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Igor Krupnik, Michael A. Lang,
and Scott E. Miller
Editors

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Inhibition of Phytoplankton and Bacterial Productivity by Solar Radiation in the Ross Sea Polynya

Patrick J. Neale, Wade H. Jeffrey, Cristina Sobrino, J. Dean Pakulski, Jesse Phillips-Kress, Amy J. Baldwin, Linda A. Franklin, and Hae-Cheol Kim

ABSTRACT. The Ross Sea polynya is one of the most productive areas of the Southern Ocean; however, little is known about how plankton there respond to inhibitory solar exposure, particularly during the early-spring period of enhanced UVB (290–320 nm) due to ozone depletion. Responses to solar exposure of the phytoplankton and bacterial assemblages were studied aboard the research ice breaker *Nathaniel B. Palmer* during cruises NBP0409 and NBP0508. Photosynthesis and bacterial production (thymidine and leucine incorporation) were measured during in situ incubations in the upper 10 m at three stations, which were occupied before, during, and after the annual peak of a phytoplankton bloom dominated by *Phaeocystis antarctica*. Near-surface production was consistently inhibited down to 5–7 m, even when some surface ice was present. Relative inhibition of phytoplankton increased and productivity decreased with increasing severity of nutrient limitation as diagnosed using F_v/F_m, a measure of the maximum photosynthetic quantum yield. Relative inhibition of bacterial production was high for both the high-biomass and postbloom stations, but sensitivity of thymidine and leucine uptake differed between stations. These results provide the first direct evidence that solar exposure, in particular solar ultraviolet radiation, causes significant inhibition of Ross Sea productivity.

Patrick J. Neale, Jesse Phillips-Kress, and Linda A. Franklin, Smithsonian Environmental Research Center, 647 Contees Wharf Road, Edgewater, MD 21037, USA. Wade H. Jeffrey and J. Dean Pakulski, Center for Environmental Diagnostics and Bioremediation, University of West Florida, 11000 University Parkway, Building 58, Pensacola, FL 32514, USA. Cristina Sobrino, Smithsonian Environmental Research Center; now at Departamento de Ecología y Biología Animal, University of Vigo, 36310 Vigo, Spain. Amy J. Baldwin, Center for Environmental Diagnostics and Bioremediation; now at Florida Department of Environmental Protection, 160 Governmental Center, Pensacola, FL 32502-5794, USA. Hae-Cheol Kim, Smithsonian Environmental Research Center; now at Harte Research Institute for Gulf of Mexico Studies, 6300 Ocean Drive, Corpus Christi, TX 78412, USA. Corresponding author: P. Neale (nealep@si.edu). *Submitted 26 October 2007; revised 21 June 2008; accepted 28 May 2008.*

INTRODUCTION

Solar radiation, particularly that in the ultraviolet waveband (UV, 290–400 nm), affects planktonic processes in the surface layer of diverse aquatic environments (polar and elsewhere) and, in particular, the metabolism and survival of bacterioplankton, phytoplankton, and zooplankton. A subject of much recent work has been the extent to which these effects are augmented by enhanced UVB (290–320 nm) due to Antarctic ozone depletion, which is most severe during the springtime "ozone hole." UVB-induced DNA damage has been measured in a wide variety of environments and trophic levels, for example, planktonic communities from tropical (Visser et al., 1999) and subtropical waters (Jeffrey et al., 1996a, 1996b), coral reefs (Lyons et al., 1998), and the Southern Ocean (Kelley et al., 1999; Buma et al., 2001; Meador et al., 2002). DNA damage in zoo-

plankton and fish larvae has been reported in the Southern Ocean (Malloy et al., 1997) and in anchovy eggs and larvae (Vetter et al., 1999).

The UV responses of Antarctic phytoplankton have been the focus of many studies (e.g., El-Sayed et al., 1990; Holm-Hansen and Mitchell, 1990; Mitchell, 1990; Helbling et al., 1992; Lubin et al., 1992; Smith et al., 1992; Boucher and Prézelin, 1996). However, there is little quantitative information on the photosynthetic response to UV in the Ross Sea and on the responses of natural assemblages of the colonial prymnesiophyte *Phaeocystis antarctica,* despite the important contribution of the Ross Sea to overall productivity of the Southern Ocean (see Smith and Comiso, 2009, and references therein). *P. antarctica* is the dominant phytoplankter in the Ross Sea, particularly during the early-spring period of ozone depletion. At this time of year most of the Ross Sea is covered by ice, so phytoplankton growth occurs in an open water area, or polynya, located just north of the Ross Ice Shelf (for more background, see DiTullio and Dunbar, 2004). Our lack of knowledge about responses to UV is not only for *P. antarctica* but also for other phytoplankton and the associated bacterioplankton community.

