Chemotaxonomic analysis of phytoplankton distribution in the Indian sector of the Southern Ocean during late austral summer

Antarctic
HNLC area
Phytoplankton
Chemotaxonomic analysis
Pigments

Antarctique
Région HNLC
Phytoplancton
Analyse Chemotaxonomique
Pigments

Caroline CAILLIAU, Hervé CLAUSTRE and Salvatore GIANNINO

Laboratoire de Physique et Chimie Marines, Observatoire Océanologique de Villefranche, (INSU-CNRS et Université Paris 6), B.P. 08, 06230 Villefranche-sur-mer, France.

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ABSTRACT

An analysis of chlorophyll *a* and of taxon-specific pigments, as measured by High Performance Liquid Chromatography (HPLC), revealed the abundance, composition and fate of phytoplankton in the Indian sector of the Southern Ocean, during the late austral summer of 1994 (ANTARES 2 cruise). In the study area (49° S-67° S, 62° E), four different sub-systems are presented from south to north: the Coastal and Continental Shelf Zone (CCSZ), the Seasonal Ice Zone (SIZ), including the Antarctic Divergence (AD), the Permanent Open Ocean Zone (POOZ) and a frontal system, the Polar Frontal Zone (PFZ). The phytoplankton biomass was low everywhere, never exceeding 0.45 mg Chl*a* m^{-3}. The highest biomass was found in the CCSZ, in the AD and in the PFZ. Diatoms were the dominant phytoplankton in the CCSZ, in the SIZ and in the AD; nanoflagellates dominated in the POOZ and in the PFZ. An analysis of physical and chemical factors indicated their influence on phytoplankton abundance, composition and fate. Thus, a high diatom biomass was found in areas where silicic acid was most abundant and where the euphotic zone was deeper than the wind-mixed layer. According to the concentrations of chlorophyll *a* and its degradation products (phaeopigments) in the water and in sediment traps (200 m), grazing pressure appeared to differ between south and north. The export rate was generally low, less than 0.3 % per day, and was maximum at the AD and in the CCSZ. A relationship appears to exist between the autotrophic biomass structure and the resulting flux of particulate organic material out of the photic zone, *i.e.* the diatom-dominated system (CCSZ and SIZ) exported more than the nanoflagellate-dominated system (PFZ).

RÉSUMÉ

Analyse chemotaxonomique de la distribution du phytoplancton dans le secteur indien de l'Océan Austral, en fin d'été.

L'abondance, la composition taxonomique, ainsi que le devenir du phytoplancton ont été étudiés dans le secteur indien de l'Océan Antarctique, en fin d'été (mission ANTARES 2, février-mars 1994), à partir de la chlorophylle *a* (Chl*a*) et des pigments spécifiques mesurés par HPLC. La zone d'investigation (49° S-67° S, 62° E) est formée, du sud vers le nord, de différents sous-systèmes: (1) la zone côtière et le plateau continental (CCSZ); (2) la zone saisonnière des glaces (SIZ), comprenant la Divergence Antarctique (AD); (3) la zone de l'Océan libre de glaces en permanence (POOZ); (4) la zone du Front Polaire (PFZ). De manière générale, la biomasse phytoplanctonique était peu

élevée, n'excédant jamais 0,45 mg Chl*a* m^{-3}. Les plus fortes biomasses furent mesurées dans la CCSZ, l'AD et le PFZ. Le phytoplancton était principalement composé de diatomées au sud (CCSZ, SIZ et plus particulièrement au niveau de l'AD), alors que les nanoflagellés dominaient aux stations de la POOZ et du PFZ. L'influence de différentes conditions environnementales vis-à-vis de la distribution phytoplanctonique a été démontrée. Ainsi, les diatomées étaient situées préférentiellement dans les zones océaniques à fortes teneurs en silicates, et où la profondeur de la couche euphotique était supérieure à celle de la couche de mélange. Les mesures des concentrations de chlorophylle a et de ses produits de dégradation dans la colonne d'eau et dans les trappes à sédiments placées à la base de la couche euphotique (200 m), indiquent une pression de broutage différente dans le nord et dans le sud. Le taux d'exportation de la matière organique particulaire était de manière générale très faible (< 0,3 % par jour), la plus forte exportation ayant été mesurée au niveau de l'AD et de la CCSZ, système dominé par les diatomées.

