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Algal pigment patterns in different watermasses of the Atlantic sector of the Southern Ocean during fall 1987

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Summary. During the autumn of 1987 a survey was carried out in the Atlantic sector of the Southern Ocean in order to study phytoplankton community structure in relation to hydrological features. The positions of the boundary zones, determined by means of hydrological and chemical properties (especially silicic acid) match with previous studies. The phytoplankton community structure was studied by means of algal pigment fingerprints. A cluster analysis of the main phytoplankton pigments revealed the presence of four distinctive phytoplankton communities in the area. In three cluster groups phytoflagellate pigments of different taxonomical groups were found which showed different relative abundance between the cluster groups. In between the Polar Front Zone and the Weddell Scotia Confluence a fourth group was found which was rich in diatoms as compared to the other cluster groups. High concentrations of the fucoxanthin related 19′-hexanoyloxyfucoxanthin indicated the relative importance of Prymnesiophyceae during fall in this area. The relative contribution of each taxonomical group to total phytoplankton biomass was estimated by using specific pigment ratios. This calculation showed that in this time of the year phytoflagellate biomass (especially Prymnesiophytes) surpasses diatom biomass.

Introduction

In contrast with the classical belief that Antarctic phytoplankton is dominated by diatoms (Hart 1942; Guillard and Kilham 1977), more recent studies stress the importance of taxonomical groups other than diatoms in Antarctic waters in terms of biomass and production (von Broeckel 1981; Buck and Garrison 1983; Hewes et al. 1985; von Bodungen et al. 1986). The Prymnesiophyte *Phaeocystis* sp. can occur in blooms in the Weddell Sea region, the Gerlache Strait and the Bransfield Strait, both in the water column as well as in the ice (Sieburth 1959; Garrison and Buck 1985; Garrison et al. 1987). Other prymnesiophytes are also found in Antarctic waters (Thomsen et al. 1988) as well as green algae (Marchant et al. 1989). Recently blooms of cryptophytes have been found in the Weddell Sea region (Smetacek and Veth 1989). Still data concerning the quantitative distribution of different taxonomical groups in Antarctic phytoplankton communities are scarce.

Quantitative studies of microalgae and especially nanoflagellates are fraught with problems. With conventional methods based on inverted microscopy reasonable counts can be made but the determination of most nanoplankton groups is difficult due to problems of preservation. The electron microscope is a powerful tool for the identification of flagellates, but counting is very time consuming. Modern techniques like flow cytometry seem promising with respect to the quantification of even very small phytoplankton cells (Veldhuis et al., in press), but it is difficult to obtain accurate taxonomical information with this method. Since determination on the basis of visual criteria does not seem to meet all demands, a combination with chemotaxonomical techniques has come into focus in recent years. Immunofluorescence is one of these (Campbell et al. 1983; Shapiro et al. 1989), algal pigment finger printing is another. The relevance of algal pigment measurements for the identification of nanoplankton groups which are difficult to identify with microscopic methods has already been demonstrated by several workers (Jeffrey 1974, 1976; Gieskes and Kraay 1983, 1986a, b; Hooks et al. 1988; Bidigare et al. 1990).

All algae contain a certain variety of pigments. Although most phytoplankton pigments are not class specific, some of them appear to be restricted to a specific taxonomical group. For instance peridinin is found only in Dinophyceae, alloxanthin in Cryptophyceae and chlorophyll *b* in green algae. The fucoxanthin related 19′-hexanoyloxyfucoxanthin has been characterised as a prymnesiophyte antenna pigment (Arpin et al. 1976; Hertzberg et al. 1977; Haxo 1985). Thus, it should be possible to obtain information on the structure of the phytoplankton community by means of quantification of these pigments. However, the conversion of specific pigment concentration to phytoplankton biomass in mixed

populations can be hampered for several reasons. First of all many pigments are not restricted to only one taxonomic group. Fucoxanthin for instance is found in diatoms as well as in several nanoflagellate groups like prymnesiophytes; 19'-butanoyloxyfucoxanthin and chlorophyll *c*3 can be found in prymnesiophytes as well as in chrysophytes (Vesk and Jeffrey 1987; Jeffrey and Wright 1987; Fawley 1989). Moreover, some class specific pigments are not found in all members of the class. Most autotrophic Dinophyceae contain peridinin, but some representatives lack peridinin and have other carotenoids instead (Jeffrey et al. 1975). 19'-hexanoyloxyfucoxanthin is a typical prymnesiophycean pigment, but it is not found in all members of the class (Wright and Jeffrey 1987; Bjørnland et al. 1988). Furthermore the relative proportion of a specific pigment to chlorophyll *a* or to cell carbon can differ from strain to strain or from species to species, as has been demonstrated for diatoms (Gallagher and Alberte 1985; Klein 1988), Chlorophyceae (Riley and Wilson 1967), Chrysophyceae (Withers et al. 1981) and Dinophyceae (Jeffrey *et al.* 1975). Finally the pigment composition of a phytoplankton cell is variable, depending on the physiological state of the cell and environmental conditions like nutrients, temperature, lightintensity and quality (Carreto and Catoggio 1976; Gallagher and Alberte 1985; Klein 1988; Kana et al. 1988; Coats and Harding 1988).

