Ultraviolet radiation enhances Arctic net plankton community production

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Abstract In this study we report the response of net community production (NCP) of plankton communities in the Arctic surface waters exposure to natural ultraviolet radiation (UVR) conditions. A possible bias in previous measurements performed using borosilicate glass bottles (opaque to most UVR) can underestimate NCP. Here we show that 77% of the sampled communities suffer, on average, 38.5% of net increase in NCP when exposed to natural UV-B condition, relative to values when UV-B radiation is excluded. UV-B tends to shift communities toward autotrophy, with the most autotrophic communities responding the strongest. This is likely explained by the inhibition of bacterial respiration during the continuous day period of the Arctic summer, corroborated by experiments where bacterial production influenced by UV-B directly affect NCP. Whereas Arctic warming is expected to lead to lower NCP, our results show that increased UV-B radiation may partially compensate this negative effect in surface waters.

1. Introduction

The discovery of the reduction of stratospheric ozone during the austral spring over the Antarctic continent has led to efforts to assess the effects of enhanced ultraviolet radiation (UVR) in marine organisms and processes [Smith and Baker, 1989; Helbling and Zagarese, 2003; Llabrés et al., 2013]. Whereas concern was initially focused on Antarctica and the Southern Ocean, recent developments have spread concern on the possible impacts of enhanced UV-B to the Arctic. A linear declining trend of 11.0% per decade in stratospheric ozone concentration has been reported over the last two decades in the Arctic [Dahlback, 2002], with stratospheric ozone levels declining to reach in the spring of 2011, for the first time in the instrumental records, those indicative of an ozone hole [Manney et al., 2011].

Although the effect of UVR on marine Arctic organisms has been assessed for macroalgae [Karsten et al., 1999; Hanelt and Sawall, 2001; Aguilera et al., 2002; Bischof et al., 2002] or zooplankton communities [Rautio et al., 2009], efforts to examine impacts of UV-B radiation on Arctic plankton communities and processes have been limited [Wängberg et al., 2006, 2008]. With an attenuation coefficient ($K_o$) of 0.34 m$^{-1}$ for UV-B radiation during the clearest Arctic water conditions [Hanelt and Sawall, 2001], UV-B radiation can penetrate to substantial depths in the Arctic ocean, with 1% of the incident ultraviolet radiation penetrating to depths between 5 and 19 m for UV-B (at 305 nm) and down to 45 m for the UV-A band at 380 nm [Duarte, 2008]. Accordingly, UV-B radiation can have significant biological impacts on Arctic plankton communities.

Evaluation of the effects of UV-B radiation on plankton processes indicates that UV-B can affect both autotrophs and heterotrophs. UV-B has been shown to increase cell mortality rates of vulnerable phytoplankton in temperate, subtropical, and Antarctic waters [Agusti and Llabrés, 2007; Llabrés and Agustí, 2010] and reduce the potential to allocate the photosynthetic production into new biomass in Arctic communities [Wängberg et al., 2008]. A decrease in plankton primary production due to inhibition of photosynthetic processes [Cullen and Neale, 1994] by 4.9% in Antarctic waters [Holm-Hansen et al., 1993] and 2.9% for Arctic communities [Wängberg et al., 2006] has been reported under ambient UV-B natural radiation. However, UV-B radiation can also affect heterotrophic organisms as bacterioplankton and viruses [Jeffrey et al., 2000] through increased mortality rates [Llabrés et al., 2013] or cellular and molecular damage [Vincent and Neale, 2000]. For instance, UV-B has been shown to play an important role on bacterioplankton community composition [Arrieta et al., 2000], decreasing bacterial activity [Herndli et al., 1993] through...
photochemical effects on the bioavailability of dissolved organic matter \citep{Obernosterer1999} and declining bacterial abundance \citep{Muller-Niklas1995}.

Since UV-B radiation can affect both photosynthetic and heterotrophic components and processes within the plankton community, UV-B radiation can affect the net community production (NCP) of plankton communities, the balance between gross primary production and respiration. Evaluations of the impacts of UV-B radiation on plankton NCP \citep{Godoy2012} reported that exclusion of UV-B radiation led, in general, to higher NCP rates, although the opposite response was also observed. Whether UV-B radiation enhances or suppresses NCP depends on the balance between the impact on photosynthetic processes and respiration. \citet{Agusti2014} confirmed, in experiments conducted in Mediterranean, Antarctic and subtropical Atlantic communities, that NCP declined with UV-B radiation. \citet{Agusti2014} demonstrated that heterotrophic activity was suppressed by UV-B radiation, but increased during the night period to exceed, over a 24 balance, that in the absence of UV-B radiation, resulting in a net suppression of NCP by ambient levels of UV-B radiation.

