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**Phytoplankton community composition and photosynthetic physiology in the
Australian sector of the Southern Ocean during the austral summer of 2010/2011**

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Abstract

Phytoplankton population dynamics play an important role in biogeochemical cycles in the Southern Ocean during austral summer. However, the relationship between phytoplankton community composition and primary productivity remains elusive in this region. We investigated the community composition and photosynthetic physiology of surface phytoplankton assemblages in the Australian sector of the Southern Ocean from Dec. 2010 to Jan. 2011. There were significant latitudinal variations in hydrographic and biological parameters along 110°E and 140°E. Surface (5 m) chlorophyll *a* (chl *a*) concentrations measured with high-performance liquid chromatography (HPLC) varied between 0.18 and 0.99 mg m⁻³. The diatom contribution to the surface chl *a* biomass increased in the south, as estimated with algal chemotaxonomic pigment markers, while the contributions of haptophytes and chlorophytes decreased. In our photosynthesis-irradiance (*P-E*) curve experiment, the maximum photosynthetic rate normalized to chl *a* ($P_{\max}^*$), initial slope (α^*), the maximum quantum yield of carbon fixation ($\Phi_{c\max}$), and the photoinhibition index (β^*) were higher in the region where diatoms contributed > 50% to the chl *a* biomass. In addition, there were statistically significant correlations between the diatom contribution to the chl *a* biomass and the *P-E* parameters. These results suggested that the changes in the phytoplankton community composition, primarily in diatoms, could strongly affect photosynthetic physiology in the Australian sector of the Southern Ocean.

45   **Keywords**   Phytoplankton community composition • Photosynthetic physiology
46   • diatoms • FRe fluorometry • Southern Ocean

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Introduction

Phytoplankton primary productivity in the Southern Ocean plays an important role in the biogeochemical cycles, including the sequestration of atmospheric CO₂ (e.g., Takahashi et al. 2002; Sarmiento et al. 2004; McNeil et al. 2007). Previous field and remote sensing studies in the Southern Ocean have linked variations in primary productivity with dominant phytoplankton communities (e.g., Korb et al. 2005; Seeyave et al. 2007; Takao et al. 2012). However, it is not clear how vital the phytoplankton community composition is to controlling primary productivity in this region. Several studies have reported taxonomic differences in photosynthetic physiology among phytoplankton communities in the Southern Ocean (e.g., Claustre et al. 1997; Bracher et al. 1999). Because the Southern Ocean is one of the largest high-nutrient low-chlorophyll (HNLC) regions, the dominant phytoplankton community, photosynthetic physiology, and primary productivity could be controlled by iron availability (e.g., Martin et al. 1990; de Baar et al. 1995; Coale et al. 2004; Lance et al. 2007; Hiscock et al. 2008). In addition, phytoplankton productivity might be light-limited in the region due to the low irradiance caused by wind-induced vertical mixing, extensive cloud cover and seasonal ice (Mitchell et al. 1991; Nelson and Smith 1991). Recently, Alderkamp et al. (2010) investigated the influence of the high light part of the light cycle, which is induced by vertical mixing, on phytoplankton productivity in the Southern Ocean. This research suggests that phytoplankton growth

in the regions with mixing of deep layers could be controlled by photoinhibition incurred during the high irradiance portion of the vertical mixing cycle, rather than the by light limitation. A small number of studies have reported that the distribution of dominant phytoplankton communities, primarily diatoms and the haptophyte *Phaeocystis antarctica*, varies as a function of the mixed layer depth, i.e., light availability, in the Ross Sea (Arrigo et al. 1999; Goffart et al. 2000) and the Indian sector off East Antarctica (Wright and van den Enden 2000). In contrast, Smith and Asper (2001) reported that there were no significant correlation between the distribution of the dominant phytoplankton communities and the mixed layer depth in the Ross Sea. Furthermore, there were no differences in the photosynthetic physiology between diatoms and *P. antarctica* in the Ross Sea (van Hilst and Smith 2002). However, the relationships among the phytoplankton community, photosynthetic physiology, and primary productivity remain elusive in most of the Southern Ocean, excluding the Ross Sea.

One of the useful methods for investigating the relationships between irradiance and the photosynthetic rate of phytoplankton is a photosynthesis–irradiance ($P-E$) curve experiment (Sakshaug et al. 1997), which provides information on the physiological state of phytoplankton (Falkowski et al. 1992). In the Indian and Australian sectors of the Southern Ocean, although several studies have examined the spatiotemporal variability in phytoplankton's physiology of photosynthesis in terms of $P-E$ parameters (e.g., Hirawake et al. 2000; Strutton et al. 2000; Yoshikawa et al. 2007;

Westwood et al. 2010), notably few studies have investigated the relationship between phytoplankton community composition and photosynthetic physiology. Recently, Uitz et al. (2009) assessed the size-class-specific primary productivity in phytoplankton of the Kerguelen Islands region of the Southern Ocean. However, these researchers used physiological parameters derived from temperate and tropical oceanic regions, and those could create errors in their estimates for the Southern Ocean. Nevertheless, a good agreement between predicted and measured size-class-specific primary productivity was observed for the bloom region, while their approach failed in the HNLC region that accounts for a significant fraction of the Southern Ocean. Therefore, an extensive field data set that includes the phytoplankton taxon- and/or size-class-specific photosynthetic properties is needed to accurately assess the relationships among the dominant phytoplankton communities, photosynthetic physiology, and primary productivity in the Southern Ocean.

The objective of this study is to estimate the characteristics of phytoplankton community composition and photosynthetic physiology in the Southern Ocean during the austral summer of 2011. Initially, two fundamental questions were raised: (1) what phytoplankton community was predominant in the region in situ? and (2) were there differences among the dominant phytoplankton communities in photosynthetic physiology?

Materials and methods

Sampling and hydrographic observations

Several observations were conducted in the Australian sector of the Southern Ocean from 25 December 2010 to 19 January 2011 on board the TR/V *Umitaka-Maru* (Tokyo University of Marine Science and Technology) as part of the project on Responses of Antarctic Marine Ecosystems to global Environmental Changes with carbonate systems (RAMEEC) of the Japanese Antarctic Research Expedition (JARE). We established 23 sampling stations along 110°E and 140°E (Fig. 1). Seawater samples were collected from 5 m in depth with acid-cleaned Teflon-coated Niskin bottles attached to a CTD system (Falmouth Scientific Inc.) that measured seawater temperature and salinity. At some stations, seawater samples were collected from a continuous flow water source that drew from the bottom of the ship (approx. 5 m below the sea surface), and vertical profiles of seawater temperature and salinity were measured using a Seabird 911+ CTD sensor. The mixed layer depth at each station was determined from individual profile based on a temperature difference (ΔT) criterion. The criterion selected is a threshold value of temperature from a near-surface value at 10 m depth ($\Delta T = 0.2$ °C: de Boyer Montégut et al. 2004; Dong et al. 2008). Nutrients (nitrite plus nitrate—hereafter denoted as nitrate, phosphate and silicate) were determined in an onshore laboratory with a BRAN + LUEBBE auto-analyzer (QuAatro) following the manufacturer's protocol.