In the present study an attempt is made to approximate phytoplankton community structure in different watermasses of the Antarctic pelagic ecosystem by means of pigment patterns. Algal pigment fingerprints in combination with hydrographical characteristics and phytoplankton counts were used to study the extent of community homogenity in the watermasses encountered. Of particular interest is the distribution of nanoflagellates at this time of the year, since few data are available on this subject.

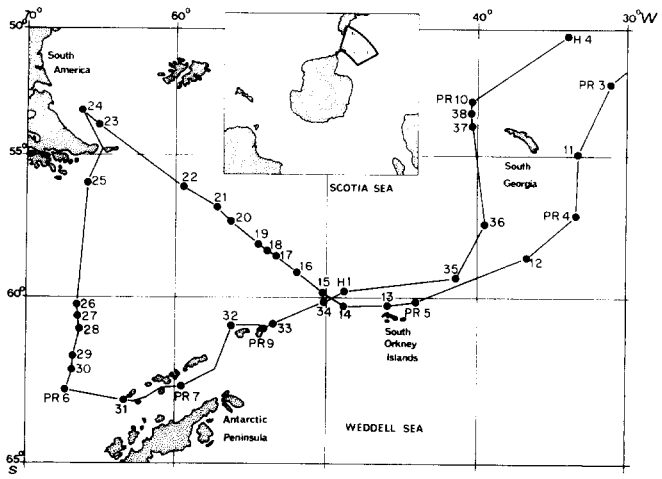

Fig. 1. Cruise track and station numbers of cruise APSARA III of *RV Marion Dufresne*, 19 March–27 April 1987

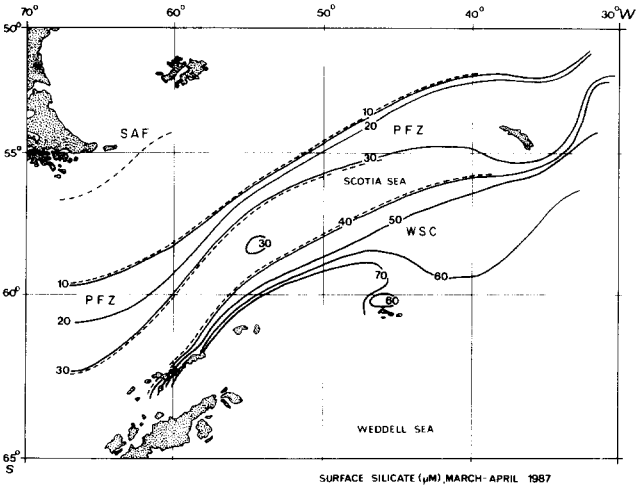

Fig. 2. Surface silicate (μM) APSARA III, March-April 1987, with positions of frontal zones (*dotted lines*): *SAF* Sub Antarctic Front; *PFZ* Polar Front Zone; *WSC* Weddell Scotia Confluence

Material and methods

Samples were taken during a cruise (APSARA III) of *RV Marion Dufresne* from March 19th to April 27th 1987 (study area and station numbers are shown in Fig. 1). Except for some large icebergs the area was free of ice. At the end of the cruise newly formed ice was encountered near the Antarctic Peninsula (Clarence Island). For the hydrographical characterisation of watermasses temperature, salinity and silicate were measured. These parameters allow a distinction between the frontal zones in the study area i.e. the Sub Antarctic Front in the North, the Polar Front in the centre, and the Weddell Scotia Confluence in the South as is shown by a number of authors (Gordon 1967; Patterson and Sievers 1980; Foster 1984; Michel 1984; Sievers and Nowlin 1988; Gordon 1988).

