INTRODUCTION

Phytoplankton primary productivity in the Southern Ocean plays an important role in modulating the global climate system by taking up anthropogenic CO$_2$ and exporting it to the deep sea (Lovenduski & Gruber 2005). In particular, coastal Antarctic ecosystems are highly productive (Arrigo et al. 2008a, Vernet et al. 2008, Long et al. 2011) and strong sinks for atmospheric CO$_2$ (Arrigo et al. 2008b). Productivity in most of the coastal Antarctic is thought to be limited by iron (Fe) or co-limited by Fe and light (Sedwick &
attenuation within the water column. Light availability depends on season, cloud cover, ice cover, depth of the upper mixed layer (UML), and attenuation within the water column.

High wind speeds in the Antarctic result in deep wind-driven vertical mixing of the water column, reducing the mean light availability to phytoplankton in the UML, but exposing them to short periods of high irradiance when they are mixed up to the surface (Denman & Gargett 1983). Thus, phytoplankton cells need to adjust their photosynthetic apparatus for optimal carbon fixation while minimizing photoinhibition due to damage to photosystems induced by excessive photosynthetically active radiation (PAR) and/or ultraviolet radiation (UVR) (MacIntyre et al. 2000). Photosystem II (PS II), most notably its D1 core protein, is more sensitive to photodamage than the rest of the photosynthetic apparatus (Aro et al. 1993). Photodamaged PS II reaction centers can be repaired via degradation and synthesis of the D1 protein, although this is a metabolically expensive pathway (Aro et al. 1993, Hazzard et al. 1997).

Photoacclimation to high irradiance decreases the effects of photodamage by reducing photosynthetic pigment content, thereby preventing the overexcitation of PS II that leads to photodamage (Falkowski & LaRoche 1991). Moreover, photoprotective mechanisms that involve non-photochemical quenching ($q_N$) of excitation energy also prevent overexcitation of PS II. An important component of $q_N$ is the thermal dissipation of excess energy via the xanthophyll pigment cycle. The xanthophyll cycle consists of enzymatic de-epoxidation of carotenoids such as diadinoxanthin (DD) to diatoxanthin (DT), the latter of which thermally dissipates excess energy (Olaizola & Yamamoto 1994, Demmg-Adams & Adams 2006, Goss & Jakob 2010). Most xanthophyll de-epoxidation reverses at low irradiance on a time scale of minutes, which causes the $q_N$ to relax. Thus, $q_N$ related to xanthophyll cycling can be measured as fast-relaxing quenching ($q_E$). The $q_N$ that results from photoinhibition relaxes through repair of damaged proteins such as D1, which is a slow process on a time scale of minutes to hours. This slow-relaxing photoinhibitory quenching is measured as $q_I$ (Maxwell & Johnson 2000).

Diatoms and *Phaeocystis antarctica* (Haptophyta) are 2 groups that dominate the phytoplankton community in most of the Southern Ocean, including productive polynyas such as those in the Ross Sea and Amundsen Sea (Schoemann et al. 2005, Wright et al. 2010, Alderkamp et al. 2012a). Laboratory studies as well as field observations suggest that there are taxon-specific differences between *P. antarctica* and Antarctic diatoms in the balancing of CO$_2$ fixation and photoprotection (Kropuenske et al. 2009, Mills et al. 2010, Van de Poll et al. 2011). The photosynthetic properties of *P. antarctica* allow for efficient usage of light when grown under a variable light regime, and therefore this species is adapted to grow efficiently in areas with a deep UML (Mills et al. 2010). Conversely, Antarctic diatoms such as *Fragilariopsis cylindrus* and *Chaetoceros brevis* contain higher levels of DD + DT, resulting in higher $q_E$ and better protection from photoinhibition (Kropuenske et al. 2009, Van de Poll et al. 2011). Thus, diatoms are better adapted to grow in the high-light environment typical of shallow UMLs (Arrigo et al. 2003, Kropuenske et al. 2009, Mills et al. 2010).

There are strong interactions between Fe limitation and photoinhibition. For example, Fe limitation decreases the synthesis of photosynthetic proteins such as the D1 reaction center protein (Greene et al. 1992, Vassilev et al. 1995). On the other hand, Fe-limited cells generally contain less chlorophyll $a$ (chl $a$), which decreases the potential for absorption of excess irradiance (Greene et al. 1992, Van de Poll et al. 2003, Van Leeuwe & Stefels 2007). Moreover, Fe limitation may increase either the cellular xanthophyll cycle pigment content (Van Leeuwe & Stefels 2007) or its ratio to light-harvesting pigments (Van Leeuwe & Stefels 1998, Alderkamp et al. 2012b). Finally, Fe limitation has been shown to either increase, decrease, or have no effect on photoprotective mechanisms such as $q_N$, depending on phytoplankton species and experimental conditions (Strzepek & Harrison 2004, Allen et al. 2008, Van de Poll et al. 2009). Thus, the net effect of Fe limitation on photoinhibition is unclear.

In the present study, we characterized photoprotective and photoinhibition mechanisms of natural phytoplankton assemblages dominated by *Phaeocystis antarctica* and diatoms when exposed to excessive in situ surface irradiance in the highly productive polynya system of the Amundsen Sea. We assessed whether photoacclimation mechanisms included adjustment of photoprotective pigment composition, and whether these adjustments in turn affected the degree of $q_E$ and $q_I$ when exposed to surface irradiance. Finally, we assessed whether acclimation to low Fe concentrations impacted the mechanisms involved in photoprotection and photoinhibition.
MATERIALS AND METHODS

In situ sampling

Seawater samples were collected from 47 stations during the NBP 09-01 cruise on the RV ‘Nathaniel B. Palmer’ in the Amundsen Sea area during the austral summer from 12 January to 17 February 2009 (Fig. 1). Vertical profiles of temperature, salinity, fluorescence, irradiance, and suspended particle abundance were obtained from the water column using a SeaBird 911+ conductivity, temperature, and depth (CTD) sensor, a Chelsea fluorometer, a PAR sensor (Biospherical), and a 25 cm WET Labs transmissometer, respectively, on a cast preceding collection of water samples. Water was sampled from discrete depths in the upper 300 m of the water column with 12 l GO-FLO samplers (General Oceanics) using trace metal clean (TMC) techniques (Gerringa et al. 2012). Sampling depths were typically 10, 25, 50, 100, 200, and 300 m.

Temperature, salinity, and derived density data were binned into 1 m intervals. The attenuation of downwelling PAR in the water column ($K_d$) was calculated from each PAR profile as described in Alderkamp et al. (2012a). The depth of the UML ($z_{UML}$) was determined for each CTD profile as the shallowest depth at which the density ($\sigma_t$) was 0.02 kg m$^{-3}$ greater than at the surface. The diffuse $K_d$, $z_{UML}$, and mean incident irradiance over the previous 5 d were used to calculate the mean PAR in the UML ($E_{UML}$) as described in Alderkamp et al. (2012a). Dissolved Fe (DFe) concentrations were determined from 44 stations as described in Gerringa et al. (2012).