Phytoplankton pigment analysis by high-performance liquid chromatography

Seawater samples (1–2 liters) collected from the 5 m depth were filtered onto 25 mm Whatman GF/F filters under a gentle vacuum (< 0.013 MPa). The GF/F filters were blotted with filter paper as much as possible after filtration. Similarly, seawater samples (1.5–3 liters) were also filtered onto 25 mm nylon-mesh filters (20 μ m in pore size). The GF/F and nylon-mesh filters were stored in liquid nitrogen or in a deep-freezer (-80°C) until analysis on land. The frozen filter was broken into small pieces and soaked in 3 ml DMF (*N,N*-dimethylformamide) containing a known amount of canthaxanthin as an internal standard. Next, the samples were sonicated with a Branson SONIFIER Model 250 to break the cell walls. The suspension was extracted for 2 h in the dark at -20°C . The extract was filtered through 0.45 μ m PTFE filters to remove fine particles. All procedures for the extraction were conducted under subdued light to prevent the photo-degradation of the pigments. The 250- μ l extract was mixed with 250 μ l 28 mM tetrabutylammonium acetate solution (pH 6.5), and 250 μ l of the mixture was injected into a Shimadzu CLASS-VP high-performance liquid chromatography (HPLC) system with a Zorbax Eclipse XDB-C8 column (4.6 $\times$ 150 mm, 3.5 μ m particle size). A binary solvent system was employed for the HPLC pigment analysis following Van Heukelem and Thomas (2001): solvent A (methanol: 28 mM tetrabutylammonium acetate solution at pH 6.5, 70:30, v:v) and solvent B (methanol).

The flow rate was held constant at 1.2 ml min⁻¹. Pigment separation was made by the linear gradient of 5 to 95% B in 22 min followed by an isocratic hold at 95% B for 8 min. The column temperature was kept at 60°C. Chlorophylls and carotenoids were detected by absorbance using a Shimadzu photodiode array detector. The identification of pigments are detailed in Suzuki et al. (2005).

In this study, the pigment data collected from the 5 m depth were interpreted by the matrix factorization program CHEMTAX (Mackey et al. 1996) to estimate the contributions of each algal class to the total chlorophyll *a* (chl *a*) biomass determined by HPLC. For the CHEMTAX calculations, 23 pigment data were treated following the methodology in Latasa (2007), with several seed values. The accessory pigment to chl *a* ratios in Table 1 are based on the initial pigment ratios of Wright et al. (1996). A dominant phytoplankton community was defined as having more than 50% contributions to chl *a* biomass.

Flow cytometry

Duplicate seawater samples (2 ml) from the surface were preserved with paraformaldehyde (0.2% final concentration), snap-frozen in liquid nitrogen, and stored in a deep-freezer at -80°C until analysis on land. An EPICS flow cytometer (XL ADC system, Beckman Coulter) equipped with a 15 mW air-cooled laser exciting at 488 nm and the standard filter setup was used to enumerate ultraphytoplankton (< 5 µm in size).

Prior to analysis, samples were thawed and then drawn through 35 μm nylon-mesh-capped Falcon cell strainer (Becton-Dickinson) to remove larger cells. For the enumeration of ultraphytoplankton, a known volume of Flow-Count fluorospheres (Beckman Coulter) and 2.0 μm Fluoresbrite YG beads (Poly Sciences) were added to each sample. The details of flow cytometric analysis are described in Suzuki et al. (2005).

Photosynthesis–irradiance (P – E) curve experiment

Seawater samples were dispensed into a set of ten 275 mL acid-cleaned polystyrene bottles, and all of the bottles were inoculated with a solution of $\text{NaH}^{13}\text{CO}_3$ (99 atom% ^{13}C , Shoko Co., Ltd.), which was equivalent to approximately 10% of dissolved inorganic carbon (DIC) in the seawater. Incubations were carried out for 2 h at 10 irradiance levels from approximately 10 to 2260 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ in a bench-top incubator. The incubator was cooled to surface seawater temperature with a temperature-controlled water circulator. The details of incubation and sample analysis were described in Isada et al. (2009). In this study, however, to determine the particulate organic carbon (POC) and the ^{13}C abundance of the sample, a mass spectrometer (DELTA V Plus, Thermo Fisher Scientific Inc.) with an in-line elemental analyzer (Flash EA1112, Thermo Fisher Scientific Inc.) was used. The amount of DIC in seawater was determined with a coulometer (Model 5012, UIC) following the

methodology in DOE (1994). Photosynthetic rates were determined following the method of Hama et al. (1983) and normalized to the chl *a* concentration measured with HPLC (see above). Photosynthesis–irradiance (*P*–*E*) parameters were obtained from the photoinhibition model of Platt et al. (1980) as follows:

$$P^* = P_s^* [1 - \exp(-\alpha^* \cdot E / P_s^*)] \cdot \exp(-\beta^* \cdot E / P_s^*) \quad (1)$$

$$P_{max}^* = P_s^* \cdot [\alpha^* / (\alpha^* + \beta^*)] \cdot [\beta^* / (\alpha^* + \beta^*)]^{\beta^* / \alpha^*} \quad (2)$$

where subscription * denotes a normalized chl *a* concentration, P^* [mg C (mg chl *a*)⁻¹ h⁻¹] is the observed photosynthetic rate, P_s^* [mg C (mg chl *a*)⁻¹ h⁻¹] is the theoretical maximum photosynthetic rate with no photoinhibition (i.e., $\beta^* = 0$), α^* { [mg C (mg chl *a*)⁻¹ h⁻¹] (μmol photons m⁻² s⁻¹)⁻¹ } is the initial slope, E (μmol photons m⁻² s⁻¹) is the irradiance, β^* { [mg C (mg chl *a*)⁻¹ h⁻¹] (μmol photons m⁻² s⁻¹)⁻¹ } is the photoinhibition index, and P_{max}^* [mg C (mg chl *a*)⁻¹ h⁻¹] is the maximum photosynthetic rate. The light saturation index, E_k , is defined by P_{max}^* and α^* (i.e., $E_k = P_{max}^* / \alpha^*$).