Continuous measurements of sea surface temperature and salinity were carried out using a Beckman thermo-salinometer. Measurements were calibrated with data acquired in parallel at 16 hydrocast stations distributed in the whole area by using reversing thermometers and a Guildline salinometer. Temperature ranged from 9°C in the North to less than −1°C near the Antarctic Peninsula (not shown). In the Drake Passage and the middle of the Scotie Sea a slight indication of the position of the Polar Front Zone was found, due to a sudden drop in temperature going south. Frontal zones were better marked by salinity gradients than by temperature. There was a tongue of water with relatively low salinity between the Polar Front Zone and the Weddell Scotia Confluence (< 33.8‰). North of the Polar Front zone and in the Weddell Scotia Confluence salinity was around 34‰ (not shown). Our data agree with other data sets (Sievers and Nowlin 1988; Foster 1984). Samples for nutrient analyses were taken with 8 l Niskin bottles mounted on a CTD rosette. Orthosilicic acid was determined aboard using a Technicon autoanalyser according to the procedure of Treguer and Le Corre (1975). Samples for the analysis of nitrate and phosphate were stored at −20°C and analysed at home.

Silicate (Fig. 2) was low north of the Polar Front Zone (< 10 μM). The Polar Front Zone itself was marked by a sudden rise in surface silicate values: from 10 to 30 μM. An even stronger silicate gradient was found at the position of the northern boundary of the Weddell Scotia Confluence, also called the Scotia Front (Cederløf et al., submitted) with a marked increase from 40 to well above 70 μM in the southern part and in the Bransfield Strait region (78 μM at PR 9, see Fig. 1). Silicate values are in agreement with earlier reports by Michel (1984), Foster (1984), Sievers and Nowlin (1988) and van Bennekom et al. (1988). Nitrate and phosphate values were high

throughout the cruise (not shown), nitrate being between 20.4 μM (H4) and 24.6 μM (PR 6) and phosphate between 1.05 μM and 1.55 μM. No consistent horizontal trends were evident for these nutrients as was also reported by other authors (Michel 1984; Foster 1984). In agreement with other authors (Patterson and Sievers 1980; Foster 1984; Michel 1984; Priddle et al. 1986; Sievers and Nowlin 1988) we have positioned the frontal zones in the Scotia Sea as drawn in Fig. 2.

Shipboard measurements of chlorophyll *a* were carried out fluorometrically (aceton extraction). Calibration was done with the classical spectrophotometric method according to the procedure of Neveux (1976). For a detailed algal pigment analysis 6 to 18 l of subsurface water were filtered over 47 mm Whatmann GF/F filters and stored at −80°C for analysis about five months later. Pigment measurements were performed following the method of Gieskes and Kraay (1986a) with minor modifications. Filters were extracted in 3 ml methanol buffered with 2% ammonium acetate and homogenised in a Braun-Melsungen CO_2 cooled homogeniser for 20 s. After filtration over a 10 mm GF/F filter 100 μl were injected in a HPLC system (Waters Associates) equipped with a 15 cm C-18 column. The solvents used were: A: 75% methanol in buffer (0.02 M ammonium acetate in distilled water), and B: 30% ethylacetate in methanol. The solvent program was linear from 1% to 100% B in 20 min with a flow rate of 0.8 ml/min. Detection of pigments was done at 436 nm and 658 nm with an absorbance detector (Waters Associates 440). Peak areas were integrated using a Hewlett Packard 3390a Reporting Integrator. Identification of the pigments was done on a Perkin Elmer Hitachi Spectrophotometer after transfer to ethanol, chloroform, acetone or methanol. Calibration of peaks was done according to Gieskes and Kraay (1983). Examples of absorption spectra of some little known pigments such as 19′-hexanoyloxyfucoxanthin have been published by Gieskes et. al. (1988). Figure 3 shows a representative HPLC chromatogramm from our research area (PR 10, Fig. 1). Samples for microscopic identification of cells were taken from Niskin bottles at the PR and H stations (Fig. 1), and with a bucket at the other stations. Counting of the Lugol fixed samples was done in 50 ml sedimentation chambers with a Zeiss inverted microscope. A cluster analysis of the pigment data was carried out according to Davis (1973) with the Eucladian distance as similarity index. To eliminate the influence of total crop size on the cluster analysis all pigments were expressed as percentages of total pigment peak area. The pigments used for the cluster analysis were, in order of retention: chlorophyll *c* 3, chlorophyll *c* 1,2, peridinin, 19′-hexanoyloxyfucoxanthin, fucoxanthin, 19′-butanoyloxyfucoxanthin, diadinoxanthin, zeaxanthin/lutein (not separated with this method) chlorophyll *b* and chlorophyll *a*.

Calculation of Prymnesiophyte biomass was done following:

Chl *c*3* $1.836^{(a)}$ = Chl *c* $(1,2)_{(Prymnesiophyceae.)}$ (peak area).