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INTRODUCTION

The very extreme climatic and hydrological conditions prevailing in the austral ocean create a unique physical and chemical environment for phytoplankton development (Sakshaug and Holm-Hansen, 1986; Bidigare *et al.*, 1986; Lancelot *et al.*, 1989; Schloss and Estrada, 1994). The productive season is restricted to a few months, corresponding to the austral summer. Known areas of high productivity and biomass are mainly represented by oceanic frontal zones (Lutjeharms *et al.*, 1985; Laubscher *et al.*, 1993), coastal zones (Mitchell and Holm-Hansen, 1991*a*; Mitchell and Holm-Hansen, 1991*b*; Bienfang and Ziemann, 1992) and near the pack-ice areas (Lancelot *et al.*, 1991*a*; Lancelot *et al.*, 1991*b*; Cota *et al.*, 1992; Lancelot *et al.*, 1993). Except for these regions, where phytoplankton productivity is limited in space and in time, the major part of the Southern Ocean is oligotrophic, with chlorophyll *a* levels rarely exceeding 1 mg m^{-3} (Jacques, 1989; Buma *et al.*, 1990; Jacques, 1991). This low phytoplankton biomass is found despite high nutrient concentrations (Jacques, 1989; Cullen, 1991; Cota *et al.*, 1992).

As in other oceanic High Nutrient Low Chlorophyll (HNLC) areas, the factors controlling phytoplankton growth and maintenance are various and interdependent, but their relative influence, which depends both on the region and on the season, is still far from being completely understood (Lancelot *et al.*, 1989; Jacques, 1991; Cullen, 1991; Laubscher *et al.*, 1993). The stability of the water column has been shown to be one of the most important factors controlling autotrophic growth (El-Sayed and Taguchi, 1981; Bidigare *et al.*, 1986; Cullen, 1991; Mitchell and Holm-Hansen, 1991*a*), particularly near the ice-edge zone (Lancelot *et al.*, 1991*a*; Lancelot *et al.*, 1991*b*; Lancelot *et al.*, 1993). The grazing pressure of zooplankton is also presented as a key limiting factor for this oceanic area (Weber and El-Sayed, 1987; Bidigare *et al.*, 1986). The incident light intensity that occurs in such high latitudes is assumed not to be a limiting factor, particularly during the summer period when the lack of ice cover allows deep light penetration (Jacques and Minas, 1981; Lancelot *et al.*, 1993). However, the light changes experienced by phytoplankton as a result of the hydrological regime largely influence algal growth (Tilzer *et al.*, 1985; Sakshaug and Holm-Hansen, 1986; Gleitz *et al.*, 1994). Two other principal factors are often proposed as growth limiting factors but their relevance is still a matter of discussion. The very low temperatures encountered in such high latitudes are supposed to allow only low phytoplankton growth rates (Jacques and Minas, 1981; Tilzer *et al.*, 1985; Sakshaug and Holm-Hansen, 1986; Jacques, 1989). Moreover the lack of micronutrients may act on both autotrophic and heterotrophic activities: in particular the role of iron, as a limiting or a non-limiting factor on phytoplankton distribution in the Southern Ocean remains debatable (Martin *et al.*, 1990; De Baar *et al.*, 1990; Buma *et al.*, 1991*a*; Martin *et al.*, 1991; De Baar *et al.*, 1995).

The correlation of qualitative and quantitative variations in the autotrophic biomass with different environmental conditions is a prerequisite for understanding, on a larger scale, the biogeochemical processes that occur in the photic zone. The phytoplankton community structure is of great interest since it most likely influences sedimentation and carbon flux (Bodungen *et al.*, 1986; Bodungen *et al.*, 1988; Jacques and Panouse, 1991; Cullen, 1991). Taxonomic composition is highly relevant to the type of production encountered: nanoflagellates characterize a "regenerated", and diatoms a "new" production system (Jacques, 1991; Claustre, 1994). The "regenerated" system, also called the "microbial loop" system (Jacques, 1989; Lancelot *et al.*, 1989), is assumed to be a weak exporter of organic matter to the deep layers (Bak *et al.*, 1992), while a large fraction of organic matter produced in the "new" production system is exported into deep water and sediments through the rapid sinking of large diatoms and fecal pellets (Jacques, 1991; Scharek *et al.*, 1994). In the former case, the f-ratio, the ratio of nitrate uptake to total nitrogen uptake (Eppley and Peterson, 1979), is generally low (< 0.5) while in the latter case, f-ratio values are high (> 0.5) (Jacques, 1991). The Antarctic Ocean has been shown to exhibit relatively high f-ratios (Jacques, 1991) compared to other oceanic HNLC ecosystems (Cullen, 1991).