The maximum quantum yield of carbon fixation ($\Phi_{c \max}$, mol C mol photons⁻¹) was derived from the following equation:

$$\Phi_{c \max} = 0.0231 \alpha^* / \bar{a}_\phi^* \quad (3)$$

where 0.0231 converts milligrams of carbon on moles, μmol photons to moles, and hours to seconds, and $\bar{a}_\phi^*$ is the mean chl *a*-specific absorption coefficient of phytoplankton (see below). The chl *a*-specific absorption spectra of phytoplankton, $a_\phi^*(\lambda)$, were measured using the glass fiber technique of Kishino et al. (1985). The optical density (OD) of all particles on the filter was measured between 350 and 750 nm

with 1 nm intervals using a MPS-2450 spectrophotometer (Shimadzu). A blank filter wetted with filtered seawater was used as a reference (Suzuki et al. 1998). The OD at 750 nm was subtracted from all wavelengths as a scattering correction assuming the lack of the absorption at 750 nm. The filter was subsequently soaked in methanol to extract phytoplankton pigments (Kishino et al. 1985), and the OD of non-algal particles (NAPs) was re-measured with the same manner as the OD of all particles mentioned above. The absorption coefficient of all of the suspended particles and NAPs were corrected for the path length amplification on the glass fiber filters using the equation in Cleveland and Weidemann (1993). The absorption coefficient of phytoplankton, $a_{\phi}(\lambda)$, was calculated as the difference between the values before and after pigment extraction. The mean chl a -specific absorption coefficient of phytoplankton, $\bar{a}_{\phi}^*$, was weighted with the spectral irradiance of an incubator lamp from 400 to 700 nm to correct for the spectral characteristics of an incubator lamp source (Cota et al. 1994):

$$\bar{a}_{\phi}^* = \int_{400}^{700} a_{\phi}^*(\lambda) \cdot E_{NL}(\lambda) d\lambda / \int_{400}^{700} E_{NL}(\lambda) d\lambda \quad (4)$$

where $E_{NL}(\lambda)$ is the normalized spectral irradiance of an incubator lamp and was estimated as follows:

$$E_{NL}(\lambda) = E_L(\lambda) / \int_{\lambda} E_L(\lambda) d\lambda \quad (5)$$

where $E_L(\lambda)$ is an incubator's lamp spectrum.

Fluorescence induction and relaxation (FIRE) fluorometry

Seawater samples were collected from the same seawater as the phytoplankton pigment samples. To open the reaction centers, the sample was acclimated in the dark for at least 30 min in an incubator, which was adjusted to the in situ seawater temperature. Variable fluorescence of phytoplankton was measured with a Fluorescence Induction and Relaxation (FIRE) fluorometer (Satlantic Inc.) in a dark room (Gorbunov et al. 1999). The FIRE fluorometer was equipped with blue (455 nm with 60 nm bandwidth) and green (540 nm with 60 nm bandwidth) light-emitted diodes (LED). The FIRE protocol involved a strong flash of saturating blue and green that initiated a rise in fluorescence in vivo from the initial value (F_0) to the maximum value (F_m) in a strong short pulse of 80 μ s duration (i.e., single-turnover flash). This change in fluorescence ($F_v = F_m - F_0$) is associated with absorption and utilization energy in photosynthesis and is normalized to F_m to deduce the photochemical quantum efficiency (F_v/F_m) of phytoplankton photosystem II (Kolber et al. 1988). The functional absorption cross-section of photosystem II (σ_{PSII} , $\times 10^{-20}$ m² quanta⁻¹) is derived from the slope where fluorescence increases from F_0 to F_m against the cumulated light energy provided with the fluorometer. Although the photosystem II action spectrum for cyanobacteria is typically much lower in blue light than in green one (e.g., Suggett et al. 2009), cyanobacteria were present in relatively low abundances in this study area (e.g., Marchant et al. 1987; Odate and Fukuchi 1995; Zubkov et al. 1998; Fouilland et al. 1999). Thus, only the blue (i.e., 455 nm) saturating light was used in this study. Triplicate samples were measured with up to 50 iterations per sample. For all analyses,

a 0.45- μm filtered seawater sample was used as a blank. The fluorescence data were processed with the MATLAB-based program fireworx developed by Audrey Barnett (Dalhousie Univ.) to obtain F_v/F_m and σ_{PSII} values.

Light microscopy

Seawater samples (500 ml) collected from the surface were preserved with 4% Lugol's iodine solution. The samples were concentrated using Utermöhl chambers (HYDRO-BIOS Apparatebau GmbH) and analyzed with an inverted microscope (BIOREVO BZ-9000, Keyence). Phytoplankton cells were identified following Tomas (1997) and Scott and Marchant (2005).

Light availability

At 10 out of 23 stations, the underwater downwelling irradiance, $E_d(\lambda, z)$, was obtained using a PRR-800 spectroradiometer (Biospherical Instruments Inc.) with a reference of PRR-810, which monitored the incident irradiance just above the sea surface. The PRR-800 has 17 wavelengths between 380 and 765 nm and was deployed on the sunny side of the ship to minimize its shadow. The value of $E_d(\lambda, z)$ at just below the sea surface was obtained by extrapolation of logarithm-transformed data from 1 to 4 m. Photosynthetic active radiation (PAR) was calculated at each depth, integrating $E_d(\lambda,$

z) over 400–700 nm. The attenuation of PAR in a water column, K_d (PAR), was determined as the slope of least-squares regression fit to logarithm-transformed E_d (PAR) as a function of depth. If PRR-800 data were unavailable, K_d (PAR) was estimated using an empirical relationship between in situ K_d (PAR) and surface fluorometric-derived chl *a* concentrations in the Southern Ocean (Venables and Moore, 2010):

$$K_d(\text{PAR}) = 0.05 + 0.057 \text{ chl } a (\text{fluorometry})^{0.58} \quad (6)$$

where chl *a* (fluorometry) is chl *a* concentration at 5 m depth as derived using the non-acidification method of Welschmeyer (1994). K_d (PAR) was used to calculate euphotic depth and total daily PAR in the upper mixed layer as described in Alderkamp et al. (2010). In this study, however, to estimate total daily surface PAR, the moderate-resolution imaging spectroradiometer (MODIS)/Aqua 8-day composite images (9 km resolution) of the Distributed Active Archive Center (DAAC)/Goddard Space Flight Center (GSFC), NASA were used.

Satellite data processing

To investigate the temporal and spatial changes in chl *a* concentration before and after our cruise, the distributions of chl *a* concentration as determined from MODIS/Aqua 8-day composite images for the period from August 2010 to March 2011 were used. To maximize available data, we averaged the each 8-day composite image

with 3×3 pixels (i.e., $27 \text{ km} \times 27 \text{ km}$) resolution.

Results

Hydrography and phytoplankton abundance

Hydrographic conditions at each station during the cruise are listed in Table 2.

Along the 110°E transect, the sea surface temperature (SST) and salinity (SSS) tended to decrease in the south and ranged from 1.3 to 15.9°C and from 33.3 to 35.3 , respectively. Surface macronutrient (nitrate, phosphate, and silicate) levels also tended to increase toward the south. Although surface nitrate and phosphate were present along the 110°E transect, surface silicate was depleted between Stations (Stn.) C01 and C02 ($< 0.17 \mu\text{mol L}^{-1}$) (Fig. 1 and Table 2). However, an ample amount of silicate ($> 20 \mu\text{mol L}^{-1}$) remained at stations south of Stn. C04 (55°S) as did the other macronutrients. Along the 140°E transect, SST decreased toward south (0.7 – 10.0°C) as with the 110°E transect. Although SSS, nitrate, and phosphate were relatively constant, silicate drastically decreased between Stns. D12 and D13 (i.e., from 20.6 to $3.0 \mu\text{mol L}^{-1}$). In the results of Wilcoxon rank sum test, no significant difference in hydrographic conditions was observed between the two transects during the cruise (SST: $p = 0.15$, SSS: $p = 0.10$, nitrate: $p = 0.08$, phosphate: $p = 0.12$, silicate: $p = 0.57$).

