Tedetti & Sempéré 2006). The Swan Estuary is characterized by more turbid, murky waters, and the resident communities might be acclimated to lower-light conditions and therefore could be more sensitive to increased doses of UVB (Villafañe et al. 2004, 2008, Litchman & Neale 2005). In contrast, communities of the clear waters at Woodman Point might be adapted to receive higher UVB radiation, with more efficient repair processes and less sensitivity to increased UVB doses.

Secondly, the seasonal light-history of the communities might influence the NCP response. We observed significant differences in the UVB radiation measured during the year, with higher UVB doses during spring and summer (Fig. 2). However, we performed the experiments during springtime (October) when these communities started to receive higher
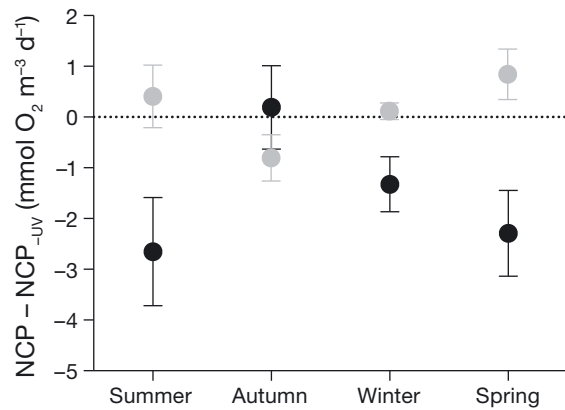
Fig. 6. Difference between mean net community production (NCP) (± SEM) under full solar radiation and when UVB was removed (NCP$_{-UV}$) by austral season for communities at the Swan River Estuary (black symbols) and Woodman Point (grey symbols)

natural UVB radiation, but they would have been exposed to very low irradiances during the previous winter and autumn (Fig. 2). Accordingly, we observed that for the *in situ* Swan Estuary communities, the strongest response (NCP – NCP$_{-UV}$) was during spring and summer (Fig. 6). The manipulated estuarine communities likely showed stronger effects of UVB on NCP than the *in situ* communities because of the light-history of the sampled communities. Therefore, if the experiments were performed in autumn after the high UVB received during spring and summer seasons, the estuarine communities might show lower or no effect of increased UVB doses on NCP. However, at the coastal Woodman Point area, NCP was differently and less affected by the experimentally increased UVB doses, and the *in situ* communities showed a similar low response, such that NCP –NCP$_{-UV}$ was close to zero across seasons (Fig. 6). Moreover, a short exposure to high UVB irradiance is more cell-damaging than a longer exposure to a lower irradiance (Cullen & Lesser 1991). Thus, a stronger effect on NCP is expected because these communities were receiving low UVB radiation during a long period (winter and autumn).

Finally, we cannot ignore the differences in trophic and community composition between ecosystems. On the one hand, the dissolved nutrient concentrations are a key environmental factor in the response to UVR (Häder 2011, Beardall et al. 2014, Cabrerizo et al. 2014). The Swan Estuary waters are nutrient-rich compared to the nutrient-limited waters of Woodman Point (Agusti et al. 2018). Nutrient-enhanced waters can counteract or unmask the inhibitory effects of solar UVR on phytoplankton photosynthesis (Carrillo et

al. 2015, Villafañe et al. 2017); however, we found stronger negative effects in the nutrient-rich estuarine waters compared to coastal waters. Indeed, under oligotrophic or low nutrient concentrations, UV can exert a negative impact on phytoplankton species, decreasing photosynthesis and quantum yield of photosystem II (Cabrerizo et al. 2014), and increasing the sensitivity of photosynthesis as a repair mechanism is less efficient (Litchman et al. 2002). On the other hand, community composition can respond differently; for example, plankton assemblages inhabiting the open ocean and clear waters can be more adapted to high UVR than the estuarine communities in darker and less transparent waters (Fritz et al. 2008, Harrison et al. 2015). Therefore, Woodman Point communities might suffer less of a negative inhibitory effect of NCP under UVR compared to the consistent pattern observed in the Swan Estuary communities.

Since the Antarctic ozone hole was described in the 1980s (Farman et al. 1985), and over the past 3 decades, the Southern Hemisphere has been receiving higher UVR than the Northern Hemisphere (Herman 2010). Thus, surface plankton communities from the Southern Hemisphere have been exposed to higher UV irradiances, and the long exposure period may have resulted in an adaptation and selection of more resistant organisms (Agustí et al. 2015). Based on our data, we postulate that plankton communities from the WA coastal communities might be photoacclimated and adapted to increased UVR, as described for similar latitudinal ranges in South Pacific waters (Montecino & Pizarro 1995). It is known that phytoplankton species have the capacity to develop photoacclimation and photoprotective strategies to UVR, by increasing pigmentation or by developing high contents of mycosporine-like amino acids, chemicals that have a high UVR-absorbing capacity and high antioxidant capacity (e.g. Navarro et al. 2014, Shang et al. 2018). In addition, strategies such as structural changes in the community composition and increases in cell aggregation that provide self-shading contribute to UVR tolerance (Navarro et al. 2008).

