Unprecedented differences in phytoplankton community structures in the Amundsen Sea Polynyas, West Antarctica

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Abstract

In the Antarctic coast, ice shelves are rapidly thinning and retreating due to global warming. Basal melt water influences marine life, particularly the phytoplankton, which are directly affected by changes in physicochemical environments. However, there is limited in situ data over large areas in the Amundsen Sea, which is currently a hotspot for rapidly thinning ice shelves in West Antarctica. During the austral summer cruise of 2020, phytoplankton species abundance was investigated along the Amundsen Sea coast using an automated continuous observation instrument, the Imaging FlowCytobot. The phytoplankton community was dominated by Phaeocystis antarctica in most coastal waters of the Amundsen Sea, as previously reported; however, unexpected blooms of diatom Dactyliosolen tenuijunctus were observed throughout the Pine Island Bay region at a high dominance rate (∼90%) and abundance (>10⁷ cells l⁻¹). D. tenuijunctus is a weakly silicified diatom and its massive bloom in the water column has been rarely reported from the Antarctic Ocean. The dramatic difference in phytoplankton compositions between these adjacent polynyas probably indicates an unstable response of phytoplankton to ice melting conditions. They could play a different role in the marine food web and carbon flux compared to other diatoms and P. antarctica. Therefore, further research is warranted to predict the biological and biogeochemical impacts of future melting conditions.

1. Introduction

In polynyas, which are open water areas surrounded by sea ice along the Antarctic coast, phytoplankton form the base of Antarctic food webs and contribute to carbon sequestration via high primary production during the austral summer (Arrigo and van Dijken 2003). Animals such as Antarctic krill, penguins, and whales adapt their life strategies to the seasonal expansion of the polynyas and subsequent phytoplankton blooms (Saba et al 2014, Riekkola et al 2018). The Amundsen Sea is among the most productive coastal systems (Arrigo et al 2012) and harbors two productive polynyas: the Amundsen Sea Polynya (ASP) and Pine Island Polynya (PIP). This region is also known for its rapidly thinning ice shelves and drastic glacial retreat owing to global warming (Rignot et al 2013, Scambos et al 2017).

Basal melt water from the ice shelves supplies iron and suspended particles to the coastal waters (Samuel et al 2017), enhances regional surface freshening (Silvano et al 2018), and consequently regulates phytoplankton biomass and community structure (Alderkamp et al 2012, Lee et al 2016).

The dominant species in this phytoplankton community, diatoms and the prymnesiophyte Phaeocystis antarctica, differ in nutrient drawdown characteristics and the food preferences for zooplankton (Arrigo et al 1999, Yang et al 2019). Thus, compositional changes have a significant impact on the biogeochemical cycles and pelagic food web structures. While some studies have examined phytoplankton ecology in the ASP, few have reported on this information in the PIP because it is difficult to access owing to the surrounding high sea ice concentrations (SIC). In January 2009, phytoplankton compositions...
were not significantly different between these two polynyas, and *P. antarctica* was dominant (>65% in biomass) (Alderkamp *et al* 2012). Since then, there have been few reports on phytoplankton compositions in the PIP over the past decade. Basal melting in PIP and ASP is expected to increase in a warming climate (Rignot *et al* 2019), and the high risk of collapse of Thwaites glacier in Pine Island Bay (PIB) has been recently reported (Bassis *et al* 2021, Crawford *et al* 2021). Because acceleration in melting and retreating of ice shelves could influence the distribution of phytoplankton, which are directly affected by changes in the chemical and physical environments, it is necessary to investigate the phytoplankton community structure in response to the rapid environmental changes in the Amundsen Sea coast.

To determine the phytoplankton community distribution in these rapidly changing areas, a field survey was conducted during the austral summer of 2020. The Imaging FlowCytobot (IFCB), an automated continuous observation instrument, provided a high-frequency spatial distribution of phytoplankton species in the coastal waters along a ship route from the Wrigley Gulf to the PIB.

2. Methods

2.1. Field survey

The field survey was conducted onboard the Korean ice-breaking research vessel (IBRV) ‘Araon’ in the Amundsen Sea during the austral summer (20 January–15 February 2020). The cruise track covered approximately 1000 km (along-shelf) from the Wrigley Gulf to the PIB in the Amundsen Sea (figure 1). The study area was geographically divided into the oceanic area (OA) and three polynyas: ASP, PIP, and Wrigley Gulf Polynya (WGP).