Addressing the effect of UV-B radiation on the NCP of Arctic plankton communities is of particular importance because Arctic plankton is exposed to 24 h of light per day during the productive season \citep{Vaquer-Sunyer2013}, with no dark period where recovery from UV-B damage maybe possible \citep{Muller-Niklas1995, Agusti2014}, and because abrupt decline in stratospheric ozone over the Arctic \citep{Manney2011} is leading to enhanced UV-B radiation \citep{Hanelt2001, McKenzie2011, Bernhard2013}. Yet the effect of UV-B on the NCP of Arctic plankton communities has not been addressed to date. Indeed, most measurements of NCP in the Arctic and elsewhere have been conducted using borosilicate bottles, which block > 90% of irradiance up to 315 nm \citep{Godoy2012, Agusti2014}. Here we examine the effect of UV-B radiation on the net metabolism of Arctic plankton communities. We do so by experimentally examining the NCP of Arctic communities exposed to the ambient light environment and those exposed to a light field where UV-B radiation was removed.

2. Materials and Methods

Experiments were performed in three different cruises: (1) the ATOS cruise from 1 to 25 July 2007, on board the Spanish R/V Hespérides, where experiments were conducted with communities at 10 stations in the Greenland Current and the Fram Strait, reaching 80°30'N; (2) the ATP-2012; and (3) the ARCTICMET 2013 cruises, conducted on board the Norwegian R/V Helmer Hanssen from 9 to 16 June 2012 and 6 to 14 June 2013, respectively, when experiments were conducted with communities sampled at eight stations in each cruise along the Svalbard region up to 80°30'N. During ARCTICMET cruise we also performed experiments at three different stations measuring bacterial production (BP) under full solar radiation and excluding UV-B (Figure 1). Surface water samples were collected between 1 and 4 m (1.64 ± 0.15 m) depth with a Rosette sampler system fitted with a calibrated CTD Sea-Bird SBE 9 and containing twelve 6 L Niskin bottles during the ATP 2012 and ARCTICMET 2013 cruises. For the ATOS 2007, samples were taken from a 30 L Niskin bottle deployed from a Zodiac and temperature and salinity at 1 m depth were determined using a Seabird CTD 19.

Seawater was carefully siphoned into 100 cm³ calibrated Winkler bottles using a silicon tube. Seven replicates were taken and fixed immediately, to provide estimates of the initial oxygen concentration. Another set of seven replicates were dispensed into transparent narrow-mouth borosilicate glass Winkler bottles and five more samples were incubated in quartz Winkler bottles. All samples were incubated for 24 h in deck incubators under natural solar radiation conditions and with running surface seawater to maintain the in situ
temperature. After 24 h, light (glass and quartz) bottles were fixed to estimate the final O\textsubscript{2} concentrations. Oxygen concentrations were determined by automated high-precision Winkler titration [Carpenter, 1965; Carrit and Carpenter, 1966]. Measurements were performed with a Mettler Toledo, DL28 titrator in the ATOS 2007 and a Metrohm 888 Titando in the ATP 2012 and ARCTICMET 2013, and in all cruises using a potentiometric electrode and automated endpoint detection [Oudot et al., 1988]. Net community production under the full solar radiation spectrum (NCP) was calculated from the difference between the oxygen concentration in the quartz bottles, which allow the full solar radiation spectrum (UV-B + UV-A + Photosynthetically active radiation (PAR)) to penetrate in the bottles and the initial oxygen concentration after incubation ([O\textsubscript{2}] light quartz bottles / [O\textsubscript{2}] initial bottles), and net community production when UV-B radiation was excluded (NCP / [O\textsubscript{2}] initial bottles). All rates are calculated as the mean of all replicate samples as mmol O\textsubscript{2} m\textsuperscript{-3} d\textsuperscript{-1}, and standard errors were calculated using error propagation techniques.

