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

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남극 동 브렌스필드 해협과 서북 웨델해 빙산주변해역의 하계 식물플랑크톤

강성호, 김동엽, 강재신, 이미영, 이상훈

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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 iceedge zone. Waters in the Bransfield Strait region were characterized by a dominance of nanoplanktonic species such as P. antarctica in motile stage, Fragilariopsis "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 Fragilariopsis 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, Fragilariopsis spp., Proboscia truncata, Chaetoceros socialis, C. dichaeta, C. neglectum, Corethron criophilum, Cylindrotheca closterium, Pseudonitzschia subcurvata, P. turgiduloides were sea ice related species, while Phaeocystis antarctica in motile stage, Fragilariopsis "nana", Cryptomonas sp., autotrophic picoflagellates, Proboscia alata, Pyramimonas sp., and Nitzschia lecointei 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 남극하계연구의 일환으로 1994년 1월 3일부터 10일까지 동 Bransfield 해협과 서북 Weddell해 얼음주변에서 식물플랑크톤이 채집되었다. 22개 연구정점에서 획득된 식물플랑크톤 시료는 종구성,생물량 및 분포양상을 이해하기 위해 정량화되었다. 연구기간 동 안 표층에서 수심 100m까지 적분된 평균 총 식물플랑크톤 탄소량은 5.8 g C m⁻²였다. Weddll해

얼음주변의 연구정점들에서 식물플랑크톤 탄소량이 가장 높았는데(7.9-14.4g C m⁻²), 이는 이 해역에 Prymnesiophyte에 속하는 Phaeocystis antarctica Karsten (colonial stage)가 우점하고 있었 기 때문이었다. 이 군체상 *P. antarctica*는 최고 7.9 g C m⁻²에 달하였으며, 평균 3.0 g C m⁻²로 총 식물플랑크톤 탄소량의 약 51%를 차지하고 있었다. Bransfield 해협과 Weddell 해 얼음주변 사이에서의 식물플랑크톤 종구성, 생물량 및 분포양상은 상당한 차이를 보여주고 있었다. Bransfield 해협에서는 nanoplankton인 P. antarctica (motile stage), Fragilariopsis "nana", Cryptomonas sp., 그리고 autotrophic picoflagellates가 전체 식물플랑크톤 탄소량의 75%를 차지 하고 있었다. 반면, Weddell 해 얼음주변 해역에서는 P. antarctica (colonial stage), Thalassiosira gravida, Fragilariopsis species가 총 식물플랑크톤 탄소량의 약 83%를 차지하고 있었다. 종 수 준에서의 식물플랑크톤 군집구조연구를 통해, 남극 하계동안 군체상의 Phaeocystis antarctica, Thalassiosira gravida, Fragilariopsis spp., Proboscia truncata, Chaetoceros socialis, C. dichaeta, C. neglectum, Corethron criophilum, Cylindrotheca closterium, Pseudonitzschia subcurvata, P. turgiduloides들은 Weddell 해 얼음과 밀접한 관계가 있었던 종이었으며, Phaeocystis antarctica, Fragilariopsis "nana", Cryptomonas sp., autotrophic picoflagellates, Proboscia alata, Pyramimonas sp. 그리고 Nitzschia lecointei들은 해빙의 영향을 적게 받는 Bransfield 해협의 외해에 적응하여 서식하는 종인 것으로 해석된다.

주요어' 남극, 식물플랑크톤, 브렌스필드 해협, 웨델해, 해빙지역

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 sopen 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 seaice 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 Compangnie 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

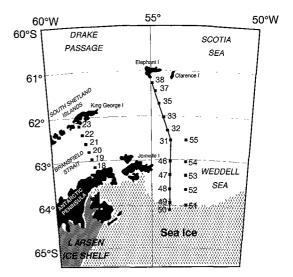


Fig. 1. A map showing the locations of the 22 stations, which were visited from 3 to 10 January 1994. The line from Station 38 in the Bransfield Strait region to Station 50 in the Weddell Sea marginal ice zone is a north-south transect where the vertical and horizontal structure of phyplankton assemblages.

