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# Macromolecular compositions of phytoplankton in the Amundsen Sea, Antarctica

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ABSTRACT

The biochemical compositions (proteins, carbohydrates, and lipids) of phytoplankton provide useful information for their environmental growth conditions and nutritional status as a basic food source for upper trophic consumers. Concentrations of these compositions were assessed at 100, 30, and 1% light penetration depths within the euphotic zone in the Amundsen Sea, Antarctica, using colorimetric techniques. The major inorganic nutrients were generally abundant throughout the study area. The average chlorophyll a (chl-a) concentration was 49.2 mg $m^{-2}$ (S.D.= ± 27.6 mg $m^{-2}$) and large phytoplankton ( > 20 μm) accounted for 64.1% of the total chl-a concentration. The biochemical compositions of the phytoplankton were not significantly different among different light depths or productivity stations. The overall compositions of proteins, carbohydrates, and lipids from all stations averaged 65.9% (S.D.= ± 12.5%), 22.4% (S.D.= ± 10.9%), and 11.7% (S.D.= ± 6.5%), respectively. Regardless of dominant phytoplankton species, nitrogen-abundant conditions sustained high protein compositions of phytoplankton in the Amundsen Sea during the cruise period. Based on the macromolecular compositions, the average food material (FM) concentration was 219.4 μg $L^{-1}$ (S.D.= ± 151.1 μg $L^{-1}$) and correlated positively with the primary productivity in the Amundsen Sea. High protein/carbohydrate ratios ( > 1) and large proportions of proteins suggest that phytoplankton provide nitrogen-sufficient foods to higher trophic consumers through a higher efficiency of protein carbon incorporated into herbivores.



## 1. Introduction

Phytoplankton consist of important biochemical components such as proteins, carbohydrates, and lipids. The proteins play a role in biological processes such as enzymatic catalysis and growth, and transfer carbon to herbivore biomass with higher efficiency than other biomolecular classes (Stryer, 1988; Lindqvist and Lignell, 1997). The lipids and carbohydrates act as an energy storage and are essential components of all membranes (Handa, 1969; Parrish, 1987).

These macromolecules are analyzed to determine the physiological condition of phytoplankton in various oceans using the carbon isotope allocations into different photosynthetic endproducts (proteins, polysaccharides, lipids, and low molecular weight metabolites) after incubation or the analysis of differences in the macromolecular composition of bulk particulate organic matter (POM) samples (Fabiano et al., 1993; Danovaro et al., 2000; Suárez and Marañón, 2003; Lee et al., 2008, 2009; Kim et al., in press). The advantage of carbon isotope method is that it elucidates the rapid response of biochemical compositions to environmental factors during short-time scales. However, previous studies have reported that carbon incorporated into their cells could change depending on the time in the day–night cycle (Lancelot and Mathot, 1985; Boëchat and Giani, 2008). Therefore, these results can not reflect patterns of the photosynthetic carbon allocations of phytoplankton for a longer period. In comparison, macromolecular compositions of bulk POM samples obtained by filtering seawater provide the physiological status of the phytoplankton over a relatively long time period, thus indicating the food quality for higher trophic levels (Fabiano et al., 1993, 1996; Boëchat and Giani, 2000; Danovaro et al., 2000; Kim et al., in press).

POM largely originates from dissolved organic substances or particulate sized organic detritus of allochthonous (terrestrial material and fecal matter) or autochthonous origin such as phytoplankton and bacteria (Volkman and Tanoue, 2002). It plays a crucial role in controlling nutritional, microbial, and geochemical cycles in various ecosystems (Wakeham and Lee, 1989; Benner et al., 1997; Danovaro et al., 2000). However, discrimination between particulate and dissolved matter by filtration is difficult because particles depend on

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different filter types and pore size. POM analysis usually requires filters of sizes from 0.2 to 0.7 μm (Fabiano et al., 1995, 1999; Volkman and Tanoue, 2002; Sugimoto et al., 2006). Fabiano et al. (1995) and Fabiano et al. (1999) used 0.2 μm pore-size polycarbonate filters and 0.4 μm pore-size filters for analyses of lipids, proteins, and carbohydrates in POM, respectively. Since POM contains pico-sized phytoplankton (0.2–2 μm) and bacterioplankton, water samples were filtered through 0.2 μm pore diameter (Fabiano et al., 1995). However, the use of GF/F glass fiber filters (nominal pore size 0.7 μm) is most common in most studies concerning particulate matter samples rather than using 0.2 μm nuclepore filters which tend to clog rapidly (Ríos et al., 1998; Danovaro et al., 1999, 2000; Khodse and Bhosle, 2012). Also, GF/F filters have good resistance to most organic and inorganic solvent and are made low blank contamination by combustion. Several studies reported that POM in the euphotic zone is mostly composed of phytoplankton (Saino and Hattori, 1980; Fabiano et al., 1993; Biddanda and Benner, 1997). Hence we analyzed the bulk biochemical components of POM to understand the overall body composition of phytoplankton in the Amundsen Sea.

Although no significant trend in the mean sea ice coverage was found for the Antarctic Ocean as a whole, the Antarctic sea ice cover has increased slightly since the late 1970s while Arctic sea ice has decreased (Parkinson and Cavalieri, 2012; Strammerjohn et al., 2012). However, regional variability is large in the Antarctic Ocean: slight increases in the Ross Sea, Weddell Sea, and Indian Ocean sectors, but significant decreases in the Amundsen-Bellingshausen Sea regions during 1979–2010, based on satellite data (Parkinson and Cavalieri, 2012). A rapid sea ice retreat in the Amundsen Sea is caused by relatively high light intensity during the austral spring–summer and an intrusion of warm Circumpolar Deep Water (CDW) (Rignot and Jacobs, 2002; Walker et al., 2007; Parkinson and Cavalieri, 2012; Strammerjohn et al., 2012). The decrease in sea ice cover from environmental change could alter physiological conditions of phytoplankton as a basic food source and thus the marine ecosystem in the Amundsen Sea. However, biochemical compositions of phytoplankton have not been investigated in the Amundsen Sea. Therefore, the main objectives of this study are to (1) understand the physiological status of phytoplankton based on macromolecular composition, (2) determine important controlling factors for the different compositions, and (3) estimate the concentrations of food material (FM) available to higher trophic levels in the Amundsen Sea.