Chl *c* $(1,2)_{Prymn.}$ /Chl *c* $(1,2)_{Total}$ *100% = Relative contribution of Prymnesiophyceae to total Chlorophyll *c* (1,2) biomass.

Conversion to Chlorophyll *a*:

Chl *c* (1,2)/Chl $a_{(diatoms)}$ = 0.97 Chl *c* (1,2)/Chl *a* $_{(Prymnesiophytes)}$ (a).

(a): Calculated from experiments with an Antarctic isolate of *Phaeocystis* sp. and several antarctic diatoms (Buma et al., submitted.)

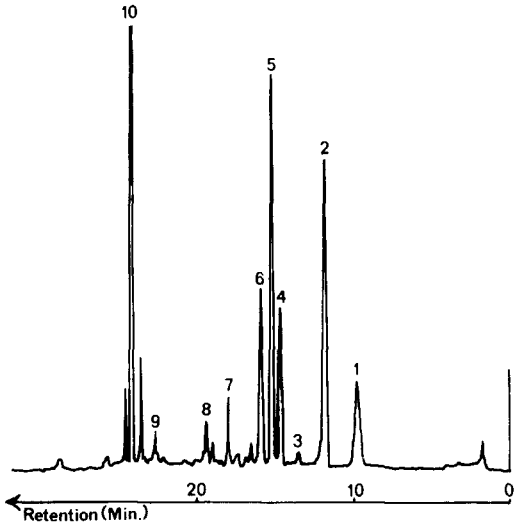

Fig. 3. Representative example of HPLC chromatogram (station PR 10, see Fig. 1). Peaks in order of retention: *1* chlorophyll *c* 3; *2* chlorophyll *c* (1,2); *3* peridinin; *4* 19′-butanoyloxyfucoxanthin; *5* fucoxanthin; *6* 19′-hexanoyloxyfucoxanthin; *7* diadinoxanthin; *8* zeaxanthin/lutein; *9* chlorophyll *b*; *10* chlorophyll *a*

Results

Chlorophyll *a* was low during the cruise, nowhere exceeding 600 ng/l. Figure 4 shows the surface distribution of chlorophyll *a* as measured with HPLC. Comparison of the HPLC data with the shipboard fluorometric method showed a good correlation ($y = -0.0346 + 0.942x$, $R = 0.95$ $n = 8$ y = fluorometric, x = HPLC), so storage of filters for later analysis on HPLC had not affected the chlorophyll *a* concentration significantly.

Besides chlorophyll *a* all samples contained a mixture of chlorophyll *c* 1,2, chlorophyll *c* 3, fucoxanthin, 19′-hexanoyloxyfucoxanthin, diadinoxanthin and peridinin in different proportions to chlorophyll *a*. Table 1 shows the concentrations of the main pigments at the stations (for station numbers see Fig. 1). Of the pigments other than chlorophyll *a* fucoxanthin had the highest concentrations. Concentration of the fucoxanthin related prymnesiophycean pigment 19′-hexanoyloxyfucoxanthin was lower than of fucoxanthin, with a few exceptions. Indicator pigments from other nanoplankton groups, notably chlorophyll *b* (green algae) and peridinin (dinflagellates) were low or undetectable except for a few stations close to the South American continent, where chlorophyll *b* was elevated. At these stations also high levels of lutein/zeaxanthin were found. Chlorophyll *c* 3 was detected in all samples, but,

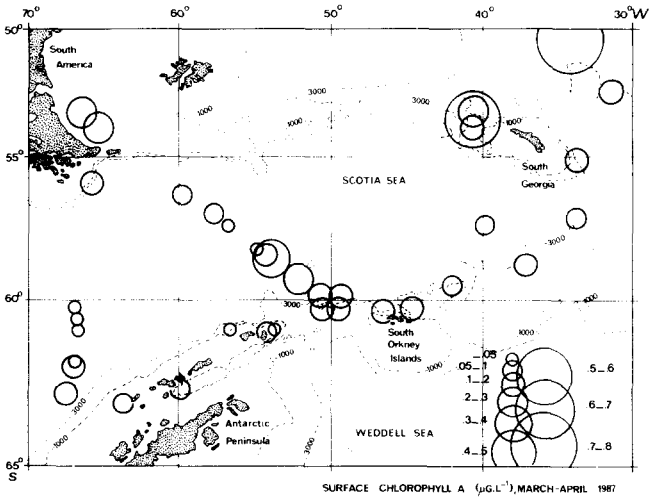

Fig. 4. Surface distribution of chlorophyll *a* (μg/l) measured with HPLC during APSARA III (March-April 1987)