In order to test the effect of UV-B on bacterial production, experiments were performed during the ARCTICMET 2013 cruise at three stations (Figure 1). Surface seawater (1 m) was sampled from 30 L Niskin, without filtering, in 2 L Nalgene bottles and immediately dispensed into three different incubation bottles: 100 mL quartz flasks (+UV treatment), 125 mL polycarbonate bottles (−UV treatment) and 125 mL dark bottles (DARK treatment). Experimental bottles were incubated at in situ temperature, with a running continuum system, in a tank installed on the deck of the vessel. Experiments lasted 26 h (Exp 1) and 24 h (Exp 2 and Exp 3). Incident UV radiation was measured every 10 min by solar light radiometer (PMA 2100 V).

Bacterial production (BP) measurements were done at the beginning (T\textsubscript{0}) and at the end (T\textsubscript{1}) of the incubation time for each light treatment. Bacterial production was estimated from the incorporation of \textsuperscript{3}H-labeled leucine as described by Smith and Azam [1992]. Briefly, five replicate subsamples (1.2 mL each) from each experimental bottle were collected into 2 mL centrifuge vials. Two of the replicates (blanks) were killed immediately by adding 120 μL of Trichloroacetic acid (TCA, SIGMA) to a final concentration of 50%. Subsequently, \textsuperscript{3}H-leucine (Perkin Elmer) was added to all the five subsamples to a final concentration of 40 nmol L\textsuperscript{-1} and incubated in the dark at in situ temperature for 2 h. In order to minimize isotope use, while maintaining the sensitivity of the assay, the commercial solution of \textsuperscript{3}H-leucine was diluted to a...
specific activity of 0.7 TBq mol\(^{-1}\) using unlabelled leucine. The incubation terminated by adding 120 \(\mu\)L of TCA (50% final concentration) to the remaining three live subsamples. The tubes were stored at \(-20^\circ\)C until come back to the radioactivity laboratory (facility of UiT), to proceed with the protocol. The tubes were centrifuged (12,000 rpm, 10 min), and the supernatant containing the unincorporated tracer was discarded. The pellets, containing the microbial biomass, were washed twice by sequentially adding 1 mL of 5% TCA, centrifuging (12,000 rpm, 10 min) and aspirating the supernatant. The amount of radioactivity incorporated in the samples was measured in a liquid scintillation counter (Packard Tri-Carb mod), after mixing of the samples with 1 mL of Opti-Fluor liquid scintillation cocktail (Perkin Elmer). The rates of leucine incorporation were calculated by subtracting the average radioactivity measured in the killed blanks from that measured in the living samples and dividing the resulting number by the incubation time. The net BP changes in Leu uptake calculated for the total incubation are expressed in pmols Leu L\(^{-1}\) h\(^{-1}\) ± SD.  

Chlorophyll \(a\) concentration was determined fluorometrically by filtering 200 mL of water through Whatman GF/F filters and extracted in 90% acetone for 24 h before spectrofluorometric determination using a Shimadzu RF-5301PC spectrofluorometer, following Parsons et al. [1984].

3. Results  
The communities exposed to the ambient solar radiation spectrum supported significantly higher NCP rates than those communities where UV radiation was removed (paired \(t\) test, \(t = 3.54, p = 0.0016\), Figure 2), with an NCP declining, on average (±SE), by 2.65 ± 0.93 mmol O\(_2\) m\(^{-3}\) d\(^{-1}\) (median 2.32 mmol O\(_2\) m\(^{-3}\) d\(^{-1}\)), significantly (\(t\) test, \(p < 0.05\)) different from zero, when UV-B was removed. NCP declined when UV-B was removed in 20 out of the 26 communities tested (77%) and the effect was sufficiently strong to drive four communities from autotrophic (NCP \(> 0\)) to heterotrophic (NCP \(< 0\)) when UV-B was removed (Figure 2). The effect of removing UV-B on NCP (i.e., NCP \(- NCP_{\text{UV}}\) increased with increasing NCP (\(R^2 = 0.44, p = 0.0002\)), and was, therefore, greatest for the more productive communities (Figure 3). The responses of bacterial production (BP) to the removal of UV-B radiation were consistent for the three experiments, where this was tested, with that of NCP, showing an opposite response to the corresponding NCP responses. BP decreased when NCP increased in response to removal of UV-B (Exp 1), the opposite was observed on Exp 3 and BP did not change in response to removal of UV-B where NCP showed no change either in Exp.2 (Figure 4).