In the present study, the abundance, structure and fate of phytoplankton biomass are determined from specific pigment signatures in the Indian sector of the Southern Ocean, during late austral summer. From south to north, the study area comprises: (1) the Coastal and Continental Shelf Zone (CCSZ), which is a restricted area characterized by low wind speeds and high vertical stability (Mitchell and Holm-Hansen, 1991*a*); (2) the seasonal ice zone (SIZ), which has been extensively studied in the Weddell-Scotia Sea (EPOS cruises), in the Ross Sea (Nelson and Smith, 1986; Nelson and Tréguer, 1992) and in Prydz Bay (Kopczynska *et al.*, in press). This zone, which is defined as delimiting the influence of the input of low density water coming from the receding pack ice (Tréguer and Jacques, 1992) and has been shown to constitute a key component of the Southern Ocean through the dynamics of sea ice retreat and formation (Lancelot *et al.*, 1989; Lancelot *et al.*, 1991*a*; Lancelot *et al.*, 1991*b*), includes the Antarctic Divergence zone (AD), a dome-like structure; (3) the Permanently Open Ocean Zone (POOZ), which is subject to violent winds and weak vertical stability (Lancelot *et al.*, 1991*a*; Lancelot *et al.*, 1991*b*); and (4) the Polar Front Zone (PFZ), a frontal system, characterized by sharp nutrient gradients (Tréguer and Jacques, 1992) and numerous mesoscale eddies (Park *et al.*, 1991; Park *et al.*, 1993).

We investigate here how the pigment signatures may characterize these different sub-systems during summer, the ice-cover melting being completed (February-March 1994). This pigment information is related to the physical (depth ratio of euphotic and wind-mixed layers), chemical (nitrate and silicic acid concentrations) and biological (grazing by heterotrophs) characteristics of the different sub-systems in order to indicate the influences on phytoplankton distribution and fate in the euphotic zone of these polar areas.

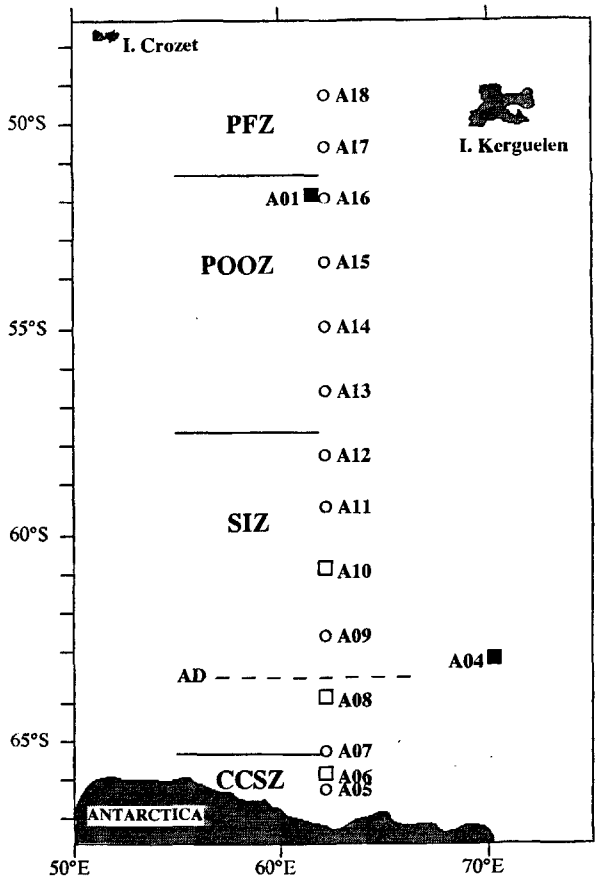

Figure 1

Location of the different stations studied during the ANTARES 2 cruise. The approximate limits between the different sub-systems are shown. (○) 1-day stations. (□) 1-day stations with deployment of sediment traps. (■) 4-day stations with deployment of sediment traps.