## 2. Materials and methods

### 2.1. Study area and water sampling

All samples were obtained in the Amundsen Sea in the western Antarctic Ocean from 11 February to 14 March, 2012 using the R/V ARAON (Fig. 1 and Table 1). Sampling was conducted at 14 stations to determine the biochemical compositions of POM. Physical properties such as water temperature and salinity and water samples for biological and chemical property analysis were obtained from a CTD—rosette sampler system equipped with 24 10-L Niskin bottles.

### 2.2. Major inorganic nutrient and chlorophyll a analyses

Samples for major inorganic nutrients and chlorophyll a (chl-a) were obtained at 3 depths with different light levels (100, 30, and 1% surface light). The major inorganic nutrients (ammonium, phosphate, nitrate+nitrite, and silicate) were measured on board using a QuAAtro auto analyzer (Seal Analytical, Germany). Seawater samples for total chl-a were filtered through 25 mm GF/F filters (Whatman, nominal 0.7 μm pore size). For size-fractionated chl-a, the samples were passed sequentially through 20 μm and 3 μm membrane filters, then 47 mm GF/F filters (Whatman, nominal 0.7 μm). Chl-a was extracted in 90% acetone for 24 h at 4 °C following Parsons et al. (1984), and quantified using a Trilogy fluorometer (Turner Designs, USA).

### 2.3. Particulate organic carbon, nitrogen, and $\delta^{13}C$ analyses

Samples for particulate organic carbon (POC), nitrogen (PON), and $\delta^{13}C$ were filtered through 25 mm GF/F filters (Whatman, nominal 0.7 μm). The filters were immediately frozen and preserved at −80 °C until analysis. After overnight HCl fuming to remove carbonate, a Finnigan Delta$^{plus}$ XL mass spectrometer was used for determining concentrations of POC and PON at the stable isotope laboratory of the University of Alaska Fairbanks.

### 2.4. Macromolecular analysis of POM and statistical analyses

Water samples to obtain the macromolecular composition (proteins, carbohydrates, and lipids) of POM were obtained from 3 depths with different light levels (100, 30, and 1%) during the cruise. One liter of each seawater sample was filtered through a pre-combusted 47 mm GF/F filter (Whatman, nominal 0.7 μm) and then was stored at −80 °C until analysis. Extractions and quantifications of biochemical classes were performed in the laboratory based on the method used by Kim et al. (in press). Proteins were analyzed quantitatively using the method of Lowry et al. (1951). Absorbance was measured at 750 nm using a spectrophotometer (Labomed, Germany). The concentration of proteins was calculated from calibration curves with a protein standard solution (2 mg $mL^{-1}$, SIGMA). Carbohydrate analyses were performed following extraction using the phenol-sulfuric method from Dubois et al. (1956). The concentration of carbohydrates was determined by measuring the absorbance of samples at 490 nm with a glucose standard solution (1 mg $mL^{-1}$, SIGMA). Lipids were extracted from POM with chloroform and methanol (1:2, v/v) according to Bligh and Dyer (1959) and Marsh and Weinstein (1966). Absorbance for lipids was measured at 360 nm. Tripalmitin solutions were used as the standard for lipid concentration. Food material (FM) was defined as the sum of particulate protein, carbohydrate, and lipid concentrations (Danovaro et al., 2000). Statistical analyses were performed using SPSS software for *t*-tests and Pearson's correlation coefficient at the level of significance ($p < 0.05$).

## 3. Results

### 3.1. Physical and chemical characteristics of the study area

Physical characteristics of the study area are presented in Table 1. Small fluctuations were observed in water temperature (−1.8 to −0.9 °C) and salinity (33.4 to 33.9 psu) within the euphotic zone at all stations (Table 1). The average temperature and salinity from the surface to the depth of 1% light were −1.5 °C (S.D.= ±0.3 °C) and 33.6 psu (S.D.= ±0.2 psu), respectively.

The vertical profiles of major inorganic nutrients (ammonium, phosphate, nitrate+nitrite, and silicate) between the surface and 1% light depths at all stations except St. 35 are shown in Table 2. Ammonium and phosphate concentrations ranged from 0.1 to 2.8 μM and 1.2 to 2.4 μM with means of 1.1 μM (S.D.= ±0.7 μM) and 1.7 μM (S.D.= ±0.3 μM), respectively. The nitrate+nitrite concentration was lowest at St. 10 (11.8 μM) and highest at a depth of 1% light at St. 63 (29.8 μM). Silicate concentration ranged from 53.6 to 91.6 μM (Table 2). Generally, major inorganic nutrient concentrations at sampling depths were not significantly different among the macromolecular stations (Table 2).

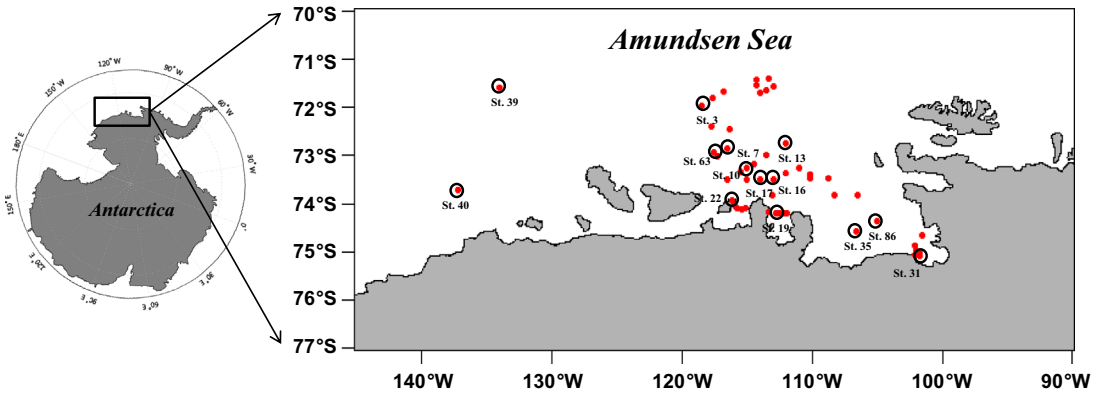


**Fig. 1.** Location of sampling area in the Amundsen Sea in 2012 (large open circles represent macromolecular stations).

