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Annually recurrent phytoplanktonic assemblages during summer in the seasonal ice zone west of the Antarctic Peninsula (Southern Ocean)

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Abstract

The distribution of phytoplankton composition, cell abundance and biomass from an area along the Western Antarctic Peninsula was studied during three summers, with the aim of understanding its dynamics over spatial and interannual scales. The studied area is characterized by seasonal sea-ice retreat and advance. Algae composition and concentration were found to be highly variable through the area as well as from year to year. Small unidentified phytoflagellates, diatoms and cryptophytes were the main phytoplankton groups, contributing the major proportion of total phytoplankton cell abundance and biomass concentration. Three annually recurrent phytoplankton assemblages were recognized in the area according to the algae composition and abundance: a diatom bloom associated with the sea-ice edge, an assemblage dominated by small unidentified phytoflagellates and cryptophytes, and a diatom-enriched assemblage in open waters. The distribution of these assemblages varied from year-to-year. During the summers preceded by early sea-ice retreat, the diatom bloom was spatially restricted and the other two assemblages occupied extended regions, whereas during the late sea-ice retreat year, the diatom bloom extended over a larger region and the other assemblages occupied smaller regions or were just absent. It was detected that these assemblages resemble different stages of the phytoplankton seasonal cycle, and that their distribution through the area can be related to a latitudinal and longitudinal gradient in the phytoplankton growth onset timing, associated with the progressive sea-ice retreat during spring. The local environmental conditions associated with each assemblage were also analyzed, but further study is needed for understanding the causes of the replacement of one assemblage by another through the area. On the other hand, the interannual variability in the distribution of the assemblages can be related to

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year-to-year differences in the timing of phytoplankton growth onset, associated with variations in the timing of the sea-ice retreat.

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1. Introduction

The Southern Ocean is considered a high-nutrient, low-chlorophyll (HNLC) ecosystem, where enhanced phytoplankton biomass is associated primarily with frontal, coastal and sea-ice edge zones (Tréguer and Jacques, 1992; Sullivan et al., 1993; Marchant and Murphy, 1994). However, the physical, chemical and biological conditions of the water have large spatial, seasonal and interannual variations, determining changes in phytoplankton composition, abundance and biomass over different spatial and temporal scales (Priddle et al., 1994; Walsh et al., 2001; Moore and Abbott, 2002). This variability in the structure of the phytoplanktonic community has important implications for the entire ecosystem, since phytoplankton, as the autotrophic component of the marine ecosystem, affects the structure and efficiency of the food web, the global biogeochemical cycles and the carbon sedimentation to deep waters (Priddle et al., 1992; Smetacek, 1996; Walsh et al., 2001).

During the past decades many studies analyzed the spatial and seasonal variability of the Antarctic phytoplankton structure and dynamics. While these studies have improved the understanding of the mechanisms that regulate the phytoplankton structure, little is known about its interannual variability/stability. This follows the fact that most research projects have included only one sampling year, or their results for different years have not been comparable because of differences from year-to-year in sampling strategies or methods (e.g. BIOMASS Programme, Priddle et al., 1994). Recently, it has become increasingly evident that interannual studies are necessary for better understanding of the dynamics of the Antarctic phytoplankton, and to discriminate the patterns of its dynamics that are annually stable from those that are a consequence of exceptional environmental conditions during the studied year. Moreover, considering that sea-ice and glacial melting highly affect the phytoplankton dynamics (Smith and Nelson, 1985; Smith and Sakshaug, 1990), and that global warming has led to an increase in sea-ice and glacial melting in the Southern Ocean (Priddle et al., 1992; Smith et al., 1999; Smith and Stammerjohn, 2001), it has been hypothesized that the ongoing global climatic changes may induce shifts in the phytoplankton composition (Moline et al., 2000). In turn, phytoplankton shifts should impact on the dynamics of higher consumers, modifying the entire ecosystem (Loeb et al., 1997; Smith et al., 2001). Therefore, interannual studies may help us to understand these topics.

Long-term studies started in 1990 along the continental shelf west of the Antarctic Peninsula, with the purpose to understand the trophic chain dynamics and their relation with the environment (Palmer Long-Term Ecological Research program, Baker et al., 1996). These studies detected a year-to-year recurrence of an on/offshore negative gradient in chlorophyll *a* (chl*a*) concentration and primary production during summer (Smith et al., 1998a, b, 2001), evidencing a high interannual stability in the spatial distribution of the phytoplankton standing stock. However, they also showed large interannual variability in the magnitude of these gradients, related to interannual changes in the sea-ice dynamics during the previous winter. In particular, during January 1997 the chl*a* gradient was coupled to changes in phytoplankton cell abundance and carbon biomass (C), and large spatial variability in the community composition was found (Garibotti et al., 2003a). During this summer nanophytoflagellates ($<20\,\mu$m) dominated numerically throughout the area, large microplanktonic diatoms ($>20\,\mu$m) contributed to the autotrophic C inshore, and cryptophytes, chlorophytes and prymnesiophytes showed distinct cell abundance and biomass peaks in restricted regions. This one-year study evidenced the complexity of the phytoplankton composition distribution within the area, but it is still to be proven whether this corresponds to a stable pattern or to an exceptional one taking place during the studied summer. Furthermore, so far it is not known if phytoplankton composition changes from year to year, and if it is related or not to the observed variability in the chl*a* on/offshore gradients.

In the present study, samples from three summer cruises to the western Antarctic Peninsula were analyzed in order to assess the phytoplankton composition variability over spatial and interannual scales. The summers of 1996, 1997 and 1999 were included in this study since they are representative of the range of primary productivity observed during the 1990s (high productivity during 1996, intermediate during 1997 and low during 1999). In addition, these summers were characterized by differences in sea-ice extent during the previous winters (high sea-ice extent in 1996, medium in 1997 and low in 1999) (Smith et al., 2001). Our specific goals were: (1) to comparatively analyze the phytoplankton composition, concentration and distribution during the three studied summers, (2) to determine whether the phytoplankton structure is stable or variable from year-to-year, and (3) to evaluate the ecological mechanisms regulating the interannual phytoplankton dynamics.

2. Methods

2.1. Study site

The studied area is located on the continental shelf west of the Antarctic Peninsula, extending between 64° and 68°S, and from the coast to approximately 200 km offshore (Fig. 1). Sampling was performed on board the R/V *Polar Duke* during the summer cruises (January and February) of 1996 and 1997, and on the ARV *L.M. Gould* in 1999. Stations were located at 20 km intervals along five across-shelf transect lines (Fig. 1), plus additional coastal stations. The stations located onshore of the line delineated by Anvers, Renauld and Adelaide Islands are referred to as being in coastal waters, and those located offshore as being in open waters.

