Antarctic Phytoplankton in the Eastern Bransfield Strait Region and in the Northwestern Weddell Sea Marginal Ice Zone during Austral Summer

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Abstract: Phytoplankton on three north-south transects of the 7th Korean Antarctic Research Program (KARP) expedition in the eastern Bransfield Strait region and in the northwestern Weddell Sea marginal ice zone were sampled during austral summer from 3 to 10 January 1994. Phytoplankton cells from discrete water bottle samples from 22 stations were counted to gain quantitative information on the composition, biomass, and distribution in water column assemblages. The mean integrated total phytoplankton carbon biomass in the upper 100 m was 5.8 g C m\(^{-2}\) during the study period. The richest phytoplankton areas (7.9-14.4 g C m\(^{-2}\)) were located at stations near the Weddell Sea ice-edge zone, and were found to be associated with increase number of prymnesiophyte Phaeocystis antarctica in colonial form. The colonial P. antarctica dominated phytoplankton stocks, reaching biomass of 7.6 g C m\(^{-2}\), and average integrated biomass (3.0 g C m\(^{-2}\)) of P. antarctica from the three N-S transects was about 51% of total phytoplankton carbon biomass. Composition, biomass, and distribution of phytoplankton showed a marked difference between the Bransfield Strait region and the Weddell Sea ice-edge zone. Waters in the Bransfield Strait region were characterized by a dominance of nanoplanctonic species such as P. antarctica in motile stage, Fragilariprissis “nana”, and Cryptomonad sp., and autotrophic picoflagellates accounting for 75% of total phytoplankton carbon biomass. In the Weddell Sea marginal ice zone, however, P. antarctica in colonial stage, Thalassiosira gravida, and Fragilariprisis spp. accounted for 83% of the total phytoplankton carbon. From measurements of structure of phytoplankton assemblages at the species-specific level, it was found that Phaeocystis antarctica in colonial stage, Thalassiosira gravida, Fragilariprisis spp., Probiscia truncata, Chaetoceros socialis, C. dichaeta, C. neglectum, Corethron criophilum, Cylindrotheca closterium, Pseudonitzschia subcurvata, P. turgidoides were sea ice related species, while Phaeocystis antarctica in motile stage, Fragilariprisis “nana”, Cryptomonas sp., autotrophic picoflagellates, Probiscia alata, Pyramimonas sp., and Nitzschia lecoinei were more closely related in open waters of the Bransfield Strait region away from the marginal ice zone where there is little impact from melt waters.

Key words: Antarctic, phytoplankton, Bransfield Strait, Weddell Sea, marginal ice zone

요약 : 제7차 대한민국 남극과학연구의 일환으로 1994년 1월 3일부터 10일까지 동 Bransfield 해협과 서북 Weddell해 일원주변에서 식물플랑크톤이 채집되었다. 22개 연구정점에서 획득된 식물플랑크톤 시료는 종구성, 생물량 및 분포양상을 이해하기 위해 정량화되었다. 연구기간 동안 표층에서 수심 100m까지 적분된 평균 총 식물플랑크톤 탄소량은 5.8 g C m\(^{-2}\)였다. Weddell해
INTRODUCTION

The Weddell Sea marginal ice zone has been identified as a region of increased phytoplankton biomass and productivity (Nelson et al. 1987, 1989; Fryxell and Kendrick 1988; Cota and Smith 1989; Smith and Nelson 1990; Garrison et al. 1987, 1993; Kang and Fryxell 1993). In contrast, open waters of the Bransfield Strait region away from the Weddell Sea marginal ice zone where there is little impact from melt waters, low phytoplankton biomass and primary production have been attributed to weak vertical stratification and deep vertical mixing which limits available irradiance (Smith 1987). A few of the many observations in the Weddell and Scotia Seas on the phytoplankton assemblages in the marginal ice zone have been published as part of the Antarctic Marine Ecosystem Research in the Marginal Ice-Edge Zone (AMERIEZ) program (Garrison and Buck 1985; Fryxell 1986, 1989; Fryxell et al. 1987, 1988, 1989; Garrison et al. 1987, 1993; Fryxell and Kendrick 1988; Kang and Fryxell 1992, 1993; Kang et al. 1993a) and the European Polarstern Study (EPOS) program (Jacques and Panouse 1991; Veth et al. 1992). Few comprehensive analysis of the phytoplankton composition, biomass, and distribution deal with summer phytoplankton assemblages in the northwestern Weddell Sea marginal ice zone and in the eastern Bransfield Strait region.

Early summer phytoplankton assemblage in the Weddell Sea ice-edge zone was closely related to the gradient in density of surface sea water across the ice-edge zone (Smith and Garrison 1990). With rapidly increasing insolation during spring and summer, an increased vertical stratification induced by ice melts forming a highly stable relatively fresh upper mixed layer over saltier deeper water concentrates and restricts phytoplankton stocks to the near surface waters of the ice-edge zone. The highlight and high-nutrient waters of the marginal ice zone (MIZ) support between 25 and 67% of the primary production in the Southern Ocean (Smith and Nelson 1986). The phytoplankton assemblage found was associated with the released epontic algae which act as seeding populations (Garrison et al. 1987). These phytoplankton increases proceed southward with the receding ice edge. The general pattern of distributions showed low abundance of phytoplankton in ice-covered waters and below the euphotic zone in contrast to assemblages in the partially ice-covered or open water (Fryxell and Kendrick 1988; Kang 1992; Kang and Fryxell 1993).

The 7th Korea Antarctic Research Program
(KARP) during the 1993/94 field season was a multidisciplinary investigation of ecosystem structure between pelagic waters in the Bransfield Strait region and waters at the marginal sea-ice zone of Weddell Sea. Information on the structure of the phytoplankton assemblage and on the relative contribution of diatom and non-diatom species to the total phytoplankton biomass is somewhat scarce and for the earlier investigations rather incomplete to quantify them. In our study, we examined phytoplankton species composition and biomass, and described their mesoscale distributions. It is anticipated that this study will provide a good database for understanding structure of phytoplankton assemblages at the Weddell Sea marginal ice region during austral summer.