Table 1. Concentrations of the main pigments and cell counts at the APSARA III stations ranked according to cluster groups. Chl *a* = chlorophyll *a*; Chl *b* = chlorophyll *b*; Chl *c* = chlorophyll *c* (1,2), Fuco = fucoxanthin; Buta = 19′-butanoyloxyfucoxanthin; Hexa = 19′hexanoyloxyfucoxanthin; Peri = peridinin, Diad = diadinoxanthin; Nano = nanoflagellates/l; ($\times 10^5$); Dino = dinoflagellates/l ($\times 10^5$); Diat = diatoms/l ($\times 10^5$)

Station no. Position		Chl *a* ng/L	Chl *b* ng/L	Chl *c* ng/L	Fuco ng/L	Buta ng/L	Hexa ng/L	Peri ng/L	Diad ng/L	Nano	Dino	Diat	Main diatoms
Group													
PR 3	52.30S 31.14W	147.6	n.d.	13.0	31.2	7.2	20.8	0.2	4.1	11.2	3.4	9.2	*Rhizosolenia* spp. *Nitzschia* spp. *Chaetoceros dichaeta Corethron criophilium*
11	55.03S 33.36W	123.8	n.d.	13.7	29.7	8.2	15.4	0.8	3.3	24.9	5.8	2.9	*Nitzschia* spp.
PR 4	57.09S 33.46W	92.6	n.d.	9.3	17.1	4.9	10.7	0.1	2.8	11.9	1.6	3.6	*Corethron criophilum Nitzschia* spp.
12	58.46S 36.53W	162.4	n.d.	16.2	42.4	7.0	19.2	0.1	4.2		n.c.		
PR 5	60.15S 44.06W	120.7	n.d.	9.7	16.6	6.3	17.7	0.2	1.6	9.2	1.3	2.0	*Nitzschia* spp. *Thalassiosira* spp.
19	58.14S 54.29W	42.1	n.d.	4.5	10.1	1.4	6.1		0.8	3.3	0.4	2.5	*Nitzschia* spp. *Thalassiosira* spp.
21	57.00S 57.32W	55.7	n.d.	5.0	8.7	3.3	15.2	0.1	1.0	13.2	1.5	1.5	*Nitzschia* spp. *Asteromphalus* sp.
22	56.10S 59.39W	60.1	1.2	5.3	11.0	5.1	11.7	0.1	0.9	11.2	1.7	16.2	*Nitzschia* spp. *Thalassiosira* spp. *Chaetoceros* sp.
26	60.13S 66.43W	48.3	0.4	4.0	7.5	4.5	7.9	0.1	1.0	3.4	0.2	2.5	*Nitzschia* spp. *Chaetoceros dichaeta Chaetoceros* spp.
27	60.30S 66.40W	27.9	0.2	2.5	5.4	1.0	6.0	0.1	0.4	9.4	1.2	0.7	*Nitzchia* spp. *Unid. central diatom* $>10\,\mu$
28	60.55S 66.35W	27.9	n.d.	2.4	5.6	1.2	5.5	0.1	0.5		n.c.		
29	61.45S 66.49W	23.3	n.d.	2.2	4.6	0.7	4.4	0.1	0.4	1.6	n.d.	2.9	*Nitzschia* spp. *Chaetoceros* spp. Unid. central diatom $>10\,\mu$
PR 10	53.24S 40.36W	265.4	1.2	29.8	66.6	27.6	29.5	0.6	8.0	8.7	0.7	2.5	*Rhizosolenia styliformis Nitzschia* spp. *Corethron criophilum*
Group 2													
23	53.50S 65.15W	213.9	8.1	9.3	14.8	3.8	24.2	0.5	3.0	11.9	0.2	0.5	*Nitzschia* spp.
24	53.00S 66.05W	249.9	8.7	13.2	35.4	n.d.	20.4	0.7	4.8	12.2	n.d.	1.7	*Nitzchia* spp.
25	55.50S 65.44W	110.6	3.2	7.6	13.1	4.6	17.1	0.1	1.9	9.4	0.5	1.7	*Nitzschia* spp.
Group 3													
31	63.03S 63.07W	89.3	0.5	6.8	15.0	1.2	5.1	0.1	2.2		n.c.		
PR 7	62.37S 59.31W	66.6	0.2	3.2	12.1	2.1	3.5	0.1	1.0	7.6	1.6	1.3	*Thalassiosira* sp. *Nitzschia* spp.
32	60.50S 56.05W	33.8	0.4	2.8	7.2	n.d.	0.8	0.4	1.0		n.c.		
PR 9	60.59S 54.01W	88.5	2.1	6.0	11.5	2.5	5.8	0.3	2.0	9.5	0.3	1.8	*Nitzschia* spp. *Corethron criophilum Thalassiosira* spp.
33	60.55S 53.45W	19.5	0.1	1.6	4.0	n.d.	n.d.	0.1	0.6	8.7	0.4	1.6	*Nitzschia* spp. *Corethron criophilum* Unid. central diatom $>10\,\mu$
34	59.41S 50.00W	101.5	1.5	6.8	15.7	n.d.	4.7	0.6	2.5		n.c.		
15	59.50S 50.19W	102.5	1.5	7.3	16.4	3.9	7.5	0.6	3.1	4.7	3.9	9.1	*Nitzschia* spp. *Thalassiosira* spp.
16	59.13S 51.51W	212.9	1.7	17.7	45.5	6.0	9.0	0.7	4.9	11.8	2.5	10.2	*Nitzschia* spp. *Chaetoceros* spp. *Thalassioira* spp.
H 1	59.50S 48.13W	156.4	1.8	8.5	22.4	1.9	2.1	0.5	4.1		n.c.		
35	59.22S 41.30W	61.6	1.3	3.2	7.8	n.d.	4.7	0.2	n.d.		n.c.		
36	57.23S 39.36W	78.2	1.7	4.7	9.8	3.8	6.0	0.1	1.4		n.c.		