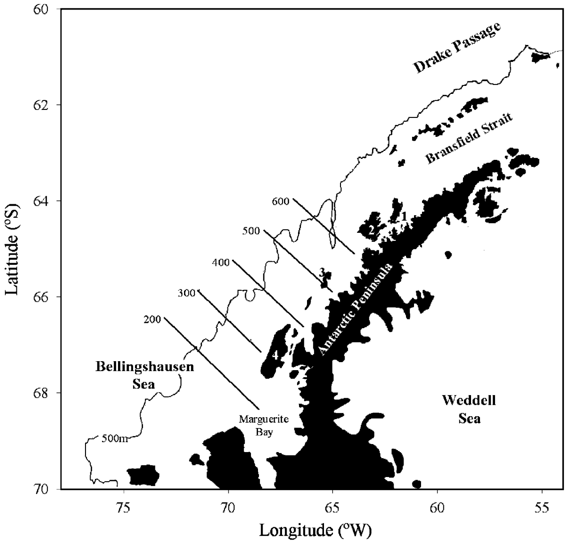

Fig. 1. Location of the sampling transect lines occupied off the western coast of the Antarctic Peninsula during the three studied summers. 200–600 correspond to transect numbers. The 500 m isobath represents the continental shelf-break. 1—Gerlache Strait, 2—Anvers Island, 3—Renaud Island, 4—Adelaide Island.

2.2. Physical variables

At each station temperature and salinity measurements were made to 500 m depth (or within a few meters from the bottom) with a Sea Bird CTD system (SBE 9/11) on a Bio-Optical Profiling System (BOPS). The BOPS included a conductivity–temperature–depth (CTD) sensor, a Biospherical Instruments MER 2040 system to determine spectral irradiance, and a SeaTech profiling fluorometer for in situ fluorescence profiles. Water density was estimated as sigma-*t* (σ_t). The depth of the upper mixed layer (UML) was estimated from the σ_t profiles. It was considered to be the depth where a change of $\sigma_t > 0.05$ occurs over a 5 m depth interval.

2.3. Sample collection

At each station a General Oceanics rosette with 10 or 121 Go-Flow Niskin bottles was used to collect discrete water samples. The depths of sampling were set at light levels, established by measuring the Photosynthetically Active Radiation (PAR) with a QSI 240 quantum sensor (Biospherical Instruments Inc.). Water aliquots were taken from six depths within the euphotic layer (100%, 50%, 30%, 13%, 4% and 0.5% PAR).

2.4. Sample analysis

For microscopic analyses water aliquots were taken from the 50% PAR depth (5–30 m) and preserved with 2% acid Lugol's iodine solution. This depth was always within the UML, so it is presumed representative of this layer. This presumption is based on previous studies performed in the area, which have shown no major phytoplankton composition variations with depth (Ross et al., 2000; Garibotti et al., 2003b).

Microscopic analysis were performed as described in Garibotti et al. (2003b). Phytoplankton cells were identified and counted with an inverted microscope (Iroscope IS-PH) according to the Utermöhl method (Utermöhl, 1958). Identification of individual cells was performed to the lowest possible taxonomical level, i.e. most diatoms were identified to species level; most phytoflagellates were identified to class level (cryptophyte, prymnesiophyte, prasinophyte and dinoflagellate); and some small (<20 μm) spherical mono- or biflagellate specimens, which could not be identified, were included in a group named unidentified phytoflagellates. Differentiation between autotrophic and heterotrophic flagellates was done either on the basis of the genus of known trophic mode or by clear presence/absence of chloroplasts.

Cell biovolumes were measured using the geometric shapes proposed by Hillebrand et al. (1999), and corrected to account for cell shrinkage due to sample fixation (Montagnes et al., 1994). Cell carbon content (C) was calculated with two different carbon-to-volume ratios, one for diatoms (Montagnes and Franklin, 2001) and one for all the other algae groups (Montagnes et al., 1994). These C concentrations are considered the best approach, but it should be noted that they are not comparable to those calculated using different cell C:cell volume ratios (Garibotti et al., 2003b). Thus, the C concentrations were also estimated using the more classical ratios proposed by Strathmann (1967), even when some studies have demonstrated that these ratios are not accurate (Montagnes et al., 1994; Menden-Deuer and Lessard, 2000; Montagnes and Franklin, 2001). These data are reported in Appendix A and may be useful to qualitatively compare our area with others in the Southern Ocean where C concentrations have been estimated using Strathmann's ratios.

To estimate nutrient concentrations water aliquots were collected from the six depths within the euphotic layer, and were analyzed within 12 h of sampling. Silicic acid, nitrate plus nitrite, ammonium and phosphate concentrations were measured according to the methods described in Johnson et al. (1985). A Perstorp/Alpken segmented flow nutrient analysis system and Labtronics data collection software were used. Because of technical problems phosphate concentrations were not estimated during the 1997 summer.

2.5. Analysis of sea-ice cover

Monthly maps of sea-ice coverage along the western Antarctic Peninsula were analyzed comparatively to evaluate the variability of the sea ice during the winter and spring seasons that preceded the studied summers. The maps analyzed are a part of a multi-year record of the sea ice for the western Antarctic Peninsula available online (Smith and Stammerjohn, 2002); full details of sea-ice coverage and dynamics in the studied area have been published by Smith and Stammerjohn (2001) and Smith et al. (2001).

2.6. Data analysis

Contour plots of the horizontal spatial distribution patterns of the phytoplankton were generated by using the inverse distance-weighting algorithm for interpolation of the grid (Jongman et al., 1995).

Tests for differences in the mean phytoplankton concentration between years were performed using paired *t*-tests. The level of significance was set at $p < 0.05$.

Cluster analyses were performed to identify groups of stations with similar phytoplankton assemblages. Station classification was based on the abundance of the six phytoplankton groups identified: diatoms, cryptophytes, prymnesiophytes, prasinophytes, dinoflagellates and unidentified phytoflagellates. The Bray-Curtis similarity coefficient was applied to construct a sample similarity matrix used for input in cluster analysis. This coefficient measures the resemblance among phytoplankton assemblages of two sites as the sum of the differences of the abundance of each phytoplankton group at each site (Jongman et al., 1995). Abundances were log-transformed so that large counts do not dominate the Bray-Curtis similarity coefficient totally. A complete-linkage hierarchical agglomerative clustering procedure was used to group similar samples (Pielou, 1984; Jongman et al., 1995).

3. Results and discussion

3.1. Phytoplankton composition variability

The main phytoplankton groups detected in the studied area were diatoms, cryptophytes and unidentified phytoflagellates, contributing more than 90% of cell abundance and 80% of C biomass of the total phytoplanktonic community (Fig. 2). Prasinophytes, prymnesiophytes and dinoflagellates were also found, but with much lower abundance and biomass. The three main phytoplankton groups are common components of the Antarctic flora, and have been frequently cited as dominating the phytoplankton of other areas of the Southern Ocean (Jacques and Panouse, 1991; Kopczynska, 1991; Fiala et al., 1998; Varela et al., 2002). Thus, it seems that they have high relevance not only in the ecosystem dynamics of our area, but in the Southern Ocean in general. In fact, it is recognized that these may be the most relevant groups regulating different processes, such as the carbon flow through the trophic chain and the CO_2 sequestration in deep waters (Walsh et al., 2001; Arrigo et al., 2003). Therefore, in this study the analysis of the phytoplankton interannual variability is focused mainly on these groups.