MATERIALS AND METHODS

Sample collection

Phytoplankton assemblages at the marginal sea-ice of the northwestern Weddell Sea and in the eastern Bransfield Strait region were sampled during early January of 1994 aboard Erebus, a 975 ton tug supply ship owned by Compagnie Nationale de Navigation in France and sailing under the command of Captain Alexandre Veyser. Data were acquired at 22 stations along three north-south transects spanning from Weddell Sea ice edge to Bransfield Strait (Fig. 1). The northern portion of the study area (Stations 18-23 and 32-38) lies over from the coastal shelf to the deep waters of Bransfield Strait, crossing the continental shelf break and slope. The southern portion of the study area (Stations 31, 46-55) lies over the continental shelf and slope near the marginal sea ice-edge of the Weddell Sea.

Temperature and salinity data were obtained using a shipboard conductivity-temperature-depth (CTD) profiling system (Sea-Bird CTD model SBE 25). In addition to the CTD system, a Sea Transmissometer (25 cm path length), pulsed fluorometer, and a solar irradiance sensor were used for recording of beam attenuation at 660 nm, for estimation of Chl a, and for recording of attenuation of photosynthetically available radiation (PAR) with depth, respectively. Water samples were obtained with a CTD/rosette unit at 7 discrete depths (1, 10, 20, 30, 50, 75, and 100 m) in 5-liter PVC Niskin bottles during the “up” casts. Aliquots of 125 ml were preserved with glutaraldehyde (final concentration of 1%). Samples were also collected via phytoplankton net tows (20-μm mesh), and preserved with glutaraldehyde (final concentration 2%); these samples were for the analysis of rare species in the phytoplankton assemblage.

Sample volumes of 50 to 100 ml were filtered through Gelman GN-6 Metricel filters (0.45-μm pore-size, 25 mm diameter; Gelman Sciences, Inc., Ann Arbor, MI, USA). The filters were mounted on microscope slides with water-soluble embedding medium (HPMA, 2-hydroxypropyl methacrylate) on board Erebus. The HPMA slides were used for estimating cell concentration and biomass. The HPMA-mounting technique, first described by Crumpton (1987), has some advantages over the classical Utermöhl sedimentation method (Kang et al. 1993b).

Cell count, biovolume, and biomass of phytoplankton

At least 300 cells were enumerated using a Zeiss
Axiophot microscope, with the combination of light and epifluorescence microscopy at 400x for microplankton, and at 1000x for autotrophic pico— and nanoplanктон (Booth 1993). For species that could not be identified under the light microscope, a Philips 515 scanning electron microscope (SEM; Polar Research Center KORDI) was used. Autotrophic pico—and nanoflagellates were filtered, dehydrated, and critical point-dried according to the standard methods (Dykstra 1992). Whole mounts coated with gold were used for the scanning electron microscopy.

Conversions from the raw cell counts to cell concentrations were done as described previously by Kang and Fryxell (1991) and Kang et al. (1993a). Cell dimensions of dominant phytoplankton species were measured to the nearest 1 μm for subsequent estimations of biolume using appropriate geometric shapes (Smayda 1978). The carbon biomass was estimated from the cell biolume with the modified Strahmann equations (Eqs. 7 and 8 in Smayda 1978). For autotrophic flagellates, the relationship log₁₀(carbon(pg)=0.94 log₁₀[cell volume (μm³)] - 0.60 was used, and for diatoms, log₁₀(carbon(pg)=0.76log₁₀[cell volume (μm³)] - 0.352.

RESULTS

Phytoplankton on three north-south transects of the 7th KARP expedition in the eastern Bransfield Strait region (BSR) and in the northwestern Weddell Sea marginal ice zone (WMIZ) were sampled during austral summer from 3 to 10 Jan. 1994 as a time series. Locations of selected stations for phytoplankton samples in the summer study are shown in relation to the ice edge and to the hydrographic conditions (Fig. 2). A pycnocline was located in the 20 to 60 m depth range (Fig. 2B). Colder temperatures (~1.0 to -1.4°C) and lower salinities (~34%) were found near the ice edges with melting sea ice (Fig. 2C, D). Hydrographic observans support previous model of auto- and water-induced stratification of the water column as an important factor responsible for the accumulation of phytoplankton biomass near the ice edge. Mixed depths near ice-edge zone during these blooms were about 30 m. The hydrographic features of the upper water column varied both horizontally and vertically. Surface water temperatures varied from -1.4°C in the WMIZ to 1.4°C in the southern portions of the BSR (Fig. 2D). Surface salinity was between 33.95% and 34.4%, with the lower values at the southern end and in the northern portions of the transects (Fig. 2C).

Phytoplankton distribution in relation to the ice edge

Vertical and horizontal structures of the surface water properties were closely related to the distribution patterns of phytoplankton. Stations near the WMIZ (Stations 46-50) showed distinct pycnoclines between 20 and 40 m with density gradients (0.32) from 0 to 100 m (Fig. 2B). Phytoplankton concentrations were high above the pycnoclines but decreased rapidly below them (Figs. 2H-M). This suggests the distributions of phytoplankton parameters were causally related to the hydrographical parameters.

The highest concentration of total phytoplankton carbon biomass (PPC) was found in subsurface layer (12 m) of WMIZ at Station 48 (465 μg C L⁻¹; Fig. 2I) and was due to mainly Phaeocystis antarctica Karsten in colonial form (Fig. 2L), a typical bloom producer in many ice-edge regions (Fryxell and Kendrick 1988; Garrison and Buck 1989; Kang and Fryxell 1993). The colonial P. antarctica can clearly be considered as an ice-related phytoplankton in this study. In contrast to the higher biomass of the colonial prymnesiophyte Phaeocystis antarctica restricted in distribution with 100 km near the ice edge (Fig. 2L), motile P. antarctica cells were higher and were distributed in the open water of the BSR (Fig. 2M).