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 ($20-\mu m$ 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 ($0.45-\mu m$ 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 Utemöhl 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 nanoplankton (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 wer 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 μ m for subsequent estimations of biovolume using appropriate geometric shapes (Smayda 1978). The carbon biomass was estimated from the cell biovolume with the modified Strahmann equations (Eqs. 7 and 8 in Smayda 1978). For autotrophic flagellates, the relationship log ₁₀carbon(pg)=0.94 log₁₀[cell volume (μ m³)] - 0.60 was used, and for diatoms, log₁₀carbon(pg)=0.76log₁₀[cell volume (μ m³)] - 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 $(-1.0 \text{ to } -1.4^{\circ}\text{C})$ and lower salinities (< 34%) were found near the ice edges with melting sea ice (Fig. 2C, D). Hydrographic observatons support previous model of melt waterinduced 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 northern 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 μ g 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 μ g C l⁻¹ at 12 m and 14.4 g C m⁻² integrated to 100 m; see Figs. 2I and 3). The average biomass of the most dominant phytoplankton is given in Table 1. The dominant phytoplankton species were *Phaeocystis antarctica* Karsten,

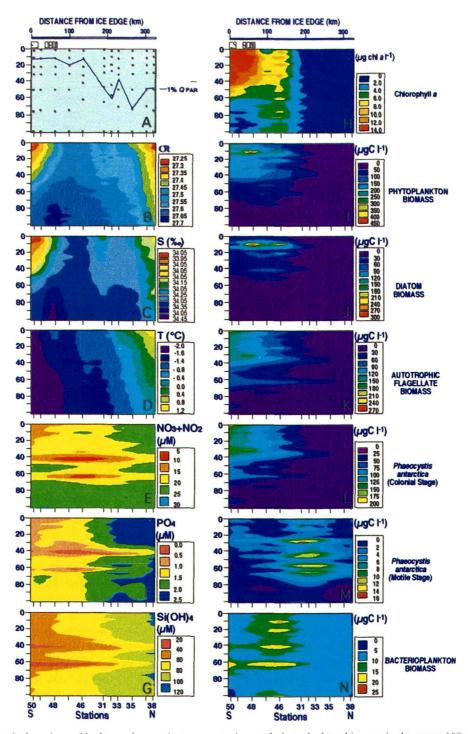


Fig. 2. Vertical sections of hydrography, nutrient concentration, and phytoplankton biomass in the upper 100 m along the north-south transect. (A) 1% Q_{PAR}, (B) density, (C) salinity, (D) temperature, (E) nitrate + nitrite, (F) phosphate, (G) silicate, (H) chlorophyll α, (I) total phytoplankton carbon biomass, (J) total diatom carbon biomass, (K) total autotrophic flagellate carbon biomass, (L) colonial *Phaeocystis antarctica* carbon biomass, (N) total bacterioplankton carbon biomass.

Table 1. Top twenty phytoplankton taxa with high carbon biomass in all stations during study period with their meanand range (g C m⁻²). (%) denotes % contribution to total biomass. Fragilariopsis "nana" is a combination ofF. cylindrus and F. pseudonana that could not be distinguished in girdle view.