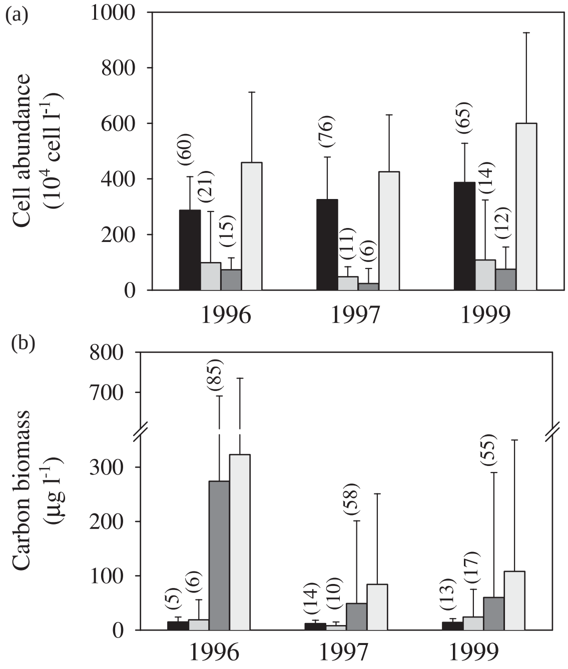

Fig. 2. Concentration of the main phytoplankton groups and of the total phytoplanktonic community averaged over the entire area during the studied summers. (a) Cell abundance, (b) carbon biomass. Black column: unidentified phytoflagellates; gray: cryptophytes; dark gray: diatoms; light gray: total phytoplankton. Relative concentration of the phytoplankton groups in brackets at the top of each column. Bars represent the standard deviation of the data.

During the three summers we found the same general distribution of total cell abundance and C biomass among the major phytoplankton groups (Fig. 2): unidentified phytoflagellates were numerically dominant but contributed with relatively low C biomass, diatoms presented low abundance but dominated the phytoplankton biomass, and cryptophytes showed intermediate cell abundance and C biomass values. This result suggests that the phytoplankton structure is relatively constant from one year to another. However, Fig. 2 also shows pronounced interannual variability in the average standing stock of each algae group,

Table 1
Results of the comparison of mean cell abundance and carbon biomass of algal groups and total phytoplankton between years

	Summer 1996 vs. Summer 1997	Summer 1996 vs. Summer 1999	Summer 1997 vs. Summer 1999
Cell abundance			
Unidentified phytoflagellates	=	*	*
Cryptophytes	*	=	*
Diatoms	*	=	*
Total phytoplankton	=	*	*
C biomass			
Unidentified phytoflagellates	*	=	*
Cryptophytes	*	=	*
Diatoms	*	*	=
Total phytoplankton	*	*	=

*Significant differences between years ($p < 0.05$), = non-significant differences.

correlating with year-to-year variations in total phytoplankton standing stock. In fact, concentrations differed significantly among years (Table 1). Furthermore, the unidentified phytoflagellate, cryptophyte and diatom distribution patterns varied from year-to-year (Fig. 3), and classification analyses of the sampling stations according to their similarity in algae composition and abundance allowed us to identify several regions with distinct phytoplankton assemblages during each year (Fig. 4). The composition and concentration of the phytoplankton in each region is summarized in Table 2.

The integrated analysis of the previous results allows us to recognize similarities among the phytoplankton assemblages differentiated during each studied summer. According to their structure (algae composition and standing stock) and distribution through the area, we distinguished three distinct yearly recurrent phytoplankton assemblages, which were named as: (1) diatom bloom associated with the sea-ice edge, (2) assemblage dominated by unidentified phytoflagellates and cryptophytes, and (3) diatom-enriched assemblage in open waters. In Tables 3 and 4 we summarize the characteristics of these assemblages. Note that unidentified phytoflagellates were numerically dominant throughout the area, but varied in their relative concentration in the three assemblages. Following we describe the characteristics of these assemblages and discuss the possible mechanisms that might have regulated their dynamics.

3.2. *Annually recurrent phytoplankton assemblages*

3.2.1. *Diatom bloom associated with the sea-ice edge*

One yearly recurrent phytoplankton assemblage was characterized by the dominance of diatoms, which represented more than 85% of the total phytoplankton C biomass (Table 3). The prymnesiophyte *Phaeocystis* spp. was also characteristic of this assemblage, contributing high cell abundance, but low biomass (Table 2). Diatom concentration peaks were found in this assemblage, reaching $210 \times 10^4\,\mathrm{cell\,l^{-1}}$ and $1563\,\mu\mathrm{g\,C\,l^{-1}}$ during 1996, $423 \times 10^4\,\mathrm{cell\,l^{-1}}$ and $888\,\mu\mathrm{g\,C\,l^{-1}}$ during 1997, and $605 \times 10^4\,\mathrm{cell\,l^{-1}}$ and $1442\,\mu\mathrm{g\,C\,l^{-1}}$ during 1999. Six diatom species dominated the assemblage during the studied summers (Table 4), evidencing year-to-year stability at the species level. Furthermore, blooms of these same species have been reported in other studies off the western Antarctic Peninsula (Holm-Hansen et al., 1989; Moline and Prézelin, 1996; Varela et al., 2002), allowing us to suggest the occurrence of a high similarity in the diatom bloom composition in this zone of the Southern Ocean. However, they differed from those of other zones, where blooms of other species are more frequently reported (e.g. Smith and Nelson, 1985; Jacques and Panouse, 1991; Bathmann et al., 1997).