**Table 1**
Locations and environmental conditions at 14 composition stations in the Amundsen Sea (temperature and salinity were averaged from surface to 1% light depth).

| Station | Latitude (°S) | Longitude (°W) | Euphotic depth (m) | Temperature (°C) | Salinity (psu) |
|---|---|---|---|---|---|
| St. 3 | 71.946 | 118.454 | 20 | −1.81 | 33.64 |
| St. 7 | 72.846 | 116.346 | 20 | −1.65 | 33.59 |
| St. 10 | 73.25 | 114.998 | 34 | −1.16 | 33.54 |
| St. 13 | 72.751 | 111.997 | 86 | −1.80 | 33.88 |
| St. 16 | 73.499 | 113.000 | 12 | −1.40 | 33.64 |
| St. 17 | 73.500 | 115.003 | 35 | −1.27 | 33.60 |
| St. 19 | 74.194 | 112.529 | 40 | −1.58 | 33.79 |
| St. 22 | 73.924 | 116.137 | 30 | −0.92 | 33.72 |
| St. 31 | 75.087 | 101.759 | 32 | −1.17 | 33.71 |
| St. 35 | 74.571 | 106.599 | 50 | – | – |
| St. 39 | 71.581 | 133.988 | 25 | −1.26 | 33.39 |
| St. 40 | 73.686 | 136.984 | 20 | −1.83 | 33.60 |
| St. 63 | 73.094 | 117.587 | 20 | −1.75 | 33.41 |
| St. 86 | 73.809 | 106.537 | 35 | −1.52 | 33.53 |

### 3.2. Total and size-fractionated chlorophyll a concentrations

Average chl-a concentration of phytoplankton integrated from 100% to 1% light penetration depths was 49.2 mg $m^{-2}$ (S.D.= ± 27.6 mg $m^{-2}$; Table 3). The lowest and highest concentrations were 8.0 mg $m^{-2}$ at St. 39 and 95.8 mg $m^{-2}$ at St. 10, respectively. The size-fractionated chl-a concentrations were averaged from 3 depths (100, 30, and 1% surface light). The phytoplankton community in the Amundsen Sea, with the exception of 4 stations (Stns. 31, 39, 40, and 86), was dominated by large-sized phytoplankton (> 20 μm) accounting for 64.1 ± 9.8% of the total chl-a concentration, followed by middle-sized (3–20 μm; 23.6 ± 3.4%), and small cells (0.7–3 μm; 12.4 ± 6.5%) (Table 3). At Stns. 31, 39, 40, and 86, middle-sized phytoplankton (3–20 μm) were predominant (50.9 ± 14.7%) in the phytoplankton community (Table 3).

### 3.3. Particulate organic carbon, nitrogen, and $\delta^{13}C$ analyses

The POC and PON concentrations averaged over depths for 100% to 1% surface light were 194.3 ± 138.9 μg $L^{-1}$, and 41.1 ± 29.0 μg $L^{-1}$, respectively (Table 3). A strong linear relationship was found between POC and PON (PON=POC*0.2101, $r^2$=0.98, $p$ < 0.001). The C/N ratio of POM was highest (6.6) at St. 3, whereas it was the lowest (4.7) at St. 39 among the 14 stations, with a mean of 5.5 (S.D.= ± 0.5). The $\delta^{13}C$ value of POM ranged from −28.0‰ to −24.7‰ with a mean of −25.8‰ (S.D.= ± 1.0‰) (Table 3).

**Table 2**
The vertical concentration profiles of major inorganic nutrient from the surface to 1% light depth in the Amundsen Sea.

| Station | Light depth (%) | Phosphate (μM) | Nitrate+Nitrite (μM) | Ammonium (μM) | Silicate (μM) |
|---|---|---|---|---|---|
| St. 3 | 100 | 1.746 | 22.621 | 0.503 | 69.717 |
| | 30 | 1.806 | 23.279 | 0.503 | 70.432 |
| | 1 | 1.821 | 23.696 | 0.591 | 70.949 |
| St. 7 | 100 | 1.750 | 21.714 | 0.797 | 85.296 |
| | 30 | 1.783 | 21.567 | 0.822 | 85.717 |
| | 1 | 1.784 | 21.459 | 0.840 | 85.916 |
| St. 10 | 100 | 1.165 | 11.763 | 0.603 | 81.009 |
| | 30 | 1.214 | 11.864 | 0.805 | 81.746 |
| | 1 | 2.359 | 28.292 | 2.762 | 91.607 |
| St. 13 | 100 | 2.127 | 28.766 | 0.252 | 71.229 |
| | 30 | 2.208 | 28.809 | 0.207 | 71.748 |
| | 1 | 2.308 | 29.824 | 0.096 | 75.154 |
| St. 16 | 100 | 1.362 | 14.893 | 0.558 | 76.457 |
| | 30 | – | – | – | – |
| | 1 | 1.405 | 15.342 | 0.665 | 77.352 |
| St. 17 | 100 | 1.418 | 16.493 | 0.592 | 78.008 |
| | 30 | 1.466 | 17.013 | 0.630 | 79.192 |
| | 1 | 2.127 | 27.775 | 0.754 | 88.523 |
| St. 19 | 100 | 1.930 | 25.104 | 0.733 | 80.107 |
| | 30 | 2.040 | 25.419 | 0.820 | 81.808 |
| | 1 | – | – | – | – |
| St. 22 | 100 | 1.321 | 12.567 | 2.016 | 84.245 |
| | 30 | 1.379 | 12.946 | 2.082 | 84.895 |
| | 1 | 1.483 | 13.932 | 2.306 | 85.802 |
| St. 31 | 100 | 1.516 | 18.657 | 2.406 | 62.999 |
| | 30 | 1.551 | 18.937 | 2.249 | 63.292 |
| | 1 | 1.583 | 19.132 | 2.348 | 63.623 |
| St. 39 | 100 | 1.926 | 25.949 | 0.775 | 54.654 |
| | 30 | 1.988 | 26.411 | 0.712 | 54.872 |
| | 1 | 2.020 | 26.343 | 0.697 | 53.617 |
| St. 40 | 100 | 2.035 | 25.504 | 1.091 | 67.025 |
| | 30 | 2.083 | 25.362 | 1.094 | 67.613 |
| | 1 | 2.087 | 26.058 | 1.089 | 67.527 |
| St. 63 | 100 | 1.437 | 18.508 | 0.763 | 80.735 |
| | 30 | 1.495 | 17.243 | 0.896 | 80.786 |
| | 1 | 1.637 | 20.695 | 1.006 | 81.429 |
| St. 86 | 100 | 1.462 | 15.640 | 1.636 | 68.285 |
| | 30 | 1.472 | 15.947 | 1.926 | 68.049 |
| | 1 | 1.650 | 18.738 | 2.017 | 66.394 |