Species	Mean	Min.	Msc.	(%)
Phaeocystis antarctica (colonial stage)	2.96±3.41	0.00	7.58	50.68
Thalassiosira gravida	0.87±1.56	0.00	4.49	14.90
Phaeocystis antarctica (motile stage)	0.46±0.40	0.07	1.18	7.88
Fragilariopsis spp. (girdle view, $< 10 \ \mu m$)	0.31±0.37	0.00	1.08	5.31
Autotrophic picoflagellates	0.17±0.07	0.07	0.32	2.91
Fragilariopsis "nana"	0.14±0.11	0.01	0.34	2.40
<i>Fragilariopsis</i> spp. (girdle view, $> 10 \mu m$)	0.13±0.23	0.00	0.64	2.23
Cryptomonas sp.	0.09±0.12	0.00	0.37	1.54
Proboscia truncata	0.08±0.12	0.00	0.39	1.37
Chaetoceros socialis	0.07±0.15	0.00	0.43	1.20
Proboscia alata	0.06 ± 0.14	0.00	0.45	1.03
Pyramimonas spp.	0.05±0.06	0.00	0.17	0.86
Chaetoceros dichaeta	0.03±0.04	0.00	0.12	0.51
Chaetoceros neglectum	0.03±0.03	0.00	0.10	0.51
Corethron criophilum	0.02±0.03	0.00	0.07	0.34
Pseudonitzschia subcurvata	0.01±0.01	0.00	0.03	0.17
Nitzschia lecointei	0.009±0.01	0.00	0.04	0.15
Pseudonitzschia lineola	0.006 ± 0.008	0.00	0.02	0.10
Pseudonitzschia turgiduloides	0.005 ± 0.008	0.00	0.02	0.09
Cylindrotheca closterium	0.004±0.009	0.00	0.02	0.07
Other	0.34			5.75
Total phytoplankton carbon biomass	5.84±5.20	0.95	14.43	100

Thalassiosira gravida Cleve, Fragilariopsis spp., autotrophic picoflagellates, Cryptomonas sp., Proboscia alata Brightwell, Chaetoceros socialis, Ch. neglectum Karsten, Ch. dichaeta Ehrenberg, Corethron criophilum Castracane, Pseudonitzschia subcurvata (Hasle) Fryxell, Nitzschia lecointei Van Heurck, Pseudonitzschia lineola Cleve, P. turgiduloides (Hasle) Hasle, Cylindrotheca closterium (Ehrenberg) Reiman et Lewin (Figs. 4, 5, and 6).

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 contributor 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*, *Chaeotoceros 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 iceregion during study period. Mean and range of biomass (g C m⁻²) of domimant 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.

Species	Mean	Min.	Msc.	(%)
Phaeocystis antarctica (colonial stage)	6.46±1.04	5.26	7.58	59.59
Thalassiosira gravida	1.89±1.93	0.22	4.46	17.44
Fragilariopsis spp. (girdle view, $< 10 \ \mu m$)	$0.63 \pm .0.32$	0.34	1.08	5.81
Fragilariopsis spp. (girdle view, > 10 μ m)	0.28±0.28	0.00	0.64	2.58
Proboscia truncata	0.17±0.13	0.07	0.39	1.57
Autotrophic picoflagellates	0.16±0.04	0.11	0.18	1.48
Chaetoceros socialis	0.14±0.20	0.00	0.43	1.29
Phaeocystis antarctica (motile stage)	0.13±0.04	0.07	0.18	1.20
Fragilariopsis "nana"	0.08±0.08	0.01	0.18	0.74
Chaetoceros dichaeta	0.06±0.03	0.04	0.12	0.55
Chaetoceros neglectum	0.05 ± 0.04	0.01	0.10	0.46
Corethron criophilum	0.04±0.07	0.00	0.17	0.37
Pyramimonas spp.	0.04±0.03	0.00	0.07	0.37
Proboscia alata	0.03±0.06	0.00	0.13	0.28
Pseudonitzschia subcurvata	0.02±0.01	0.00	0.03	0.18
Pseudonitzschia lineola	0.01±0.008	0.00	0.02	0.09
Pseudonitzschia turgiduloides	0.01±0.01	0.00	0.02	0.09
Cylindrotheca closterium	0.009±0.01	0.00	0.02	0.08
Cryptomonas sp.	0.0008 ± 0.002	0.00	0.004	0.01
Nitzschia lecointei	0.00±0.00	0.00	0.00	0.00
Other	0.63			5.81
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) Krieger, F. kerguelensis (O'Meara), F. pseudonana (Hasle) Hasle, F. ritscheri Hustedt were important diatoms in the iceedge 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 μ m) are generally found in lower cell numbers than the smaller-celled species (< 20 μ m) 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 domimant 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.