Integrated phytoplankton biomass

The average integrated absolute and relative PPC (g C m⁻²) throughout a water column weighted by depth 0 to 100 m for three north-south transects are tabulated (Tables 1-3). Total PPC ranged from 0.95 to 14.4 g C m⁻² (mean value of 5.8 ± 5.2 g C m⁻²). In three transects, the total PPC was concentrated in the upper 50 m and near the ice edge (Fig. 2H-M). Total phytoplankton peaked in biomass at Station 48 with 465 μg C L⁻¹ at 12 m and 14.4 g C m⁻² integrated to 100 m; see Figs. 2I and 3). The biomass of the most dominant phytoplankton species was Phaeocystis antarctica Karsten,
Fig. 2. Vertical sections of hydrography, nutrient concentration, and phytoplankton biomass in the upper 100 m along the north-south transect. (A) 1% QPAR, (B) density, (C) salinity, (D) temperature, (E) nitrate + nitrite, (F) phosphate, (G) silicate, (H) chlorophyll α, (I) total phytoplankton carbon biomass, (J) total diatom carbon biomass, (K) total autotrophic flagellate carbon biomass, (L) colonial *Phaeocystis antarctica* carbon biomass, (M) total bacterioplankton carbon biomass.
Table 1. Top twenty phytoplankton taxa with high carbon biomass in all stations during study period with their mean and range (g C m⁻²). (%) denotes % contribution to total biomass. *Fragilariopsis “dana”* is a combination of *F. cylindrus* and *F. pseudonana* that could not be distinguished in girdle view.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean</th>
<th>Min.</th>
<th>Misc.</th>
<th>(%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Phaeocystis antarctica</em> (colonial stage)</td>
<td>2.96±3.41</td>
<td>0.00</td>
<td>7.58</td>
<td>50.68</td>
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<tr>
<td><em>Thalassiosira gravida</em></td>
<td>0.87±1.56</td>
<td>0.00</td>
<td>4.49</td>
<td>14.90</td>
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<tr>
<td><em>Phaeocystis antarctica</em> (motile stage)</td>
<td>0.46±0.40</td>
<td>0.07</td>
<td>1.18</td>
<td>7.88</td>
</tr>
<tr>
<td><em>Fragilariopsis</em> spp. (girdle view, &lt;10 μm)</td>
<td>0.31±0.37</td>
<td>0.00</td>
<td>1.08</td>
<td>5.31</td>
</tr>
<tr>
<td>Autotrophic picoflagellates</td>
<td>0.17±0.07</td>
<td>0.07</td>
<td>0.32</td>
<td>2.91</td>
</tr>
<tr>
<td><em>Fragilariopsis “dana”</em></td>
<td>0.14±0.11</td>
<td>0.01</td>
<td>0.34</td>
<td>2.40</td>
</tr>
<tr>
<td><em>Fragilariopsis</em> spp. (girdle view, &gt;10 μm)</td>
<td>0.13±0.23</td>
<td>0.00</td>
<td>0.64</td>
<td>2.23</td>
</tr>
<tr>
<td><em>Cryptomonas</em> sp.</td>
<td>0.09±0.12</td>
<td>0.00</td>
<td>0.37</td>
<td>1.54</td>
</tr>
<tr>
<td><em>Proboscia truncata</em></td>
<td>0.08±0.12</td>
<td>0.00</td>
<td>0.39</td>
<td>1.37</td>
</tr>
<tr>
<td><em>Chaetoceros socialis</em></td>
<td>0.07±0.15</td>
<td>0.00</td>
<td>0.43</td>
<td>1.20</td>
</tr>
<tr>
<td><em>Proboscia alata</em></td>
<td>0.06±0.14</td>
<td>0.00</td>
<td>0.45</td>
<td>1.03</td>
</tr>
<tr>
<td><em>Pyramimonas</em> spp.</td>
<td>0.05±0.06</td>
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<td>0.17</td>
<td>0.86</td>
</tr>
<tr>
<td><em>Chaetoceros dichta</em></td>
<td>0.03±0.04</td>
<td>0.00</td>
<td>0.12</td>
<td>0.51</td>
</tr>
<tr>
<td><em>Chaetoceros neglectum</em></td>
<td>0.03±0.03</td>
<td>0.00</td>
<td>0.10</td>
<td>0.51</td>
</tr>
<tr>
<td><em>Corethron criophilum</em></td>
<td>0.02±0.03</td>
<td>0.00</td>
<td>0.07</td>
<td>0.34</td>
</tr>
<tr>
<td><em>Pseudonitzschia subcurvata</em></td>
<td>0.01±0.01</td>
<td>0.00</td>
<td>0.03</td>
<td>0.17</td>
</tr>
<tr>
<td><em>Nitzschia lecontei</em></td>
<td>0.009±0.01</td>
<td>0.00</td>
<td>0.04</td>
<td>0.15</td>
</tr>
<tr>
<td><em>Pseudonitzschia lineola</em></td>
<td>0.006±0.008</td>
<td>0.00</td>
<td>0.02</td>
<td>0.10</td>
</tr>
<tr>
<td><em>Pseudonitzschia turgiduloides</em></td>
<td>0.005±0.008</td>
<td>0.00</td>
<td>0.02</td>
<td>0.09</td>
</tr>
<tr>
<td><em>Cylindrotheca closterium</em></td>
<td>0.004±0.009</td>
<td>0.00</td>
<td>0.02</td>
<td>0.07</td>
</tr>
<tr>
<td>Other</td>
<td>0.34</td>
<td></td>
<td></td>
<td>5.75</td>
</tr>
<tr>
<td>Total phytoplankton carbon biomass</td>
<td>5.84±5.20</td>
<td>0.95</td>
<td>14.43</td>
<td>100</td>
</tr>
</tbody>
</table>


A Prymnesiophyte *Phaeocystis antarctica* in colonial stage, was a major contributor to total PPC, accounting for 2.96 g C m⁻² (~51% of the total PPC; see Table 1), WMIZ and open-water stations in BSR in their biomass of the colonial *P. antarctica* cells. Furthermore, *Phaeocystis* showed a distinct distribution pattern depending on their life stages. The colonial *P. antarctica* cells attained higher mean integrated numbers near the ice-edge stations (Fig. 5C), accounting for 6.5 g C m⁻² (~60% of total PPC; Table 2), while the motile *P. antarctica* dominated in the BSR (Fig. 5D), accounting for 0.73 g C m⁻² (~43% of total PPC; Table 3).