### 3.4. Biochemical compositions of POM

Biochemical compositions and FM (food material) of POM at 100, 30, and 1% light penetration depths for each station are summarized in Table 4. The average concentrations of the proteins, carbohydrates, and lipids from the 14 stations were 146.8 μg $L^{-1}$ (S.D.= ± 97.3 μg $L^{-1}$), 53.5 μg $L^{-1}$ (S.D.= ± 52.2 μg $L^{-1}$), and 19.1 μg $L^{-1}$ (S.D.= ± 6.3 μg $L^{-1}$), respectively. Proteins and carbohydrates were relatively high, ranging from 5.9 to 396.2 μg $L^{-1}$ and

2.8 to 216.0 μg $L^{-1}$, respectively, whereas lipids had a narrow range from 13.2 to 36.9 μg $L^{-1}$. For the 14 stations, the percentage of each biochemical component of POM at the depth of each of the three tested light levels is shown Fig. 2. The proteins contributed approximately >60% to the biochemical compositions regardless of depth, whereas the contribution of lipids was the lowest (<15%). The depth-averaged macromolecular composition of POM was dominated by proteins (mean ± S.D. = 65.9 ± 12.5%), followed by carbohydrates (mean ± S.D. = 22.4 ± 10.9%), and lipids (mean ± S.D. = 11.7 ± 6.5%) (Fig. 3). Based on the composition of proteins, carbohydrates, and lipids, the average FM concentration of POM was 219.4 μg $L^{-1}$ (S.D. = ± 151.1 μg $L^{-1}$) in this region (Fig. 4). The highest value of FM (639.4 μg $L^{-1}$) was observed at St. 16, whereas the lowest was 42.7 μg $L^{-1}$ at St. 13 (Fig. 4).

### 3.5. Biochemical composition in relation to environmental factors

Based on Pearson's correlation analysis, the percentage of carbohydrates was found to have a positive relationship only with silicate ($r$=0.36, $n$=37, $p$<0.05) and a negative relationship with proteins ($r$=−0.85, $p$<0.01; Table 5). Proteins had negative relationships with lipids, phosphate, and dissolved inorganic nitrogen (DIN=nitrate+nitrite+ammonium concentration) ($r$=−0.50, −0.48, and −0.39, respectively, $p$<0.01), whereas lipids had a negative relationship with silicate ($r$=−0.47, $p$<0.01). We also assessed the relationship between the biochemical composition and physical properties. Temperature was correlated only with lipids

**Table 3**
Total chl-a concentrations (mg $m^{-2}$), percentage of size-fractionated chl-a (%), POC, PON, and $\delta^{13}C$ (Total chl-a was integrated from surface to 1% depths, whereas the remaining parameters were averaged from 100, 30, and 1% light penetration depths).

| Station | Integrated chl-a (mg $m^{-2}$) | Size-fractionated chl-a | | | POC (μg $L^{-1}$) | PON (μg $L^{-1}$) | $\delta^{13}C$ (‰) |
|---|---|---|---|---|---|---|---|
| | | >20 μm (%) | 3–20 μm (%) | 0.7–3 μm (%) | | | |
| St. 3 | 43.2 | 68.1 | 23.6 | 8.3 | 188.6 | 33.3 | −24.7 |
| St. 7 | 67.0 | 63.7 | 23.4 | 12.9 | 227.7 | 55.1 | −25.8 |
| St. 10 | 95.8 | – | – | – | 361.4 | 77.9 | −25.3 |
| St. 13 | 29.3 | – | – | – | 86.3 | 17.8 | −25.0 |
| St. 16 | 74.5 | 76.3 | 18.7 | 5.0 | 660.8 | 138.3 | −26.2 |
| St. 17 | 65.7 | 67.3 | 22.9 | 9.8 | 237.3 | 46.7 | −25.7 |
| St. 19 | 26.8 | 46.9 | 29.5 | 23.6 | 85.7 | 18.7 | −27.0 |
| St. 22 | 56.3 | 62.0 | 23.5 | 14.5 | 301.6 | 56.6 | −24.8 |
| St. 31 | 91.2 | 22.8 | 64.1 | 13.1 | 237.3 | 54.5 | −28.0 |
| St. 35 | 30.7 | – | – | – | 110.3 | 23.2 | −26.3 |
| St. 39 | 8.0 | 27.6 | 52.3 | 20.1 | 125.9 | 31.2 | −25.3 |
| St. 40 | 8.2 | 37.3 | 30.0 | 32.7 | 100.2 | 18.8 | −25.5 |
| St. 63 | 43.7 | – | – | – | 175.5 | 37.8 | −24.8 |
| St. 86 | 48.2 | 23.1 | 57.0 | 19.9 | 136.8 | 32.1 | −26.6 |
| **Average** | **49.2** | **49.5** | **34.5** | **16.0** | **194.3** | **41.1** | **−25.8** |
| **S.D. (±)** | **27.6** | **20.5** | **16.7** | **8.2** | **138.9** | **29.0** | **1.0** |