Position des différentes stations étudiées durant la campagne Antares 2. Les limites approximatives entre les différents sous-systèmes sont indiquées : (○) stations de 24 h ; (□) stations où des trappes à sédiments ont été déployées ; (■) stations de 4 jours, avec déploiement de trappes à sédiments.

MATERIAL-METHODS

The ANTARES 2 cruise (France-JGOFS) was conducted aboard the R.V. *Marion- Dufresne* from 10 February to 9 March 1994. The beginning of the cruise was devoted to the study of two five-day stations (called "long stations"), A01 (52° S-62° E) and A04 (63° S-70° 20 E). Then a south-north transect between 49° S and 67° S was performed along 62° E (13 daily stations or "short stations", A05 to A18, taken at each degree latitude) (*see* Fig. 1). By the time of arrival in the southern part of the transect, the pack-ice had retreated to the Antarctic continent and except for some large icebergs, the study area was free of ice.

At each station, continuous vertical profiles of temperature, salinity, and oxygen were obtained from a Sea-Bird CTD. The CTD was equipped with a Chelsea Fluorimeter. Concentrations of dissolved inorganic nutrients (nitrate, nitrite, phosphate and silicic acid) were determined by Masson and Oriol (Fiala, 1995) using automated analyzers, according to the method of Tréguer and Le Corre (1975). The depth of the wind-mixed layer (Z_m, m) was determined, either by direct examination of the salinity, temperature and density profiles (Mitchell and Holm-Hansen, 1991*a*), either by noting the depth at which the density gradient is greater than 0.05 kg. m^{-3} over a 10 m depth interval. The euphotic zone depth (Z_e, *m*), corresponding to the depth where 1 % of the surface Photosynthetically Available Radiation is measured, was calculated from an optical model (Morel, 1988), which uses the discrete integrated vertical Chl*a* concentrations (ΣChl*a*, mg Chl*a* m^{-2}) to back-calculate light depths. For some stations, direct measurements of the euphotic depth were missing; for the other stations, the euphotic zone depth as calculated was in good agreement with that directly measured during the cruise (data not shown). Therefore, for sake of consistency, we have preferred always to apply the model of Morel (1988) to determine the depth of the euphotic zone.

Water samples for pigment analysis were collected from Niskin bottles (12 L) (General-Oceanics Rosette coupled to the Sea-Bird CTD) tripped at different depths according to the fluorimetric profiles. For each depth, 2 L were filtered through 25 mm GF/F Whatman filters, at a vacuum differential of < 20 cmHg. Filters were stored in liquid

nitrogen before laboratory analysis using HPLC (High Performance Liquid Chromatography).

Sediment traps (PPS5 Technicap-collecting surface of 1 m^2), equipped with 24 glasses, were deployed over a four-day period for the two "long stations" (A01 and A04), and over a period of one day for some "short stations" (A06, A08 and A10), in order to estimate the different pigment fluxes (mg m^{-2} d^{-1}). The traps were located just below the photic zone (200 m), so that decomposition of particulate matter during its vertical descent was minimized, and thus vertical fluxes of organic particulate matter represent export production. For the "long stations", each of the 24 glasses (280 ml) was sampled at four-hour intervals; at the three "short stations", glasses were sampled at four-hour (A08 and A10) or eight-hour (A06) intervals. Aliquots of 30 to 50 ml were filtered through 25 mm GF/F filters and stored in liquid nitrogen before HPLC analysis. The export rate (% d^{-1}) was then defined for the different pigments as the pigment flux (mg m^{-2} d^{-1}) divided by the pigment integrated concentrations (mg m^{-2}) measured in the 0-200 m water column.