Diatoms in such genera as *Thalassiosira*, *Fragilariopsis*, *Proboscia*, *Chaetoceros*, *Corethron*, *Pseudonitzschia*, *Cylindrotheca*, and *Nitzschia* were also important contributors for the enhanced marginal ice-edge phytoplankton biomass, accounting for about 30% of total PPC (Table 1). Diatoms were generally observed in samples with higher biomass near the ice-edge zone like the other autotrophic flagellates (Fig. 3). The integrated total diatom carbon biomass (DIC) showed its peak in Sta. 48 (6.0 g C m⁻²; Fig. 3B) and consisted principally of *Thalassiosira gravida*, *Fragilariopsis* spp., *Proboscia truncata*, *Chaetoceros socialis* (Figs. 4-6).

*Thalassiosira gravida* was the most important carbon contributor to total diatom biomass, with 1.9 g C m⁻², accounting for ~17% of total PPC (Table 2). *T. gravida* forms gelatinous colonies, as does the colonial *P. antarctica*. Smetacek (1985)
Table 2. Top twenty phytoplankton taxa ranking high in carbon biomass in stations of the Weddell Sea marginal ice region during study period. Mean and range of biomass (g C m⁻²) of dominant phytoplankton species. (%) used as % contribution to total biomass. *Fragilariopsis* "*nana*" is a combination of *F. cylindrus* and *F. pseudonana* that could not be distinguished in girdle view during analysis.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean</th>
<th>Min.</th>
<th>Misc.</th>
<th>(%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Phaeocystis antarctica</em> (colonial stage)</td>
<td>6.46±1.04</td>
<td>5.26</td>
<td>7.58</td>
<td>59.59</td>
</tr>
<tr>
<td><em>Thalassiosira gravida</em></td>
<td>1.89±1.93</td>
<td>0.22</td>
<td>4.46</td>
<td>17.44</td>
</tr>
<tr>
<td><em>Fragilariopsis</em> spp. (girdle view, &lt; 10 µm)</td>
<td>0.63±0.32</td>
<td>0.34</td>
<td>1.08</td>
<td>5.81</td>
</tr>
<tr>
<td><em>Fragilariopsis</em> spp. (girdle view, &gt; 10 µm)</td>
<td>0.28±0.28</td>
<td>0.00</td>
<td>0.64</td>
<td>2.58</td>
</tr>
<tr>
<td><em>Proboscia truncata</em></td>
<td>0.17±0.13</td>
<td>0.07</td>
<td>0.39</td>
<td>1.57</td>
</tr>
<tr>
<td>Autotrophic picoflagellates</td>
<td>0.16±0.04</td>
<td>0.11</td>
<td>0.18</td>
<td>1.48</td>
</tr>
<tr>
<td><em>Chaetoceros socialis</em></td>
<td>0.14±0.20</td>
<td>0.00</td>
<td>0.43</td>
<td>1.29</td>
</tr>
<tr>
<td><em>Phaeocystis antarctica</em> (motile stage)</td>
<td>0.13±0.04</td>
<td>0.07</td>
<td>0.18</td>
<td>1.20</td>
</tr>
<tr>
<td><em>Fragilariopsis</em> &quot;<em>nana</em>&quot;</td>
<td>0.08±0.08</td>
<td>0.01</td>
<td>0.18</td>
<td>0.74</td>
</tr>
<tr>
<td><em>Chaetoceros dicaeata</em></td>
<td>0.06±0.03</td>
<td>0.04</td>
<td>0.12</td>
<td>0.55</td>
</tr>
<tr>
<td><em>Chaetoceros neglectum</em></td>
<td>0.05±0.04</td>
<td>0.01</td>
<td>0.10</td>
<td>0.46</td>
</tr>
<tr>
<td><em>Corethron criophilum</em></td>
<td>0.04±0.07</td>
<td>0.00</td>
<td>0.17</td>
<td>0.37</td>
</tr>
<tr>
<td><em>Pyramimonas</em> spp.</td>
<td>0.04±0.03</td>
<td>0.00</td>
<td>0.07</td>
<td>0.37</td>
</tr>
<tr>
<td><em>Proboscia alata</em></td>
<td>0.03±0.06</td>
<td>0.00</td>
<td>0.13</td>
<td>0.28</td>
</tr>
<tr>
<td><em>Pseudonitzschia subcurvata</em></td>
<td>0.02±0.01</td>
<td>0.00</td>
<td>0.03</td>
<td>0.18</td>
</tr>
<tr>
<td><em>Pseudonitzschia lineola</em></td>
<td>0.01±0.008</td>
<td>0.00</td>
<td>0.02</td>
<td>0.09</td>
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<tr>
<td><em>Pseudonitzschia turgiduloides</em></td>
<td>0.01±0.01</td>
<td>0.00</td>
<td>0.02</td>
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<td><em>Cylindrotheca closterium</em></td>
<td>0.009±0.01</td>
<td>0.00</td>
<td>0.02</td>
<td>0.08</td>
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<tr>
<td><em>Cryptomonas</em> sp.</td>
<td>0.0008±0.002</td>
<td>0.00</td>
<td>0.004</td>
<td>0.01</td>
</tr>
<tr>
<td><em>Nitzschia lecoinei</em></td>
<td>0.00±0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Other</td>
<td>0.63</td>
<td></td>
<td></td>
<td>5.81</td>
</tr>
</tbody>
</table>

Total phytoplankton carbon biomass 10.84±3.14 7.90 14.43 100

states that mucus secretion in diatoms leads to entanglement and rapid sinking into different current regimes and constitutes a strategy of survival. Protection against grazing could be one advantage of this strategy (Fryxell and Kendrick 1988).