Pigments

Phytoplankton were collected by filtering 0.2 to 1.0 l of seawater onto GF/F filters (25 mm, Whatman) under gentle vacuum pressure. Filters for determination of chl a were extracted overnight in 90% [v/v] acetone and measured on a Turner Designs fluorometer before and after acidification (Holm-Hansen et al. 1965). Filters for determination of pigment composition by high-pressure liquid chromatography (HPLC) were immediately flash-frozen in liquid nitrogen and stored at −80°C until analysis. Chl a, chlorophyll c3 (chl c3), 19'-butanoyloxyfucoxanthin (19'-But), fucoxanthin (Fuc), 19'-hexanoyloxyfucoxanthin (19'-Hex), DD, and DT were quantified as described in Alderkamp et al. (2012a). Pigment composition derived from HPLC analysis was used to determine the phytoplankton community composition based on CHEMTAX analysis (Mackey et al. 1996, Wright et al. 1996) as described in Alderkamp et al. (2012a) and to determine the photoprotective pigment ratio of (DD + DT)/chl a.

Fluorescence parameters

The maximum photochemical efficiency of PS II ($F_v/F_m$, the ratio of variable fluorescence $F_v$ to maximum fluorescence $F_m$) was determined using a pulse-amplitude modulated (PAM) fluorometer (Water PAM, Heinz Walz) at ambient seawater temperature. Prior to analysis, the PAM was blanked with GF/F-filtered seawater from the same station. After sampling from the GO-FLO bottles, phytoplankton samples were acclimated in the dark at ambient seawater temperature for 30 min to fully oxidize the photosynthetic reaction centers and epoxidate the xantho-
phyll cycle pigments. Minimum fluorescence ($F_o$) and $F_m$ were measured on triplicate 4 ml subsamples. $F_o$ was determined using the measuring (non-photochemistry-inducing) light of the PAM, and $F_m$ was measured by applying a saturating light pulse of 4000 μmol photons m$^{-2}$ s$^{-1}$ for 0.8 ms to close all PS II reaction centers. The maximum dark-acclimated efficiency of PS II ($F_v/F_m$) was calculated as (Krause & Weis 1991):

$$F_v/F_m = \frac{F_m - F_o}{F_m}$$

(1)

**Surface irradiance exposure experiments**

The sensitivity of phytoplankton photosynthesis to various levels of in situ surface irradiance exposure (SIE) was tested as described by Alderkamp et al. (2010, 2011). Briefly, at 30 stations, phytoplankton from the surface (S) and the subsurface (D; see Table 2 for sampling depth) were exposed to near-surface irradiance (see Tables 1 & 2) for 20 min while floating in a deck incubator at in situ water temperature in 50 ml polystyrene culture flasks (Becton Dickinson). The polystyrene flasks were transparent to PAR and ultraviolet A (UVA), whereas ultraviolet B (UVB) was blocked, which was confirmed by measuring light absorption (200 to 800 nm) by the wall of the flask on a Perkin-Elmer Lambda 35 spectrophotometer. After 20 min of SIE (time $t = 20$ min), maximum ($F_m$) and minimum ($F_o$) fluorescence were determined without applying far-red illumination and compared to $F_m$ and $F_o$ measurements before SIE. The $qN$ was calculated as (Van Kooten & Snell 1990):

$$qN = 1 - \frac{F_m - F_o}{F_m - F_o}$$

(2)

The $qN$ represents the ratio of quenched to maximum variable fluorescence and can be used to compare quenching characteristics of phytoplankton with a range of variable fluorescence. The $qN$ may also be calculated as NPQ, which represents the ratio of quenched to remaining fluorescence using the Stern-Volmer equation (Krause & Weis 1991); however, NPQ may underestimate $qN$ when $F_o$ is low (Krause & Weis 1991, Maxwell & Johnson 2000, Lavaud et al. 2007). Moreover, the NPQ calculation requires a stable fluorescence baseline over the time of the measurement (110 min). In our study, variations in the baseline, due either to phytoplankton biomass near the detection limit of the PAM fluorometer (Alderkamp et al. 2010) or sample heterogeneity when colonial *Phaeocystis antarctica* was dominant, produced inconsistent values of NPQ.

Following SIE, samples were placed at low light (5 μmol photons m$^{-2}$ s$^{-1}$) under cool white fluorescent lamps at ambient seawater temperature to monitor recovery for 2 h, during which $F_v/F_m$ was measured at approximately 30 min intervals after dark acclimation for 5 min. Two treatments were tested, one with no addition of metabolic inhibitors and the other with the addition of 0.6 × 10$^{-3}$ mol l$^{-1}$ (final concentration) of lincomycin (Sigma, from a 100× stock solution freshly prepared in 96% ethanol). Lincomycin inhibits transcription of chloroplast-encoded proteins such as the D1 reaction center protein (Bouchard et al. 2005). Experiments were carried out in triplicate, and a single control sample for each treatment was not exposed but kept at ambient seawater temperature under low light (5 μmol photons m$^{-2}$ s$^{-1}$).

The short dark acclimation time for $F_v/F_m$ measurements during recovery allowed us to resolve relaxation of $qN$, so that both $qE$ and $ql$ could be determined in the treatments without lincomycin (Alderkamp et al. 2010). Briefly, measurements of $F_v/F_m$ after 30 min of recovery ($t = 50$ min to $t = 110$ min) were linearly regressed and extrapolated back to the time immediately after SIE ($t = 20$ min) to determine the value of $qN$ that would have been attained if only $ql$ had been present; $qE$ was then calculated as the difference between $qN$ and $ql$ (Maxwell & Johnson 2000, Kropuenske et al. 2009).

**Bioassays**

Fe effects on the (DD + DT)/chl $a$ ratio and quenching parameters were studied in bioassays, where Fe was added to the surface (10 m) phytoplankton community (see Table 3). Experimental details are described in Mills et al. (2012). Briefly, TMC 2 l poly-carbonate incubation bottles were randomly filled from GO-FLO bottles, Fe was added to the +Fe treatment (final concentration 4.0 nmol l$^{-1}$), while no amendments were made to the control (C) treatment. Triplicate treatments of +Fe and C were incubated at in situ water temperature in deck incubators covered with neutral density screening to reduce the light level to 20% of in situ surface irradiance. After 4 to 5 d, bottles were opened and analyzed for pigment content, and $F_v/F_m$ and quenching parameters were measured after SIE, as described in the previous section. Additional biochemical data are described in
Mills et al. (2012). Fe effects on SIE were tested by comparing +Fe and C treatments of the same bioassay, allowing us to test for Fe effects on phytoplankton with an equal light history over the 4 to 5 d of the bioassay.

**Statistics**

Means are presented ± SD. Data were checked for homoscedasticity and normality. Assumptions of homoscedasticity were always met, and data were log10 transformed when the assumption of normality was not met. Data were analyzed using 1-way ANOVA (Statistica, release 7, StatSoft) and accepted as significant at p < 0.05. Effects of sampling depth, lincomycin addition, and Fe additions on recovery after SIE were tested using repeated-measures ANOVA. Simple linear regression was used to examine the dependent relationships between measured variables.