Overall, these observations suggest that plankton communities from WA waters are not as strongly affected by the high UVR received, compared to the stronger negative response of plankton communities over the global ocean receiving much lower UVR doses (Godoy et al. 2012, Agustí et al. 2014, García-Corral et al. 2014, 2015, 2017, Regaudie-de-Gioux et al. 2014). We observed smaller differences between NCP and NCP$_{-UV}$ than expected, given the high measured UVR. When UVB was artificially increased, we found a UV dose-dependent inhibition

of NCP in estuarine communities (i.e. higher inhibition with higher UVB doses), while NCP of the coastal communities was less affected by UVB, only occasionally showing dose-dependent inhibition.

Therefore, based on all of the above, we conclude that UVR plays an important role in biological processes, from an evolutionary perspective. In the case of marine biota in the Southern Hemisphere, exposure to high UV irradiance (Häder et al. 2007, Herman 2010) resulted in the selection of plankton communities that are more resistant and adapted to UV, compared to those from the Northern Hemisphere (García-Corral et al. 2014), as described for a variety of organisms and processes (Agustí et al. 2015). The most recent scientific assessment concluded that there is enough evidence showing the negative effects of the stratospheric ozone depletion on Southern Ocean marine ecosystems (Williamson et al. 2019, World Meteorological Organization 2019). Moreover, the ozone in the lower stratosphere between 60° S and 60° N, contrary to the upper stratospheric ozone layer, has declined since 1998 (Ball et al. 2018). Because we cannot ignore the existing threat, we believe it is essential to perform more UV-exposure experiments with natural sunlight, increase monitoring data and incorporate UV photoinhibition into models of primary production in the world's oceans (Neale & Thomas 2017) in order to understand the ultimate overall effects of UVR on marine ecosystems.

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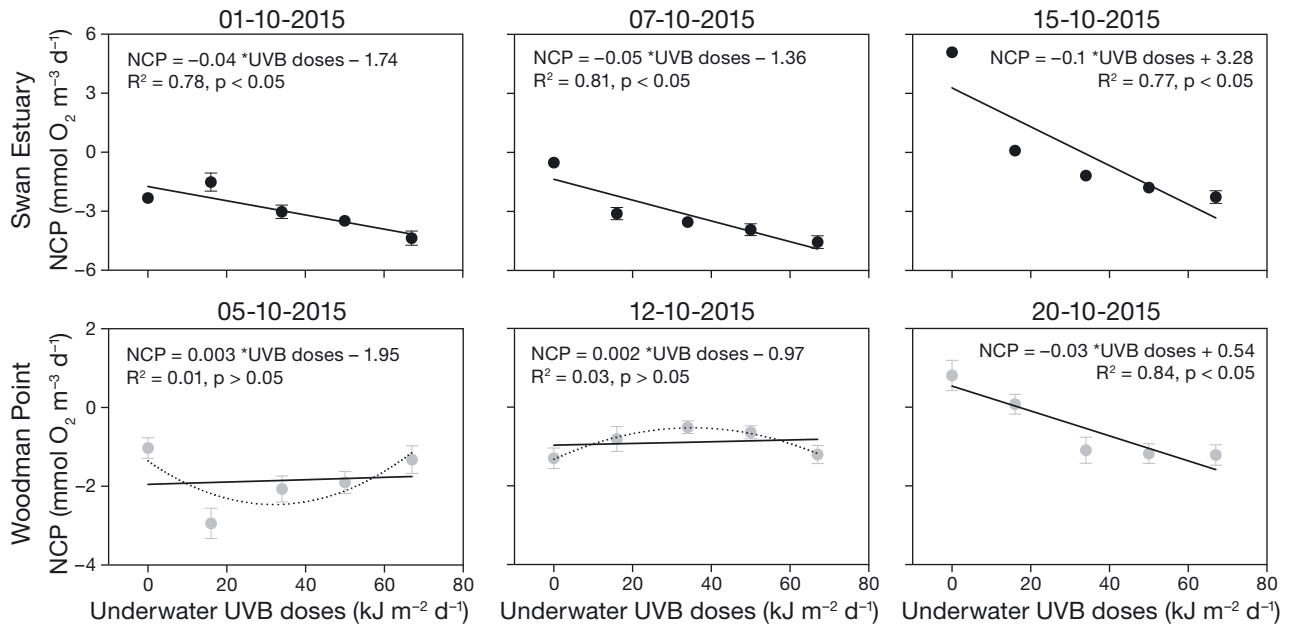
Appendix 1. Additional data

Fig. A1. Responses of net community production (NCP; mean ± SEM) to an experimental gradient of increasing underwater UVB daily doses (UVB from lamps + photosynthetically active radiation, PAR), tested on plankton communities from the Swan Estuary (black dots, upper panel) and Woodman Point (grey dots, lower panel). The solid lines indicate the fitted Type II linear regression for each experiment and the dotted curves represent the best fitting second-order polynomial regression. NCP at dose = 0 represents communities exposed only to PAR (NCP$_{-UV}$)