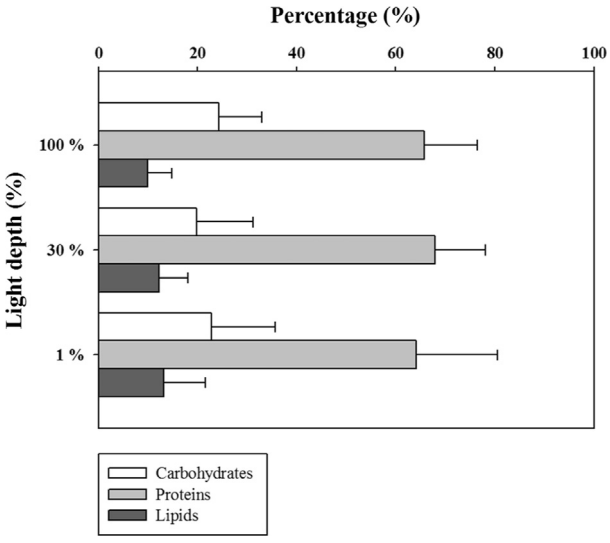


**Fig. 2.** The macromolecular compositions (carbohydrates, proteins, and lipids) of phytoplankton from depths at three light levels (100, 30, and 1%).

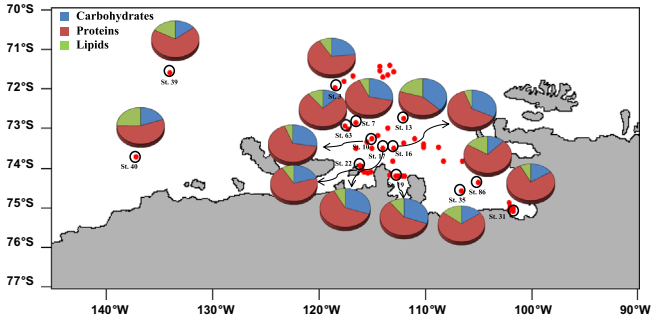


**Fig. 3.** Macromolecular composition of phytoplankton averaged from three depths at different light levels (100, 30, and 1%) at each station in the Amundsen Sea.

**Table 4**
The concentrations of different macromolecular classes (carbohydrates, proteins, and lipids) of phytoplankton at three light penetration depths (100, 30, and 1%).

| Station | Carbohydrate concentration (μg $L^{-1}$) | Protein concentration (μg $L^{-1}$) | Lipid concentration (μg $L^{-1}$) | FM concentration (μg $L^{-1}$) |
|---|---|---|---|---|
| St. 3 | 38.3 (36.8–40.6) | 112.1 (105.6–120.6) | 14.1 (14.0–14.2) | 164.5 (160.5–172.2) |
| St. 7 | 83.2 (72.4–90.7) | 190.7 (178.3–204.2) | 19.7 (15.9–21.9) | 293.5 (286.6–297.8) |
| St. 10 | 128.8 (76.3–193.5) | 299.1 (248.6–395.4) | 24.8 (18.5–34.4) | 452.7 (348.1–623.2) |
| St. 13 | 27.7 (23.4–33.3) | 44.7 (5.9–89.9) | 14.2 (13.4–15.1) | 86.6 (42.7–137.4) |
| St. 16 | 204.5 (193.0–216.0) | 391.4 (386.5–396.2) | 34.4 (31.8–36.9) | 630.2 (621.0–639.4) |
| St. 17 | 87.3 (74.1–97.8) | 180.2 (156.1–212.9) | 21.6 (16.3–28.9) | 289.1 (261.9–331.7) |
| St. 19 | 41.4 (35.6–47.2) | 80.2 (62.4–98.0) | 13.2 (13.2–13.2) | 134.7 (111.1–158.3) |
| St. 22 | 67.1 (39.8–107.5) | 221.4 (188.4–245.2) | 26.9 (16.6–33.5) | 315.3 (244.8–383.2) |
| St. 31 | 37.7 (22.8–59.1) | 184.1 (177.9–190.8) | 17.1 (16.3–17.8) | 238.9 (230.0–254.2) |
| St. 35 | 18.2 (13.4–23.9) | 88.3 (62.0–103.2) | 17.1 (15.9–18.9) | 123.5 (95.1–142.4) |
| St. 39 | 13.0 (6.5–19.7) | 63.4 (51.1–84.2) | 14.9 (14.2–15.9) | 91.3 (72.2–111.3) |
| St. 40 | 12.5 (2.8–29.4) | 35.3 (21.3–45.5) | 15.8 (14.4–17.2) | 63.6 (61.6–65.0) |
| St. 63 | 23.0 (19.0–26.2) | 140.1 (114.5–152.9) | 18.5 (18.0–19.5) | 181.6 (158.8–194.6) |
| St. 86 | 13.4 (6.1–22.7) | 83.0 (74.1–92.7) | 18.2 (17.6–19.1) | 114.6 (105.9–121.9) |
| **Average** | **53.5** | **146.8** | **19.1** | **219.4** |
| **S.D. (±)** | **52.2** | **97.3** | **6.3** | **151.1** |

and salinity correlated with carbohydrates ($r=-0.35$ and 0.37, respectively, $p<0.05$; Table 5).