Bacterioplankton abundance can reach 3×10^9 cells/L in the Ross Sea, equal to bacterial blooms in other oceanic systems. Bacterioplankton do bloom in response to the *Phaeocystis* bloom, but with a delay of one or two months after the onset of the phytoplankton bloom (Ducklow et al., 2001). DOC release by *Phaeocystis* is low, but is believed to be labile (Carlson et al., 1998) and may limit bacterial production in the upper water layer (Ducklow et al., 2001). Bacterial production in deeper waters is relatively high (Ducklow et al., 2001) and may be related to sinking *Phaeocystis* POC (DiTullio et al., 2000).

There are many other measurements to suggest that enhanced UVB and environmental UV in general have effects on organismal physiology and survival (reviewed in de Mora et al., 2000). Direct measurements of quantitative in situ effects, on the other hand, are difficult to make for most cases. However, estimates can be made using mathematical models. The quantitative response to UV exposure is characterized well enough for some processes that statements can be made about integrated effects over the water column as a function of vertical mixing in the surface layer (Neale et al., 1998; Huot et al., 2000; Kuhn et al., 2000). These model results, together with profiles of UV-specific effects like DNA damage under qualitatively different mixing conditions (Jeffrey et al., 1996b; Huot et al., 2000), argue that mixing significantly modifies water column effects (Neale et al., 2003). However, there are no instances where UV responses and vertical mixing have been quantitatively measured at the same time.

Here we present results from field work conducted in the Ross Sea polynya to assess the quantitative impact of UV on the phytoplankton and bacterioplankton communities. Both communities play a crucial role in carbon and nutrient cycling. They are also tightly coupled, so it is important to examine both communities simultaneously to understand UV impacts on the system as a whole. For example, a decrease in phytoplankton production may result in a decline in bacterial production that may be compounded by direct UVB effects on bacterioplankton. A primary physical factor controlling exposure of these communities to UV is vertical mixing. Thus, our work examined the effects of vertical mixing using a combination of field measurements and modeling approaches.

Our assessments of UV responses of Ross Sea plankton used three approaches: laboratory spectral incubations, surface (on deck) time series studies, and daylong in situ incubations. The first two approaches enable estimation of spectral response (biological weighting functions, Cullen and Neale, 1997) and kinetic response. From this information we are constructing general, time-dependent models of UV response to variable irradiance in the mixed layer. While providing less detail on specific responses, in situ incubations have the advantage of using natural irradiance regimes. However, they are not sufficient in themselves in measuring actual water column effects since they introduce the artifact of keeping samples at a constant depth throughout the day. For example, depending on the kinetics of UV inhibition, a static incubation may overestimate the response at the surface but underestimate the integrated response over the water column (Neale et al., 1998).

Nevertheless, in situ incubations still provide useful information on responses of natural plankton assemblages. They provide direct evidence that UV exposure is sufficiently high to cause some effect, in particular, inhibition of near-surface productivity. Moreover, in situ observations can be compared to predictions of laboratory-formulated models evaluated using measured irradiance at the incubation depths and thus provide an independent validation of the models.

Here we present measurements of phytoplankton productivity (^{14}C-$HCO3^-$ incorporation) and bacterial production (^3H-leucine and ^3H-thymidine incorporation) for daylong incubations conducted in the near surface (upper 10 m) of the Ross Sea polynya for three dates spanning the early-spring through summer period.

MATERIALS AND METHODS

IRRADIANCE MEASUREMENTS

Radiometers were mounted on top of a science mast (nominally 33 m above ocean surface). Photosynthetically available radiation (PAR, 400–700 nm) incident on a flat plane (2-π collector) was measured with a Biospherical Instruments (San Diego, California, USA) GUV 2511. Spectral UV irradiance was recorded with a Smithsonian-designed multifilter radiometer, the SR19, which measures between 290 and 324 nm with 2-nm bandwidth (FWHM) and resolution and at 330 nm with 10-nm bandwidth (technical description in Lantz et al., 2002). Broadband UV measurements (nominal 10 nm bandwidth) in the UV were also made by the GUV 2511. The transmission of downwelling irradiance ($E_d[\lambda]$) through the water column was measured by a free-fall, profiling radiometer, the Biospherical Instruments PUV 2500. Four to five casts were made near solar noon from 0 to 50 m, and attenuation coefficients ($k_d[\lambda]$) were computed from the regression of log($E_d[\lambda]$) versus depth. Profiles of E_d were recorded at 305, 313, 320, 340, and 395 nm (only $k_d[\lambda]$ are presented here) and for PAR.