The separation procedure of chlorophylls and carotenoids by HPLC was carried out as follows. Three millilitres of acetone 90 % were added to the filters, which were then placed at –80 °C for 30 min before extraction using a sonication probe (less than 30 s). The solution was clarified by filtration (25 mm GF/C filters) and mixed with ammonium acetate (two parts of extract for one part of ammonium acetate), and 150 µl of this mixture were injected into the HPLC system through a 7 125 Rheodyne valve. The HPLC system consisted of a LDC Milton Roy pump, a 10 cm (4.6 mm ID) Hypersil ODS 3 µm column, and two spectrophotometers (LDC spectro monitor SM 3 000 and SM 3 100) set respectively at 440 nm (detection of chlorophylls and carotenoids) and at 667 nm (chlorophylls and phaeopigments). The gradient elution conditions were as in Mantoura and Llewellyn (1983) except that the flow rate was 1 ml min^{-1}. The chemotaxonomic significance of pigments recorded in this study may be described as follows. Chlorophyll *a* (Chl*a*) is the marker of total autotrophic biomass. The sum of 19'- hexanoyloxyfucoxanthin and 19'-butanoyloxyfucoxanthin (19' HF + 19' BF) characterizes nanoflagellates (prymnesiophytes and chrysophytes), while fucoxanthin is most likely a diatom marker (Wright and Jeffrey, 1987; Wright *et al.*, 1991). Although some species of the prymnesiophyte *Phaeocystis* may contain significant amounts of fucoxanthin (Buma *et al.*, 1991*b*), there is evidence that this contribution remains low for Antarctic strains (Wright and Jeffrey, 1987; Vaulot *et al.*, 1994; Bidigare *et al.*, 1996). The possible contribution of *Phaeocystis* to the fucoxanthin signal is here assumed to be negligible. The chlorophyll degradation products of grazing and senescence are, in descending order, phaeophytin *a* (Phin*a*), phaeophorbide *a* (Phbd*a*) and pyrophaeophorbide *a* (Pyro*a*), all of which are detected by HPLC. The identification of the different phaeopigments was realized by comparing retention time and visible absorption spectra with those of standards provided by D.J. Repeta (Department of Chemistry, Woods Hole Oceanographic Institution). Peak areas of pigments and phaeopigments were recorded and calculated by computer, using Nelson Analytical software. The quantification procedure of pigments and of phaeopigments was performed from detector response factors, previously established by injection of known amounts of the pigment standards. The extinction coefficients we used at 440 nm in the HPLC solvent were 50.0, 53.6 and 93.5 l g^{-1} cm^{-1} for Phin*a*, Phbd*a* and Pyro*a*, respectively (Bustillos-Guzman *et al.*, 1995). Grazing also results in colourless products, not detected by HPLC. The phaeopigments were used here as qualitative and not quantitative indices of macrozooplankton grazing.

In addition to individual pigment concentration, two criteria were analysed. (1) The (Diadinoxanthin + Diatoxanthin) per Chl*a* ratio [(DD + DT)/Chl*a*, concentrations ratio] the vertical distribution of which was here used to characterize the photoadaptation processes of phytoplankton in relation to the degree of the water column stability (Claustre *et al.*, 1994). The two indices Diadinoxanthin/Diatoxanthin (DT/DD), and (Diadinoxanthin + Diatoxanthin)/Chl*a* [(DD + DT)/Chl*a*], have been both proposed as tools for retracing phytoplankton light histories in the water column (Welschmeyer and Hoepffner, 1986; Bidigare *et al.*, 1987). However, in our *in situ* study, sampling time was too long and too variable compared to the expected rate of change of the ratio DT/DD (Olaizola *et al.*, 1992). Thus the (DD + DT)/Chl*a* ratio was here assumed to be more appropriate than DT/DD ratio for characterizing the photoadaptation processes of phytoplankton. (2) The F_p-ratio, defined as the sum of integrated fucoxanthin and peridinin concentrations divided by the sum of integrated concentrations of all the pigments, characterizes the proportion of microphytoplankton within the whole phytoplankton community (Claustre, 1994). This pigment index is considered as an estimator of the biomass derived from new production, and was proposed as an alternative for the traditional f-ratio as defined by Eppley and Peterson (1979).

RESULTS

Physical and chemical environment

The inorganic dissolved nitrogen concentrations were relatively high along the entire transect, and qualitatively represented by nitrate (from about 23 to 28 µM, north to south). Surface silicic acid [$Si(OH)_4$] concentrations increased from about 3 to 48 µM from the northernmost to the southernmost stations (cruise report ANTARES 2, 1994).