## 4. Discussion and conclusions

### 4.1. Origin of POM

Since POM is derived from different sources, the C/N ratio and stable carbon isotope ratio ($\delta^{13}C$) are useful tools to assess major components of organic matter in the oceans (Lobbes et al., 2000; Lee and Whitledge, 2005). The average C/N ratios for fresh living phytoplankton and bacteria are generally 6–10 and 3–5, respectively, whereas it varies from 15 or higher for the terrestrial POM (Redfield et al., 1963; Goldman et al., 1987; Lee and Fuhrman, 1987; Zweifel et al., 1993; Montagnes et al., 1994; Fagerbakke et al., 1996; Ríos et al., 1998; Lobbes et al., 2000). The $\delta^{13}C$ signature of oceanic POM provides the key evidence for a marine origin. According to earlier studies, $\delta^{13}C$ values ranged from −27.5‰ to −26.4‰ for POM (mainly consisting of diatoms) in samples collected from the Antarctic Australian Sector (Wada et al., 1987) and $-25.6\pm1.9$‰ for phytoplankton (< 62 μm) near King George Island, Antarctica (Corbisier et al., 2004). Moreover, Lee et al. (2012) observed $\delta^{13}C$ values of POM (mostly dominated by *Phaeocystis* sp.) between −29.3‰ and −27.7‰ in the Amundsen Sea polynyas. In this study, the C/N ratio and $\delta^{13}C$ value of POM ranged from 4.7 to 6.6 (mean ± S.D. = 5.5 ± 0.5) and from −28.0‰ to −24.7‰ (mean ± S.D. = −25.8 ± 1.0‰), respectively. In addition, material inputs in the Amundsen Sea are more likely to be driven by the seasonal Sea ice rather than riverine source (Jenkins et al., 2010). This implies that the POM was mostly derived from phytoplankton and not greatly influenced by terrestrial organic matter and bacteria. Therefore, the biochemical compositions of POM are believed to have been affected largely by growth conditions of phytoplankton in this study.

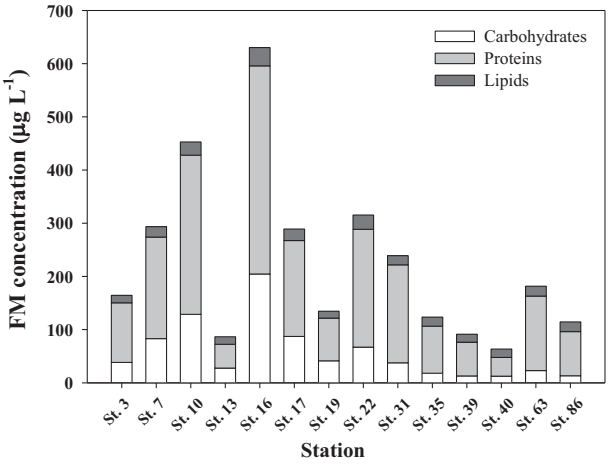


**Fig. 4.** FM (Food Material) concentrations (sum of carbohydrates, proteins, and lipids concentrations) of phytoplankton averaged from three depths at different light levels (100, 30, and 1%) at each station.

### 4.2. Phytoplankton biomass

The phytoplankton biomass in the Antarctic Ocean shows a strong seasonal variability (El-Sayed and Weber, 1982; Moline and Prézelin, 1996; Smith et al., 1998, 2000). Smith et al. (1998) found that the average chl-a concentration peaked in summer and decreased in winter within the top 30 m near the western Antarctic Peninsula. Moline and Prézelin (1996) observed a high chl-a concentration in December during their observation period from August 1993 to January 1994 in shelf waters adjacent to Palmer Station, Antarctica. In our study, the mean chl-a concentrations integrated from surface to the 1% light depth was 49.2 mg $m^{-2}$ (S.D. = ± 27.6 mg $m^{-2}$; Table 3). In comparison, Lee et al. (2012) reported that the average chl-a concentration was 190.3 mg $m^{-2}$, ranging widely (6.7–742.5 mg $m^{-2}$) in the Amundsen Sea in 2010/2011. The integrated chl-a concentration in this study was significantly lower than in 2010/2011 (Lee et al., 2012), mainly due to a large seasonal variation of primary production in the Amundsen Sea (Kim et al., 2015). Our measurement was conducted during the late summer period (February–March) after a large phytoplankton bloom, whereas the phytoplankton biomass in Lee et al. (2012) was measured during late December to January within the bloom period (Arrigo and van Dijken, 2003; Arrigo et al., 2012).

### 4.3. Biochemical composition in relation to environmental factors

In our study, overall protein composition was highest (65.9 ± 12.5%) and lipid composition was lowest (11.7 ± 6.5%). This pattern is the reverse of the trend in the Arctic Ocean, where the lipid composition was highest (50 ± 12.5%) and the protein contribution was lowest (15 ± 11.2%), reported by Kim et al. (in press). According to earlier reports, the macromolecular composition of phytoplankton is highly variable depending on various environmental factors such as light conditions (Morris et al., 1974; Smith and Morris, 1980), growth stages (Smith et al., 1997), species (Liebezeit, 1984; Moal et al., 1987; Rivkin and Voytek, 1987), and nutrient availability (Morris et al., 1974; Kilham et al., 1997). Therefore, we would like to address these main controlling factors one by one.

A higher light intensity usually results in diminished protein content and relatively enhanced lipid content, as suggested by several studies (Smith and Morris, 1980; Smith et al., 1987, 1997; Suárez and Marañón, 2003; Lee et al., 2008). Boëchat and Giani (2008) reported that the diel cycle of light clearly plays a primary role

**Table 5**
Pearson's correlation matrix of macromolecular compositions and environmental factors. DIN: total dissolved inorganic nitrogen.

| | %Carbohydrates | %Proteins | %Lipids | $PO_4$ | $SiO_2$ | DIN | Salinity | Temperature |
|---|---|---|---|---|---|---|---|---|
| **%Carbohydrates** | 1 | | | | | | | |
| **%Proteins** | −0.85** | 1 | | | | | | |
| **%Lipids** | – | −0.50** | 1 | | | | | |
| **$PO_4$** | – | −0.48** | 0.56** | 1 | | | | |
| **$SiO_2$** | 0.36* | – | −0.47** | – | 1 | | | |
| **DIN** | – | -0.39* | 0.51** | 0.98** | – | 1 | | |
| **Salinity** | 0.37* | – | – | – | – | – | 1 | |
| **Temperature** | – | – | −0.35* | −0.36* | – | −0.35* | – | 1 |

"–" indicates not significant.
* $p<0.05$.
** $p<0.01$.

in the biochemical composition of phytoplankton. However, no significant relationship between biochemical compositions and the light levels at our sampled depths was found in our study (Fig. 2). The mean mixed layer depth (mean ± S.D. = 34.7 ± 13.7 m) was similar to the mean euphotic depth in this study (mean ± S.D. = 32.8 ± 18.3 m) (*t*-test, $p > 0.05$), which implies that light conditions of the phytoplankton during growth could be similar within the euphotic layer given a well mixed water column condition during our cruise period.