PRODUCTIVITY ASSAYS

Sample water for the incubations was obtained with 30-L "Go-Flo" Niskin bottles (General Oceanics) mounted on a conductivity-temperature-depth (CTD) rosette. The CTD cast was made in open water at 5-m depth at approximately 0500 local time (LT) (GMT+13), ensuring minimal exposure to UV prior to incubation. The sample was immediately dispensed through wide-bore tubing and stored in the dark at 0°C until use. For photosynthesis assays, UV-transparent polyethylene sample bags (113-mL Whirl-Pak bag) were prepared by extensive rinsing with sample water. Then ^{14}C-bicarbonate was added to 700 mL of sample water (~1 μCi/mL), which was distributed into 14 sample bags in 50-mL aliquots. The unfilled portion of the bag was tightly rolled and twist sealed to prevent leakage. A second set of bags was prepared for measurements of bacterial productivity. Tritium (^{3}H) labeled thymidine (60 Ci/mmol) or ^{3}H-leucine (60 Ci/mmol) was added to 175 mL of seawater to a final concentration of 10 nM for 19 January and 21 November and 20 nM for 28 November. Five milliliters of the amended solution were added to each of three Whirl-Pak bags, as for photosynthesis, such that triplicates for each substrate were placed at each depth. After inoculation, the bags for both photosynthesis and bacterial productivity were secured with plastic ties to 25 × 25 cm "crosses" made of UV-transparent acrylic sheet (Plexiglas) (Figure 1). Each "arm" was 10 cm wide; one set of replicate photosynthesis bags was fastened to one set of opposing arms, and triplicate ^{3}H-thymidine incorporation and triplicate ^{3}H-leucine incorporation bags were attached to each of the other two arms. Crosses were kept at 0°C and in the dark until just before deployment. These Plexiglas pieces were then secured at 1-, 2-, 3-, 4-, 5-, 7.5- and 10-m depth to a weighted line which passed through the center of each cross. A primary float was attached at the surface along with a second float containing a radar reflector and a radio beacon. The array was hand deployed from the stern of the research vessel and followed for 12 h. Upon retrieval of the array, bags were quickly removed from the arms and transported to the laboratory in the dark. For photosynthesis, five replicate aliquots (5 mL) were removed from the bags and analyzed for incorporated organic ^{14}C-carbon by acidification, venting and scintillation counting. Replicate 1.5-mL samples for ^{3}H-thymidine or ^{3}H-leucine incorporation were removed from each Whirl-Pak bag and placed in 2-mL microfuge tubes containing 100 μL of 100% trichloroacetic acid (TCA). Samples were processed via the

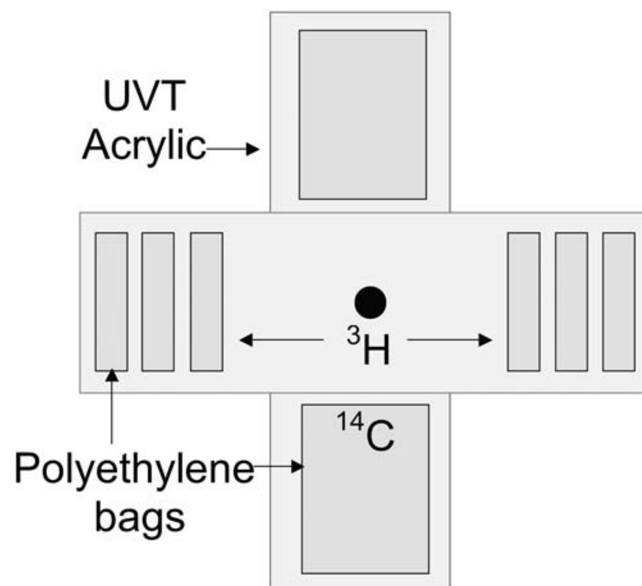

FIGURE 1. Schematic diagram of "cross" supports for the in situ array. The cross pieces are 25 cm in length. Darker shaded boxes indicate position of the UV-transparent polyethylene (Whirl-Pak) incubation bags. The center circle indicates where the support attached to the incubation line.

microcentrifugation method described by Smith and Azam (1992) as modified by Pakulski et al. (2007).