Species of the diatom genus *Fragilariopsis* in girdle view such as *F. curta* (Van Heurck) Hustedt, *F. cylindrus* (Grunow) Kriege, *F. kerguelensis* (O’Meara), *F. pseudonana* (Hasle) Hasle, *F. ritscheri* Hustedt were important diatoms in the ice-edge zone, accounting for 8% of total PPC (Table 2). The *Fragilariopsis* spp. were restricted with in the WMIZ (Figs. 5A, B). The nanoplanktonic diatom *F. "*nana*" which is a combination of *F. cylindrus* and *F. pseudonana* that could not be distinguished in girdle view during analysis accounted for 2.4% of total PPC.

**DISCUSSION**

The dominance of three genera was striking in our material from austral summer ice-edge water samples. These three genera have been reported in large populations and blooms in the water column near the ice edge: *Phaeocystis* Lagerheim from the Weddell Sea (Buck and Garrison 1983; Garrison and Buck 1985; Garrison et al. 1987; Fryxell and Kendrick 1988; Fryxell 1989; Kang and Fryxell 1993), the Ross Sea (El-Sayed et al. 1983; Palmisano and Sullivan 1983; Palmisano et al. 1986; Knox 1990), and the Prydz Bay (Perrin and Marchant 1987; Davidson and Marchant 1992) and diatom genera *Thalassiosira* Cleve and *Fragilariopsis* Hustedt from the Weddell Sea (Buck and Garrison 1983; Garrison and Buck 1985; Fryxell and Kendrick 1988; Kang and Fryxell 1993), the Ross Sea (Smith and Nelson 1985; Wilson et al. 1986), and Prydz Bay (Kang and Fryxell 1991).

Although the larger-celled phytoplankton species (> 20 µm) are generally found in lower cell numbers than the smaller-celled species (< 20 µm) in
Table 3. Top twenty phytoplankton taxa ranking high in carbon biomass in stations of the Bransfield Strait region during study period. Mean and range of biomass (g C m\(^{-2}\)) of dominant phytoplankton species. (%) used as % contribution to total biomass. *Fragilaripsis “nana”* is a combination of *F. cylindrus* and *F. pseudonana* that could not be distinguished in girdle view during analysis.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean</th>
<th>Min.</th>
<th>Msc.</th>
<th>(%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Phaeocystis antarctica</em> (motile stage)</td>
<td>0.73±0.36</td>
<td>0.24</td>
<td>1.18</td>
<td>43.45</td>
</tr>
<tr>
<td><em>Fragilaripsis “nana”</em></td>
<td>0.19±0.11</td>
<td>0.06</td>
<td>0.34</td>
<td>11.31</td>
</tr>
<tr>
<td>Cryptomonas sp.</td>
<td>0.17±0.09</td>
<td>0.06</td>
<td>0.37</td>
<td>10.12</td>
</tr>
<tr>
<td>Autotrophic picophytoplanktates</td>
<td>0.16±0.09</td>
<td>0.07</td>
<td>0.32</td>
<td>9.52</td>
</tr>
<tr>
<td>Proboscia alata</td>
<td>0.09±0.18</td>
<td>0.00</td>
<td>0.45</td>
<td>5.36</td>
</tr>
<tr>
<td>Pyramimonas spp.</td>
<td>0.06±0.04</td>
<td>0.008</td>
<td>0.10</td>
<td>3.57</td>
</tr>
<tr>
<td><em>Phaeocystis antarctica</em> (colonial stage)</td>
<td>0.05±0.08</td>
<td>0.00</td>
<td>0.19</td>
<td>2.98</td>
</tr>
<tr>
<td><em>Fragilaripsis</em> spp. (girdle view, &lt;10 (\mu m))</td>
<td>0.04±0.05</td>
<td>0.0002</td>
<td>0.14</td>
<td>2.38</td>
</tr>
<tr>
<td>Nitzschia lecoinei</td>
<td>0.02±0.04</td>
<td>0.00</td>
<td>0.10</td>
<td>1.99</td>
</tr>
<tr>
<td>Thalassiosira gravida</td>
<td>0.02±0.02</td>
<td>0.00</td>
<td>0.04</td>
<td>1.19</td>
</tr>
<tr>
<td>Corethron criophillum</td>
<td>0.01±0.01</td>
<td>0.00</td>
<td>0.04</td>
<td>0.60</td>
</tr>
<tr>
<td>Chaetoceros neglectum</td>
<td>0.006±0.008</td>
<td>0.00</td>
<td>0.02</td>
<td>0.36</td>
</tr>
<tr>
<td>Pseudonitzschia subcurvata</td>
<td>0.005±0.006</td>
<td>0.00</td>
<td>0.001</td>
<td>0.30</td>
</tr>
<tr>
<td>Chaetoceros dichaeta</td>
<td>0.001±0.002</td>
<td>0.00</td>
<td>0.005</td>
<td>0.06</td>
</tr>
<tr>
<td>Pseudonitzschia lineola</td>
<td>0.001±0.002</td>
<td>0.00</td>
<td>0.005</td>
<td>0.06</td>
</tr>
<tr>
<td><em>Fragilaripsis</em> spp. (girdle view, &gt;10 (\mu m))</td>
<td>0.0003±0.0006</td>
<td>0.00</td>
<td>0.002</td>
<td>0.02</td>
</tr>
<tr>
<td>Chaetoceros socialis</td>
<td>0.00±0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Cylindrotheca closterium</td>
<td>0.00±0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Proboscia truncata</td>
<td>0.00±0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Pseudonitzschia turgiduloides</td>
<td>0.00±0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Other</td>
<td>0.13</td>
<td></td>
<td></td>
<td>7.54</td>
</tr>
<tr>
<td>Total phytoplankton carbon biomass</td>
<td>1.68±0.54</td>
<td>0.95</td>
<td>2.25</td>
<td>100</td>
</tr>
</tbody>
</table>