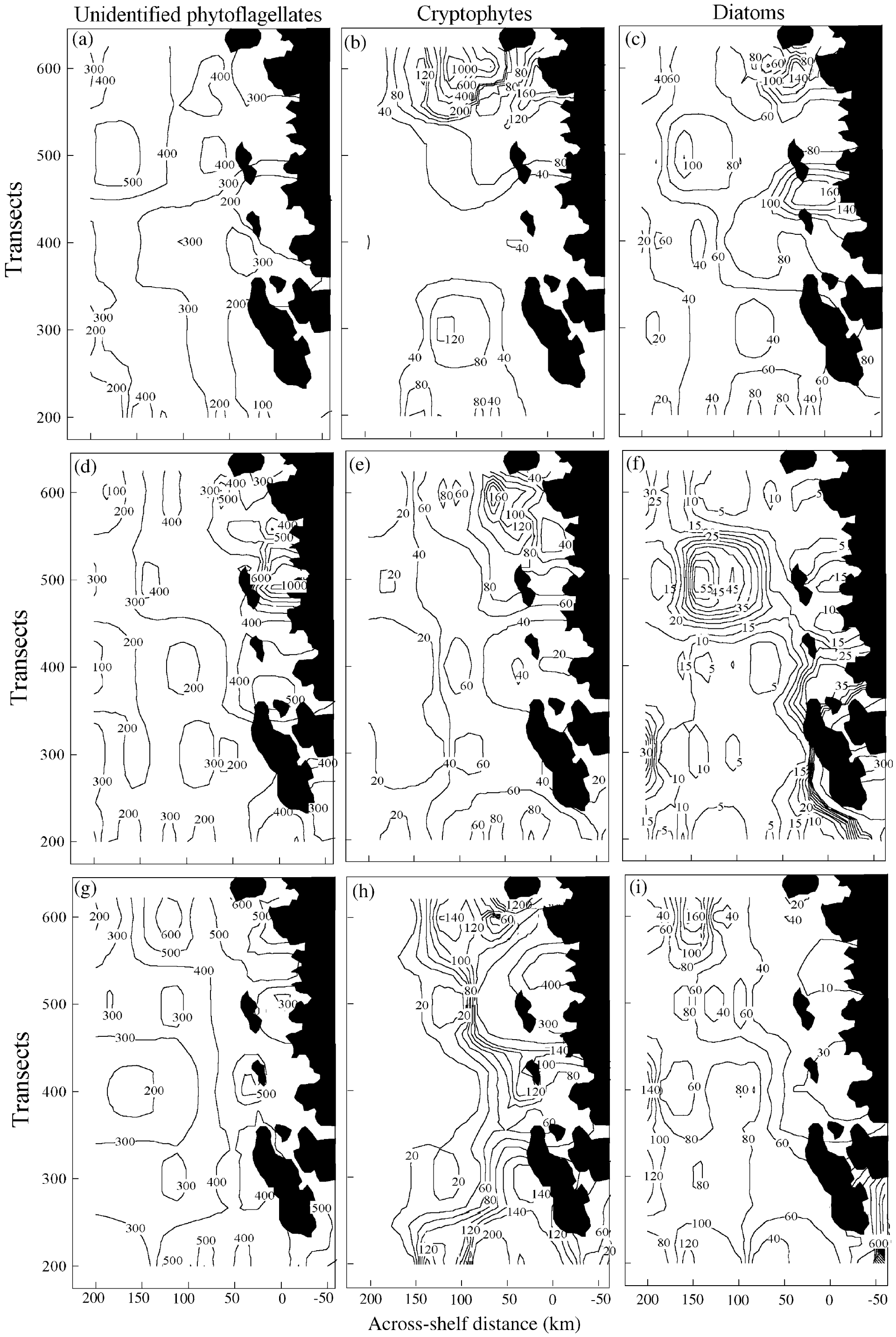

Fig. 3. Distribution of the abundance (10^4 cell l^{-1}) of the main phytoplankton groups at the 50% PAR depth. (a–c) Summer 1996, (d–f) summer 1997, (g–i) summer 1999. (a,d,g) Unidentified phytoflagellates, (b,e,h) cryptophytes, (c,f,i) diatoms. Transect numbers are as in Fig. 1.

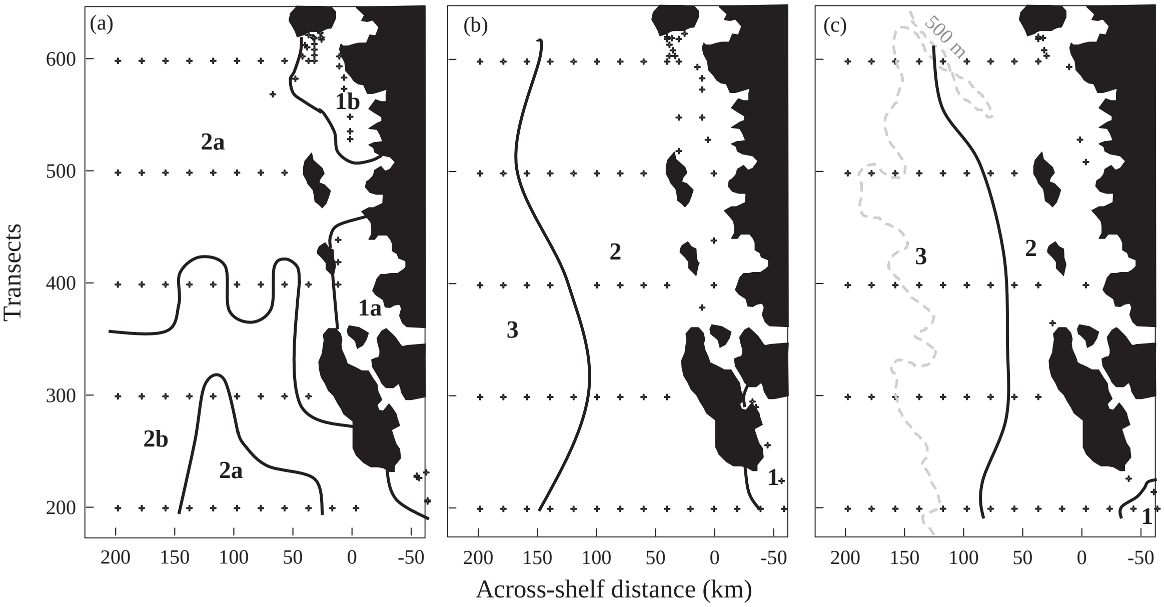

Fig. 4. Classification analysis of the sampling stations according to their algal composition and abundance. (a) Summer 1996, (b) summer 1997, (c) summer 1999. Region numbers correspond to: (1) diatom bloom associated with the sea-ice edge, (2) assemblage dominated by unidentified phytoflagellates and cryptophytes, (3) diatom-enriched assemblage in open waters. Crosses correspond to sampling stations. Transect numbers are as in Fig. 1. The dashed gray line in plot c corresponds to the 500 m isobath, which represents the continental shelf-break.

The diatom bloom was found at Marguerite Bay during all summers and also south of Anvers Island during 1996 (Fig. 4: Regions 1). The sea-ice cover was located in the southern part of Marguerite Bay during the three summers (Smith and Stammerjohn, 2002), indicating that the diatom bloom found in this bay was associated with the sea-ice edge. The dominance of diatoms and *Phaeocystis* spp. in the marginal sea-ice zone can be related to their release to the water column from epontic communities during sea ice melting, where they may act as inoculum of phytoplankton assemblages (Garrison and Buck, 1985; Buma et al., 1992). It can also be related to the water column stratification that characterized this region (see the low UML depth, Table 5), which may have allowed algae cells to remain in the upper portion of the water column, and to grow under a propitious light regime, favoring their bloom. As well, the region south of Anvers Island was characterized by a low UML depth during 1996 (Table 5: Region 1b). Thus, it seems that water column stratification was also responsible for the diatom concentration in this region, although it was not directly associated with the sea-ice edge.

The extended distribution of the diatom bloom observed during the 1996 summer is noteworthy (Fig. 4a). Moreover, a diatom bloom was also detected at the same time in the Gerlache Strait (Varela et al., 2002), indicating that a major portion of the coast of the western Antarctic Peninsula, from Marguerite Bay to the Gerlache-Bransfield Confluence, was dominated by diatom blooms during this summer. Thus, it is evident that the diatom blooms exhibited interannual variability in their distribution. To explain this variation we consider it relevant to take into account the sea-ice dynamics during the previous winter and spring seasons. With this purpose, we analyzed comparatively the extent of the sea ice in the studied area from the monthly maps of Smith and Stammerjohn (2002). From these maps it can be seen that sea ice retreats progressively from north to south and from offshore to inshore,

Table 2
Phytoplanktonic community structure during the three studied summers in distinct regions differentiated within the study area

	Total phytoplankton		Unidentified phytoflagellates		Cryptophytes		Diatoms		Prymnesiophytes		Prasinophytes		Dinoflagellates	
	Cells	Biomass	Cells	Biomass	Cells	Biomass	Cells	Biomass	Cells	Biomass	Cells	Biomass	Cells	Biomass
Summer 1996														
Region 1a	232±81	637±421	110±26	6±2	4±2	1±0	84±45	620±416	25±20	2±2	2±2	0±1	7±2	7±4
Region 1b	537±131	684±459	283±67	10±8	136±101	26±20	101±52	633±471	2±2	0	8±16	1±3	5±3	4±4
Region 2a	589±297	86±83	372±101	21±8	132±260	25±53	64±28	23±37	0	0	11±18	1±1	9±5	10±8
Region 2b	282±108	46±25	212±91	15±7	23±27	4±4	39±24	13±13	0	0	0	0	7±3	9±9
Summer 1997														
Region 1	733±175	603±224	306±77	8±6	24±20	3±2	154±137	520±221	220±186	19±16	7±3	1±1	14±5	18±5
Region 2	447±177	43±17	363±159	14±6	62±34	11±7	11±13	7±7	1±6	0	1±1	0	7±5	8±5
Region 3	253±115	25±11	216±103	7±3	15±10	2±2	44±15	7±5	1±3	0	0	0	4±2	5±2
Summer 1999														
Region 1	1141±470	1039±621	409±47	13±7	18±23	3±4	312±260	965±610	384±528	35±48	4±6	0	11±2	12±1
Region 2	769±323	91±71	493±114	18±5	223±288	51±68	38±20	13±18	0	0	1±2	0	9±5	6±3
Region 3	426±136	40±18	306±94	11±5	21±32	4±7	88±37	18±10	0	0	5±5	0	5±2	4±2