Biomass and Photosynthetic Quantum Yield

Chlorophyll concentration and bacterial cell abundance was measured on aliquots of the early-morning 5-m sample at all cruise stations (including the incubation stations). Samples for chlorophyll were concentrated on glass fiber filters (GF/F, Whatman Inc., Florham Park, New Jersey, USA) and extracted with 90% acetone overnight at 0ºC. After extraction, chlorophyll concentration was measured as the fluorescence emission in a Turner 10-AU fluorometer calibrated with pure chlorophyll *a* (Sigma Chemical, St. Louis, Missouri, USA). Bacterial abundances were determined by epifluorescence microscopy of 5–10 mL of 4′, 6-diamidino-2-phenylindole (DAPI) stained samples collected on black 0.2-μm polycarbonate filters (Porter and Feig, 1980). A pulse-amplitude-modulated fluorometer (Walz Water PAM, Effeltrich, Germany) with red LED (650 nm) excitation was used to assess the maximum photosynthetic efficiency (quantum yield) of the samples. Measurements on the 5-m sample were made after at least one hour of dark incubation at 0ºC. The data are expressed as the PSII quantum yield, $F_v/F_m = (F_m\text{-}F_0)/F_m$, which has been correlated with the maximum quantum yield of photosynthesis (Genty et al., 1989). F_0 is the steady-state yield of in vivo chlorophyll fluorescence in dark-adapted phytoplankton, and F_m is the maximum yield of fluorescence obtained from the same sample during application of a saturating light pulse (400-ms duration).

SITE DESCRIPTION

The Ross Sea polynya was sampled in two research cruises aboard the R/V *Nathaniel B. Palmer* taking place in December 2004 to January 2005 (NBP0409) and October through November 2005 (NBP0508). Overall trends in surface biomass are shown in Figure 2. During both years, this south central region of the Ross Sea supported a strong bloom of *P. antarctica* in November, peaking in early December (on the basis of Moderate Resolution Imaging Spectroradiometer (MODIS) satellite images). The bloom slowly declined through January, becoming mixed with other species, mostly diatoms. Bacterial biomass displayed a more complex pattern, with biomass peaks occurring during each of the cruise periods. Bacterioplankton