the Southern Ocean waters, they were considered as significant biomass source due to their large cell volumes (Kang and Fryxell 1991; Kang et al. 1993b; Kang and Lee in press). They found that the larger-celled diatoms served as better indicators and tracers of water masses than the smaller-celled diatoms species. When *Thalassiosira gravida* was compared with other dominant diatom species such as *Fragilaripsis* species, *T. gravida* showed higher biomass than other dominant species which were frequently dominant in number. During the austral spring cruise in the marginal ice-edge zone the more opportunistic diatom genera such as *Thalassiosira* increased in numbers in the open water near the ice edge and appeared to outcompete the pennate diatoms (Fryxell and Kendrick 1988). That centric diatom genus is known to be opportunistic ecologically, reproducing rapidly and often dominating in early spring blooms in temperate areas or when growth conditions improve or in upwelling areas.

Although diatoms were important carbon contributor to total phytoplankton biomass during early summer 1994 in the WMIZ, *Phaeocystis antarctica* was the supreme dominant in our material from austral early summer ice-edge water samples and a significant biomass source due to their high numerical abundance (Table 2). Integrated *Phaeocystis* carbon in the upper 100 m of the water column ranged from 5.3 g C m\(^{-2}\) to 7.6 g C m\(^{-2}\), while integrated *Thalassiosira gravida* carbon ranged from 0.22 to 4.5 g C m\(^{-2}\) (Table 2). Although larger-celled diatom species such as *Thalassiosira gravida* and *Fragilaripsis* species were considered to be important biomass sources due to their large cell volumes in other ice-edge zones (Fryxell and Kendrick 1988; Kang and Fryxell 1993), *Phaeocystis antarctica* in colonial stage appeared to outcompete the larger-celled diatoms during the study period in the WMIZ.

Sournia (1988) outlined diagnostic features of *Phaeocystis* at the various life stages and pointed
out the difficulty of identification of *Phaeocystis* at the species level because of (1) the existence of poorly described taxa, (2) the alternation of different stages in the life cycles, and (3) practical difficulties of observation at the ultrastructural level. Although *P. pouchetii* has been considered as an important Antarctic species and has been well described under both the motile and non-motile stages, Sournai (1988) advised the use of *P*. sp. for the present to avoid further confusion. Recently, Medlin *et al.* (1993, 1994), however, have found morphological, physiological, and genetic differences between the *P. pouchetii* from the northern hemisphere and *P. antarctica* from Antarctic waters.

The distribution of *Phaeocystis antarctica* showed a similar pattern to that of their respective diadinoxanthin, and the distribution of the total diatoms exhibited similar pattern as fucoxanthin (see Figure 2 in Bidigare *et al.* 1992). A good agreement was observed between microscopically enumerated phytoplankton counts and pigment concentration.
Chlorophyll $a$ concentration during austral spring in the Bellingshausen Sea marginal ice zone followed more closely the biomass of the colonial *P. antarctica* cells than the biomass of the diatoms, suggesting that *P. antarctica* cells were more important as biomass source (Bidigare et al. in press).

**Comparisons between the Bransfield Strait region and the Weddell Sea marginal ice zone**

Hydrographic observations during the 7th KARP cruise illustrate substantial differences in the physical conditions between the BSR and the WMIZ. In the BSR the density structure was heterogeneous with mixed layer depths varying from 60 to 100 m (Fig. 2B). In contrast, in the WMIZ the ice was in bands, it was retreating to south; there was not melting of the pack ice; and the distribution of density was uniform, with the pycnocline consistently occurring between 20 and 40 m (Fig. 2B). Stratification was comparatively much stronger in the WMIZ than in the BSR. The phytoplankton species composition and biomass between two regions also showed differences (Figs. 3-6).

The BSR and the WMIZ were different in their total PPC distributions of the overall spatial patterns. The WMIZ exhibited about six times higher total PPC than that in the BSR (Tables 2 and 3).

The mean total PPC in the WMIZ was 10.8 g C m$^{-2}$ (S.D. = 3.1 since the conditions varied from under the ice to the open ocean), while the mean value in the BSR was 1.7 g C m$^{-2}$ (S.D. = 0.54). Thus taken as a whole, the significant differences of phytoplankton carbon biomass between near ice edge and in open ocean were observed throughout this study.

We found intraspecific differences of *Phaeocystis antarctica* life stages, biomass, and distributional patterns between sea ice-edge waters and open water. The mean biomass of *P. antarctica* in colonial stage was much higher (124 times) in the WMIZ (6.5±1.0 g C m$^{-2}$) than in the BSR (0.05±0.08 g C m$^{-2}$), but the mean biomass of *P. antarctica* in motile stage was about six times higher in the BSR (0.73±0.36 g C m$^{-2}$) than in the WMIZ (0.13±0.04 g C m$^{-2}$; see Tables 2 and 3). The biomass and relative dominance of the different phytoplankton species may have changed with time in the ice-edge zone of the northwestern Weddell Sea. The differences in biomass and distributional patterns of diatoms and *Phaeocystis* between the two regions could have resulted from different physical conditions such as depth of mixed layer, light limitation, micronutrient availability, and grazing or other removal processes. Smith and Garrison (1990) pointed out that the spatial variations in pigment levels in autumn were not to be associated with a stratified density structure alone, but instead were related to the length of time the regon had been ice-free. Comiso et al. (1990) observed higher pigment values in the south than in the north with satellite ocean color study, indicating that latitudinal gradient of irradiance was not the only factor controlling spatial distribution of phytoplankton pigment concentrations at this time.

It is possible that the differences we did observe between the two regions and between near sea ice waters and open waters resulted from biological removal processes that were moderating the phytoplankton increase with time and intensified grazing pressure. Daly and Macaulay (1991) found different distribution and abundance of krill in different life history stages during austral autumn in the marginal ice zone. In general, mean density of all stages was higher in the open water than near sea ice, but maximum densities of juveniles and immature adults occurred under the ice and in the north-
ern transect. The mean ratio of the full diatoms to empty diatoms was 1.5 in the northern transect and 3.2 in the southern transect (Kang and Fryxell 1993), suggesting a generally declining population, possibly including more grazing pressure on the diatoms in the northern transect and a healthier, growing population capable of reproducing when light was available in the southern transect during austral summer in the WMIZ.