**RESULTS**

Chl a distribution, phytoplankton community composition, Fe, and light

The Pine Island and Amundsen polynyas (PIP and AP, respectively) are bordered by a band of sea ice to the north and by ice shelves to the south, which include several major glaciers such as the Pine Island Glacier (PIG), Dotson ice shelf, Crosson ice shelf, and Getz Glacier (Fig. 1). Dense phytoplankton blooms developed in surface waters of PIP, Pine Island Bay (PIB), and AP, and are described in detail in Alderkamp et al. (2012a). The phytoplankton blooms in the polynyas consisted of high surface (upper 10 m) chl a concentrations of up to 14 μg l⁻¹ (Fig. 2A). The highest surface chl a concentration was found in the PIP and was largely restricted to the UML (Fig. 2B). Surface chl a in PIB was lower than in the PIP, but the UML was deeper (Fig. 2E), resulting in similar depth-integrated chl a biomass (Alderkamp et al. 2012a). Considerable spatial heterogeneity was observed in surface chl a of the AP, with chl a concentrations similar to the PIB. Chl a was also variable in the surrounding sea ice zone (SIZ), with mean chl a approximately half of that in the polynyas (Table 1). The lowest chl a concentrations in the SIZ were observed in the northeast region, and the highest were observed bordering the PIP and the AP. The phytoplankton community in the polynyas was consistently dominated by *Phaeocystis antarctica*, while in the SIZ, some stations were dominated by diatoms while others were either dominated by *P. antarctica* or had a mixed phytoplankton population (Fig. 1).

The phytoplankton bloom in PIB and PIP was fuelled largely by DFe input from the PIG (Gerringa et al. 2012). High DFe concentrations were observed in surface waters near the PIG (>0.43 nmol l⁻¹) and Crosson Ice Shelf (0.67 nmol l⁻¹), and lower DFe concentrations near the Dotson (0.13 nmol l⁻¹) and Getz Ice Shelves (0.12 nmol l⁻¹; Fig. 2C). Surface DFe concentrations decreased with distance from the ice shelves into the polynyas, while chl a concentrations increased (Fig. 2A,C), indicating uptake of DFe by phytoplankton. This resulted in very low DFe concentrations (<0.09 nmol l⁻¹) in surface waters of the PIP. Surface DFe concentrations in the SIZ were similar to those in the polynyas but more variable (Table 1). In general, DFe concentrations increased with depth at all locations (Fig. 2D).

Mean daily light levels in the UML (*E*<sub>UML</sub>) are calculated from incident irradiance, ice cover,

### Table 1. Mean ± SD of the depth of the upper mixed layer (UML) (*z*<sub>UML</sub>) and the daily light in the UML (*E*<sub>UML</sub>) and dissolved iron (DFe) concentration, chl a concentration, photoprotective pigment ratio (diadinoxanthin [DD] + diatoxanthin [DT])/chl a, and maximum efficiency of Photosystem II (*F*<sub>v</sub>/F<sub>m</sub>) at all stations, stations located in the Antarctic Circumpolar Current (ACC), sea ice zone (SIZ) and polynyas, and stations dominated (>50% of chl a) by diatoms, *Phaeocystis antarctica*, or mixed populations.

Means are significantly different if they are connected by the same symbol * p < 0.05, ** p < 0.01, *** p < 0.001

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th><em>z</em>&lt;sub&gt;UML&lt;/sub&gt; (m)</th>
<th><em>E</em>&lt;sub&gt;UML&lt;/sub&gt; (μmol quanta m⁻² s⁻¹)</th>
<th>DFe (nmol l⁻¹)</th>
<th>Chl a (μg l⁻¹)</th>
<th>(DD + DT)/chl a</th>
<th><em>F</em>&lt;sub&gt;v&lt;/sub&gt;/F&lt;sub&gt;m&lt;/sub&gt;</th>
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<tr>
<td>All stations</td>
<td>47</td>
<td>25.8 ± 23.9</td>
<td>120 ± 60</td>
<td>0.15 ± 0.20</td>
<td>5.0 ± 4.2</td>
<td>0.12 ± 0.05</td>
<td>0.46 ± 0.07</td>
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<td>ACC</td>
<td>1</td>
<td>37</td>
<td>111</td>
<td>0.04</td>
<td>0.36</td>
<td>0.09</td>
<td>0.30</td>
</tr>
<tr>
<td>SIZ</td>
<td>15</td>
<td>15.7 ± 6.1</td>
<td>119 ± 52</td>
<td>0.13 ± 0.09</td>
<td>3.1 ± 3.0*</td>
<td>0.13 ± 0.05</td>
<td>0.47 ± 0.07</td>
</tr>
<tr>
<td>Polynya</td>
<td>31</td>
<td>30.3 ± 28.0</td>
<td>119 ± 64</td>
<td>0.17 ± 0.23</td>
<td>6.2 ± 4.3*</td>
<td>0.11 ± 0.04</td>
<td>0.46 ± 0.07</td>
</tr>
<tr>
<td>Diatoms</td>
<td>8</td>
<td>23.3 ± 12.1</td>
<td>136 ± 53</td>
<td>0.11 ± 0.03</td>
<td>1.1 ± 1.1**</td>
<td>0.17 ± 0.06***</td>
<td>0.44 ± 0.09</td>
</tr>
<tr>
<td><em>P. antarctica</em></td>
<td>37</td>
<td>26.8 ± 26.3</td>
<td>117 ± 63</td>
<td>0.19 ± 0.24</td>
<td>6.2 ± 4.0**</td>
<td>0.11 ± 0.03***</td>
<td>0.46 ± 0.06</td>
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<tr>
<td>Mixed</td>
<td>2</td>
<td>17.5 ± 10.6</td>
<td>109 ± 26</td>
<td>0.20 ± 0.02</td>
<td>0.7 ± 0.7</td>
<td>0.11 ± 0.08</td>
<td>0.60 ± 0.04</td>
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Fig. 2. (A,B) Chl a concentration, (C,D) dissolved iron (DFe) concentration, (E) upper mixed layer (UML) depth \( z_{\text{UML}} \), and (F) mean photosynthetically active radiation (PAR) in the UML \( E_{\text{UML}} \). Characteristics are shown for (A,C) surface waters (10 m), as well as (B,D) the upper 100 m of the water column on a transect from the southwestern end of the Pine Island Glacier (PIG) to the northwest, transecting the Pine Island Bay (PIB) and Pine Island Polynya (PIP) as shown with solid line in (A).
and $z_{UML}$ and $K_d$, the latter being primarily related to phytoplankton biomass. Since all these factors showed considerable spatial variation, the mean $E_{UML}$ in our study region ranged >10-fold, from 19 to 267 μmol photons m$^{-2}$ s$^{-1}$, with a mean of 120 ± 60 μmol photons m$^{-2}$ s$^{-1}$ for all stations (Fig. 2F). In general, however, the lowest $E_{UML}$ was observed at stations with a deep $z_{UML}$ while the highest were associated with a shallow $z_{UML}$. Surprisingly, the mean $E_{UML}$ of SIZ stations was almost identical to that of polynyas at 119 μmol photons m$^{-2}$ s$^{-1}$ (Table 1), likely a consequence of high phytoplankton biomass in the polynyas reducing light penetration. Likewise, there was no difference between the mean $E_{UML}$ of Phaeocystis antarctica-dominated stations (>50% of chl $a$ attributed to $P. antarctica$) and those dominated by diatoms (Table 1).