In both transects, there were relatively high abundances of *Synechococcus*

measured with the flow cytometry only at Stns. C01 and S02 ($> 20.0 \times 10^3$ cells ml^{-1}) (Fig. 1 and Table 2). Except at those stations, *Synechococcus* concentrations were relatively low ($< 3.0 \times 10^3$ cells ml^{-1}). The surface chl *a* concentrations measured with HPLC varied from 0.18 to 0.99 mg m^{-3} , and no significant difference was observed between the transects (Wilcoxon rank sum test, $p = 0.48$). The highest chl *a* value was observed in water with low temperature and salinity (Stn. S09), where micro-sized ($> 20 \mu\text{m}$) phytoplankton accounted for 25% of the total chl *a* biomass. Overall, the contribution of micro-sized phytoplankton to the total chl *a* biomass was relatively low ($< 50\%$), and nano- and pico-sized ($< 20 \mu\text{m}$) phytoplankton dominated the phytoplankton assemblages during our cruise.

Phytoplankton community composition as estimated by CHEMTAX

Figure 2 shows the contributions of each algal class to the total chl *a* biomass estimated by CHEMTAX. Along the 110°E transect, haptophytes type6 (presumably coccolithophores *Emiliana huxleyi*; Zapata et al., 2004), haptophytes type8 (presumably *P. antarctica*; Zapata et al., 2004), and chlorophytes were the major algal groups between Stns. C01 and C03 (Fig. 2a). The relatively high contributions of cyanobacteria to the chl *a* biomass were only found at Stns. C01 and S02 (19% and 12%, respectively). Although diatoms were the minor constituents between Stns. C01 and C03, they contributed to the chl *a* biomass with $> 50\%$ between Stns. C04 and C10.

Along the 140°E transect, diatoms contributed to the chl *a* biomass with > 50% except Stn. D15 (Fig. 2b). At Stn. D15, diatoms contributed to the chl *a* biomass with 44%, haptophytes (type6 and type8) and chlorophytes accounted for 56% of the total chl *a* biomass. As a result, the area south of 55°S was defined as a diatom-dominated area in this study (i.e., Stns. C04, C05, C06, S09, C08, C10, C17, S15, D07, D08, D10, D12, D13, S21, and D14). Along both transects, dinoflagellates, cryptophytes, and prasinophytes were minor algal groups, and their contributions to the chl *a* biomass were < 14%.

Light availability in the upper mixed layer

There were significant latitudinal variations in the depth of upper mixed layer (z_{UML}) and euphotic zone (z_{eu}), incident surface PAR, and total daily PAR in the upper mixed layer (E_{UML}) along the 110°E and 140°E transects (Fig. 3). Along the 110°E transect, z_{UML} ranged from 11 to 92 m, and the shallowest values were observed at Stns. C08, C10, and C17 (Fig. 3a). Along the 140°E transect, z_{UML} ranged from 13 to 68 m (Fig. 3b), and no significant difference was observed relative to the 110°E transects (Wilcoxon rank sum test, $p = 1.0$). In general, z_{UML} was shallower than z_{eu} along the both transects with a few exceptions. Incident surface PAR tended to decrease in the south along the 110°E transect, while relatively high E_{UML} values ($> 10 \text{ mol photons m}^{-2} \text{ d}^{-1}$) were also observed in the south due to the shallow z_{UML} (Fig. 3c). Along the 140°E

transect, both incident surface PAR and E_{UML} were similar to values along the 110°E transect (Fig. 3d), and no significant differences in the both parameters were observed between the two transects (Wilcoxon rank sum test, PAR: $p = 0.57$, E_{UML} : $p = 0.74$). There was no significantly correlation between total daily PAR in the upper mixed layer (E_{UML}) and surface chl *a* concentration (Nonparametric Kendall's rank correlation, $p = 0.26$).

The value of z_{UML} in the diatom-dominated and non-diatom-dominated areas varied from 11 to 92 m and from 13 to 84 m, respectively (Figs. 2 and 3). In the diatom-dominated area, the value of E_{UML} varied from 4.0 to 22.7 mol photons $m^{-2} d^{-1}$. While the minimum value in the non-diatom-dominated area was higher than that in the diatom-dominated area (i.e., 8.8 mol photons $m^{-2} d^{-1}$), the maximum value was almost same (i.e., 23.0 mol photons $m^{-2} d^{-1}$). In the results of Wilcoxon rank sum test, no significant differences were observed in z_{UML} and E_{UML} between the diatom-dominated and non-diatom-dominated areas (z_{UML} : $p = 0.86$, E_{UML} : $p = 0.12$). Furthermore, there were no statistically significant correlations between the diatom contribution to the chl *a* biomass and z_{UML} as well as E_{UML} (Nonparametric Kendall's rank correlation, z_{UML} : $p = 0.19$, E_{UML} : $p = 0.92$).

P–E parameters

In the diatom-dominated area, significantly higher values of the maximum

photosynthetic rate normalized to chl *a* ($P_{\max}^*$), initial slope (α^*), photoinhibition index
 (β^*), and maximum quantum yield of carbon fixation ($\Phi_{c\max}$) were observed compared
 with the non-diatom-dominated area (Wilcoxon rank sum test, $P_{\max}^*: p < 0.05$, $\alpha^*: p <$
 0.05 , $\beta^*: p < 0.05$, $\Phi_{c\max}: p < 0.01$). The value of $P_{\max}^*$ in the diatom-dominated and
 non-diatom-dominated areas varied from 0.95 to 1.87 mg C (mg chl *a*)⁻¹ h⁻¹ and from
 0.74 to 1.26 mg C (mg chl *a*)⁻¹ h⁻¹, respectively (Fig. 4a). In this study, α^* values
 increased toward the south (Fig. 4b). The values of α^* in the diatom-dominated area
 varied from 0.0069 to 0.0134 mg C (mg chl *a*)⁻¹ h⁻¹ ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)⁻¹, while the
 maximum value in the non-diatom-dominated area was 0.0078 mg C (mg chl *a*)⁻¹ h⁻¹
 ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)⁻¹. As for α^* , β^* also increased toward the south (Fig. 4c). The
 values of $\Phi_{c\max}$ in the diatom-dominated area varied from 0.009 to 0.016 mol C (mol
 photons)⁻¹, and the minimum value was higher than the maximum value (i.e., 0.007 mol
 C (mol photons)⁻¹) observed in the non-diatom-dominated area (Fig. 4d). The values of
 $\bar{a}_{\phi}^*$ in the diatom-dominated and non-diatom-dominated areas varied from 0.017 to
 0.030 m² (mg chl *a*)⁻¹ and from 0.021 to 0.035 m² (mg chl *a*)⁻¹, respectively (Fig. 4e).
 Relatively high E_K values were observed at Stns. C01 and D15 in the
 non-diatom-dominated area (Fig. 4f). However, no significant differences were
 observed in $\bar{a}_{\phi}^*$ and E_K between the diatom-dominated and non-diatom-dominated areas
 (Wilcoxon rank sum test, $\bar{a}_{\phi}^*: p = 0.16$, $E_K: p = 0.31$).