The increased concentrations of *Phaeocystis antarctica* in colonial stage near the ice edge during the summer were probably not due only to a physical mechanism but were probably due to other factors, as well, such as lower light intensity. This hypothesis seems feasible because *Phaeocystis* is capable of physiologically adapting to low irradiances (Palmisano *et al.* 1986), and under light limitation, protein synthesis by the colonial cells of *Phaeocystis* continues at the expense of the extracellular mucopolysaccharides synthesized in the light (Lancelot and Mathot 1985). This feature gives *Phaeocystis* a selective advantage over other phytoplankton in light-controlled or light-limited environments. *Phaeocystis* could have been seeded from any melting ice at the end of the summer and from the water under the ice; certainly much more enhanced biological activity was observed at the ice edge, which suggested an even higher estimation of available source of food in the study area.

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REFERENCES


**APPENDIX I. Classification of the observed species**

**Division BACILLARIOPHYTA**

**Order Centrales**

Suborder coscinodiscinae

Family Thalassiosiaceae Lebour 1930.

_emend Hasle 1973_

_Thalassiosira antarctica_ Comber
_Thalassiosira gracilis_ (Karst.) Hustedt
_Thalassiosira gravida_ Cleve
_Thalassiosira sp._

Family Melosiraceae Kützing 1844

_Corethron criphilum_ Castracane

Family Coscinodiscaceae Kützing 1844

_Stellarina microtrias_ (Ehrenberg) Hasle & Sims

Family Hemidiscaceae Hendey 1937 emend Simonsen 1975

**Actinocyclus actinochilus** (Ehrenberg)

**Simonsen**

Suborder Rhizosoleniinae

Family Rhizosoleniaceae Petit 1888

_Dactyliosolen antarcticus_ Castracane
_Dactyliosolen tenuijunctus_ (Mang.) Hasle
_Rhizosolenia chunii_ Karsten
_Rhizosolenia inermis_ Castracane

Suborder Biddulphineae

Family Biddulphiaceae kützing 1844

Subfamily Hemiaulioideae Jous, Kiselev & Poretskii 1949

_Eucampia antarctica var. recta_ (Mangin)
_Fryxell et Prasad_

Subfamily Chaetoceraceae Smith 1872

_Chaetoceros bulbosum_
_Chaetoceros criophilum_ Castracane
_Chaetoceros dichtaeta_ Ehrenberg
_Chaetoceros flexuosum_ Mangin
_Chaetoceros neglectum_ Kartsen
_Chaetoceros shimpertani_ Kartsen
_Chaetoceros socialis_ Lauder

Family Eupodiscaceae Kützing 1849

Subfamily Eupodiscoidae Kützing 1849

_Odontella weissflogii_ (Janisch) Grunow

Order Pennales

Suborder Araphidinae

Family Diatomaceae Dumortier 1822

_Trichotoxon reinboldii_ (Van Heurck) Feid et Round

Suborder Raphidinae

Family Naviculaceae Kützing 1844

_Pseudogomphonema arcticum_ Grunow

Family Nitschiaceae Grunow 1860

_Cylindrotheca closterium_ (Ehrenberg) Reimann

_Fragilariopsis curta_ (Van Heurck) Hasle
_Fragilariopsis obliquecostata_ (Van Heurck) Hasle
_Fragilariopsis ritscheri_ (Hustedt) Hasle
_Fragilariopsis vanheurckii_ (M. Per.) Hasle
_Pseudonitzschia heinii_ Manguin
_Pseudonitzschia turgiduloides_ Hasle

Division CHROMOPHYTA

Class Prymnesiophyceae

_Phaeocystis antarcticai_ Karsten
APPENDIX II. Taxonomic Study

Order Centrales

Suborder Coscinodiscinae

Family Thalassiosiraceae Lebour 1930. Emend Hasle 1973

*Thalassiosira antarctica* Comber

*Thalassiosira gracilis* (Karst.) Hustedt
Fryxell 1983. p. 95, fig. 3(c); Johansen and Fryxell 1985. p. 167, figs. 58, 59; Krebs 1985. p. 214b, fig. 8; Fryxell and Johansen 1990. p. 101, PL. 11.8, fig. 4.

*Thalassiosira gravida* Cleve

Family Melosiraceae Kützing 1844

*Corethron criophilum* Castracane

Family Coscinodiscaceae Kützing 1844

*Stellarima microtrias* (Ehrenberg) Hasle & Sims

Family Hemidiscaceae Hendey 1937 emend Simonsen 1975

*Actinocyclus actinochilus* (Ehrenberg) Simonsen
Simonsen 1982. p. 113-116, PL. 1-4, figs. 1-9;
Krebs 1985. p. 287, PL. 1, fig. 6; Priddle and Fryxell 1985. p. 103; Fryxell 1990. p. 113, PL. 14.1, fig. 1; El-Sayed and Fryxell 1993. p. 75, fig. 2.6(2).

Suborder Rhizosoleniinae

Family Rhizosoleniaceae Petit 1888

*Dactyltosolen antarcticus* Castracane
Cupp 1943. p. 76, fig. 37; Priddle and Fryxell 1985. p. 59, figs. A-E.

*Dactyltosolen tenuijunctus* (Mang.) Hasle
Priddle and Fryxell 1985. p. 61, figs. A, B.

*Rhizosolenia chunii* Karsten

*Rhizosolenia inermis* Castracane
Priddle et al. 1990. p. 125, fig. 6a, b

Suborder Biddulphiinae

Family Biddulphiaceae Kützing 1844

Subfamily Hemiauloideae Jous, Kiselev & Poretskii 1949

*Eucampia antarctica* var. *recta* (Mangin) Fryxell et Prasad

Subfamily Chaetoceraceae Smith 1872

*Chaetoceros bulbosus* complex
Priddle and Fryxell 1985. p. 25, figs. A-J.