**Xanthophyll cycle pigments and phytoplankton fluorescence**

The mean photoprotective ratio (DD + DT)/chl $a$ of phytoplankton in surface waters was 0.12 ± 0.05 (wt/wt), with ratios ranging from 0.04 to 0.27 (Fig. 3A). The (DD + DT)/chl $a$ ratio was higher at the surface than at depth, particularly below $z_{UML}$ (Fig. 3B), indicating that phytoplankton acclimated to high light at the surface by increasing their (DD + DT)/chl $a$ ratio. The surface (DD + DT)/chl $a$ ratio in the SIZ (mean 0.13 ± 0.05) was not different from that of the polynyas (mean: 0.11 ± 0.04; Table 1). However, when stations were grouped according to their dominant phytoplankton class, diatom-dominated stations had a 55% higher (DD + DT)/chl $a$ ratio (mean: 0.17 ± 0.06) than Phaeocystis antarctica-dominated stations (mean: 0.11 ± 0.03; Table 1).

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**Fig. 3.** (A,B) Photoprotective ratio of xanthophyll cycle pigments, (diadinoxanthin [DD] + diatoxanthin [DT])/chl $a$, and (C,D) maximum efficiency of Photosystem II ($F_v/F_m$), in (A,C) surface waters (10 m), as well as (B,D) the upper 100 m of the water column on the same transect as that described in Fig. 2, shown by solid line in (A)
There was a weak, yet significant, positive relation-
ship between the \( \frac{(\text{DD} + \text{DT})}{\text{chl} \ a} \) ratio of surface
phytoplankton and \( E_{\text{UML}} \) for all stations (Fig. 4A,
Table 2) with \( E_{\text{UML}} \) values ranging from 19 to 267 \( \mu \text{mol quanta m}^{-2} \text{s}^{-1} \), consistent with phytoplankton accli-
mating to higher growth irradiance by increasing
their \( \frac{(\text{DD} + \text{DT})}{\text{chl} \ a} \) ratio. When stations were
grouped according to their dominant phytoplankton
taxa, this relationship was stronger at the stations
dominated by diatoms and absent at stations domi-
nated by \( P. \text{antarctica} \) (Fig. 4A, Table 2).

There was no relationship between the \( \frac{(\text{DD} + \text{DT})}{\text{chl} \ a} \) ratio and \( \text{DFe} \) concentration when all
stations were considered together (Fig. 4B, Table 2).
At \( P. \text{antarctica} \)-dominated stations, the
relationship was weak, slightly positive, but non-
significant. The relationship at diatom-dominated
stations was stronger and negative, although also
non-significant due to the low sample size (Table 2).

The \( F_v/F_m \) of phytoplankton in surface waters averaged 0.46 ± 0.07, ranging from 0.29 at the ACC sta-
tion to 0.63 at Stn 140 in the SIZ (Fig. 3C). Generally,
\( F_v/F_m \) was higher close to the ice shelves, higher in
PIB than in the PIP, and variable in the SIZ. \( F_v/F_m \) was
lower at the surface than at depth (Fig. 3D) as a result

![Graphs showing relationships between (A,B) photoprotective ratio of xanthophyll cycle pigments, \( \frac{(\text{DD} + \text{DT})}{\text{chl} \ a} \), and (C,D) maximum efficiency of Photosystem II \( (F_v/F_m) \) in surface waters (10 m) to (A,C) mean photosynthetically
active radiation (PAR) in the upper mixed layer \( E_{\text{UML}} \) and (B,D) log of dissolved iron (DFe) concentration. \( R^2 \) of simple linear
regressions are shown; other statistics are given in Table 2]
of high surface light, consistent with the negative relationship between \( F_v/F_m \) and \( E_{UML} \) (Fig. 4C, Table 2). This relationship was similar for stations dominated by \textit{Phaeocystis antarctica} and diatoms (Table 2). Surface \( F_v/F_m \) in the SIZ (mean: 0.47 ± 0.07) was the same as that of the polynya (mean: 0.46 ± 0.07; Table 2). Moreover, the surface \( F_v/F_m \) at \textit{P. antarctica}-dominated stations (mean: 0.46 ± 0.06) was the same as that of diatom-dominated stations (mean: 0.44 ± 0.09; Table 2).

The \( F_v/F_m \) was positively related to DFe concentrations (Fig. 4D, Table 2), indicating that low DFe conditions resulted in a decrease in \( F_v/F_m \) both at stations dominated by \textit{Phaeocystis antarctica} and by diatoms (Table 2). Although the latter relationship was not significant due to the low number of samples, it nevertheless shows a steeper slope.

### SIE experiments

SIE for 20 min caused quenching of \( F_v/F_m \) (Fig. 5; Table S1 in the supplement at www.int-res.com/articles/suppl/m475p015_supp.pdf), resulting in a considerably high \( qN \) in all experiments (Fig. 6A,B; Table S1 in the supplement). The lowest \( qN \) was observed when samples were exposed to relatively low SIE (<700 μmol photons m\(^{-2}\) s\(^{-1}\)). In all experiments, the quenching relaxed during incubation under low irradiance. In 8 of the experiments, relaxation of quenching in surface samples were assessed by high temporal resolution sampling during the first 30 min (Stns 37, 94, 105, 118, 129, 135, 158, and 160; Fig. 5A,B; Table S1 in the supplement). In 3 of these experiments exposed to relatively low irradiance and with relatively low \( qN \) (Stns 105, 118, and 129), \( qE \) had relaxed after 10 min of recovery (see Fig. 5A for a typical example from Stn 105). It took longer for \( qE \) to relax in the 5 other experiments (see Fig. 5B for an example from Stn 135). However, in all 8 experiments, \( qE \) was fully relaxed by \( t = 50 \) min (20 min of exposure + 30 min of recovery used to calculate the slow relaxing quenching).

Most of the quenching was fast-relaxing during the first 30 min of recovery under low irradiance, resulting in a high \( qE \) in most experiments, especially in surface waters where \( qE \) was the major component of \( qN \) (Fig. 6E,F). At depth, however, \( qE \) was lower, and occasionally the minor component of \( qN \) (Fig. 6F).