2.2. Automated continuous measurements

Continuous variables were measured while underway using the seawater supply of the ship at a nominal depth of 7 m along the cruise track. Seawater temperature and salinity were measured using a thermosalinograph (SBE43). Chlorophyll fluorescence was measured using a Turner Designs 10-AU equipped with a continuous flow cuvette and calibrated against chlorophyll-a (chl-a) concentrations determined from discrete water samples using fluorometry. Variable fluorescence measurements of phytoplankton were conducted using a mini-FIRe (Lin *et al* 2016). Surface photosynthetically active radiation (PAR) was determined using a quantum sensor (LI-1400, LI-COR Inc., USA) every 5 min during the cruise.

Phytoplankton species abundance was acquired with the IFCB, which collects images of particles containing chlorophyll fluorescence (Olson and Sosik 2007). The seawater continuously flowed into a sample reservoir (approximately 2 l), and the bottom water (typically 5 ml) of the reservoir was pumped into the sample syringe of the IFCB. A Nitex screen with a mesh size of 150 μm was placed over this sample intake to prevent larger particles from clogging the flow cell.

All digital micrographs were automatically classified using a supervised machine learning strategy (Laney and Sosik 2014), and 37 taxa were identified in these samples (table S1). These results were manually verified for 57 selected samples to ensure the highest possible accuracy in taxonomic identifications, as discussed subsequently.

2.3. Sample processing

Discrete water samples were collected while underway to measure the macronutrient and photosynthetic pigment concentrations. Macronutrient concentrations, including nitrate + nitrite (NOx), ammonium, phosphate (P), and silicate (Si), were measured onboard using standard colorimetric methods adapted for use with a four-channel autoanalyzer (QuAAtro; Seal Analytical, USA) according to the manufacturer’s instructions (QuAAtro Applications). Chl-a concentrations were determined onboard using samples that were immediately filtered through glass-fiber filter paper (47 mm; Gelman GF/F), extracted with 90% acetone for 24 h (Parsons *et al* 1984), and then measured using a fluorometer (Trilogy, Turner Designs, USA), which was previously calibrated against a chl-a standard (Sigma). Samples for photosynthetic pigment analysis were filtered through a 47 mm GF/F Whatman filter and stored in a freezer at −80 °C. Pigments were extracted by adding 3 ml of 100% acetone to each filter, which was subsequently ultrasonicated for 30 s and maintained at 4 °C in the dark for 15 h. Debris was removed by filtering through a 0.45 μm Teflon syringe filter. Immediately before injection, the extracts were diluted with distilled water (1 ml of extract + 0.3 ml of water) to avoid peak distortions for the first eluting pigments. Pigments were assessed by high-performance liquid chromatography (HPLC) (Zapata *et al* 2000). Prior to the analysis, the series 1200 chromatographic system (Agilent, USA) was calibrated using the following standard pigments (DHII, Denmark): chl-a, chl-b, chl-c2, chl-c3, 19-butanoyloxyfucoxanthin, fucoxanthin (fuco), 19-hexanoyloxyfucoxanthin (hex-fuco), diadinoxanthin, dinoxanthin, diatoxanthin, neoxanthin, prasinoxanthin, violaxanthin, alloxanthin, zeaxanthin, lutein, and peridinin. A 250 mm × 4.6 mm, 5 μm, C8 column (XDB-C8; Agilent, USA) was used for pigment separation. The pigments were identified by their retention times and absorbance spectra. After determining the pigment concentrations, the response factor was calculated as the weight of the injected standard divided by the area.
of the pigment. The concentrations of standard pigments were calibrated by spectrophotometry using known absorption coefficients (Jeffrey et al. 1997).