Average ± standard deviation cell abundance (10^4 cell l^{-1}) and carbon biomass (μg l^{-1}). Regions were differentiated by a classification analysis of the sampling stations according to their similarity in algae composition and abundance (Fig. 4).

and that the summers analyzed in the present research were preceded by seasons that differed in the timing of the sea-ice retreat. In fact, preceding the 1996 summer, sea ice started to retreat in October and partially covered the studied area until December; preceding the 1997 summer, the retreat started in September and no sea ice remained by December; and preceding the 1999 summer, the retreat started early in spring and no sea ice remained by November. Therefore, it can be argued that during the 1996 summer, because of the delayed sea-ice retreat, meltwater input must have recently influenced the waters all along the coast, creating the observed stratification of the water column (Table 5), and allowing the diatom growth and bloom in large regions of the studied area (Fig. 4a). In contrast, during the 1997 and 1999 summers, because of the early sea-ice retreat, the influence of melting waters was limited to the region surrounding the ice edge, determining the stratification of the water column only at Marguerite Bay (Table 5), and leading to a restricted distribution of the diatom bloom (Fig. 4b,c).

We concluded that in the studied area diatom blooms are associated with the sea-ice retreat. Moreover, since in the Southern Ocean phytoplankton growth starts when the sea-ice melts (Smith and Sakshaug, 1990), we assume that the diatom blooms constitute the first stage of the phytoplankton seasonal cycle in the studied area.

3.2.2. Assemblage dominated by unidentified phytoflagellates and cryptophytes

Another yearly recurrent assemblage was dominated by unidentified phytoflagellates and had the highest proportion of cryptophytes of the area (Table 3). Diatoms contributed also with a relatively high C biomass (Table 3). This assemblage occupied extended regions during the studied summers (Fig. 4: Regions 2), in agreement with the conception that small phytoflagellates dominate the phytoplanktonic community throughout most of the Southern Ocean (von Bröckel, 1981; Jacques and Panouse, 1991).

In particular, the presence of cryptophytes during the three summers is outstanding (Fig. 3),

Table 3
Percent of total cell abundance and carbon biomass contributed by unidentified phytoflagellates, cryptophytes and diatoms (%) in the three annually recurrent assemblages differentiated within the area. Regions are as in Fig. 4

		Unidentified phytoflagellates		Cryptophytes		Diatoms	
		Cells	Biomass	Cells	Biomass	Cells	Biomass
Diatom bloom associated with the sea-ice edge							
1996	Region 1a	47	1	2	0	36	97
	Region 1b	53	2	25	4	19	93
1997	Region 1	42	1	3	0	21	86
1999	Region 1	36	1	2	0	27	93
Assemblage dominated by unidentified phytoflagellates and cryptophytes							
1996	Region 2a	63	24	22	29	11	27
	Region 2b	75	33	8	8	14	28
1997	Region 2	81	32	14	26	3	17
1999	Region 2	64	21	29	56	5	14
Diatom-enriched assemblage in open waters							
1997	Region 3	85	28	6	9	6	27
1999	Region 3	72	27	5	10	21	46

Table 4
Dominant diatom species in the annually recurrent phytoplankton assemblages differentiated within the area

	1996		1997	1999
Diatom bloom associated with the sea-ice edge				
	Region 1a	Region 1b	Region 1	Region 1
Chaetoceros socialis	2.0±2.4	14.9±11.0	19.5±31.6	167.3±181.4
Coscinodiscus bouvet	47.6±80.0	78.4±76.1	0±0	601.9±327.0
Eucampia antarctica var. *antarctica*	508.7±387.8	203.3±157.4	96.0±70.7	40.0±50.0
Odontella weissflogii	27.3±27.2	246.5±222.9	298.0±160.0	17.7±30.6
Stellarima microtrias	0±0	0±0	0±0	53.3±92.4
Thalassiosira spp.	11.6±12.2	61.1±42.5	47.5±46.7	22.2±15.7
Assemblage dominated by unidentified phytoflagellates and cryptophytes				
	Region 2a	Region 2b	Region 2	Region 2
Actinocyclus actinochilus	1.6±6.0	1.6±5.5	0±0	3.4±12.5
Corethron pennatum	0±0	0±0	3.4±5.4	0.2±0.6
Fragilariopsis curta	1.7±2.1	0.9±1.0	0.2±0.4	0.2±0.2
Fragilariopsis curta, *F. cylindrus* and *F. pseudonana* (<10 μm)	5.3±2.4	3.2±2.0	1.0±1.4	4.3±2.2
Nitzschia spp.	2.7±3.2	1.9±2.4	1.0±1.4	0.5±1.5
Thalassiosira spp.	5.4±7.3	4.8±5.6	1.2±2.2	2.3±10.9
Diatom-enriched assemblage in open waters				
			Region 3	Region 3
Corethron pennatum			2.9±5.0	2.4±4.8
Fragilariopsis curta			0.4±0.6	1.8±1.2
Fragilariopsis curta, *F. cylindrus* and *F. pseudonana* (<10 μm)			1.4±1.1	9.8±4.3
Nitzschia spp.			0.9±1.5	0.8±0.9
Thalassiosira spp.			1.1±2.7	0.5±0.8

Average±standard deviation carbon biomass (μg l^{-1}). Regions are as in Fig. 4.

Table 5
Environmental variables in distinct regions within the study area

		Temperature	Salinity	UML depth	Silicate	Nitrate plus nitrite	Amonium	Phosphate
Diatom bloom associated with the sea-ice edge								
1996	Region 1a	−0.99±0.45	33.13±0.16	7±7	58.0±12.4	13.4±6.7	2.1±0.3	1.0±0.4
	Region 1b	−0.25±0.48	33.35±0.18	17±12	75.8±8.8	14.8±5.0	1.8±0.4	1.2±0.6
1997	Region 1	0.37±0.47	33.13±0.14	12±10	58.0±3.4	5.1±5.0	1.6±0.9	
1999	Region 1	0.46±0.38	33.57±0.09	16±5	33.7±2.5	8.5±3.7	2.6±1.2	0.9±0.1
Assemblage dominated by unidentified phytoflagellates and cryptophytes								
1996	Region 2a	0.60±0.55	33.62±0.16	34±19	65.2±7.7	20.0±4.2	2.3±0.7	1.5±0.3
	Region 2b	0.86±0.51	33.67±0.14	47±21	57.2±10.7	23.1±1.5	2.4±1.3	1.7±0.2
1997	Region 2	0.75±0.46	33.52±0.25	40±36	72.0±10.6	22.1±4.0	2.8±1.1	
1999	Region 2	0.28±0.50	33.66±0.14	35±22	54.9±19.0	19.0±5.3	2.0±0.8	1.5±0.3
Diatom-enriched assemblage in open waters								
1997	Region 3	1.26±0.26	33.80±0.03	53±9	47.5±9.7	25.0±3.1	2.0±1.2	
1999	Region 3	0.78±0.24	33.82±0.05	57±22	43.2±13.5	21.0±3.4	1.7±0.4	1.5±0.2