Slowly relaxing quenching \( (qI) \) was present in most experiments (Figs. 5 & 6C,D; Table S1 in the supplement), although in surface samples, it was the minor component of \( qN \) (Fig. 6A,C). In some subsurface samples, \( qI \) was the major component of \( qN \) (Fig. 6B,D). The presence of \( qI \) suggests that some photoinhibition was incurred following SIE. Moreover, inhibiting D1 repair by the addition of lincomycin negatively affected recovery in most (87%) experiments (except Stns 13, 17, and 158; Tables 1 & 2) in both surface and deep samples, indicating that D1 repair is a basic response of these phytoplankton when exposed to excessive irradiance. In most experiments, the \( F_v/F_m \) of lincomycin-treated samples following SIE recovered to 50–60% of the untreated samples (see Fig. 5A–C,E for examples), but in some experiments, \( F_v/F_m \) in lincomycin-treated samples recovered to >90% of the untreated samples (see Fig. 5D,F for examples). There was no apparent difference between \textit{Phaeocystis antarctica}- or diatom-dominated experiments in their response to lincomycin (compare Stn 105 in the PIP dominated by \textit{P. antarctica} and Stn 135 in the sea ice dominated by diatoms; Fig. 5A,B). Recovery of lincomycin-treated samples was generally more similar to untreated samples at
relatively low SIE (see Fig. 5F for an example from Stn 133 exposed to 335 μmol photons m⁻² s⁻¹); however, in some experiments, the effect of lincomycin was small even at high SIE (see Fig. 5D for an example from Stn 7 exposed to 1991 μmol photons m⁻² s⁻¹).

**Effects of photoacclimation state on phytoplankton response to SIE**

In 17 SIE experiments, quenching characteristics of phytoplankton were collected from both the surface (S) and the subsurface (D) to study how light history impacts the response by phytoplankton to exposure to high surface light (Fig. 5C–F). Photoacclimation to higher light levels in the S sample was reflected in a higher (DD + DT)/chl a ratio in 88% of stations (except Stns 14 and 131; Table S1 in the supplement). Moreover, $F_v/F_m$ was lower in the S sample in 94% of stations (except Stn 131; Table S1 in the supplement). Out of 17 experiments, 4 experiments (24%; (Stns 7, 46, 91, and 127) exhibited a major negative effect of increased sampling depth on recovery (repeated-measures ANOVA, $p < 0.05$, Table S1 in the supplement; see Fig. 5C for a typical example at Stn 46). In 10 other experiments (59%; (Stns 11, 14, 17, 36, 99, 102, 104, 119, 131, and 140), there was a small negative effect of greater sampling depth on $F_v/F_m$ recovery (repeated measures ANOVA, $p < 0.05$), and overlap between the recovery of S and D samples was observed in the controls without lincomycin (see Fig. 5E for a typical example at Stn 104). Finally, recovery of $F_v/F_m$ was not affected by sampling depth in 3 experiments (18%; repeated-measures ANOVA, $p > 0.05$; Stns 13, 89, and 133; Table S1 in the supplement; see Fig. 5F for a typical example at Stn 133). The enhanced recovery of S samples was reflected in lower $q_I$ and higher $q_E$ (Fig. 6D,F; Table S1 in the supplement), with differences in $qN$ between S and D samples being smaller (Fig. 6B). In accordance with lower $q_I$, effects of blocking D1 repair by lincomycin addition were generally less pronounced in the S than the D samples (Fig. 5C–F).

Generally, phytoplankton community composition was vertically uniform and the percent contribution of the dominant phytoplankton group in S and D samples differed by <15%, except for Stns 17 and 133, where differences were larger. Thus, at most stations, differences in phytoplankton community composition did not affect the response to SIE. In most experiments, the D sample was taken from below $z_{UML}$, whereas in 3 experiments, both S and D
samples were collected within the UML (Stns 99, 119, and 140; Table S1 in the supplement). These experiments showed minimal effects of sampling depth, indicating that sampling depth within the UML did not affect the magnitude of the response on quenching parameters.
Controls on phytoplankton quenching parameters

The relationship between SIE, photoprotective pigment content, and phytoplankton quenching parameters was studied using the S samples of the SIE experiments (n = 30). There was a positive relationship between $q_N$ and the magnitude of SIE during the 20 min exposure (Fig. 7A, Table 3). This relationship resulted mainly from the $q_I$ component of $q_N$ (Fig. 7C, Table 3) and less so from $q_E$, which was less sensitive to incident irradiance during the SIE experiments (Fig. 7E). These results suggest that $q_E$ remains relatively constant in response to different degrees of excessive irradiance exposure. In contrast, $q_I$ increased with exposure irradiance level; however, only when SIE exceeded 1700 μmol photons m$^{-2}$ s$^{-1}$ did $q_I$ exceed $q_E$.

We could not discern any relationship between $E_{UML}$ and the quenching parameters $q_N$, $q_I$, or $q_E$ (Table 3). Thus, within the light climate to which the surface phytoplankton within the UML were acclimated, the $E_{UML}$ did not affect their quenching parameters during SIE.

Relationships between the photoprotective ratio (DD + DT)/chl a and quenching parameters were analyzed for (1) S samples only, (2) S and D samples together to include phytoplankton from below the UML that were acclimated to very low light levels and had a low (DD + DT)/chl a ratio, and (3) S and D samples exposed to high SIE (>1500 μmol photons m$^{-2}$ s$^{-1}$) to specifically address the effects of the (DD + DT)/chl a ratio on quenching parameters at high irradiance. There was no statistically significant relationship between the (DD + DT)/chl a ratio and $q_N$ for any of the experimental treatments, including the S samples alone, both S and D samples, and when S and D samples were exposed to >1500 μmol photons m$^{-2}$ s$^{-1}$ (Fig. 7B, Table 3). The relationship between the (DD + DT)/chl a ratio and $q_I$ was also non-significant for the S samples alone (Fig. 7D, Table 3). However, the relationship was stronger and slightly negative when S and D samples were analyzed together, although the $R^2$ was still rather low but significant (Fig. 7D, Table 3), indicating that the photoprotective effects of the xanthophyll cycle pigment content became apparent when considered over a wider range of (DD + DT)/chl a ratios. When SIE of the S and D samples exceeded 1500 μmol photons m$^{-2}$ s$^{-1}$, the slope of the regression between the (DD + DT)/chl a ratio and $q_I$ was more negative and had a higher coefficient of de-
Alderkamp et al.: Photoacclimation and photoinhibition (Fig. 7E, Table 3), indicating that a high (DD + DT)/chl a ratio protects against photoinhibitory quenching at high irradiance. Finally, there was a small but statistically significant positive relationship between the (DD + DT)/chl a ratio and qE when S samples were analyzed alone (Fig. 7F, Table 3). This positive relationship was stronger when both S and D samples were analyzed together and was stronger still when SIE for both S and D samples exceeded 1500 μmol photons m−2 s−1 (Fig. 7F, Table 3). These results indicate that a high (DD + DT)/chl a ratio increases the capacity for qE at high irradiance, which reduces the amount of photoinhibition (i.e. qI is lower).