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

the Southern Ocean waters, they were considered as significan 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 Fragilariopsis species, T. gravida showed higher biomass than other dominat 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 largercelled diatom species such as Thalassiosira gravida and Fragilariopsis species were considered to be important biomasss 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

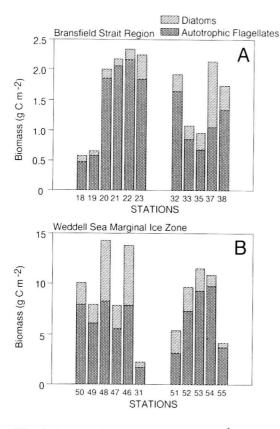


Fig. 3. Carbon biomass (gram carbon m⁻²) of total diatoms and autotrophic flagellates integrated in the upper 100 m in the Bransfield Strait region (A) and in the Weddell Sea marginal ice zone (B).

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 ultra sturctural level. Although *P. pouchetii* has been considered as an important Antarctic species and has been well described under both the motile an 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

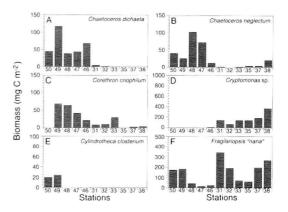


Fig. 4. Carbon biomass (gram carbon m⁻²) of phytoplankton species integrated in the upper 100 m along the north-south transect (A) Chaetoceros dichaeta, (B), Chaetoceros neglectum, (C) Corethron criophilum, (D) Cryptomonas sp., (E) Cylindrotheca closterium, (F) Fragilariopsis "nana".

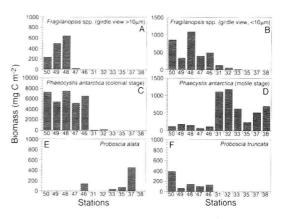


Fig. 5. Carbon biomass (gram carbon m⁻²) of phytoplankton species integrated in the upper 100 m along the north-south transect (A) *Fragilariopsis* spp. (girdle view, > 10 μ m), (B), *Fragilariopsis* spp. (girdle view, < 10 μ m), (C) *Phaeocystis* antarctica (colonial stage), (D) *Phaeocystis* antarctica (motile stage), (E) *Proboscia alata*, (F) *Proboscia truncata*.

dianostic pigments 19'-hexanoyloxyfucoxanthin, 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.

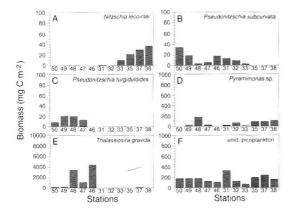


Fig. 6. Carbon biomass (gram carbon m⁻²) of phytoplankton species integrated in the upper 100 m along the north-south transect (A) Nitzschia lecointei, (B), Pseudonitzscia subcurvata, (C) Pseudonitzscia turgiduloides, (D) Pyramimonas sp., (E) Thalassiosira gravida, (F) unidentified autotrophic picoplankton.

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 net 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 diferences (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 $(6.5\pm1.0 \text{ g C m}^{-2})$ than in the BSR $(0.05\pm0.08 \text{ g C m}^{-2})$, but the mean biomass of P. antarctica in motile stage was about six times higher in the BSR $(0.73 \pm 0.36 \text{ g C m}^{-2})$ than in the WMIZ (0.13 \pm 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 n 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 maxmum densities of juveniles and immature adults occurred under the ice and in the northern 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 muco-polysaccharides synthesized n 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 oberved at the ice edge, which suggested an even higher estimation of available source of food in the study area.