Variable fluorescence of phytoplankton

The relationship between the photochemical quantum efficiency (F_v/F_m) and the functional absorption cross-section (σ_{PSII}) of photosystem II for the phytoplankton community at 5 m along the 110°E and 140°E transects are shown in Figure 5. Along the transects, F_v/F_m values were consistently low (≤ 0.25), and no significant difference in F_v/F_m was observed between the diatom-dominated and non-diatom-dominated areas (Wilcoxon rank sum test, $p = 0.21$). The values of σ_{PSII} varied from 141 to $513 \times 10^{-20} \text{ m}^2 \text{ quanta}^{-1}$, and no significant difference in σ_{PSII} was observed (Wilcoxon rank sum test, $p = 0.68$). There was no statistically significant correlation between the values of F_v/F_m and σ_{PSII} in the transects (Nonparametric Kendall's rank correlation, $p = 0.21$).

Temporal and spatial changes in chl *a* concentration derived from satellite ocean-color

Figure 6 shows temporal and spatial changes in the distributions of satellite-derived chl *a* concentration (chl_{sat}) in the study area from August 2010 to March 2011 along 110°E and 140°E. Along the 110°E transect, chl_{sat} in the area between Stns. C02 and C03 were relatively high before our cruise (i.e., from October to November) and decreased significantly from December to March (Fig. 6a). However, there were relatively constant chl_{sat} in the area between Stns. C03 and C05 until March. In the area south of Stn. C06, clear blooming events ($\text{chl}_{\text{sat}} > 1 \text{ mg m}^{-3}$) occurred before and after our cruise. Along the 140°E transect, chl_{sat} in the area north of Stn. D12 were

relatively high before our cruise and decreased after our cruise (Fig. 6b). In the area south of Stn. D10, clear blooming events occurred after our cruise.

Discussion

Latitudinal changes in the abundance and community composition of phytoplankton

There were considerable changes in the abundance and community composition of phytoplankton with latitude in the Australian sector of the Southern Ocean during the austral summer of 2010/2011. The contributions of each algal class to the total chl *a* biomass estimated by CHEMTAX drastically changed toward south, particularly along the 110°E transect (Fig. 2). Although the contribution of cyanobacteria to the chl *a* biomass and the cell densities of *Synechococcus* measured with flow cytometry were relatively high at Stns. C01 and S02, a dramatic decrease in both the contributions and the cell concentrations occurred to the south of those stations (Table 2 and Fig. 2a). As a result, cyanobacteria were minor algal groups in most of the study area. Those latitudinal patterns were consistent with the previous reports for the Southern Ocean (e.g., Marchant et al. 1987; Odate and Fukuchi 1995; Wright et al. 1996; Zubkov et al. 1998; Fouilland et al. 1999). Along the 110°E transect, haptophytes type6, haptophytes type8, and chlorophytes were the major algal groups in the area north of 50°S, while diatoms contributed to the chl *a* biomass with more than 50% in the

area south of 55°S. Those latitudinal gradients in each algal class were consistent with the previous CHEMTAX interpretations of HPLC pigment data in the Australian sector of the Southern Ocean (e.g., Wright et al. 1996).

Since the Southern Ocean is a HNLC region, the abundance and community composition of phytoplankton were thought to be mainly controlled by availability of light (e.g., Mitchell et al. 1991; Nelson and Smith 1991; Arrigo et al. 1999; Goffart et al. 2000; Wright and van den Enden 2000) and iron (e.g., de Baar et al. 1995; Boyd et al. 2000; Lance et al. 2007) from the perspective of bottom-up control. A shallow mixed layer leads to a higher E_{UML} that stimulates phytoplankton growth (Mitchell et al. 1991). During our cruise, most z_{UML} were shallower than z_{eh} (Fig. 3). However, there was no significantly correlation between E_{UML} and surface chl *a* concentration. Previous studies in the Southern Ocean have reported that the distribution of dominant phytoplankton communities varies as a function of the mixed layer depth (Arrigo et al. 1999; Goffart et al. 2000; Wright and van den Enden 2000), while there were no significant correlations between the diatom contribution to the chl *a* biomass and z_{UML} as well as E_{UML} in this study. These results suggested that latitudinal changes in the abundance and community composition of phytoplankton might not be light limited during our cruise.

The surface macronutrient levels for all substances except silicate (Table 2) were generally higher than the mean half-saturation constant, K_s , of each macronutrient for diatoms (Sarhou et al. 2005) and for haptophytes *phaeocystis* (Schoemann et al. 2005), indicating that nitrate and phosphate were not the dominant factors controlling

latitudinal changes in the algal photosynthetic physiological condition. Nelson and Tréguer (1992) reported that silicate was a limiting factor the growth of diatoms and/or silicoflagellates at the stations where silicate was less than $5 \mu\text{mol L}^{-1}$ at the time of sampling. Along the 140°E transect, the surface silicate was less than $5 \mu\text{mol L}^{-1}$ at Stns. D13, S21, D14, and D15 (Table 2), while diatoms contributed $> 50\%$ to the chl *a* biomass except at Stn. D15 (Fig. 2b). According to the light microscopy, the chain-forming pennate diatom *Fragilariopsis kerguelensis* was also present at Stns. D14 and D15 (Fig. 7). Satellite-derived chl *a* concentrations were relatively high in the area north of Stn. D12 before our cruise (Fig. 6b). These results suggested that the low silicate level in the area north of Stn. D13 could be due to the consumption by diatoms and/or silicoflagellates.

It is known that iron availability was very low in the Australian sector of the Southern Ocean (e.g., Sohrin et al. 2000; Bowie et al. 2004; Sedwick et al. 2008). Iron and nitrate limitations lead to a decrease in F_v/F_m of algal photosystem II (e.g., Greene et al. 1992; Kolber et al. 1994; Boyd and Abraham 2001; Suzuki et al. 2002). Although the surface nitrate was abundant in this study (Table 2), the F_v/F_m values were considerably lower (≤ 0.25 ; Fig. 5) than the empirical maximum (approximately 0.65: Falkowski et al. 1994). These results suggested that the abundance of phytoplankton in this area could be controlled by iron availability. However, chl *a* concentrations were relatively high in the southern part of the transects (Table 2). The chl *a* concentration derived from satellite ocean-color was also relatively high before our cruise in the

southern part of the transects where sea ice covered until October (Fig. 6). Sea ice melting caused the changes in the mixed layer depth (e.g., Mitchell and Holm-Hansen 1991) and iron availability (e.g., Lannuzel et al. 2007), affecting phytoplankton abundance (e.g., Boyd et al. 2000). Thus, relatively high chl *a* concentration in the region might be caused by improved growth conditions before our cruise.