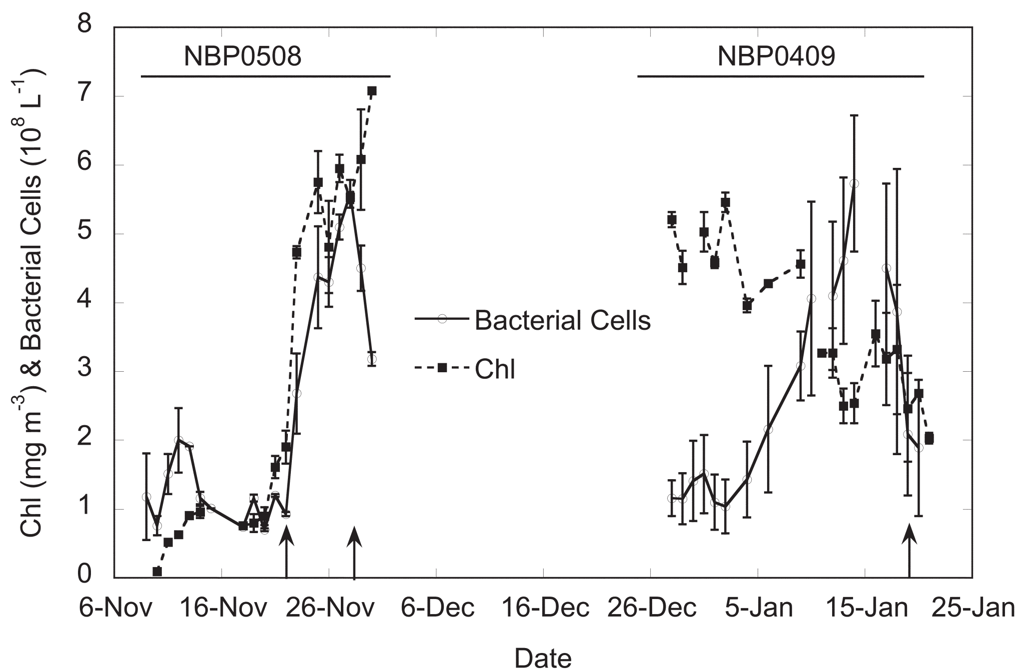

FIGURE 2. Time series of chlorophyll and bacterial cell concentration at 5 m for all stations in two cruises to the Ross Sea polynya. Bars indicate standard deviation of triplicate determinations. The two sampling periods for NBP0409 (December 2004 to January 2005) and NBP0508 (November 2005) are indicated by horizontal lines, and vertical arrows indicate dates of incubations.

are seen to increase along with the onset of the bloom followed by a second peak occurring in mid-January as the bloom receded. Our data from October–November is very similar to Ducklow et al. (2001), but this previous study and ours differ for the December–January period. We observed relatively low bacterial numbers at the end of December when the cruise began. Bacterioplankton then increased to a second peak occurring at approximately the same time as that reported by Ducklow et al. (2001) but at a maximum density of only 0.6×10^9 cells/L compared to the $\sim 2 \times 10^9$ cells/L reported in the previous study. These contrasting observations may be due to differences in specific bloom conditions between years or specific sampling locations within the Ross Sea. Deployment locations and times of the incubations are given in Table 1. During the early-spring (October–November) cruise, the surface was covered with moderate to heavy pack ice interspersed with leads until the last week in November. For the first incubation (21 November), samples were obtained and the array was deployed while the ship was in a lead. Shortly after deployment, the array became surrounded with a raft of "pancake" ice extending at least a 100 m in all directions (Figure 3), and this continued until retrieval. The 28 November and 19 January deployments were conducted in open water.

FIGURE 3. Typical surface conditions during the 21 November incubation. The surface float of the array sitting on top of the ice is approximately 75 cm in diameter.

RESULTS

Solar Irradiance

Surface UV and PAR were similar between all three days, with midday PAR in the range of 1000–1200 μmol m^{-2} s^{-1} and midday UV at 320 nm between 100 and 150 mW m^{-2} nm^{-1} (Figure 4). Transmission of UV and PAR varied between dates in inverse relation to phytoplankton biomass. Attenuation coefficients were similar for the prebloom and postbloom stations but were considerably higher in both UV and PAR for the station on 28 November near the peak of the bloom (Table 1).

Photosynthesis

All in situ profiles exhibited lowest rates at the surface and higher rates with depth, with the near-surface "photoactive" zone of inhibitory effect extending to at least 5 m on all dates (Figure 5). The 21 November profile shows an inhibitory trend over the full profile, but differences below 4 m are not significant due to high sample variability. This high variability may be associated with ice-cover-generated heterogeneity in the underwater light field. Interestingly, relative inhibition at 1 m is only 10% less than in the 28 November profile, despite the presence of ice cover on 21 November (Figure 2). On 28 November, the depth maximum in productivity was observed at 5 m, which was much shallower than the other dates. This is consistent with the relatively low transparency to both PAR and UV on this date due to high phytoplankton biomass (5.5 mg m^{-3}), mostly

TABLE 1. Background information on the three stations where in situ incubations were conducted. LT = local time.

Date (LT)	Latitude	Longitude	Chl *a* (mg m^{-3})	k_d[320] (m^{-1})	k_d PAR (m^{-1})
21 Nov 2005	−77°35.113′	178°23.435′	1.9	0.32	0.15
28 Nov 2005	−77°34.213′	−178°57.763′	5.5	0.54	0.27
19 Jan 2005	−74°30.033′	173°30.085′	2.8	0.32	0.17