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APPENDIX I. Classification of the observed species

Division BACILLARIOPHYTA

Order Centrales

Suborder coscinodiscinae
Family Thalssiosiraceae Lebour 1930. emend Hasle 1973
Thalassiosira antarctica Comber
Thalassiosira gracilis (Karst.) Hustedt
Thalassiosira gravida Cleve
Thalassiosira sp.
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 Suborder Rhizosoleniineae Family Rhizosoleniaceae Petit 1888 Dactyliosolen antarcticus Castracane Dactyliosolen tenuijunctus (Mang.) Hasle Rhizosolenia chunii Karsten Rhizosolenia inermis Castracane Suborder Biddulphineae Family Biddulphiaceae kützing 1844 Subfamily Hemiauloideae Jous, Kiselev & Poretskii 1949 Eucampia antarctica var. recta (Mangin) Fryxell et Prasad Subfamily Chaetoceraceae Smith 1872 Chaetoceros bulbosum Chaetoceros criophilum Castracane Chaetoceros dichaeta Ehrenberg Chaetoceros flexuosum Mangin Chaetoceros neglectum Kartsen Chaetoceros shimperianum Chaetoceros socialis Lauder Family Eupodiscaceae Kützing 1849 Subfamily Eupodiscoideae Kützing 1849

Odontella weissflogii (Janisch) Grunow

Order Pennales Suborder Araphidineae Famly Diatomaceae Dumortier 1822 Trichotoxon reinboldii (Van Heurck) Feid et Round Suborder Raphidineae 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 heimii 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

Fryxell *et al.* 1981. p. 324-330, figs. 1-33; Johansen and Fryxell 1985. p. 163, figs. 37-39; Krebs 1983. p. 294, PL.5, figs. 4a-f; Fryxell and Johansen 1990. p. 103, PL. 11.9, figs. 1, 2; Wasell and Håkansson 1992. p. 187, figs. 130, 131.

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

Johansen and Fryxell 1985. p. 164, fig. 43; Krebs 1985. p. 214b, fig. 9; Fryxell and Johansen 1990. p. 103, PL. 11.9, fig. 13.

Family Melosiraceae Kützing 1844

Corethron criophilum Castracane

Priddle and Fryxell 1985. p. 55, figs. A-I; Krebs 1985. p. 205b, fig. 11; Thomas and Bonham 1990. p. 101, PL. 12, figs. 1, 3, 5; El-Sayed and Fryxell 1993. p. 97, figs. 2-4; Crawford and Hinz 1995. p. 96-103, figs. 1-38.

Family Coscinodiscaceae Kützing 1844

Stellarima microtrias (Ehrenberg) Hasle & Sims

Syvertsen 1985. p. 115, figs. 1-9; Hasle and Sims 1986. p. 104-105, figs. 18-27; Fryxell 1989. p. 5-6, figs. 6-17; Round *et al.* 1990. p. 189-1981, figs. a-i; Hasle and Syvertsen 1990. p. 109, PL. 13.1, figs. 1-2; El-Sayed and Fryxell 1993. p. 73, figs. 2.4(1-2).

Family Hemidiscaceae Hendey 1937 emend Simonsen 1975

Actinocyclus actinochilus (Ehren berg) 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 Rhizosoleniineae

Family Rhizosoleniaceae Petit 1888

Dactyliosolen antarcticus Castracane

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

Dactyliosolen tenuijunctus (Mang.) Hasle

Priddle and Fryxell 1985. p. 61, figs. A, B.

Rhizosolenia chunii Karsten

Priddle and Fryxell 1985. p. 70, figs. A-E; Priddle *et al.* 1990. p. 125, fig. 2.

Rhizosolenia inermis Castracane

Priddle et al. 1990 p. 125, fig. 6a, b

Suborder Bioddulphineae

Family Biddulphiaceae Kützing 1844

Subfamily Hemiauloideae Jous, Kiselev & Poretskii 1949

Eucampia antarctica var. recta (Mangin) Fryxell et Prasad

Priddle and Fryxell 1985. p. 67; Hasle and Syvertsen 1990. p. 131, figs. 7-13; Fryxell and Prasad 1990. p. 30-32, figs. 2-16; El-Sayed and Fryxell 1993. p. 92, fig. 2.17.

Subfamily Chaetoceraceae Smith 1872

Chaetoceros bulbosus complex

Priddle and Fryxell 1985. p. 25, figs. A-J.

Chaetoceros criophilum Castracane

Fryxell and Madlin 1981. p. 28, figs. 53; Priddle and Fryxell 1985. p. 31, figs. A-D; Fryxell 1989. p. 10, figs. 33-34.