From north to south along the transect, the depths of the wind-mixed layer and of the euphotic zone decreased; this was particularly notable in the case of the wind-mixed layer, which decreased from 100 m in the POOZ to 25-35 m in the CCSZ (Fig. 2). The depth values of the euphotic zone were much the same (at 70-80 m) in the CCSZ and PFZ, and higher (100 m) in the POOZ (Fig. 2). Thus, for stations located in the CCSZ and SIZ, the limit of the

euphotic zone was deeper (by 50-70 %) than the limit of the wind-mixed layer, while for the stations located in the POOZ and PFZ, the two limits were also much the same (Fig. 2).

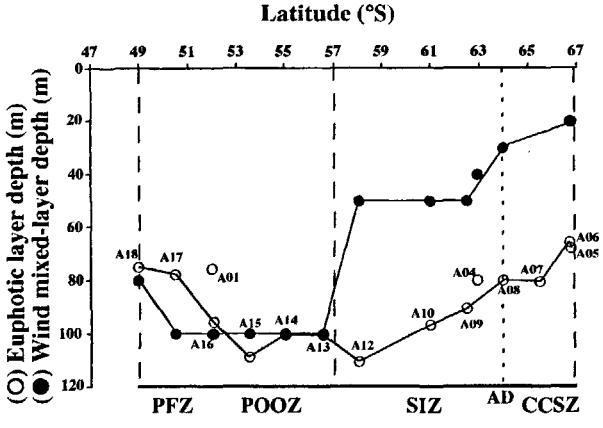

Figure 2

Latitudinal variations of the euphotic (Z_e) and wind-mixed (Z_m) layer depths (m).

Variations latitudinales des profondeurs (*m*) de la couche de mélange (Z_m) et de la couche euphotique (Z_e).

Phytoplankton distribution and physiological state

Integrated concentrations (up to 200 m) of Chl*a* (ΣChl*a*) varied between 10 and 35 mg Chl*a* m^{-2} (Fig. 3*a*), the lowest values being found at the oceanic stations A14, A15 and A16, and the highest at the continental stations (A05 and A06), at the Antarctic Divergence station (A08) and at the northernmost stations, in the PFZ (A17 and A18). An increase in phytoplankton biomass concentration was observed at station A13 (56° S) in comparison with neighbouring stations. Diatoms and nanoflagellates were the dominant phytoplankton all along the transect. Values of integrated concentrations of fucoxanthin (ΣFuco) and of the sum 19′-hexanoyloxyfucoxanthin and 19′-butanoyloxyfucoxanthin [Σ(19′ HF + 19′ BF)] varied from 4 to 25 mg m^{-2} and from 4 to 20 mg m^{-2} respectively. These pigment concentrations were normalized to Chl*a* in order to avoid quantitative variations and to reveal the taxonomic variations only (Fig. 3*b*). While the highest values of the ΣFuco:Chl*a* ratio were found at the southernmost stations and at station A08, the highest values of the (19 HF + 19 BF):(Chla ratio were found at the northernmost stations (Fig. 3*b*). The inversion in phytoplankton group dominance was observed at about 57° S, between stations A12 and A13, which is occasionally the northern winter limit of the pack ice in this sector. Comparison of stations A01 and A16, geographically located on the same site on the transect in the PFZ, revealed integrated pigment concentrations to be very different in the one-month interval, presenting a 38 % higher biomass at station A01. Furthermore, station A04 was located at an eastern longitude with respect to the transect, and at a latitude between that of stations A08 and A09. Concerning quantitative and