Average ± standard deviation. Regions are as in Fig. 4.

coinciding with Moline et al. (2000), who mentioned their recurrence during summer near the Anvers Island coast (northeast of the area). Our results demonstrate that the coastal cryptophyte blooms reported by these authors are part of a more extended assemblage. Furthermore, another outstanding characteristic is given by the cryptophyte concentration peaks that we found (Fig. 3), reaching values as high as $1132\times10^{4}\,\mathrm{cell\,l^{-1}}$ and $229\,\mu\mathrm{g\,C\,l^{-1}}$ during 1996 (off Anvers Island), $193\times10^{4}\,\mathrm{cell\,l^{-1}}$ and $36\,\mu\mathrm{g\,C\,l^{-1}}$ during 1997 (south of Anvers Island), and $1571\times10^{4}\,\mathrm{cell\,l^{-1}}$ and $369\,\mu\mathrm{g\,C\,l^{-1}}$ during 1999 (south of Anvers Island). Although the importance of cryptophytes in other areas of the Southern Ocean has been previously reported (Jacques and Panouse, 1991; Kopczynska, 1991; Buma et al., 1992; Kang and Lee, 1995; Rodríguez et al., 2002), as far as we know, the maximum concentrations measured were much lower than ours, ranging between 30 and $600\times10^{4}\,\mathrm{cell\,l^{-1}}$. Therefore, we conclude that cryptophytes are a distinctive and annually recurrent component of the phytoplankton of a large region of the studied area, exhibiting blooms which can be considered a peculiarity of our area.

The distribution of cryptophytes showed high interannual variability. During the 1996 summer they were limited to some restricted sites in open waters (Fig. 3b), while during the 1997 summer they were ubiquitous along the area, showing a maximum concentration south of Anvers Island (Fig. 3e), and during the 1999 summer they were distributed with relatively high abundance throughout most of the coastal and mid-shelf waters (Fig. 3h). Fig. 3 also shows that cryptophytes and diatoms presented a divergent distribution through the area. In fact, during the 1996 summer, peaks of cryptophyte and diatom standing stock were found along the Transect 600 line, but as the diatoms concentrated in the inner stations, the cryptophytes concentrated in the middle portion of the transect (Fig. 3b,c). During the 1997 summer, high cryptophyte abundance and biomass were found south of Anvers Island, in coincidence with a very low diatom concentration (Fig. 3e,f). Furthermore, the diatom maximum found at Marguerite Bay coincided with a relatively low cryptophyte concentration. Finally, during the 1999 summer, high diatom concentration was detected at Marguerite Bay, coinciding with a minimum in cryptophytes, and throughout the rest of the coastal and mid-shelf

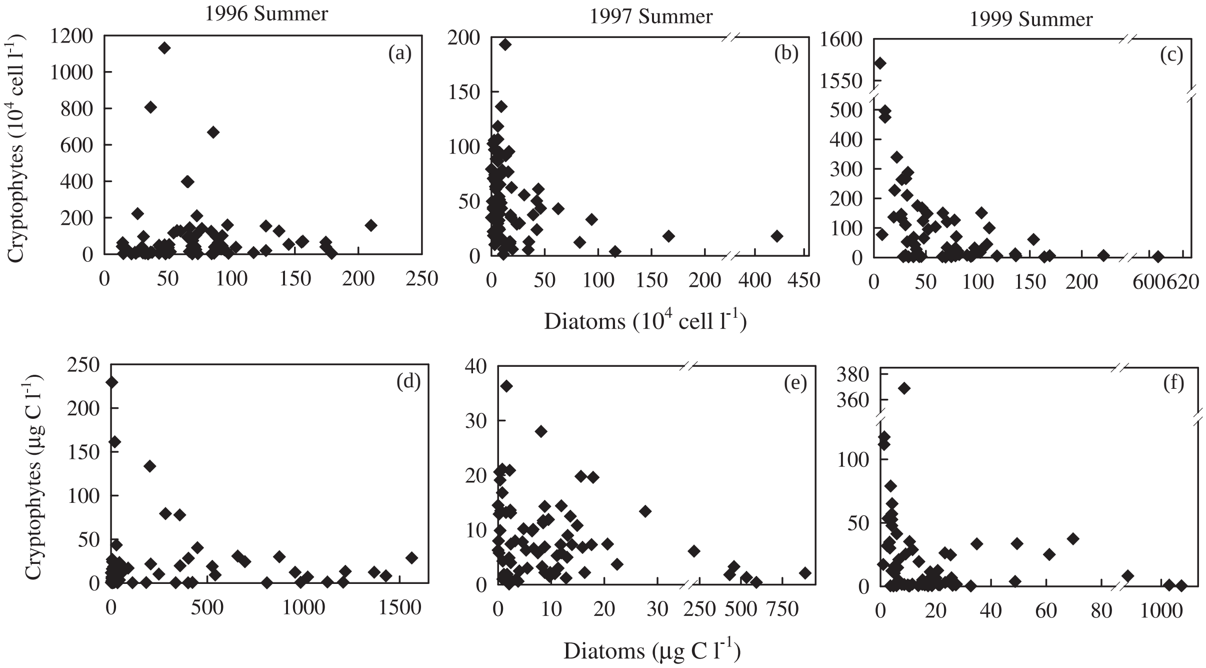

Fig. 5. Relationship between cryptophyte and diatom concentrations. (a–c) Cell abundance, (d–f) carbon biomass. (a,d) Summer 1996, (b,e) summer 1997, (c,f) summer 1999.

waters, cryptophytes exhibited high concentration associated with the lowest diatom abundance and biomass estimated for the area (Fig. 3h,i). In fact, the scatter-plots of cryptophyte versus diatom standing stock clearly show an inverse relationship for the three studied summers (Fig. 5).

These previous results emphasize that the spatial replacement of cryptophytes and diatoms is a characteristic of the phytoplankton structure of the studied area, despite the high interannual variability in the extent of the region occupied by each group. Some studies reported that similar cryptophyte-enriched assemblages developed after a sea-ice edge diatom bloom, and considered them as a secondary stage of the seasonal phytoplankton succession (Jacques and Panouse, 1991; Kang and Lee, 1995; McMinn et al., 2000; Moline et al., 2000; Bode et al., 2002). Therefore, here we hypothesize that the cryptophyte-enriched assemblages we found constitute a secondary stage of the seasonal phytoplankton succession, following the diatom blooms, and that the vicariate spatial distribution of cryptophytes and diatoms observed may be related to their succession in the seasonal cycle.