Fe effects on phytoplankton responses to SIE

The +Fe and C treatments of 9 bioassays were used to study Fe effects on phytoplankton photoprotection and photoinhibition after 4 to 5 d of incubation. The full presentation of these Fe-addition bioassays and discussion of their results with respect to Fe limitation at sample locations can be found in Mills et al. (2012). In 2 out of 9 experiments, Fe additions resulted in a ~30% increase in Fv/Fm and a 35% rise in phytoplankton biomass expressed as chl a (Stn 5 in the SIZ on the shelf break and Stn 160 in the ACC) (Table 4), suggesting that phytoplankton in the C treatment were Fe-limited in their growth. Both experiments were dominated by diatoms (Table 4). Fe additions in these 2 bioassays resulted in a 35% and 18% lower (DD + DT)/chl a ratio at Stns 5 and 160, respectively. After SIE, Fv/Fm in the +Fe treatments recovered to higher values than in the C treatments (Fig. 8A). Although there were only minor effects of Fe addition on qN and qE (<10% difference), qI increased by 167% and 64% at Stns 5 and 160, respectively (Table 4). Thus, despite Fe additions resulting in recovery to higher Fv/Fm, qI was still
Table 4. Mean ± SD of triplicate samples from bioassays and mean ± SD of quenching analysis of triplicate surface irradiance exposure (SIE) experiments with control (C) and Fe addition (+Fe) treatments from the sea ice zone (SIZ), Pine Island Bay (PIB), and Amundsen Gulf (AG). Effects of Fe and of lincomycin addition before SIE exposure were tested with repeated-measures ANOVA and were significant at *p < 0.05, **p < 0.01, or ***p < 0.001. na: no CHEMTAX analysis available for phytoplankton species composition; ns: not significant.

<table>
<thead>
<tr>
<th>Stn</th>
<th>Region</th>
<th>Dominant Phytomplankton</th>
<th>Fe</th>
<th>Lincomycin (p)</th>
<th>DO+DT</th>
<th>yE</th>
<th>qN</th>
<th>yE</th>
<th>qE</th>
<th>yE</th>
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<tr>
<td>5</td>
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<td>941 ± 0.03</td>
<td>0.15</td>
<td>4.92 ± 0.14</td>
<td>941</td>
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<td>0.40 ± 0.02</td>
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<tr>
<td>10</td>
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<td>P. antarctica (0.89)</td>
<td>C</td>
<td>14.92 ± 1.44</td>
<td>0.23</td>
<td>4.98 ± 0.47</td>
<td>1099</td>
<td>0.69 ± 0.05</td>
<td>0.61 ± 0.02</td>
<td>0.08 ± 0.02</td>
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<tr>
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<td>14.92 ± 1.44</td>
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<td>4.98 ± 0.47</td>
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<tr>
<td>47</td>
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<td>4.98 ± 0.47</td>
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<td>4.98 ± 0.47</td>
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<tr>
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<td>4.92 ± 0.14</td>
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<td>4.92 ± 0.14</td>
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<td>4.92 ± 0.14</td>
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<td>0.39 ± 0.03</td>
<td>0.40 ± 0.02</td>
<td>0.06 ± 0.04</td>
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Notes:
- Samples for high-pressure liquid chromatography (HPLC) analysis were pooled because of low biomass.
- Higher in the +Fe treatments than in the C treatment due to a higher Fv/Fm at t = 0. On the other hand, the Fe-limited, diatom-dominated phytoplankton assemblages in the C treatment recovered to approximately their initial Fv/Fm after SIE exposure and showed less qE. There was no clear effect of Fe on D1 repair in the lincomycin addition treatments at either Stn 5 or 160, since lincomycin negatively affected recovery in both +Fe and C treatment (Fig. 8A).

In the other 7 experiments in the polynyas and SIZ, Fe addition resulted in a 27 ± 10% increase in Fv/Fm, with no change in chl a concentrations, indicating that phytoplankton in the C treatment were experiencing some Fe stress but not to a degree sufficient to affect biomass over the course of the experiment. These bioassays were either dominated by Phaeocystis antarctica or contained a mixed phytoplankton population (Stn 129). Additionally, Fe additions resulted in a 41 ± 13% lower (DD + DT)/chl a ratio in 5 bioassays (Table 4), with no effect in 2 others (bioassays on Stns 129 and 148; Table 4). After SIE, there were differences in the recovery of the +Fe and the C treatment in almost all experiments (except in the bioassay of Stn 129), with the Fv/Fm in the +Fe treatments increasing to values higher than in the C treatment (see Fig. 8B). Generally, both the C and Fe treatments of these mostly P. antarctica-dominated phytoplankton assemblages showed similar recovery characteristics with respect to their initial Fv/Fm values (Fig. 8B), and there was little effect on quenching parameters (Table 4). There was no effect of Fe addition on qN, except for Stn 158 (−33%). Similarly, Fe addition generally did not affect qE, except for Stns 37 (−15%) and 159 (−35%). Finally,
Fe rarely affected $q_I$, except for Stn 37 (+33%). Moreover, blocking D1 repair by lincomycin negatively affected recovery in both the C and +Fe treatments to a similar degree (see Fig. 8B for a typical example at Stn 47), suggesting that Fe did not affect the D1 repair response in Fe-stressed, *P. antarctica*-dominated phytoplankton assemblages.

**DISCUSSION**

**Photoacclimation and photoinhibition in *Phaeocystis antarctica* and diatoms**

The upper water column in the Amundsen Sea was generally not very deeply mixed, with a mean $z_{UML}$ of 26 ± 24 m over all 46 stations. However, due to the high biomass at the time of sampling, light attenuation was high, and mixing extended below the euphotic zone at almost all stations within the PIP, PIB, and the AP (Alderkamp et al. 2012a). Moreover, moderate to high wind speeds throughout the cruise period actively mixed the UML with a high turnover rate on the order of 0.5 to 2.0 h (estimated according to Denman & Gargett 1983). Thus, phytoplankton residing in the UML were subjected to a dynamic light climate that regularly exceeded 1500 μmol photons m$^{-2}$s$^{-1}$ at the surface, while $E_{UML}$ was 1 to 2 orders of magnitude lower, ranging from 22 to 267 μmol photons m$^{-2}$ s$^{-1}$. Consequently, phytoplankton in the UML needed to balance photoprotection with CO$_2$ fixation under conditions ranging from light limitation to overexposure.

Both *Phaeocystis antarctica* and diatoms used heat dissipation by xanthophyll cycling for short-term photoprotection (Olaizola & Yamamoto 1994, Lavaud et al. 2002a, Van de Poll et al. 2005, Van Leeuwe & Stefels 2007), which resulted in the relatively high $q_E$ observed in all SIE experiments. While traces of violaxanthin and alloxanthin were present in some of the northern SIZ surface (10 m) waters, DD and DT were the main xanthophyll cycle pigments that were observed throughout the Amundsen Sea. At all stations, the (DD + DT)/chl $a$ ratio was higher within the UML than below, confirming that both diatoms and *P. antarctica* increase their photoprotective/photosynthetic pigment ratio under high light in the UML. The (DD + DT)/chl $a$ ratio in surface waters of diatom-dominated stations was higher than that of *P. antarctica*-dominated stations, although there was no difference in the $E_{UML}$ between stations dominated by these 2 groups. This observation is consistent with culture studies in which the Antarctic diatoms *Fragilaropsis cylindrus* and *Chaetoceros brevis* had a higher (DD + DT)/chl $a$ ratio than *P. antarctica* grown over a range of light conditions (Kropuenske et al. 2009, Arrigo et al. 2010, Van de Poll et al. 2011). Moreover, the (DD + DT)/chl $a$ ratio in surface waters increased with the $E_{UML}$ at diatom-dominated stations but not at those dominated by *P. antarctica,* also consistent with trends in culture studies under dynamic light with different mean light levels (Kropuenske et al. 2009). Finally, culture studies showed that the chemical inhibitors preventing the conversion of DD into heat-dissipating DT resulted in a stronger increase in photoinhibition in *F. cylindrus* than in *P. antarctica* (Kropuenske et al. 2009), suggesting that xanthophyll cycling is more important for photoprotection in diatoms than in *P. antarctica*.