*Chaetoceros criophilum* Castracane

*Chaetoceros dichaeta* Ehrenberg

*Chaetoceros flexuosum* Mangin

*Chaetoceros neglectum* Kartsen
Priddle and Fryxell 1985. p. 47, figs. A-C.

*Chaetoceros socialis* Lauder
Family Eupodiscaceae Kützing 1849
Subfamily Eupodiscoideae Kützing 1849

*Odontella weissflogii* (Janisch) Grunow

**Order Pinnales**

**Suborder Araphidineae**
Family Diatomaceae Dumortier 1822

*Trichotomyx reinboldii* (Van Heurk) Feid et Round

**Suborder Raphidineae**
Family Naviculaceae Kützing 1844

*Pseudogomphonema arcticum* Grunow
Medlin 1990. p. 158, fig. 6; Medlin and Round 1986a. p. 211, 220, fig. 38, 92-100
Family Nitzschiaeae Grunow 1860

*Cylindrotheca closterium* (Ehrenberg) Reimann

*Fragilariopsis curta* (Van Heurck) Hasle
Hasle and Medlin 1990b. p. 193, PL. 24.6, figs. 2-5.

*Fragilariopsis obliquecostata* (Van Heurck) Hasle

*Fragilariopsis ritscheri* (Hustedt) Hasle

*Fragilariopsis vanheurckii* (M. Per.) Hasle

*Pseudonitzschia heimii* Manguin

*Pseudonitzschia turgiduloides* Hasle

**REFERENCES FOR APPENDIX**


Hasle, G.R. (19650 *Nitzschia* and *Fragilariopsis* Species Studied in the Light and Electron Microscopes II. The Group *Pseudonitzschia*. Universitetsforlaget, pp. 79.


Plate 1. 1-5. *Thalassiosira* spp. External view of girdle. Connected by multiple chitin threads twisted, rope-like. (Scale bars: 1, 2 = 20 µm; 3-5 = 40 µm)

Plate 2. 6. *Thalassiostra antarctica* (external view of valve)
7-8. *Thalassiostra gravida* (external view of valves and girdles. colony formed)
9. *Corethron criophilum*. (external view of girdle)
10. *Corethron criophilum*. (external view of girdle. auxospore formed)
(Scale bars: 6 = 10 µm; 7, 9, 10 = 40 µm; 8 = 20 µm)

Plate 3. 11. *Corethron criophilum*. (external view of girdle)
12. *Corethron criophilum*. (external view of girdle. normal cell and auxospore)
13-14. *Stellarima microtrias* (external view of girdle)
15. *Stellarima microtrias* (external view of valve)
16. *Stellarima microtrias* (external view of valve)
(Scale bars: 11-13 = 40 µm; 14, 15 = 20 µm; 16 = 10 µm)

Plate 4. 18-19. *Actinocyclus actinochilus* (external view of valve)
20. *Actinocyclus actinochilus* (internal view of valve)
21. *Dactylisolen antarcticus* (external view of girdle)
22. *Dactylisolen tenuijunctus* (external view of girdle)
23. *Proboscia chunnii* (external view of girdle)
(Scale bars: 18-20 = 10 µm; 21, 22 = 20 µm; 23 = 40 µm)

Plate 5. 24. *Proboscia chunnii* (external view of girdle)
25. *Proboscia inermis* (external view of girdle)
26-28. *Eucampia antarctica var. recta* (external view of girdle)
29. *Chaetoceros criophilum* (external view of girdle)
(Scale bars: 24, 25, 28 = 20 µm; 26, 27, 29 = 20 µm)

Plate 6. 30. *Chaetoceros criophilum* (external view of girdle)
31-33. *Chaetoceros dicaeta* (external view of girdle)
34. *Chaetoceros flexuosum* (external view of girdle)
(Scale bars: 30, 32, 34 = 40 µm; 31, 33 = 20 µm)

Plate 7. 35. *Chaetoceros neglectum* (external view of girdle)
36. *Chaetoceros shimperiaum* (external view of girdle)
37. *Chaetoceros socialis* (external view of girdle)
38-39. *Odontella weissflogii* (external view girdle)
(Scale bars: 35, 36, 39 = 20 µm; 37, 38 = 40µm)

Plate 8. 40-41. *Trichotoxon reinboldii* (colony formed)
42. *Trichotoxon reinboldii* (external view of valve)
43. *Pseudogromphonema arcticum* (internal view of valve)
44-45. *Cylindrotheca closterium*
(Scale bars: 40, 41 = 100 µm; 42, 43 = 10 µm; 44, 45 = 20 µm)

(Scale bars: 46, 48 = 10 µm; 47, 49 = 20 µm; 50 = 40 µm)

Plate 10. 51. Siliated protozoa containing many small *Fragilariopsis cylindrus*
52. *Fragilariopsis curtaii* (external view of valve)
53-54. *Fragilariopsis ritscheri* (External view of valve)
55-56. *Fragilariopsis obliquecostata* (external view of valve)
57. *Fragilariopsis vanheurckii* (external view of valve)
(Scale bars: 51 = 20 μm; 52-54 = 5 μm; 55-57 = 10 μm)

**Plate 11.**
58. *Pseudonitzschia heimii.* (colony formed)
59. *Pseudonitzschia subcurvata*
60-61. *Pseudonitzschia turgiduloides* (colony formed)
62-63. *Pseudonitzschia turgiduloides* (external view of valve)
(Scale bars: 58-61 = 20 μm; 62, 63 = 10 μm)

**Plate 12.**
64-66. *Phaeocystis antarctica* (colonial stage)
67-68. Choanoflagellate *Parvicorcula socialis* (colony formed)
(Scale bars: 64, 65, 68 = 10 μm; 66, 67 = 20 μm)
Plate 1
Plate 5
Plate 7

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