Furthermore, we consider that the observed spatial distribution pattern of cryptophytes and diatoms can be related to their seasonal succession. This follows the fact that, as the sea ice retreats progressively from north to south and from offshore to inshore, there should exist a similar gradient in the timing of phytoplankton growth onset. Diatoms must have started growing in the northwestern portion of the area, and should have progressively moved to coastal and southern regions following the sea-ice retreat, to be finally found during our sampling period throughout the coast (1996 summer) or at Marguerite Bay (1997 and 1999 summers). Cryptophytes, as the secondary stage of the seasonal phytoplankton succession, should have progressively occupied those sites when the diatom bloom had already disappeared, thus explaining their distribution in northern and more offshore waters than diatoms (Figs. 3 and 4). This discussion concurs with Hart, who in 1934 and 1942 suggested the existence of a latitudinal gradient in the timing of Antarctic phytoplankton growth initiation. Notably, this was not considered in further studies as a possible major factor explaining the phytoplankton spatial distribution.

The observed interannual variability in the diatom and cryptophyte distributions is also consistent with the previous discussion. During 1996 the diatom bloom was distributed throughout large regions of the area, and cryptophytes were spatially restricted (Figs. 3b,c, and 4a). Since during this season sea ice retreated late in spring, phytoplankton growth must have started late, and therefore the seasonal succession of phytoplankton was in an early stage during the sampling period. In addition, the restricted distribution of the diatom bloom, and the higher concentration and extended distribution of cryptophytes during the other two summers (Figs. 3e,f,h,i, and 4b,c), suggest that the phytoplankton seasonal succession was more advanced than in 1996 because of the earlier sea-ice retreat registered during these years. Thus, we conclude that the interannual variability in the cryptophyte abundance and distribution, and in the spatial replacement of diatoms by cryptophytes through the area, was related to the year-to-year variations in the sea-ice retreat timing, which regulated the phytoplankton seasonal cycle progression.

Another aspect that could be analyzed in connection with the previous discussion is the determination of the local environmental factors responsible for the replacement of diatoms by cryptophytes as the seasonal succession progresses. In this regard we comparatively analyzed the environmental conditions in the regions dominated either by diatoms or by cryptophytes. Previous seasonal studies performed in different areas of the Southern Ocean reported several variables as possible regulators of the diatom–cryptophyte seasonal replacement, considered as follows.

(1) At Anvers Island coast, Moline et al. (2000) estimated a negative relationship between the salinity and the percentage of cryptophytes in the community, and associated the growth of these algae with the initiation of glacial melting and freshwater input to the water column. Thus, they suggested this as the cause of the diatom–cryptophyte replacement through the seasonal cycle. Dierssen et al. (2002) suggested that glacial meltwater may move offshore, influencing the offshore phytoplankton communities. However, we found a high abundance of cryptophytes under variable salinity conditions (from 32.80 to 33.84, Table 5). Moreover, we estimated a low correlation between the percentage of cryptophytes in the community and the salinity throughout the area ($R^2 = 0.002$, $p < 0.01$). Therefore, the mechanism proposed as regulating cryptophyte assemblages in coastal waters cannot a priori be applicable to those we found widespread in a large region.

(2) Other studies explained the phytoplankton succession from diatoms to cryptophytes by considering the variables that might put an end to the diatom bloom. Furthermore, it is considered that cryptophytes are competitors of diatoms for nutrients and light, so that the diatom disappearance facilitates a cryptophyte bloom (Walsh et al., 2001). One cause invoked to explain the diatom bloom demise is macronutrient exhaustion by phytoplankton consumption (Holm-Hansen et al., 1989; Moline et al., 1997). However, macronutrients clearly did not limit diatom growth in our area, since their concentrations exceeded those found to be limiting for phytoplankton growth (Table 5). Another possible cause is the deepening of the mixed layer (Mitchell and Holm-Hansen, 1991; Varela et al., 2002), but although in our area diatoms dominated in a stable water column, cryptophyte dominance occurred under different mixing conditions (Table 5). Thus, mixing is not likely the factor determining the observed divergent distribution of diatoms and cryptophytes. Hence, the causal mechanism underlying the diatom–cryptophyte replacement still remains under study.

3.2.3. Diatom-enriched assemblage in open waters

A third phytoplankton assemblage was differentiated during the 1997 and 1999 summers. It occupied the mid-shelf and open water stations (Fig. 4b,c: Regions 3) and was characterized by the dominance of unidentified phytoflagellates and diatoms (Table 3). It is remarkable that during these two summers the unidentified phytoflagellate concentration decreased towards offshore, while diatom concentration increased (Fig. 3). Thus, diatoms represented a higher proportion of the total cell abundance and biomass in this assemblage than in that located more inshore (Table 3: compare diatom relative concentration in Regions 2 and 3). The dominant diatom species were small cells of *Fragilariopsis curta, F. pseudonana* and *F. cylindrus*, and the micro-diatom *Corethron pennatum* (Table 4). These species are considered typical of Antarctic pelagic waters (Hasle, 1969), indicating that the increased concentration of diatoms found was due to the accumulation of local species.

In addition to the diatom-enriched assemblage we found in offshore waters during two summers, Prézelin et al. (2000) mentioned a similar one in the same region for summer 1993. These observations indicate that this assemblage is common in open waters of the studied area. This represents a peculiar characteristic for a seasonal sea-ice zone (SIZ) of the Southern Ocean, since it is generally considered that once the diatom bloom associated with the sea-ice edge disappears, the community that develops in the ice-free waters has the characteristics typical of those found in permanently open waters (i.e. low biomass concentration and dominance of nano-phytoflagellates and diatoms) (Smetacek et al., 1990; Tréguer and Jacques, 1992). Moreover, it is assumed that the composition and concentration of this community is fairly stable over space and time (Smetacek et al., 1990; Bathmann, 1998). However, our results showed a more complex model than that previously considered for the phytoplankton structure of a SIZ, as detailed below.

(1) The presence of two assemblages, the assemblage dominated by unidentified phytoflagellates and cryptophytes and the diatom-enriched assemblage (Fig. 4), shows the existence of spatial variability in the phytoplankton structure of the waters liberated by the sea ice. (2) According to our assumption that the diatom bloom associated with the sea-ice edge and the assemblage dominated by unidentified phytoflagellates and cryptophytes must have dominated offshore waters earlier in the growing season, and must have progressively moved onshore as the sea ice retreated, it can be assumed that the diatom-enriched assemblage is the third one growing in offshore waters during the seasonal cycle. Hence, it seems that the phytoplankton community of the ice-free waters exhibited seasonal variability. (3) The presence of a diatom-enriched assemblage occupying a large region during the 1997 and 1999 summers, and its absence during the 1996 summer (Fig. 4), indicate that the community of the ice-free waters also changed on an interannual scale.

These previous results open new questions about the environmental conditions that favored the concentration of diatoms in open waters during summer. During our studied summers the diatom-enriched assemblage was found in well-mixed and macronutrient-rich waters (Table 5). These conditions did not differ greatly from those found in more onshore waters (Table 5: compare conditions in Regions 2 and 3), suggesting it was unlikely that they were responsible for the shift from the dominance of unidentified phytoflagellates and cryptophytes in more onshore waters, to the concentration of diatoms in offshore waters. Previously, Prézelin et al. (2000) associated the diatom-enriched assemblage with a frontal system in the continental shelf-slope, which might produce the upwelling of a macronutrient-rich water mass (Upper Circumpolar Deep Waters), thus enhancing the diatom growth. However, as shown in Fig. 4c, during 1999 this assemblage extended well over the continental shelf, indicating that it could not be only a result of a phenomenon associated with the continental shelf-break. Our results suggest either a protrusion of upwelled water over the continental shelf, or a different mechanism for the increased diatom standing stock offshore. In fact, Garibotti et al. (2003a) suggested that iron concentration could have been regulating the growth of this assemblage during January 1997. While no iron measurements have yet been done in the area, this is a plausible explanation, since it is well known that iron concentration is an important factor determining a shift of phytoplankton composition from a phytoflagellate-dominated to a diatom-dominated assemblage (Boyd et al., 2000). Therefore, in situ measurements of iron concentration should be performed in future studies to determine whether it is the factor that regulates the growth of the diatom-enriched assemblage in open waters.