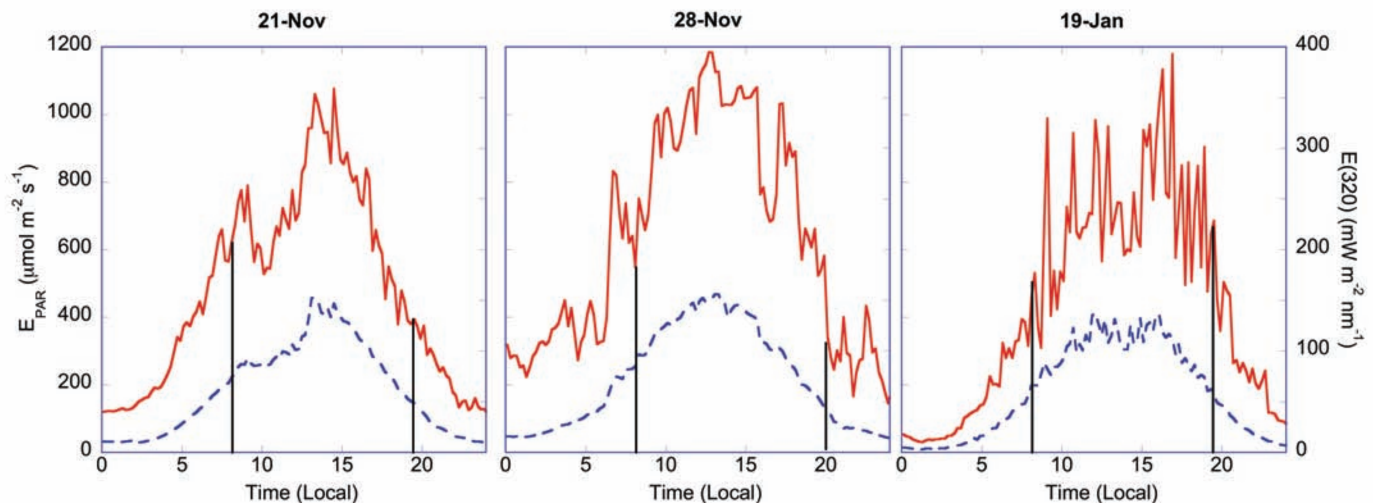

FIGURE 4. Daily variation in the surface quantum flux of photosynthetically available radiation (µmol m^{-2} s^{-1} PAR, 400–700 nm, solid line) and spectral irradiance at 320 nm (mW m^{-2} nm^{-1}, 2.0-nm bandwidth at half maximum, dashed line). Vertical lines indicate period of incubation on each date.

comprised of *P. antarctica* (data not shown). The presence of *P. antarctica* decreased not only PAR transparency because of absorbance by photosynthetic pigments but also UV transparency (Table 1). The decreased UV transparency is caused in part by the presence of UV screening pigments, the mycosporine-like amino acids, which are known to be accumulated by this species and were present in separate absorbance scans of particulates (data not shown). The 19 January incubation was at a postbloom station for which the depth of UV effects is comparable to the prebloom 21 November station and relative inhibition at 1 m was the highest of all profiles.

If the three profiles are regarded as showing the sequential development of the Ross Sea polynya bloom (despite the 19 January station being from the previous season), a couple of trends are apparent. One is the large increase in productivity associated with the high biomass on 28 November. Also, productivity was higher in the prebloom station compared to the postbloom station despite similar biomass. In other words, biomass-specific maximum productivity in the profile (P^{B}_{max}, at 5 m on 28 November and 10 m on 21 November and 19 January) was highest before the bloom and actually decreased with time (Figure 6). Parallel to this result was a decrease in the maximum quantum yield of photosynthesis as measured by PAM fluorometry (Figure 6). The most likely reason for the declining quantum yield, which has been observed previously for postbloom phytoplankton in the Ross Sea (e.g., Peloquin and Smith, 2007), is the depletion of dissolved iron, the limiting nutrient for phytoplankton growth in most areas of the Ross Sea (Smith et al., 2000). An additional factor could be the cumulative effect of recurring inhibitory solar exposure on the functioning of the photosynthetic apparatus.

Bacterioplankton Production

Similar to the pattern observed for photosynthetic rates, bacterial incorporation of either leucine or thymidine was most inhibited at the high-biomass and postbloom stations. For leucine incorporation, the lowest rates and least inhibition at 1 m were observed for the early-season sample, while the highest production rates were observed in the high-biomass sample. The pattern was similar for thymidine incorporation, although there was minimal difference between the high-biomass and postbloom samples. The pattern of dark leucine rates generally followed bacterial biomass (Figure 2), with minor variation in rates per cell (not shown). In contrast, thymidine rates remained high at the postbloom station.