Chaetoceros dichaeta Ehrenberg

Priddle and Fryxell 1985. p. 33, figs. A-H; El-Sayed and Fryxell 1993. p. 85, fig. 2-12(2).

Chaetoceros flexuosum Mangin

Fryxell and Madlin 1981. p. 19, 21, 22, figs. 1-8, 16-28; Priddle and Fryxell 1985. p. 35, figs. A-D.

Chaetoceros neglectum Kartsen

Priddle and Fryxell 1985. p. 47, figs. A-C.

Chaetoceros socialis Lauder

Priddle and Fryxell 1985. p. 53, figs. A-I.

Family Eupodiscaceae Kützing 1849

Subfamily Eupodiscoideae Kützing 1849

Odontella weissflogii (Janisch) Grunow

Priddle and Fryxell 1985. p. 71. A-H

Order Pennales Suborder Araphidineae

Family Diatomaceae Dumortier 1822

Trichotoxon reinboldii (Van Heurk) Feid et Round

Reid and Round 1987. p. 221-222, figs. 2-16; Hasle 1990. p. 135, figs. 7-8.

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 Nitzschiaceae Grunow 1860

Cylindrotheca closterium (Ehrenberg) Reimann

Hasle and Medlin 1990a. p. 178, PL. 23.1, figs. 1-4.

Fragilariopsis curta (Van Heurck) Hasle

Hasle and Medlin 1990b. p. 193, PL. 24.6, figs. 2-5.

Fragilariopsis obliquecostata (Van Heurck) Hasle

Hasle and Medlin 1990b. p. 187, PL. 24.3, figs. 2-7.

Fragilariopsis ritscheri (Hustedt) Hasle

Hasle and Medlin 1990b. p. 187, PL. 24.3, figs.

8.

Fragilariopsis vanheurckii (M. Per.) Hasle

Hasle and Medlin 1990b. p. 193, PL. 24.6, figs. 13-16.

Pseudonitzschia heimii Manguin

Hasle 1965. p. 67. figs. 1-7; Hasle and Medlin 1990b. p. 172, PL. 22.2, figs. 9-13.

Pseudonitzschia turgiduloides Hasle

Hasle 1965. p. 69, figs. 9-16; Hasle and Medlin 1990b. p. 173, PL. 22.3, figs. 9-14.

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- **Plate 1.** 1-5. *Thalassiosira* spp. External view of girdle. Connected by multiple chitin threads twisted, rope-like. (Scale bars: $1, 2 = 20 \ \mu m$; $3-5 = 40 \ \mu m$)
- Plate 2. 6. *Thalassiosira antarctica* (external view of valve)
 7-8. *Thalassiosira 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. Dactyliosolen antarcticus (external view of girdle)22. Dactyliosolen tenuijunctus (external view of girdle)23. Proboscia chunii (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 girde)
 (Scale bars: 24, 25, 28 = 20 μm; 26, 27, 29 = 20 μm)
- Plate 6. 30. Chaetoceros criophilum (external view of girde) 31-33. Chaetoceros dichaeta (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 girde)
 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. Pseudogomphonema arcticum (internal view of valve)
 44-45. Cylindrotheca closterium
 (Scale bars: 40, 41 = 100 μm; 42, 43 = 10 μm; 44, 45 = 20 μm)
- **Plate 9.** 46-50. *Fragilariopsis* spp. External view of girdle. Colony formed. (Scale bars: 46, 48 = 10 μ m; 47, 49 = 20 μ m; 50 = 40 μ m)
- Plate 10.
 51. Siliated protozoa containing many small Fragilariopsis cylindrus

 52.
 Fragilariopsis curtai (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: $51 = 20 \ \mu m$; $52-54 = 5 \ \mu m$; $55-57 = 10 \ \mu m$)

- 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 *Parvicorbicula socialis* (colony formed) (Scale bars: 64, 65, 68 = 10 μ m; 66, 67 = 20 μ m)