On the other hand, a remarkable characteristic is that during the 1996 summer no diatom-enriched assemblage was found in open waters, which instead were completely occupied by the assemblage dominated by unidentified phytoflagellates and cryptophytes (Fig. 4a). Additionally, during 1997 the diatom-enriched assemblage occupied a large region, and diatoms represented a relatively high proportion of the total biomass; and during 1999 its extent was even larger, with diatoms dominating the biomass (Fig. 4, Table 3). Thus, it seems that during the 1997 and 1999 summers the community had already changed into the diatom-enriched assemblage, while this shift still had not occurred during the 1996 summer. These year-to-year variations can be related to the early/late sea-ice retreat, which triggers the onset of phytoplankton growth earlier/later in the season, regulating a longer/shorter length of time during which phytoplankton had been growing in offshore waters at the time of sampling. This is in agreement with the mechanism we proposed above as the one regulating the interannual distribution variability of the other two recurrent phytoplankton assemblages. That is in the sense that the interannual variability in the distribution of all three annually recurrent assemblages was associated with the sea-ice dynamics during the previous winter and spring seasons.

4. Summary for the three studied summers

According to the interpretation we propose, the main characteristics of the phytoplanktonic community during each summer can be summarized as follows:

During the 1996 summer, the late retreat of sea ice from the area might have retarded the initiation of phytoplankton growth during the spring/summer season, and the summer phytoplanktonic community seems to have been in an early stage of the seasonal succession. The diatom bloom occupied a large region of the area, cryptophytes were spatially restricted, and no diatom enrichment was found offshore.

During the 1997 summer, the phytoplanktonic community seems to have been in a more advanced stage of the seasonal succession, possibly because of the earlier initiation of phytoplankton growth, as sea ice retreated during mid-spring. The diatom bloom was spatially restricted to the southeastern portion of the area, cryptophytes exhibited a widespread distribution, with high abundance in the coastal and northern portions of the area, and a diatom-enriched assemblage was detected offshore.

During the 1999 summer, the retreat of sea ice in early spring might have allowed the early initiation of phytoplankton growth, and the summer community appears to have been in an even more advanced stage of the seasonal succession. The diatom bloom was spatially restricted to the coastal and southernmost stations, cryptophytes were present with high concentration throughout the coastal and mid-shelf waters, and diatoms dominated throughout most of the open waters.

5. Conclusions

The phytoplanktonic community of the studied area exhibited three yearly recurrent algae assemblages: a diatom bloom associated with the sea-ice edge, an assemblage dominated by small unidentified phytoflagellates and cryptophytes, and a diatom-enriched assemblage in open waters. The diatom bloom associated with the sea-ice edge and the assemblage dominated by small unidentified phytoflagellates and cryptophytes resemble different stages of the phytoplankton seasonal succession. The diatom-enriched assemblage might be the third one growing in offshore waters through the seasonal cycle, following the other two recurrent assemblages, which might have grown in this region earlier in the season. Thus, the phytoplankton community of the area seems to be characterized by a mosaic of assemblages corresponding to different stages of the phytoplankton seasonal cycle.

We propose that the presence of the three recurrent assemblages and their distribution through the area was related to a northwest–southeast gradient in the timing of phytoplankton growth onset. In turn, this gradient must have been regulated by the progressive retreat of the sea-ice cover. We also propose that the interannual variability in the distribution of the annually recurrent assemblages reflects the year-to-year differences in the progression of the phytoplankton seasonal cycle, associated with interannual variations in the timing of the sea-ice retreat from the area. With this interpretation, we conclude that the summer phytoplankton community was in a delayed stage of its seasonal cycle during the coldest year (1996), and in an advanced stage during the warmer years (1997 and 1999). We point out that the observed interannual variation in the summer phytoplankton composition represented a temporal shift of the seasonal progression, and not an algae compositional change. Therefore, we predict that changes in the sea-ice dynamics due to global warming (e.g. early sea-ice retreat) would not affect the composition of the Antarctic phytoplankton, but its seasonal dynamics instead.

In this study we analyzed the variability in the physico-chemical environmental conditions, and associated it with the occurrence of the annually recurrent assemblages. Moreover, we compared our results with those reported for other areas of the Southern Ocean, where similar assemblages were found. This allowed us to propose different mechanisms to explain the shift from one assemblage to another through the area. Hereafter these hypotheses must be further studied in order to better understand the dynamics of the phytoplankton in the area. Moreover, further studies should focus on the analysis of the relationship between the spatial distribution of the recurrent assemblages and the phytoplankton seasonal evolution, and of the mechanisms determining the assemblage shift through the seasonal cycle. We should note that the Southern Ocean presents difficulties at the time of sampling, due to the unstable weather conditions and logistics involved. Thus, it would be very difficult to analyze the seasonal progression of the phytoplankton in an area as large as that studied here. Therefore, indirect evidence of the phytoplankton seasonal cycle, arising from analyses of the phytoplankton distribution as presented here, are a major contribution to understanding of Antarctic phytoplankton dynamics.

Finally, considering that the phytoplankton is the main autotrophic component of Antarctic waters, it is interesting to think about the possible impact the observed interannual phytoplankton variability may have on the upper trophic levels. In fact, given that it is usually assumed that diatoms are grazed mainly by krill, and phytoflagellates by salps and microzooplankton, interannual shifts in the structure of the trophic chain during summer may be expected. Cold years should be dominated by a short food chain composed by diatoms, krill and higher consumers, and warm years by a complex food chain based on a microbial foodweb of bacteria, nanophytoplankton and microzooplankton, with salps as the main macrozooplankton component. This agrees with previous observations reporting that krill is more abundant during the summer of cold years, and salps during the summer of warm years (Loeb et al., 1997).

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Appendix A. Average ± standard deviation of the algal and total phytoplankton carbon biomass ($\mu g\, l^{-1}$) calculated using the cell carbon:cell volume ratios proposed by Strathmann (1967). Regions are as in Fig. 4.

	Total phytoplankton	Unidentified phytoflagellates	Crypto-phytes	Diatoms	Prymnesio-phytes	Prasino-phytes	Dino-flagellates
Summer 1996							
Region 1a	218±134	8±2	1±0	198±130	3±2	0±1	7±3
Region 1b	256±133	14±10	34±26	197±145	0	1±3	4±3
Region 2a	85±80	27±9	33±68	9±12	0	1±2	10±7
Region 2b	42±17	19±8	5±6	6±5	0	0	8±8
Summer 1997							
Region 1	251±76	13±8	3±3	162±71	27±23	1±1	18±5
Region 2	48±17	20±9	14±9	3±2	0±1	0	8±5
Region 3	24±9	10±4	3±2	3±2	0	0	5±2
Summer 1999							
Region 1	394±206	19±4	4±6	299±190	50±68	0	12±1
Region 2	105±87	26±7	65±86	5±5	0	0	6±3
Region 3	36±17	15±6	5±9	9±4	0	0	4±2

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