Growth stage is another controlling factor of the biochemical composition of phytoplankton. Some studies reported that actively growing phytoplankton is mainly associated with protein synthesis (Morris, 1981; Ríos et al., 1998), while the proportion of storage compounds (carbohydrates and lipids) decreases. In other words, under stationary phase conditions or as phytoplankton become degraded, the protein proportion tends to decrease. The growth rate of phytoplankton in this study could be lower than that in developing bloom conditions since our measurements were done during a later stage of bloom development (Smith et al., 2000). In fact, Kim et al. (2015) reported an average specific carbon uptake rate (not considering phytoplankton biomass) significantly lower in this study year than that in Lee et al. (2012). This indicated that phytoplankton was not active growth condition in this study. Nevertheless, we found high protein concentrations during a later bloom stage in this study (Table 4). This result is consistent with result of Fabiano et al. (1993) who reported that proteins are always dominant in a marginal ice zone regardless of the bloom stage in the Ross Sea, Antarctica.

In our study, the large differences in the phytoplankton size structure were mainly attributed to a different species composition in the Amundsen Sea. The phytoplankton community at all stations except 4 (Stns. 31, 39, 40, and 86) was dominated by large-sized phytoplankton (> 20 μm) accounting for 64.1 ± 9.8% of the total chl-a concentration (Table 3). At Stns. 31, 39, 40, and 86, middle-sized phytoplankton (3–20 μm) were predominant (50.9 ± 14.7%; Table 3). The dominant species was *Phaeocystis antarctica* at most of our stations, but *Dactyliosolen tenuijunctus* (diatoms) was the most dominant species at 4 of the stations (Stns. 31, 39, 40, and 86). Several studies have shown that the biochemical composition of marine phytoplankton depends on species composition (Liebezeit, 1984; Moal et al., 1987; Rivkin and Voytek, 1987; Harrison et al., 1990). The different sizes of phytoplankton, based on isotope-labeled experiments, incorporate different quantities of macromolecular classes (Lee et al., 2009). Lee et al. (2009) reported that small phytoplankton (< 5 μm) incorporated much more carbon into proteins than large-sized phytoplankton (> 5 μm) under substantially high ammonium concentrations (~5 μM) in the Bering Strait and the Chukchi Sea. However, proteins were predominant at all stations in this study. A possible reason for no discernable differences in biochemical composition among stations dominated by different species could be environmental factors such as nutrients, which are a more important factor than species composition in allocation into different macromolecular compositions. In $^{14}C$-labeling experiments, Suárez and Marañón (2003) reported that patterns in photosynthate partitioning among macromolecules were not related to the species composition of phytoplankton over an entire annual cycle. Our data also support that phytoplankton species are, therefore, less important than environmental factors in controlling patterns in macromolecular compositions.

Nutrient availability is an important factor that determines the biochemical composition of phytoplankton. Generally, protein contents increases under nitrogen-replete conditions or those where nutrients are not limited. In nutrient-limited conditions, triglyceride content (energy storage) increases because of shifts from protein to lipid metabolism (Lombardi and Wangersky, 1991; Smith et al., 1997; Takagi et al., 2000). Subsequently, lipids and carbohydrates increase under conditions of nutrient stress (Shifrin and Chisholm, 1981; Harrison et al., 1990). In this study, high concentrations of major inorganic nutrients in the euphotic layer and high protein contents in POM (> 60%) were observed (Fig. 3 and Table 2). Our results were similar to those reported previously in the Ross Sea, Antarctica, which showed a predominance of proteins (> 50%), extracted using a similar method (Fabiano et al., 1993, 1996). In contrast, overall lipid composition in the Arctic Ocean accounted for approximately 50% of POM and the proteins were generally low (< 15%) during the summer season (Kim et al., in press). One of the major reasons for these differences in protein compositions is likely to be an ambient nutrient availability, particularly for nitrogenous compounds. In the Arctic Ocean, the concentration of nitrate + nitrite was mostly depleted in the upper mixed layer (~20 m) and the ammonium concentration was lower than 1 μM (Kim et al., in press). In contrast, the Amundsen Sea has nitrogen-replete conditions (Minas et al., 1986; Lee et al., 2012). The nitrate + nitrite concentration in this study was > 10 μM and the average ammonium was 1.1 μM (S.D = ± 0.7 μM) within the euphotic zone (Table 2). Normally, the protein/carbohydrate ratio of phytoplankton indicates the nitrogen availability. Values higher than 1 were generally observed in high productivity or bloom regions under nitrogen-abundant conditions (Fabiano et al., 1984, 1992, 1993), whereas the values lower than 1 indicated nitrogen-limited conditions (Mayzaud et al., 1989; Lizotte and Sullivan 1992; Danovaro et al., 2000). The average protein/carbohydrate ratio in this study was 4.2 (S.D = ± 3.4), which suggests sufficient nitrogen availability for the phytoplankton. Along with the high ratio of protein/carbohydrate, high proportions of protein indicate no nitrogen-limiting conditions affecting growth; this provides a higher efficiency in carbon transfer to higher trophic levels in the Amundsen Sea during the cruise period.