### 2.4. Comparisons of phytoplankton species abundance using the IFCB and microscope

The IFCB results were compared with microscopically-analyzed phytoplankton species abundances. For microscopic analysis, water samples were subsampled using 200 ml high-density polyethylene bottles, preserved with glutaraldehyde (final concentration 1%), and stored at 4 °C until processed. Subsequently, sample volumes of 20–100 ml were filtered through Nuclepore filters (0.8 μm pore size, black, 25 mm diameter) until 5 ml remained in the filtration tower. Concentrated 4′,6-diamidino-2-phenylindole (50 μg ml⁻¹ final concentration) was then added to the remaining volume, which was also filtered after a 5 s incubation (Lee et al. 2016). The filters were mounted on glass slides with immersion oil and coverslips. Phytoplankton were distinguished and enumerated using epifluorescence microscopy with blue light excitation (Axiohot, Zeiss) (Tomas 1997, Scott and Thomas, 2005). Cells were counted in random fields at magnifications of 200–1000× until a total of 50 fields or 300 cells were observed. Because colonies can break during processing, we were not able to determine whether individual *P. antarctica* cells were previously colonial or always single cells.

*P. antarctica* abundances analyzed by the IFCB and microscopy were consistent (figure S1(a), R² = 0.949). However, diatoms showed much higher abundances in the IFCB results for some samples dominated by *D. tenuijunctus*, which resulted in inconsistencies in the total biomass of those samples (figures S1(b) and (c)). *D. tenuijunctus* is a fragile and small species; therefore, it can break and escape through pores in the Nuclepore filters when preparing microscopic slides. This species was almost entirely absent on the slides but was observed by the IFCB, which enables the investigation of seawater in its natural condition. Furthermore, this species was previously reported mainly in studies in which concentrated water samples were observed under a microscope (Kopczynska et al. 1986, Mikaelyan and Belyaeva 1995, Saggiomo et al. 2017). Thus, these studies showed that appropriate observational methods are needed to investigate this species.

Although IFCB has an advantage in capturing images of *D. tenuijunctus*, it also has limitations. Nano- and micro- size phytoplankton are captured with the IFCB, but pico- and large- (>ca. 300 μm) size fractions are difficult to capture due to low fluorescence intensities and mesh screen, respectively. Although most phytoplankton in the Amundsen Sea were within the size range measured by the IFCB, the technical limitation of the phytoplankton size observable by the IFCB should be taken into account to investigate phytoplankton community structure. In addition, some micrographs of *D. tenuijunctus* acquired with IFCB were not classified into the appropriate taxa because the fragile siliceous cell wall was too faint to be recognized during the automated image processing, and therefore manual classification was required. The IFCB, an automated continuous observation instrument, has the advantage of acquiring information regarding phytoplankton species composition with higher spatio-temporal accuracy.
resolution; however, to accurately investigate their community structure, comparison and verification with the results using a microscope, a HPLC, and a flow cytometer could be required.

2.5. Satellite data
SIC with a horizontal resolution of 3.125 km along the ship track were derived from the Advanced Microwave Scanning Radiometer-2 (Spreen et al. 2008), which was used to obtain the 7 d average SIC prior to the sampling periods and the January mean SIC. The former was used as SIC data for the statistical analysis because the ice concentrations varied substantially during the melting period.

2.6. Statistical analysis
Statistical analyses were carried out using the R4.0.5 software (R Development Core Team, www.r-project.org) and supplemented with the vegan package. The spatial environmental status of the four habitats was summarized using principal component analysis based on log-transformed/normalized abiotic data from the surface layer. To examine the differences between habitats, one-way analysis of variance (ANOVA, Kruskal–Wallis test) and post hoc analysis (Bonferroni correction) were performed using normalized abiotic data, such as seawater temperature, salinity, and SIC, because most of the data did not satisfy assumptions of normality (Clarke and Gorley 2006). A Bray–Curtis dissimilarity matrix was constructed from the square root transformed dominance rate of phytoplankton species, and non-metric multidimensional scaling (NMDS) was performed using the metaMDS function, which was visualized using the ggplot2 package. Differences among the phytoplankton compositions of the samples were determined using an analysis of similarities test (ANOSIM test, anosim function) from the square root-transformed phytoplankton species dominance rate.

3. Results

3.1. Environmental characteristics of the Amundsen Sea habitats
In this study, the OA was characterized by a higher SIC and lower sea surface temperature and salinity, indicating different environmental characteristics from those of the three polynyas (figures 2 and S2(a)). However, there were no clear differences between the
Figure 3. Variation in phytoplankton composition in the Amundsen Sea. (a) Phytoplankton species abundance (cells l\(^{-1}\)) from the IFCB and (b) photosynthetic pigment ratios from the HPLC along the cruise track in four geographic areas of the Amundsen Sea.