The observed values of F_v/F_m in this study (Fig. 5) was comparable to the ranges reported outside an iron enriched patch during SOIREE, a past in situ iron enrichment experiment in the Australian sector of the Southern Ocean (Boyd and Abraham 2001). However, the ranges of the two parameters in this study were very narrow compared to other previous studies in the Mertz Glacier Region of East Antarctica (Vaillancourt et al. 2003) and in the vicinity of the Crozet Plateau (Moore et al. 2007). These studies reported that values of F_v/F_m and σ_{PSII} were highly correlated (Vaillancourt et al. 2003; Moore et al. 2007). On the other hand, there was no statistically significant correlation between the two parameters in this study (Fig. 5). Suggett et al. (2009) reported that F_v/F_m and σ_{PSII} varied principally with broad-scale changes in community structure, and the slope of the F_v/F_m versus σ_{PSII} relationship was much steeper for cyanobacteria than it is for diatoms and haptophytes. However, since cyanobacteria were minor algal groups in this study areas, the absence of relationship between F_v/F_m and σ_{PSII} might be caused by other reasons. Moore et al. (2007) indicated that responses of the variable fluorescence parameters (i.e., F_v/F_m and σ_{PSII}) to a drop in iron availability may be more varied in a condition approximating steady-state

limitation occurs, although rapid changes in the parameters tend to follow increased iron availability to a starved population. Thus, further studies are needed to examine the relationships between the variable fluorescence parameters and phytoplankton community compositions in as the Southern Ocean, where phytoplankton growth is often limited by low iron availability.

Differences in photosynthetic physiology between the dominant phytoplankton communities

Significant higher $P-E$ parameters ($P_{\max}^*$, α^* , β^* , and $\Phi_{c\max}$) in the diatom-dominated area were observed (Figs. 4a-d). It is well known that $P_{\max}^*$ is dependent on temperature because it is controlled by the activity of enzymes such as RuBisCO (Sukenik et al. 1987; MacIntyre and Geider 1996). Although high temperatures increase enzymatic activity and carbon fixation (Davison 1991; Sakshaug et al. 1997), the seawater temperature in the diatom-dominated area was significantly lower than that in the non-diatom-dominated area (Wilcoxon rank sum test, $p < 0.05$). These results suggested that factors other than temperature may play a more important role in the control of $P_{\max}^*$.

Several studies have reported a significant effect of irradiance levels on the photosynthetic physiology of phytoplankton in the Southern Ocean (e.g., Bracher et al. 1999; van Hilst and Smith 2002). In the Atlantic sector, Bracher et al. (1999) reported

that beyond frontal zones, $P_{\max}^*$ values at the 1% irradiance level were significantly higher than those at the surface (i.e., 100% irradiance level). However, in the Ross Sea, no differences existed between $P_{\max}^*$ values at the 1% irradiance level and those at the 50% irradiance level, while significant differences in α^* and E_k were observed between the two irradiance levels (van Hilst and Smith 2002). In this study, although significant higher $P_{\max}^*$, α^* , β^* , and $\Phi_{c \max}$ were observed in the diatom-dominated area, no significant differences were observed in z_{UML} and E_{UML} between the diatom-dominated and non-diatom-dominated areas. Indeed, no significant difference was observed in E_k between the diatom-dominated and non-diatom-dominated areas. Thus, the differences in photosynthetic physiology between the diatom-dominated and non-diatom-dominated areas may have resulted from factors other than light availability.

In the past in situ iron enrichment experiments, several studies reported photosynthetic physiology of phytoplankton communities in HNLC regions was affected by changes in iron availability (e.g., Gervais et al. 2002; Hiscock et al. 2008; Suzuki et al. 2009). In the Southern Ocean during EisenEx (Gervais et al. 2002) and SoFeX (Hiscock et al. 2008), α^* became higher inside the iron enriched patch, whereas there was no difference in $P_{\max}^*$ between inside and outside the iron patch. However, in the Western Subarctic Gyre (WSG) during SEEDS-II (Suzuki et al. 2009), higher $P_{\max}^*$ values were observed inside the iron enriched patch, but α^* was little affected by the iron additions. Although several studies reported F_v/F_m increased inside the iron patch, temporal changes in the $P-E$ parameters and F_v/F_m were not always correspond with

each other (Gervais et al. 2002; Suzuki et al. 2009). In this study, the F_v/F_m values in the diatom-dominated and non-diatom-dominated areas were considerably low, while significant higher $P_{\max}^*$, α^* , β^* , and $\Phi_{c\max}$ in the diatom-dominated area were observed. These results suggested that changes in the $P-E$ parameters might not always be related to absolute values of F_v/F_m .

In this study, there was strong covariation between the $P_{\max}^*$ and α^* (Table 3), indicating E_k -independent variability (Behrenfeld et al. 2004). Covariability in $P_{\max}^*$ and α^* was frequently observed in the Southern Ocean (Tilzer et al. 1986; Claustre et al. 1997; Moline et al. 1998; Moore et al. 2007). Photosynthetic process is divided into two processes, i.e., the photosynthetic electron transfer (PET) process (e.g., light-harvesting and reductant production) and downstream processes of PET (e.g., carbon fixation). The $P-E$ parameters were related to both processes (i.e., PET and the downstream processes of PET), whereas the variable fluorescence parameters measured with FRe fluorometer (i.e., F_v/F_m and σ_{PSII}) were solely related to the PET process. Comparing these parameters, there were no statistically significant correlations between F_v/F_m or σ_{PSII} and most of the $P-E$ parameters, except for β^* (Table 3), indicating that the PET processes did not play important roles in the changes in most of the $P-E$ parameters. Previous studies also showed the importance of the downstream processes of PET for the E_k -independent variability (Behrenfeld et al. 2004; Yoshie et al. 2010). Although several factors have been suggested as drivers for the E_k -independent variability (Behrenfeld et al. 2004), Claustre et al. (1997) suggested that changes in phytoplankton

community composition were largely responsible for the E_k -independent variability in the Antarctic Peninsula shelf. However, the mechanism of the E_k -independent variability is largely unresolved. Therefore, further studies are needed to clarify the factors controlling the E_k -independent variability in the Southern Ocean.