### 4.4. Estimation of FM concentration

Food material (FM) is defined for the sum of protein, lipid, and carbohydrate concentrations of POM (Danovaro et al., 2000). In this study, the average FM concentration was 219.4 μg $L^{-1}$ (S.D. = ± 151.1 μg $L^{-1}$) (Fig. 4). This value is lower compared to those reported previously from the Antarctic region (Table 6). Fabiano et al. (1996) reported a relatively higher FM concentration with a mean of 374 μg $L^{-1}$ in the upper mixed layer (< 48 m) in Terra Nova Bay (Table 6). In the Ross Sea, the average FM concentration measured by Fabiano et al. (1993) was 294.4 μg $L^{-1}$ (S.D. = ± 228.1 μg $L^{-1}$) with the highest concentration at 699 μg $L^{-1}$.

**Table 6**
Comparison of proteins, carbohydrates, lipids, and FM concentrations from different areas in the Antarctic and Arctic Oceans.

| Area (depth) | Proteins (μg $L^{-1}$) | Carbohydrates (μg $L^{-1}$) | Lipids (μg $L^{-1}$) | FM (μg $L^{-1}$) | Authors |
|---|---|---|---|---|---|
| Ross Sea, Antarctica (euphotic zone, < 66 m) | 18–650 | 18–279 | 2–94 | 81–699 | Fabiano et al. (1993) |
| Terra Nova Bay, Antarctica (mixed layer; < 48 m) | 108–632 | 32–444 | 3–64 | – | Fabiano et al. (1996) |
| Cretan Sea (0–1500 m) | 7–92 | 13–149 | 4–63 | 54–200 | Danovaro et al. (2000) |
| Off Princess Astrid Coast, Antarctica (0–100 m) | 24–200 | 23–138 | 15–174 | 148–393 | Dhargalkar et al. (1996) |
| Chukchi Sea, Arctic (euphotic zone) | 1–86 | 22–147 | 50–105 | 94–246 | Kim et al. (in press) |
| **Amundsen Sea, Antarctica (euphotic zone, < 86 m)** | **6–396** | **3–216** | **13–37** | **43–639** | **Present study** |

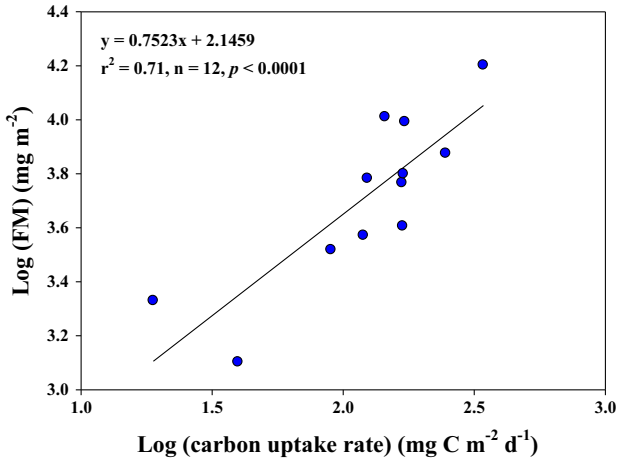


**Fig. 5.** Linear regression between FM concentration and daily primary productivity in the Amundsen Sea. FM concentration and daily primary productivity were integrated from euphotic water depths and converted to log scale for linear regression.

However, similar values (mean=217.5 μg $L^{-1}$) were observed along the Princess Astrid Coast, Antarctica in May (Dhargalkar et al., 1996). The difference in the FM concentration is likely to be induced by a regional difference in phytoplankton production. The mean daily carbon uptake rate was 0.2 g C $m^{-2}$ $d^{-1}$ (S.D.= ± 0.1 g C $m^{-2}$ $d^{-1}$) in this study (Kim et al., 2015). The Ross Sea is considered as the most productive in the Southern Ocean, with a daily production reaching up to 2.6 g C $m^{-2}$ $d^{-1}$ (El-Sayed et al., 1983; Smith et al., 1996, 2000; Arrigo et al., 1998). In comparison, the FM concentrations ranged from 93.6 to 245.9 μg $L^{-1}$ with an average of 149.2 μg $L^{-1}$ (S.D.= ± 36.5 μg $L^{-1}$) in the northern Chukchi Sea (the western part of the Arctic Ocean) during summer, recently reported by Kim et al. (in press). This concentration is approximately 70% of our FM concentration in this study (Table 6). According to Yun et al. (2014), the northern Chukchi Sea has a relatively low primary production ( < 0.2 g C $m^{-2}$ $d^{-1}$). A strong positive linear relationship ($y=0.7523x+2.1459$, $r^2=0.71$) on a log–log scale was found between FM concentration and the daily primary productivity vertically integrated from the euphotic depth (Fig. 5). Thus, the FM concentrations can reflect the regional primary production and a valuation of potential food sources for higher trophic consumers in marine ecosystems. However, to prove the FM concentration as an indicator for potential food sources to consumers, more detail studies are needed.

In this study, the $\delta^{13}C$ signature of oceanic POM was used for determining its origin. In fact, $\delta^{13}C$ measurements have been widely applied to the dietary relationships between animals and their foods because stable isotope ratios in animal tissues are related to those of their foods (DeNiro and Epstein, 1978; Fry et al., 1984; Hobson et al., 1997; Lee et al., 2005; Stowasser et al., 2012). A further investigation for the $\delta^{13}C$ pathways between POM and their potential grazers such as zooplankton could provide a better insight.

This result is based solely on one time measurement in the Amundsen Sea. In this study, we discussed only POM for potential food material. However, dissolved organic matter (DOM) such as accumulation of DOM and extracellular polymeric substances (EPS) produced by microorganisms such as prokaryotes (bacteria) and eukaryotes (phytoplankton and fungi) could be a potential energy and matter source for some other organisms in marine ecosystems (Passow, 2002). Therefore, a further investigation for the contribution of DOM will be warranted for a better estimation for the FM concentration in the marine ecosystem of the Amundsen Sea. Moreover, further studies are needed for a better understanding of potential effects on the biochemical composition of POM including phytoplankton, and the roles in the biological pump under current environmental changes such as melting sea ice in Antarctica.

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