3.2. Phytoplankton species compositions of the Amundsen Sea habitats

In the WGP and ASP, the predominant phytoplankton species with a high biomass was *P. antarctica*; in contrast, diatoms, especially *Fragilariopsis* spp., formed a major group with low biomass in the marginal sea ice zone (MSIZ) of the OA (figure 3(a)). These are among the previously reported dominant species in this area, and our results are consistent with those of previous studies that noted the effects of environmental factors, such as sea ice, iron, light, and mixed layer depth, on phytoplankton community distribution in this area (Alderkamp *et al* 2015, Lee *et al* 2016, 2022). However, phytoplankton in the PIP exhibited an unprecedented community structure. The diatom *D. tenuijunctus* predominated with an average abundance of 1.5 × 10^7 cells l\(^{-1}\) and an average dominance rate of 76% (and a maximum of 90%) along the entire route through the PIP up to a width of more than 100 km. These massive *D. tenuijunctus* blooms lasted throughout the research cruise in the PIP, from 29 January to 15 February 2020.

Phytoplankton compositions were clearly differentiated among OA, WGP, and PIP, as shown by the results of the NMDS analysis (figure S2(b)), indicating that *Fragilariopsis* spp., *P. antarctica*, and *D. tenuijunctus* were the predominant species in the three areas, respectively. The phytoplankton communities in the ASP were dominated by...
**Discussion and conclusion**

During the austral summer of 2020, unexpected *Dactyliosolen* blooms occurred in PIB, Antarctica, while, as previously reported, *P. antarctica* was the predominant species in the phytoplankton community in adjacent polynyas. *D. tenuijunctus* is a weakly silicified diatom, and its presence and distribution in Antarctic coastal waters is understudied. Some reports note its presence as a minor species in water columns, sea ice cores, and near free-floating icebergs in the Weddell and Ross Seas (Kopczynska et al. 1986, Günther and Dieckmann 2001, Cefarelli et al. 2011, Moreau et al. 2013, Saggiomo et al. 2017). In this study, *D. tenuijunctus* was also observed in the MSIZ of the OA, with a dominance rate of approximately 20%. Recently, it has been reported as a major species in some waters near the Ross Ice Shelf (Saggiomo et al. 2021). However, as was the case in the PIP, massive blooms over a large area had not previously been reported. Moreover, the relatively low ratio of hex-fuco to fuco in our results have rarely been reported in this region, further indicating that these massive *D. tenuijunctus* blooms were not common (figure 3(b), table S1).

The effects of *D. tenuijunctus* blooms on biogeochemical cycles and ecosystems have also been rarely reported from the Southern Ocean. However, these effects can be predicted based on the findings of the multidisciplinary studies from the Amundsen Sea coastal waters, including the PIP and the ASP, conducted during the post-bloom period in 2012. Kim *et al.* (2014) described that *P. antarctica* colony and *D. tenuijunctus* were the predominant species in the ASP and the PIP, respectively, based on microscopic observations to explain the spatial variation in primary production. Moreover, in terms of chl-a size fraction, micro- and nano-size fractions were more than 60% dominant in the ASP and the PIP, respectively, suggesting that *Phaeocystis* colony (>20 µm) and *D. tenuijunctus* (<20 µm) were the major contributors in the ASP and the PIP, respectively (Kim *et al.* 2014). However, data on the dominant rate and abundance of phytoplankton species were not presented in that study. Since the phytoplankton community structures in the two polynyas had been reported to be similar in previous studies undertaken during the bloom period of 2007 and 2009 (Alderkamp *et al.* 2012, Fragasso *et al.* 2012) and there was no clear evidence for *Dactyliosolen* dominance throughout the PIP in 2012 (Kim *et al.* 2014), the studies conducted in 2012 did not take into account the phytoplankton community structures in the two polynyas to understand spatial variations in phytoplankton physiological characteristics (Hahm *et al.* 2014, Kim *et al.* 2014, Park *et al.* 2017). Nevertheless, the descriptions in Kim *et al.* (2014) imply that phytoplankton size and community structures were considerably different between the two polynyas and *D. tenuijunctus* was one of the dominant species in some areas of the PIP during the austral summer in 2012.