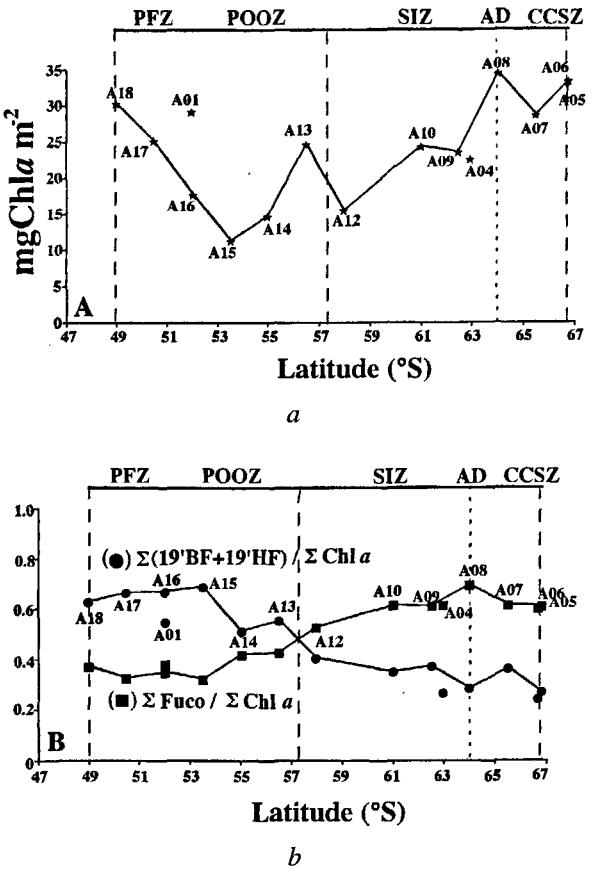

Figure 3

Latitudinal variations of A: the integrated (0-200 m) Chlorophyll a concentrations (ΣChla, mg Chla m^{-2}). B: the ΣFuco per ΣChla ratio (■) and the Σ(19′ HF + 19′ BF) per ΣChla ratio (•).

Variations latitudinales des: **A**: concentrations intégrées (0-200 m) de la Chl*a* (★, (Chl*a*, mg Chl*a* m^{-2}); **B**: concentrations intégrées en fucoxanthine (■) et en (19′ BF + 19′ HF) (•), normalisées par les concentrations intégrées en Chl*a*.

qualitative phytoplankton distribution, station A04 was very different from station A08, but similar to station A09. The very low (< 2 mg m^{-2}) and variable concentrations of peridinin, alloxanthin and zeaxanthin measured suggested that dinoflagellates, cryptophytes and prokaryotes were not major components of the phytoplankton biomass (data not shown). Chlorophyll *b* (Chl*b*) is here considered as a biomarker of green algae, since a small quantity of zeaxanthin, which is contained in prochlorophytes (which may also contain Chl*b*), was found in the transect. The latitudinal variations of the Chl*b* integrated concentrations indicated that green algae were not very abundant along the transect (mean value found at 3.5 mg m^{-2}), and were preferentially located in the Polar Front Zone (mean value at 6.6 mg m^{-2}) (data not shown).

In the 0-200 m water column, Chl*a* concentrations were low during the cruise, and never exceeded 0.45 mg Chl*a* m^{-3} (Fig. 4*a*). Generally speaking, Chl*a* concentrations at the surface were very low, ranging from 0.10 to 0.20 mg Chl*a* m^{-3}, the highest values being recorded at the CCSZ stations (A05 and A06, 66.7° S-62° E) and at the PFZ stations (A17 and A18, 49° S-62° E). The SIZ stations situated between 66° S and 57° S (station A04