DISCUSSION

The results presented here show some of the first observations of the effects of full-spectrum, near-surface solar exposure on plankton assemblages in the Ross Sea polynya from which we can already make several conclu-

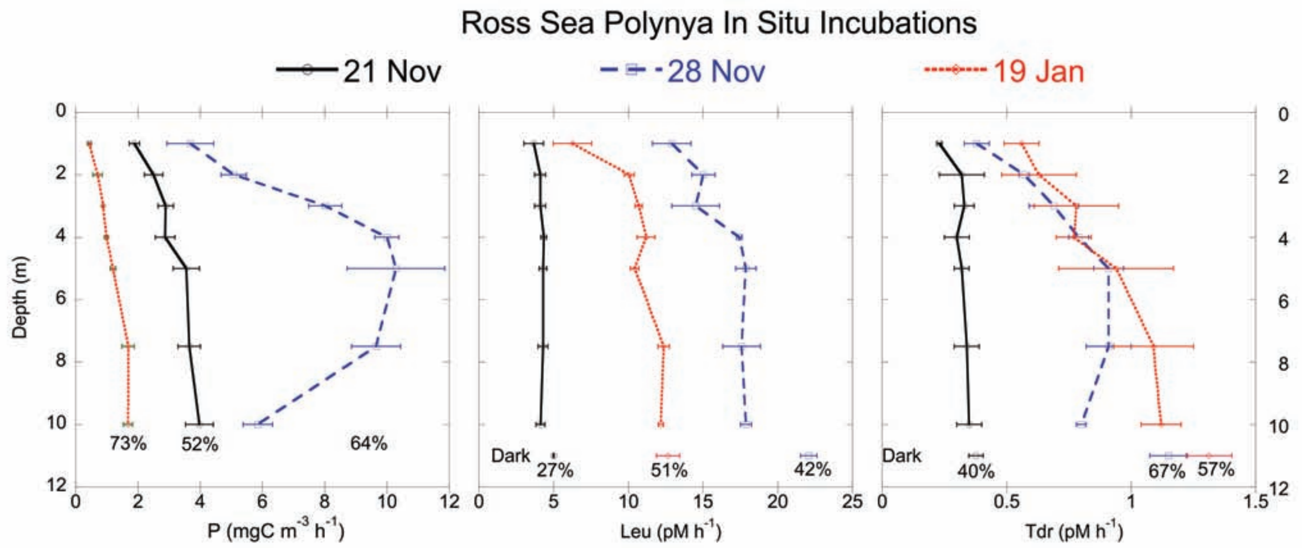

FIGURE 5. Hourly productivity rates for photosynthesis (P) and bacterial incorporation of leucine (Leu) and thymidine (Tdr) for the incubations on 21 November, 28 November, and 19 January (all in 2005). The bottom symbols for Leu and Tdr show rates for samples incubated in the dark. Horizontal bars indicate assay standard deviation (P, n = 10; Leu/Tdr, n = 6). The numbers below each profile show the percent inhibition at 1 m relative to the peak rate in the profile (photosynthesis) or rate in the dark (bacterial incorporation).

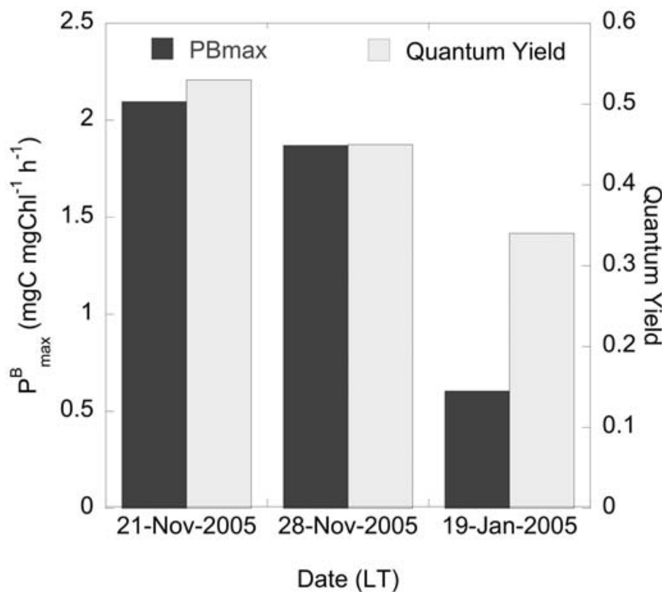

FIGURE 6. Measurements on the early-morning 5-m sample used for the in situ incubations. Maximum chlorophyll-specific rate of photosynthesis of the in situ incubation (black bars, left axis) and maximum photosynthetic quantum yield as measured with PAM fluorometry (gray bars, right axis). These are two independent approaches to indicate the relative variation in the overall photosynthetic capacity of the sampled phytoplankton assemblage.

sions. First, it is clear that incident solar exposure is sufficiently high and plankton assemblages are sufficiently sensitive that inhibition of near-surface algal and bacterial productivity is a regular occurrence during the spring–summer period in the southern Ross Sea. Photosynthesis was more strongly inhibited than bacterial productivity, such that effects on phytoplankton could even be observed below light ice cover (21 November). These effects were also observed even though UVB exposure was not significantly enhanced by ozone depletion. Although low ozone can occur throughout November in the Ross Sea region (Bernhard et al., 2006), the “ozone hole” was not present during the NBP0508 incubations.