4. Discussion  
Our results, based on 26 experiments conducted across different regions of the Eastern Arctic Ocean, show that UV radiation strongly affects net community production (NCP) in Arctic plankton communities. In particular, our results show that ambient UV-B radiation levels enhance net community production relative to communities where UV-B is excluded. This suggests that previous analysis have underestimated NCP in Arctic communities, as all measurements reported were derived using borosilicate bottles [e.g., Regaudie-de-Gioux and Duarte, 2010; Vaquer-Sunyer et al., 2013], which exclude UV-B radiation. This underestimation is highest at high NCP rates, typically observed in the spring [Vaquer-Sunyer et al., 2013], and corresponds to an underestimation, for surface waters, where this bias is highest of 26% (Figure 3). The impact on integrated rates is smaller, as these effects are only important in surface waters, where UV-B levels are highest.

Incubation-free methods offer alternatives to estimate NCP, particularly through the evaluation of \(O_2/Ar\) ratios, free of possible impacts on the light field [Williams et al., 2013]. Unfortunately, these methods assume...
that the photic layer is well mixed, whereas in the Arctic shallow pycnoclines resulting from freshwater released from ice melting are prevalent and render this assumption invalid [Duarte et al., 2013].

The trend for UV-B radiation to shift NCP of plankton communities toward greater net autotrophy in the Arctic is in contrast to results published for communities sampled in the SE Pacific Ocean of the Chilean Coast [Godoy et al., 2012] and in the Atlantic, Mediterranean, and Southern Ocean communities [Regaudie-de-Gioux et al., 2014; Agustí et al., 2014a] where UV-B radiation generally suppressed NCP, resulting in predominant heterotrophic communities in surface waters. Moreover, the effects of excluding UV-B radiation on NCP were also of a greater magnitude in the Arctic Ocean, with a reduction of 2.65 ± 0.93 mmol O$_2$ m$^{-3}$ d$^{-1}$, on average, when UV-B was excluded, compared to an overall mean increase of NCP by 1.1 ± 0.35 mmol O$_2$ m$^{-3}$ d$^{-1}$ when UV-B was excluded [Regaudie-de-Gioux et al., 2014].

Whereas the results reported for the Arctic Ocean appear, because of the decrease rather than increase of NCP when UV-B is excluded, in conflict with previous results [e.g., Godoy et al., 2012; Regaudie-de-Gioux et al., 2014; Agustí et al., 2014a], this finding is consistent with the analysis of the underlying mechanisms derived from the experiments reported by Agustí et al. [2014a]. In particular, Agustí et al. [2014a] report that bacterial activity is suppressed by UV-B radiation, but increases greatly in the dark following this exposure. A suppression of bacterial activity in the presence of UV-B radiation is consistent with the observed reduction in NCP of Arctic plankton communities when UV-B radiation is excluded, as in the absence of a dark period in the summer Arctic day, prevents recovery to occur. In particular, the night period has been found to be essential for repair of UV-B-induced damages, including three different dark repair mechanisms: nucleotide excision repair, postreplication recombinational repair, and error-prone repair [Zenoff et al., 2006]. The lack of a dark period when repair from UV-B damage can occur, contributes to suppress heterotrophic activity during the Arctic summer, thereby enhancing the effects of UV-B. Also, respiration and BP have been showed to be enhanced in the dark following exposure to UV-B radiation, overcompensating for the inhibition of BP when communities are exposed to the light [Agustí et al., 2014a]. Therefore, the increase in NCP under the midnight sun period is likely explained by a strong inhibition of bacterial respiration during the continuous day of the Arctic summer. Hence, both processes, UV-B bacterial activity inhibition and lack of a dark period allowing for recovery, may explain the difference, both in magnitude and direction, between the reduced NCP with UV-B removal found for Arctic communities and the increase in NCP with UV-B removal found for SE Pacific communities [Godoy et al., 2012] and Mediterranean, Atlantic, and Southern oceans [Agustí et al., 2014a; Regaudie-de-Gioux et al., 2014].