Group 4												
13	60.22S	46.09W	111.8	n.d.	19.4	68.3	3.8	3.2	0.9	5.9	12.4	n.d.	6.8	*Nitzschia* spp. *Thalassiosira* spp.
14	60.10S	49.14W	12.5	1.2	19.6	70.7	4.3	6.0	0.5	6.4	4.2	6.3	41.1	*Nitzschia* spp. *Thalasiosira* spp.
17	58.31S	53.43W	343.4	n.d.	55.6	155.4	4.8	14.7	0.7	10.4	27.3	1.2	19.5	*Nitzschia* spp. *Chaetoceros dichaeta* *Thalassiosra* spp.
18	58.25S	53.59W	109.8	n.d.	16.1	45.6	3.9	10.1	0.2	3.8	11.8	1.0	3.3	*Rhizosolenia* spp. *Corethron criophilum* *Nitzschia* spp.
20	57.26S	56.26W	31.1	n.d.	5.6	18.2	1.1	6.8	0.1	1.1	8.2	1.7	6.7	*Nitzschia* spp. *Chaetoceros* spp. *Thalassiosira* sp.
30	61.59S	66.51W	116.4	n.d.	19.8	41.0	1.7	8.2	0.3	2.0	10.7	0.2	4.7	*Nitzschia* spp. *Chaetoceros* spp. *Thalassiothrix* sp.
PR 6	62.39S	67.03W	174.3	n.d.	26.5	60.5	25.4	12.6	0.6	4.4	32.3	4.5	23.9	*Chaetoceros dichaeta Nitzschia* spp. *Chaetoceros* spp.
37	53.52S	40.31W	140.3	0.5	18.5	40.0	19.4	13.6	0.2	5.7	12.4	n.d.	6.2	*Rhizosolenia stylíformis Rhizosolenia* spp. *Nitzschia* spp.
38	53.29S	40.34W	528.3	0.6	83.4	186.0	58.6	18.1	0.3	13.1		n.c.		
H 4	51.50S	34.40W	577.4	0.6	49.0	250.7	35.0	19.3	2.6	16.5	42.2	5.0	15.5	*Corethron criophilum Nitzschia* spp. *Rhizosolenia* spp.

since extinction coefficients of this pigment are not known yet, concentrations were not calculated.

Figure 5 shows the distinction into four cluster groups as a result of the cluster analysis of the main pigments. Stations of group 2 are located north of the Sub Antarctic Front, close to the South American Continent (Fig. 5); Group 1 is situated in the region of the Polar Front Zone and around South Georgia whereas the stations of Group 3 are situated in the Weddell Scotia Confluence region. In the area between Group 3 and 1a fourth cluster group was found situated between the Polar Front Zone and the Weddell Scotia Confluence (Fig. 5).