Indeed, UV and PAR exposure in the Ross Sea polynya were not high compared to other observations in Antarctic waters (Kieber et al., 2007; Pakulski et al., 2007). Thus, the assemblages must be particularly sensitive to solar exposure in order for effects to be so pronounced despite moderate exposure levels. This conclusion is consistent with the preliminary results of our laboratory measurements of biological weighting functions for UV inhibition. These showed the highest sensitivity to UV yet recorded for Antarctic phytoplankton and modest sensitivity to UV for Ross Sea bacterioplankton (Neale et al., 2005; Jeffrey et al., 2006). They also showed that most of the inhibitory effect of near-surface irradiance on photosynthesis was

due to UV, with PAR having only a small effect. Similarly, Smith et al. (2000) did not observe significant near-surface inhibition when they measured daily in situ primary productivity in the Ross Sea using UV-opaque enclosures, although PAR inhibition was observed in on-deck incubations receiving higher than in situ irradiance. This high sensitivity to UV may be a consequence of the acclimation to low-irradiance conditions in the early-season assemblage (before iron depletion) and iron limitation during the late season. The lower sensitivity of bacterioplankton to UVR may have been related to nutrient replete conditions. Three separate experiments over the course of the sampling period during November 2005 indicated that the bacterioplankton were not nutrient (Fe, N, C) limited (data not shown). Our previous work has suggested that alleviation of nutrient limitation often reduced UVR sensitivity (Jeffrey et al., 2003). Unfortunately, no data is available for the summer 2005 samples. Bacterioplankton abundance increased as did chl *a* during this period, in contrast to the lags reported by others. Our observation may be, in part, due to the apparent replete nutrient conditions we observed. Although Ducklow et al. (2001) reported low DOC production by the *Phaeocystis* bloom, it is labile (Carlson et al., 1998) and it has been hypothesized that macronutrient depletion seldom occurs in the Ross Sea (Ducklow et al., 2001).

Results have been combined for two years; however, the time course of phytoplankton biomass in the Ross Sea for both 2004–2005 and 2005–2006 followed the normal pattern of peak biomass at the end of November (Peloquin and Smith, 2007). Although species composition shifted between the cruises, inhibition was consistently high for all profiles. In contrast, bacterial response was less consistent between the cruises. The ratio between leucine and thymidine dark uptake was >10 in November 2005 but <10 in January 2005, suggesting basic metabolic differences between assemblages. The abundance patterns during the cruises also show separate growth "events" occurring during each cruise (though some of the variation may be due to spatial differences). These observations suggest that the two cruises sampled physiologically distinct bacterial assemblages, a conclusion that is consistent with differences in sample genetic composition as determined using terminal restriction fragment length polymorphisms (TRFLP) analysis (A. Baldwin, University of West Florida, and W. H. Jeffrey, University of West Florida, personal communication).

In summary, our results provide direct evidence that in situ UV irradiance in the Ross Sea is inhibitory for both phytoplankton photosynthesis and bacterioplankton production. In terms of the magnitude of the responses observed in the incubations, these should be conservative estimates of the effects of solar exposure on in situ planktonic production. Models of UV- and PAR-dependent photosynthetic response, when evaluated for the exposure occurring at each depth in the array, predict a comparable response as observed in situ (Neale et al., 2005). In contrast, vertical profiles of fluorescence-based photosynthetic quantum yield showed that inhibited phytoplankton are found deeper in the water column than the 5-7 m depth of the photoactive zone in the incubations. This enhancement of inhibition in the water column is consistent with vertical exchange due to both Langmuir ciculation and near-surface internal waves, both of which increase the proportion of surface layer phytoplankton exposed to inhibiting irradiance. The operation of these mechanisms was confirmed by physical measurements. Detailed comparisons of production estimates using these multiple approaches will be presented in subsequent reports.

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