The net community production, primary production, and phytoplankton carbon uptake rate were lower in the PIP than those in the ASP in February 2012 (Hahm *et al.* 2014, Kim *et al.* 2014). Because there were no clear differences in physicochemical properties between the two polynyas, it has been suggested that the differences in phytoplankton production and physiology in the two polynyas were likely influenced by different observational periods and bloom timing (Hahm *et al.* 2014, Kim *et al.* 2014). Simultaneously, low chl-a and high Fv/Fm were reported from the PIP due to the lower solar irradiance and lower Fe stress in the PIP than those in the ASP (Park *et al.* 2017). During the bloom period in 2020, lower chl-a concentration and higher Fv/Fm were observed in the PIP than those in the ASP, indicating consistent results in 2012. Since the physicochemical environment was not significantly different between the two areas during our cruise (figure 2), bloom timing and duration are possible two of the important influencing factors contributing to the spatial differences of phytoplankton biomass and physiological characteristics. However, the timing of blooming differed by approximately 10 d between the two polynyas (Arrigo *et al.* 2012) and the observations were made at the end of January and early February in the ASP and PIP, respectively, indicating that it is not likely to depend on the sampling period. In addition, light and iron possibly influenced the Fv/Fm during the 2020 cruise because they are well known to be the important limiting factors for phytoplankton growth in this area (Alderkamp *et al.* 2015, Lee *et al.* 2022). However, our study demonstrated that physiological properties in the two adjacent polynyas could be influenced by phytoplankton community structure because diatoms tend to have a higher Fv/Fm than that of *P. antarctica* (Smith *et al.* 2014).

*P. antarctica* and *D. tenuijunctus* could have different sinking rates. Previous studies have shown that large diatoms and *P. antarctica* colonies have higher...
sinking rates than small diatoms and \textit{P. antarctica} single cells (Lee et al 2016, 2022, Smith et al 2017). \textit{D. tenuijunctus} is a lightly silicified diatom with a diameter of less than 15 µm and floats longer in the water column due to its higher buoyancy. Therefore, \textit{D. tenuijunctus} bloom could influence carbon sequestration from the surface to the ocean bottom. Moreover, their dominance could play a different role as a food source in the marine food web in comparison with those of \textit{P. antarctica} and other diatoms.

The mechanism by which the predominant phytoplankton species differed dramatically between the ASP and PIP remains unclear. Basal melting in the PIP possibly influences phytoplankton physiology (Rignot et al 2015, Park et al 2017). Additionally, Antarctic coastal currents flowing from the Amundsen Sea to the Ross Sea could explain the intermediate characteristics of the phytoplankton communities in the ASP, which is located between the PIP and WGP (Jacobs et al 2002). \textit{D. tenuijunctus} that are entrapped in ice during the autumn are released into the water column in spring (Saggiomo et al 2017) and may have grown and accumulated near the ice shelves by currently unknown physical processes. Meltwater-driven gyres in the PIB (Yoon et al 2022) could be a physical phenomenon that explains the distribution of this species in the PIP. The waters dominated by \textit{D. tenuijunctus} could have different sinking rates, Fv/Fm ratios, net community productions, and carbon uptake rates than those in \textit{P. antarctica}-dominated waters. Since there are few reports of \textit{D. tenuijunctus} blooms in the Southern Ocean, it is also necessary to compare the physiological and ecological characteristics in the waters that are dominated by this species and other diatoms such as \textit{Fragilariopsis}, \textit{Pseudonitzschia}, and \textit{Chaetoceros}, even though they all belong to the group of diatoms. Massive \textit{D. tenuijunctus} blooms could significantly impact biological carbon pumps and food web structures along the melting Antarctic coasts in the future. Therefore, it is urgent to elucidate the mechanisms of massive \textit{D. tenuijunctus} blooms in the PIP and their physiological and ecological characteristics.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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Conflict of interest

The authors have declared that no competing interests exist.

Ethics statement

The authors declare that our article does not contain any studies involving human or animal participants.

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