In Table 2 the mean proportions of the most important pigments relative to chlorophyll *a* are listed (in % w/w). Relative amounts of chlorophyll *c* (1,2) and fucoxanthin were highest in Group 4; 15.2% and 44% respectively. Microscopic counts (Table 1) revealed a small numerical dominance of flagellates in this group although differences in the relative abundance of phytoplankton groups were large between stations (between 20% and 81% flagellates). The diatom composition within group 4 showed differences, depending on the geographical position, with a dominance of small pennates in the Peninsula region, a mixed population of pennates, *Chaetoceros* spp. and *Thalassiosira* spp. in the Drake Passage. Near South Georgia pennates, *Corethron criophilum* and *Rhizosolenia*

Fig. 5. Grouping of stations as a result of a cluster analysis of phytoplankton pigments in surface waters during APSARA III (March-April 1987)

Table 2. Mean pigment ratios (w/w · 100%) in different cluster groups (1 to 4). Chl *c* (1,2) = chlorophyll *c* (1,2); Chl *a* = chlorophyll *a*, fuco = fucoxanthin; hexa = 19′-hexanoyloxyfucoxanthin

Cluster group	Chl*c*(1,2)/Chl *a* (w/w · 100%)	Fuco/Chl *a* (w/w · 100%)	Hexa/Chl *a* (w/w · 100%)
1	9.52 ± 1.05	20.04 ± 3.70	16.65 ± 4.65
2	6.23 ± 1.82	11.58 ± 3.66	7.58 ± 1.10
3	6.74 ± 1.31	16.69 ± 3.59	4.79 ± 2.78
4	15.17 ± 2.70	43.99 ± 11.27	7.39 ± 5.70

sp. dominated the phytoplankton community. The diatom assemblages found in this study match with data for this and other seasons. (Hayes et al. 1984; Heywood and Whitaker 1984; Priddle et al. 1986; Garrison et al. 1987).

Cluster group 1 showed much lower ratios of chlorophyll *c* (1,2) and fucoxanthin to chlorophyll *a*, but these ratios were higher than for Group 2 and 3, which were similar in this respect. The prymnesiophycean pigment 19′-hexanoyloxyfucoxanthin was highest in Group 1 and lowest in Group 3. Microscopic counts showed that Group 2 had high numbers of nanoflagellates (numerical dominance of flagellates: 91%). The diatoms present were mainly small pennates. Considering the Groups 1 and 3 diatom composition was comparable with the diatom distribution of Group 4 from the same area, but numbers of flagellates were much higher in the Groups 1 and 3 (70.7% and 72.8% respectively) than in Group 4 (61.7%). The flagellates counted were mainly small (< 10 μm) and difficult to identify. No colonies of *Phaeocystis* sp. were observed in living material. Numbers of dinoflagellates, mainly small naked dinoflagellates < 10 μm were low in the whole area.

Discussion

At this time of the year phytoplankton biomass, expressed as chlorophyll *a*, is low, as was found earlier by Hayes *et al.* (1984) and El-Sayed (1988), with a mean of 500 ng/l. South of the Polar Front Zone and at the northern boundary of the Weddell Scotia Confluence (Group 4 in the cluster analysis), especially around South Georgia, slightly elevated chlorophyll *a* levels were spotted. Yet phytoplankton-standing stock despite high nutrient levels nowhere exceeded 1000 ng/l. It is still a matter of discussion which factor(s) cause the discrepancy between actual production and standing stock and potential production on the basis of available nutrients in Antarctic waters (Jacques (1989)).

Striking are the large scale similarities in phytoplankton pigment composition in the area. Despite the fact that diatom assemblages seem to be related mainly to the geographical position of the stations, the overall pigment fingerprint of the whole community seems to be linked mainly to the watermasses and not primarily to geographical position. As can be seen in Figs. 2 and 5 the positions of the cluster groups match well with watermass distribution as defined by silicate and salinity gradients in surface waters. Only in the region south and east of South Georgia mixing phenomena cause blurring of watermass characteristics (Priddle et al. 1986) which at the same time complicate interpretation of pigment data. On the other hand, if, as our data imply, pigment fingerprints can be used as supplementory indicators of watermasses, this would lead to the suggestion that the waters South and East of South Georgia originated from the Polar Front Zone system (Fig. 5). It is questionable whether this coupling between pigment pattern and watermass exists during all seasons. In spring, features like the supply of algae from the ice through melting, water column stability, light availability and grazing events among other factors likely determine the phytoplankton community structure, resulting in heterogenity in phytoplankton populations in a certain watermass. Moreover bloom populations, -often diatoms-, seem to have only minor resemblance with the original more stable "winter" population. In the austral autumn constancy in environmental conditions, due to the fact that the whole area has been free of ice for a prolonged period, presumably in combination with low mesozooplankton activity causes large-scale similarity of phytoplankton populations in the area. Differences between phytoplankton communities are then due only to the geographical and long-term ecological history of the watermass.