A role for bacteria activity in driving the responses observed here is supported by the consistency in the opposite responses of BP and NCP to UV-B removal observed in the three experiments conducted here, and the evidence accumulated elsewhere for impacts of UV-B radiation on bacterioplankton [Jeffrey et al., 2000] increasing mortality rates [llabrés et al., 2013], cellular and molecular damage [Vincent and Neale, 2000; Jeffrey et al., 1996], changing community composition [Arrieta et al., 2000], decreasing bacterial activity [Herndl et al., 1993] and abundance [Müller-Niklas et al., 1995]. Hence, impacts of UV-B radiation on heterotrophic processes, leading to reduced community respiration rates, can lead to increased NCP in the presence of UV-B radiation, as observed here.

On the other hand, whereas phytoplankton can be negatively impacted by UV-B radiation [e.g., Larkum and Wood, 1993; Hessen et al., 1997; Döhler, 1997], the results presented suggest that Arctic phytoplankton is more resistant to ambient UV-B doses than heterotrophs. Arctic plankton communities can contain substantial contributions from colonial Phaeocystis pouchetti, the dominant (82%) phytoplankton species in the stations sampled at the Eastern Fram Strait-Svalbard region during ATOS 2007 cruise [Lasternas and Agustí, 2010]. The colonies of these species reach 500–1000 μm in diameter and should be more resistant than single-celled species of smaller size, as the vulnerability to UV-B has been shown to be size dependent [Boelen et al., 2000]. Furthermore, Phaeocystis pouchetti colonies are characterized by a mucilage secretion that can act as a sunscreen, reflecting and preventing the penetration of UV-B radiation [Banaszak, 2003]. Moreover, Arctic phytoplankton communities often synthesize micosporine-like aminoacids [Ha et al., 2012], metabolic subproducts that absorb UV radiation and may offer a photoprotective mechanism against UV exposure by serving as a cellular-level sunscreen [Day and Neale, 2002].

The results presented here are significant beyond providing evidence that NCP may have been underestimated in the past through the use of procedures that excluded UV-B radiation. Stratospheric ozone
has been declining and a small but continuing ozone losses for at least the next two decades, [Brune et al., 1991; Austin et al., 2000] should lead to increase UV-B radiation over the Arctic. Climate change with the associated changes in tropospheric and stratospheric temperature and heat flows is now affecting stratospheric ozone dynamics [Rex et al., 2006]. Ozone depletion in the Arctic is strongly influenced by the dynamics of the polar atmosphere: changes in circulation, and particularly changes that affect air temperatures in the polar region, can have a substantial effect [Weatherhead et al., 2005]. Intense warming over the Arctic is affecting polar stratospheric ozone dynamics, leading to a steep decline and the recent development of an Arctic ozone hole, with a record stratospheric ozone depletion registered in early 2011 [Manney et al., 2011]. Hence, there is a need to examine what consequences increased UV-B radiation could have in the Arctic ecosystem, which is challenging, since the Arctic ozone hole is still smaller and more irregular than the Southern Ocean one [Dahlback, 2002; Weatherhead and Andersen, 2006]. Consequences of the Arctic ozone hole have been suggested to be high for the Arctic biota, due to the higher sensitivity to UV-B of the Northern Hemisphere marine organisms [Agustí et al., 2014b]. In addition, thinning and loss of sea ice is enhancing incoming solar radiation levels in the Arctic Ocean [Duarte et al., 2012], further enhancing the doses of UV-B radiation received by plankton communities.

In summary, the results presented here suggest that the ongoing tendency toward increasing UV-B radiation level in Arctic surface waters is expected to lead to increased NCP, thereby enhancing the CO$_2$ sink capacity of Arctic plankton communities and the production available to the food web. This is an important trend to add to the number of ongoing changes in the Arctic Ocean [Duarte et al., 2012], because NCP is a key trait, acting as a tipping element in the Arctic ecosystem that may switch the role of plankton communities between that of CO$_2$ sinks and CO$_2$ sources with climate change [Duarte et al., 2012]. Whereas warming has been shown to lead to a switch of Arctic communities from CO$_2$ sinks to CO$_2$ sources beyond a 5°C threshold [Vaquer-Sunyer et al., 2010; Holding et al., 2013], the possible effect of increased UV-B radiation had not been considered as yet. Our results suggest that enhanced UV-B radiation may partially compensate for the negative effects of warming on NCP in shallow layers, where significant levels of UV-B penetrate.