Culture studies further suggested that the higher (DD + DT)/chl $a$ ratios in diatoms enables them to grow at higher light levels and be less prone to photoinhibition than *Phaeocystis antarctica* (Kropuenske et al. 2009, Van de Poll et al. 2011). However, the SIE experiments in our study did not show lower $q_I$ at diatom-dominated stations, and lincomycin additions negatively affected recovery of $F_v/F_m$ at both diatom- and *P. antarctica*-dominated stations. These results indicate that there was no difference in photoinhibition between diatoms and *P. antarctica* in the UML of the Amundsen Sea. Thus, differences in photoinhibition do not seem to control the relative abundances of *P. antarctica* and diatoms at stations with a dynamic light climate. However, much higher (DD + DT)/chl $a$ ratios have been reported in diatom cultures grown at higher light levels than we encountered in our study area (Ruban et al. 2004, Van de Poll et al. 2005, 2006), suggesting that diatoms have the potential for higher $q_E$ than measured here, which would be beneficial in areas with a shallow UML and lower biomass resulting in higher $E_{UML}$.

**Effects of photoacclimation state on photoinhibition**

Photoacclimation to high light by phytoplankton within the UML generally resulted in higher (DD + DT)/chl $a$ ratios, higher $q_E$, and lower $q_I$ than phytoplankton growing at greater depths. These results are consistent with culture studies where high (DD + DT)/chl $a$ ratios for high light-acclimated phytoplankton provided a greater potential for $q_E$ and decreased $q_I$ in both diatoms and *Phaeocystis antarctica* (Lavaud et al. 2002a, Van de Poll et al. 2006, 2011). Moreover, high light-acclimated cultures
showed faster de-epoxidation of xanthophyll cycle pigments after high light exposure, resulting in greater dissipation of energy, less over-excitation of PS II, and reduced photoinhibitory quenching (Van de Poll et al. 2006). Unfortunately, de-epoxidation could not be assessed in our study since sample handling and filtration took longer than the time scale of epoxidation, which is on the order of minutes (Van de Poll et al. 2006).

The $q_I$ of surface phytoplankton was independent of $E_{\text{UML}}$, despite a 10-fold range in intensity (19 to 267 μmol photons m$^{-2}$ s$^{-1}$). Thus, the light climate in the UML of the Amundsen Sea, however variable, allowed for photoacclimation of phytoplankton such that $q_I$ was relatively minor at all stations. In contrast, phytoplankton in surface waters from pelagic stations in the Pacific and Atlantic sectors of the Southern Ocean and in the Drake Passage exhibited high $q_I$ and low $q_E$ (Alderlarmkamp et al. 2010, 2011, Petrou et al. 2011). We do not know whether these differences were related to lower $E_{\text{UML}}$ in the open-ocean studies, a different sampling season, or higher susceptibility to photoinhibition by open-ocean phytoplankton (Strzepek & Harrison 2004, Lavau et al. 2007). The only open-ocean station in our study (Stn 160) had a relatively high $E_{\text{UML}}$ and similar quenching characteristics to the polynya stations.

Even though it was a minor fraction of $q_N$, some $q_I$ was observed in most SIE experiments. Elevated $q_I$ and inhibition of $F_v/F_m$ recovery by lincomycin show that repair of D1 is a basic response by natural populations of both diatoms and Phaeocystis antarctica to excessive irradiance. A low level of repair after excessive irradiance exposure was previously observed in natural Antarctic sea-ice communities (Petrou et al. 2010) and pelagic phytoplankton communities from Palmer Stn, in response to both UVA and UVB or UVA only (Fritz et al. 2008), the latter resembling results from the SIE experiments in our study. In stations with significant $q_I$ repair resulted in recovery of $F_v/F_m$ to $\geq 90\%$ of its initial values within 90 min, thus minimizing photoinhibitory effects on CO$_2$ fixation. Rapid and continuous repair of D1 was previously reported for the green algae Dunaliella salina, whose rates of repair were proportional to growth irradiance (Kim et al. 1993). Also, when sea-ice diatoms from East Antarctic pack ice were exposed to excessive irradiance levels, the rate of D1 repair increased with increasing irradiance (Petrou et al. 2010). The rapid recovery of $F_v/F_m$ to initial values in experiments exhibiting $q_I$ suggests that D1 damage in Antarctic phytoplankton is also repaired at low irradiance when phytoplankton are mixed down in the UML after high light exposure, thereby minimizing effects of photoinhibition on CO$_2$ fixation.

Lincomycin addition negatively affected the recovery of $F_v/F_m$ in 90% of the SIE experiments, although several lincomycin-treated samples exhibited some increase in $F_v/F_m$ after $t = 50$ min, similar to what was observed in SIE experiments in the ACC (Alderlarmkamp et al. 2010, 2011). This apparent ability for some recovery may be due either to lincomycin not completely blocking D1 synthesis or to recovery mechanisms other than D1 repair. Immunochemistry blots of the D1 protein in natural phytoplankton samples treated with lincomycin showed a strong decrease in the D1 protein when compared to untreated controls (Bouchard et al. 2005), although some D1 remained present in lincomycin-treated samples, and thus complete inhibition of D1 synthesis could not be confirmed. Slow recovery of $F_v/F_m$ may also be due to slow epoxidation of DT to DD during recovery after high light exposure (Goss et al. 2006), as was reported in cultures of Antarctic diatoms Thalassiosira antarctica (Van de Poll et al. 2006) and Fragilariopsis cylindrus (Kropuenske et al. 2009). The slow recovery in lincomycin-treated samples was generally more pronounced in D samples than S samples, which corroborates results from the culture studies of Van de Poll et al. (2006), who describe slower epoxidation during recovery after high light exposure in low light-acclimated cultures than in high light-acclimated cultures. Moreover, light conditions during recovery also affect epoxidation rates (Goss et al. 2006). However, in Antarctic field samples, epoxidation was fast, and 90% of DT was converted to DD in the first 20 min of low light recovery following high light exposure (Van de Poll et al. 2011). If slow epoxidation of DT to DD affected recovery of $F_v/F_m$ in our study, not all measured $q_I$ was the result of photodamage. Thus, our estimates of $q_I$ represent an upper limit of photoinhibition in the Amundsen Sea.