Few data are available on the quantitative contribution of phytoflagellates to total biomass in Antarctic ecosystems. The abundance of small dinoflagellates and prymnesiophytes, mainly *Phaeocystis* sp. has been reported (Burkholder and Sieburth 1961; El-Sayed et al. 1983; Buck and Garrison 1983; Hayes et al. 1984; von Bodungen et al. 1986). Gieskes and Elbraechter (1986) and Wright and Jeffrey (1987) demonstrated the presence of prymnesiophytes in different regions of the Antarctic by measuring indicator pigments from this taxonomical group, namely chlorophyl *c* 3 and 19′ hexanoyloxyfucoxanthin. Other workers who used pigment patterns to trace phytoflagellate groups (Bidigare et al. 1986) measured considerable concentrations of chlorophyll *b* in the Weddell Scotia Confluence region, revealing the presence of green algae. Our data show that in the austral autumn in the Atlantic sector of the Southern Ocean Prymnesiophyceae are as common as diatoms. Pigments patterns indicated the presence of other non-diatom groups as well (green algae and dinoflagellates).

Factors like low taxon-specificity of certain pigments and variations in pigment ratios within algal classes complicate an accurate conversion of pigment concentration to phytoflagellate biomass. Nevertheless we tried to approximate phytoflagellate biomass by using indicator pigments from the Prymnesiophyceae, Dinophyceae and green algae. When we consider a mean chl *b* to chl *a* ratio of 0.5 (w/w) in green algae (Riley and Wilson 1967) the phytoplankton biomass of the stations of cluster group 2 would contain not more than 7.5% green algae (concentration chl*b*/(concentration chl *a*·0.5)·100%). The stations of the other cluster groups would contain less than that, with a maximum of 4.7% at station PR 9. In general the contribution of this taxonomical group to total phytoplankton stock in terms of chl *a* is small. The same holds for photosynthetic dinoflagellates. Jeffrey et al. (1975) calculated a mean ratio peridinin to chl *a* to be in the order of 0.3 (w/w). In our study this would mean a contribution of phototrophic dinoflagellates to total phytoplankton biomass of not more than 1.5% (station H4, Fig. 1). However, this group could be underestimated due to the fact that not all photosynthetic dinoflagellates contain peridinin (Jeffrey et al. 1975).

Since 19′hexanoyloxyfucoxanthin is a pigment specific for prymnesiophytes it should be possible to use this pigment in a calculation of prymnesiophyte biomass. However it seems that the ratio 19′hexanoyloxyfucoxanthin to chl *a* is very variable between species and strains, being much higher in *Emiliania huxleyi* than in certain

Antarctic strains of *Phaeocystis* sp. (Jeffrey and Wright. 1987; Buma et al., submitted). High levels of this pigment in cluster group 1 could thereby be explained by a higher abundance of *Emiliania huxleyi* in this group rather than higher overall prymnesiophyte biomass. In contrast, chl *c*3 seems more useful for calculation of prymnesiophyte stock since the ratio chlorophyll *c*3 to chlorophyll *c* (1,2) seems to be relatively constant (Buma et al., submitted). We used a ratio taken from own experiments with *Phaeocystis* sp. to calculate prymnesiophyte chl *c* (1,2) from our stations on the basis of peak area (see "Material and methods"). The relative proportion of Prymnesiophyte *c*(1,2) to total chlorophyll *c* 1,2 (peak area) also gives information on diatom biomass since diatoms form the other important chlorophyll *c* (1,2) containing group. Conversion of chlorophyll *c* 3 to Prymnesiophyte biomass (% of total chlorophyll *a*) gave highest Prymnesiophyte abundance in cluster group 1 (mean of 91.9% of chlorophyll *a*), the group which also contained highest amounts of 19'hexanoyloxyfucoxanthin relative to chlorophyll *a* (Table 2). Groups 2,3 and 4 contained 62.9%, 70.9% and 71.1% prymnesiophyte biomass respectively. Diatoms would form approximately 25% of total biomass in groups 2,3 and 4, whereas Group 1 contained less than 10% diatom biomass. So in all groups Prymnesiophytes would form the majority of phytoplankton stock. Comparing these pigment conversions with cell counts (Table 1) it seems evident that cell counts indeed underestimate phytoflagellate biomass; phytoflagellate numbers were generally lower than was suggested on the basis of pigment calculation, considering also the presumed lower pigment biomass per number of phytoflagellate than per number of diatom (Proportion of phytoflagellates to total phytoplankton numbers: Group 1:70.7%; Group 2:91%; Group 3:72.8%; Group 4:61.7%). It is evident that exact estimation of the biomass of different taxonomical groups cannot be done until more experimental data is gathered on variability of indicator pigments on the species level or the effects of environmental conditions on concentrations of these pigments.

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