The observed values of P - E parameters in this study (Fig. 4) were comparable to the ranges previously reported for the Australian sector of the Southern Ocean during austral summer (Hirawake et al. 2000; Yoshikawa et al. 2007). Yoshikawa et al. (2007) and Hirawake et al. (2000) reported that $P^*_{\max}$, α^* , and $\Phi_{c\max}$ tended to be high toward south at approximately 140°E in the Southern Ocean during the austral summer, and their results were consistent with this study. However, their studies did not examine phytoplankton community composition. On the other hand, Bracher et al. (1999) reported that $P^*_{\max}$ and $\Phi_{c\max}$ tended to be high in the polar front (PF) positioned approximately 50°S and low in the marginal ice zone (MIZ) approximately 64°S in the Atlantic sector of the Southern Ocean during austral summer. Although the latitudinal pattern reported by Bracher et al. (1999) showed an opposite trend in this study, Bracher et al. (1999) reported that diatoms dominated the phytoplankton community in the PF and the haptophyte *Phaeocystis* sp. dominated in the MIZ. As a result, both $P^*_{\max}$ and $\Phi_{c\max}$ in the diatom-dominated area (i.e., the PF) were higher than those observed in the non-diatom-dominated area (i.e., the MIZ), as found in this study. In the Antarctic coastal waters, Claustre et al. (1997) also reported that the depth-averaged values of $P^*_{\max}$ and α^* for diatoms were higher than those for

cryptophytes, although cryptophytes were minor constituents in this study (Fig. 2). To assess the effect of the phytoplankton community composition on changes in the $P-E$ parameters, the relationships between the diatom contribution to the chl a biomass and the $P-E$ parameters were examined (Table 3). There were statistically significant correlations between the diatom contribution to the chl a biomass and most of the $P-E$ parameters, except for α^* and E_k . Thus, latitudinal changes in the $P-E$ parameters could be accompanied by changes in the phytoplankton community composition, mainly diatoms. Although this study primarily focused on the community composition and photosynthetic physiology of phytoplankton at the sea surface, vertical changes in the distribution and abundance of phytoplankton communities were found in the Southern Ocean (e.g., Wright and van den Enden 2000; Wright et al. 2010; de Salas et al. 2011). Therefore, further studies are needed to examine the responses of the community composition and photophysiology of phytoplankton assemblages to vertical changes in the underwater light field in the Southern Ocean.

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Figure Captions

Fig. 1. Location of sampling stations along 110°E and 140°E in the Australian sector of the Southern Ocean. Closed circles and stars represent the stations where seawater was sampled and Photosynthesis–irradiance curve experiments were conducted, respectively. Each line represents the climatological location of one of the four fronts (Orsi et al., 1995): STF, Subtropical Front; SAF, Subantarctic Front; PF, Polar Front; SB, Southern Boundary of the Antarctic Circumpolar Current.

Fig. 2. Contributions of each algal class to the total chl *a* biomass at 5 m estimated by CHEMTAX along (a) 110°E and (b) 140°E.

Fig. 3. Changes in the depth of upper mixed layer (z_{UML}) and euphotic zone (z_{eu}), incident surface PAR, and total daily PAR in the upper mixed layer (E_{UML}) along (a, c) 110°E and (b, d) 140°E.

Fig. 4. Changes in the photosynthetic parameters at 5 m along 110°E and 140°E: (a) maximum photosynthetic rate (P^*_{max} : mg C (mg chl *a*)⁻¹ h⁻¹), (b) initial slope of the P – E curve (α^* : [mg C (mg chl *a*)⁻¹ h⁻¹] (μmol photons m⁻² s⁻¹)⁻¹), (c) photoinhibition index (β^* : [mg C (mg chl *a*)⁻¹ h⁻¹] (μmol photons m⁻² s⁻¹)⁻¹), (d) maximum quantum yield of carbon fixation ($\Phi_{c\ max}$: mol C (mol photons)⁻¹), (e) mean chl *a*-specific absorption

coefficient of phytoplankton ($\bar{a}_{\phi}^*$: $\text{m}^2 (\text{mg chl } a)^{-1}$), and (f) light saturation index (E_k : $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) in the study area.

Fig. 5. Relationship between the photochemical quantum efficiency (F_v/F_m) and the functional absorption cross-section (σ_{PSII}) of photosystem II for the phytoplankton community at 5 m along 110°E and 140°E.

Fig. 6. Temporal and spatial changes in the distributions of satellite-derived chl *a* concentration in the study area from August 2010 to March 2011 along (a) 110°E and (b) 140°E. Data points were extracted with 3×3 pixels (i.e., $27 \text{ km} \times 27 \text{ km}$) resolution from MODIS/Aqua 8-day composite images. Areas in white represent lack of satellite data due to sea-ice cover and/or cloudiness. Arrows indicate sampling stations in Fig. 1.

Fig. 7. Light microscopy images of the pennate diatom *Fragilariopsis kerguelensis* with chains: (a) D14 (b) D15. The black bar in the images is $20 \mu\text{m}$.

Table 1. CHEMTAX analysis of accessory pigment to chl *a* ratios in the major algal class: (a) initial ratios and (b) final ratios. Perid, peridinin; 19'-But, 19'-butanoyloxyfucoxanthin; Fucox, fucoxanthin; 19'-Hex, 19'-hexanoyloxyfucoxanthin; Neox, neoxanthin; Prasinox, prasinoxanthin; Violax, violaxanthin; Allox, alloxanthin; Chl *b*, chlorophyll *b*; Chl *a*, chlorophyll *a*.

	Perid	19'-But	Fucox	19'-Hex	Neox	Prasinox	Violax	Allox	Zeax	Chl <i>b</i>	Chl <i>a</i>
(a)											
Prasinophytes	0	0	0	0	0.039	0.069	0.097	0	0	2.235	1
Dinoflagellates	0.781	0	0	0	0	0	0	0	0	0	1
Cryptophytes	0	0	0	0	0	0	0	0.118	0	0	1
Haptophytes6	0	0.041	0.112	0.957	0	0	0	0	0	0	1
Haptophytes8	0	0.327	0.069	0.613	0	0	0	0	0	0	1
Chlorophytes	0	0	0	0	0.003	0	0.01	0	0.003	0.006	1
Cyanobacteria	0	0	0	0	0	0	0	0	0.507	0	1
Diatoms	0	0	0.664	0	0	0	0	0	0	0	1
(b)											
Prasinophytes	0	0	0	0	0.039	0.067	0.097	0	0	2.235	1
Dinoflagellates	0.781	0	0	0	0	0	0	0	0	0	1
Cryptophytes	0	0	0	0	0	0	0	0.118	0	0	1
Haptophytes6	0	0.043	0.117	1.398	0	0	0	0	0	0	1
Haptophytes8	0	0.327	0.069	0.613	0	0	0	0	0	0	1
Chlorophytes	0	0	0	0	0.003	0	0.01	0	0.003	0.006	1
Cyanobacteria	0	0	0	0	0	0	0	0	0.507	0	1
Diatoms	0	0	0.664	0	0	0	0	0	0	0	1

Table 2. Summary of hydrographic conditions and phytoplankton abundance along 110°E and 140°E. SST: sea surface temperature (°C), SSS: sea surface salinity, N: nitrate (= nitrate + nitrite) concentration ($\mu\text{mol L}^{-1}$), P: phosphate concentration ($\mu\text{mol L}^{-1}$), Si: silicate concentration ($\mu\text{mol L}^{-1}$), chl *a*: chlorophyll *a* concentration, chl *a*_{micro}: chlorophyll *a* concentration by micro-sized (>20 μm) phytoplankton, micro-size contribution: ratio of chl *a*_{micro} to chl *a* (%).