In linear photosynthetic electron flow, a decrease in $F_v/F_m$ due to photoinhibition would decrease oxygen evolution and CO$_2$ fixation (Long et al. 1994), although these responses do not always covary (Suggett et al. 2009). Particularly at high light, electron flow through PS II may outperform CO$_2$ fixation (Wagner et al. 2006, Alderlarmkamp et al. 2012b), and electrons may be shuttled to alternative electron sinks or photoprotective cycling of electrons around PS II (Lavaud et al. 2002b, Feikema et al. 2006, Alderlarmkamp et al. 2012b). Therefore, at high light, the effect of a lower $F_v/F_m$ on CO$_2$ fixation may be minimal. Since $q_I$ was low in surface waters of the Amundsen Sea, effects of photoinhibition on CO$_2$ fix-
atation are likely to be even smaller. Accordingly, no photoinhibition of CO₂ fixation was apparent in photosynthesis versus irradiance curves generated for phytoplankton that were incubated at light levels up to 600 μmol photons m⁻² s⁻¹ (Alderkamp et al. 2012a).

**Effects of Fe on qN and photoinhibition**

Low Fe concentrations in the bioassays resulted in a decrease in F₆/F₅ and an increase in the photosynthetic pigment ratio (DD + DT)/chl a in all diatom- and most *Phaeocystis antarctica*-dominated experiments. An increase in the (DD + DT)/chl a ratio under Fe limitation was also observed in laboratory studies in the diatom *Chaetoceros brevis* (Van de Poll et al. 2005) and in *P. antarctica* (Van Leeuwe & Stefels 1998, 2007, Alderkamp et al. 2012b). Moreover, bioassays in the Australian Sub-Antarctic Zone (SAZ) showed an increase in the (DD + DT)/chl a ratio under Fe limitation in a mixed phytoplankton assemblage where haptophytes were the most abundant group (Petrou et al. 2011). The increase in this ratio may be due to a decrease in cellular chl a content, an increase in cellular DD + DT concentration, or both (Greene et al. 1992).

Fe limitation may affect the ratio of components of the photosynthetic apparatus, since the amount of Fe-rich components, such as cytochrome b₅f and Photosystem I (PS I), decrease more than others, such as those associated with PS II (Allen et al. 2008). As a result, lower cellular content of the Fe-rich cytochrome b₅f and PS I decreases the efficiency of electron flow downstream of PS II. Since cytochrome b₅f complexes are crucial to the build-up of the ΔpH across the thylakoid membrane that drives xanthophyll de-epoxidation, and thus heat dissipation and qE (Goss et al. 2006, Goss & Jakob 2010), Fe limitation may limit photoprotection through qE. Moreover, it has been shown that adaptations to chronic low Fe concentrations in open-ocean diatoms that have lower concentrations of the Fe-rich cytochrome b₅f and PS I reduced their potential for qN and increased their susceptibility to photoinhibition (Strzepek & Harrison 2004). However, qN was mostly unaffected by Fe in the bioassays, whereas qE was either unaffected or increased in the −Fe treatment. This suggests that either xanthophyll de-epoxidation was unaffected under most *in situ* conditions in our study, or lessened de-epoxidation was offset by a higher (DD + DT)/chl a ratio under Fe stress. The increase in qE under Fe limitation is consistent with similar observations made in culture studies of the diatoms *Phaeodactylum tricornutum* (Allen et al. 2008) and *Fragilariopsis cylindrus* (Alderkamp et al. 2012b), whereas Fe limitation did not affect qN in *Phaeocystis antarctica* (Alderkamp et al. 2012b). Moreover, the increase in qE under Fe limitation in our study corroborates increased qE in an Fe-limited bioassay with a mixed phytoplankton assemblage in the open ocean of the Australian SAZ (Petrou et al. 2011), suggesting that Fe limitation increases qE in natural phytoplankton assemblages.

Because of the decrease in downstream electron acceptors, acclimation to low Fe may result in a higher fraction of reduced PS II reaction centers that are more prone to photodamage (Greene et al. 1992). Despite this, acclimation to low Fe concentrations did not result in higher qI in either diatom-dominated or *Phaeocystis antarctica*-dominated bioassays. Nor did blocking D1 repair by lincomycin affect recovery differently in −Fe versus +Fe treatments. Rather, qI was diminished by Fe limitation in the 2 diatom-dominated bioassays, corroborating a lower qI in a Fe-limited bioassay conducted in the Australian SAZ (Petrou et al. 2011). Likely, the reduced chl a content of low Fe-acclimated phytoplankton reduced light absorption and over-excitation of PS II (Geider & LaRoche 1994, Van de Poll et al. 2005, Alderkamp et al. 2012b), thereby offsetting damaging effects of more reduced PS II components. These results are consistent with culture studies showing that photoinhibition is unaffected by Fe limitation in both *P. antarctica* and *Fragilariopsis cylindrus* (Alderkamp et al. 2012b) and lessened in *Chaetoceros brevis* (Van de Poll et al. 2005).

**CONCLUSIONS**

Results from our field study are consistent with previous culture studies showing that Antarctic diatoms and *Phaeocystis antarctica* exhibit different photoacclimation strategies. Specifically, diatoms have a higher (DD + DT)/chl a ratio that can be adjusted to reflect mean light levels in a dynamic light climate, whereas the (DD + DT)/chl a ratio was lower for *P. antarctica* and did not track light levels in a dynamic light climate (Kropuenske et al. 2009, Mills et al. 2010, Van de Poll et al. 2011). However, despite the higher (DD + DT)/chl a ratios of diatoms, qI was similar at diatom- and *P. antarctica*-dominated stations. Moreover, qI from surface samples was relatively low, even following an SIE as high as 1500 μmol quanta m⁻² s⁻¹, and effects of lincomycin addition were minor, never fully blocking recovery of
Thus, photoinhibition is generally low for both diatoms and *P. antarctica* residing in the UML of the Amundsen Sea.

The low photoinhibition in UML samples resulted from photoacclimation to the available light climate, as samples acclimated to much lower light below the UML showed lower (DD + DT)/chl a ratios and higher qL. Despite differences in photoacclimation above and below the UML, differences in *E* *UML* between various surface samples did not affect quenching characteristics of surface phytoplankton, indicating that the light climate in the UML of the study region enabled phytoplankton to photoacclimate to minimize photoinhibition. The increased qL in samples below the UML suggests photoinhibition may be more important for phytoplankton that are mixed up to the surface from below the UML during strong mixing (e.g. during high winds). Moreover, *E* *UML* may be much lower than observed in our study region when deep UMLs are combined with high light attenuation by phytoplankton blooms. These conditions have been observed in the Ross Sea Polynya, where the UML during *Phaeocystis antarctica* blooms often exceed 40 m, with phytoplankton biomass in the order of 6 to 10 µg l⁻¹ chl a (Arrigo et al. 1999, Neale et al. 2012). In addition, early in the season, during the onset of the bloom, the shorter day-length period reduces incident irradiance. The resulting low *E* *UML* under those conditions may prevent photoacclimation from minimizing photoinhibition.

Finally, we found no evidence that Fe limitation increases photoinhibition under realistic *in situ* light conditions. Although Fe limitation makes photosystems more prone to photodamage through the presence of more reduced components of the photosynthetic apparatus (Greene et al. 1992), this is likely offset by reduced excitation due to lower chl a content in combination with more photoprotection by xanthophyll pigment cycling. Thus, when phytoplankton blooms in Antarctic polynyas become Fe-limited (Sedwick & DiTullio 1997), this is not likely to increase photoinhibition.

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LITERATURE CITED

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