Station	Date	Latitude	Longitude	SST	SSS	N	P	Si	<i>Synechococcus</i>	chl <i>a</i>	chl <i>a</i> _{micro}	Micro-size contribution
		(°S)	(°E)	(°C)		($\mu\text{mol L}^{-1}$)	($\mu\text{mol L}^{-1}$)	($\mu\text{mol L}^{-1}$)	($\times 10^6 \text{ cells ml}^{-1}$)	(mg m^{-3})	(mg m^{-3})	(%)
110°E												
C01	26 Dec 2010	40.0	110.0	14.8	35.2	1.72	0.31	0.00	28.5	0.30	0.00	0.0
S02	26 Dec 2010	41.0	110.0	15.9	35.3	0.58	0.24	0.00	21.5	0.47	0.01	1.4
S03	26 Dec 2010	43.3	110.0	13.3	34.7	6.96	0.62	0.17	2.5	0.68	0.09	13.4
C02	26 Dec 2010	45.0	110.0	11.3	34.5	11.32	0.93	0.00	2.0	0.18	0.00	0.0
S05	27 Dec 2010	47.6	110.0	9.6	34.2	17.67	1.26	1.70	1.4	0.18	0.00	0.0
C03	28 Dec 2010	50.0	110.0	8.0	33.9	22.59	1.64	6.70	0.5	0.19	0.00	2.4
S06	28 Dec 2010	51.6	110.2	4.6	33.9	24.93	1.85	10.05	0.3	0.40	0.04	10.6
C04	29 Dec 2010	55.0	110.0	5.0	33.9	26.41	1.97	23.21	0.2	0.49	0.06	12.9
C05	30 Dec 2010	58.4	110.0	3.1	33.9	26.46	1.82	24.42	0.2	0.37	0.15	39.0
C06	31 Dec 2010	60.0	110.0	2.2	33.9	26.09	1.84	29.21	0.2	0.65	0.28	42.6
S09	1 Jan 2011	62.1	109.9	1.3	33.4	23.30	1.64	36.81	0.2	0.99	0.25	24.8
C08	1 Jan 2011	63.0	110.0	1.3	33.3	22.10	1.36	37.80	0.2	0.78	0.14	18.4
C10	2 Jan 2011	65.0	110.0	2.6	33.8	21.17	1.25	52.52	0.2	0.57	0.05	7.9
C17	4 Jan 2011	63.0	115.0	2.0	33.7	23.17	1.59	34.70	0.2	0.67	0.12	17.2
140°E												
S15	9 Jan 2011	66.0	140.4	0.7	33.9	26.08	1.85	54.53	0.2	0.69	0.06	8.4
D07	10 Jan 2011	65.0	140.0	0.9	33.6	26.74	1.90	47.09	0.2	0.27	0.02	7.3
D08	11 Jan 2011	64.0	140.1	1.7	33.5	26.30	1.81	40.78	0.2	0.26	0.01	4.8
D10	14 Jan 2011	62.5	140.0	1.7	33.7	24.57	1.77	30.82	0.2	0.92	0.46	49.7
D12	15 Jan 2011	60.0	140.0	2.5	33.9	26.31	1.75	20.59	0.2	0.30	0.02	8.1
D13	16 Jan 2011	58.6	140.0	4.8	33.7	24.67	1.78	3.04	0.3	0.34	0.06	16.5
S21	16 Jan 2011	57.0	140.0	4.8	33.7	22.77	1.53	2.23	0.2	0.32	0.10	29.9
D14	17 Jan 2011	55.0	140.0	5.0	33.8	23.92	1.68	0.18	0.2	0.31	0.13	43.0
D15	18 Jan 2011	50.0	143.7	10.0	34.1	17.36	1.28	0.00	1.6	0.30	0.00	0.0

Table 3. Nonparametric Kendall's rank correlations between photosynthetic parameters and the diatom contribution to the chl *a* biomass ($n = 11$). $P_{\max}^*$: maximum photosynthetic rate ($\text{mg C (mg chl } a)^{-1} \text{ h}^{-1}$), α^* : initial slope of the $P-E$ curve ($[\text{mg C (mg chl } a)^{-1} \text{ h}^{-1}] (\mu\text{mol photons m}^{-2} \text{ s}^{-1})^{-1}$), β^* : photoinhibition index ($[\text{mg C (mg chl } a)^{-1} \text{ h}^{-1}] (\mu\text{mol photons m}^{-2} \text{ s}^{-1})^{-1}$), $\Phi_{\text{c max}}$: maximum quantum yield of carbon fixation ($\text{mol C (mol photons)}^{-1}$), $\bar{\alpha}_{\phi}^*$: mean chl *a*-specific absorption coefficient of phytoplankton ($\text{m}^2 (\text{mg chl } a)^{-1}$), E_K : light saturation index ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), F_v/F_m : photochemical quantum efficiency of photosystem II, σ_{PSII} : functional absorption cross-section of photosystem II ($\times 10^{-20} \text{ m}^2 \text{ photon}^{-1}$), Diatom contribution: diatom contribution to the chl *a* biomass.

	$P_{\max}^*$	α^*	β^*	$\Phi_{\text{c max}}$	$\bar{\alpha}_{\phi}^*$	E_K	F_v/F_m	σ_{PSII}
α^*	0.71 **							
β^*	0.49 *	0.42						
$\Phi_{\text{c max}}$	0.64 **	0.71 **	0.56 *					
$\bar{\alpha}_{\phi}^*$	-0.05	-0.50	0.42	-0.35				
E_K	-0.09	-0.38	0.05	-0.24	-0.13			
F_v/F_m	-0.09	0.05	-0.54 *	-0.09	0.35	-0.17		
σ_{PSII}	0.20	0.13	0.20	0.05	0.09	0.20	-0.28	
Diatom contribution	0.53 *	0.45	0.75 ***	0.67 **	-0.53 *	-0.05	-0.28	0.09

Bold numbers denote statistical significance; $*0.01 < P \leq 0.05$, $**0.001 < P \leq 0.01$, $***P \leq 0.001$.

Takao et al. Figure 1

(a) 110°E

(b) 140°E

Takao et al. Figure 2

Takao et al. Figure 3

Takao et al. Figure 4

Takao et al. Figure 5

Takao et al. Figure 6

(a)

(b)

Takao et al. Figure 7