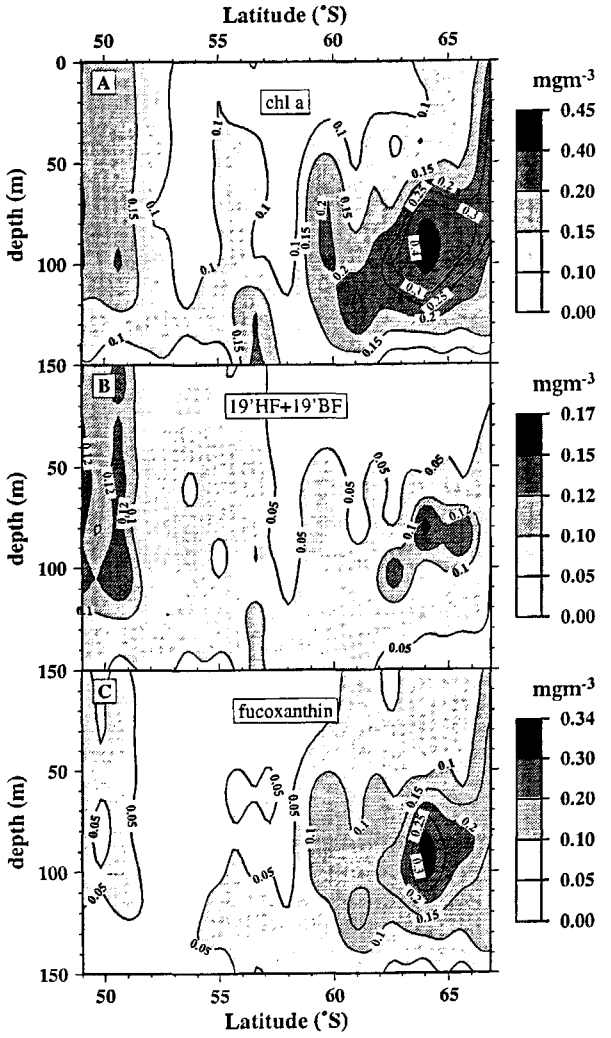

Figure 4

Latitudinal variations of the vertical distribution of pigment concentrations (mg m^{-3}). A: Chla . B: (19′ BF + 19′ HF). C: fucoxanthin.

Variations selon la latitude des distributions verticales des concentrations de différents pigments (mg m^{-3}). **A**: Chl*a*. **B**: (19′ BF + 19′ HF). **C**: fucoxanthine.

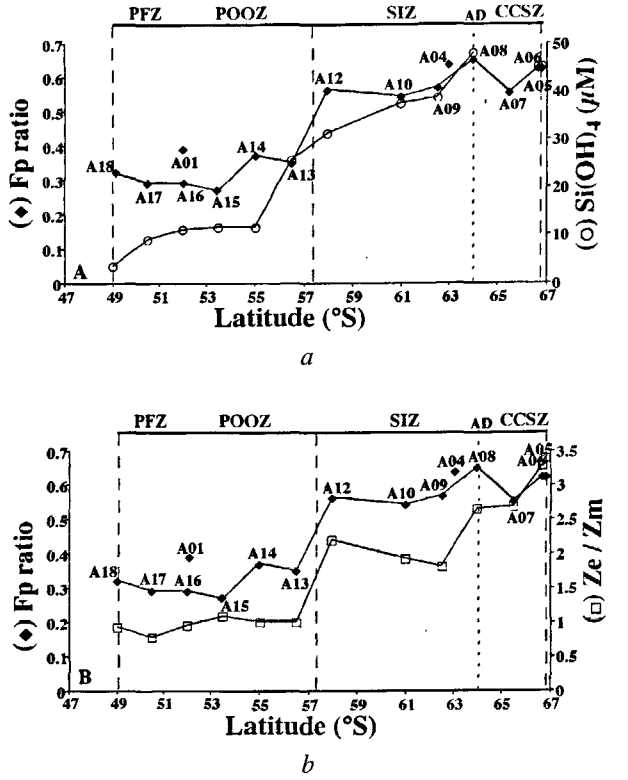

Figure 5

Comparison of the horizontal variations of the F_p-ratio (♦) with A: silicic acid ($Si(OH)_4$) surface concentrations (○). B: the euphotic zone per wind-mixed layer depth ratio (□).

Comparaison des variations suivant la latitude du F_p-ratio (♦) avec : **A** : concentrations moyennes de l'acide silicique [$Si(OH)_4$] en surface (○) ; **B** : rapport des profondeurs de la couche de mélange avec la couche euphotique (□).

and on the transect stations A07 to A13) presented a deep Chl*a* maximum (DCM), with values reaching 0.45 mg Chl*a* m^{-3} at station A08. The depth of the DCM was about 70 m in the south, increasing northwards to reach 150 m at stations A12 and A13. For stations beyond 57° S (POOZ stations), Chl*a* was uniformly distributed throughout the euphotic zone. The maximal values of the sum (19′ HF + 19′ BF) and of fucoxanthin, were respectively 0.14 mg m^{-3}, measured at the PFZ and at the AD stations (Fig. 4*b*), and 0.35 mg m^{-3} measured at the AD station (Fig. 4*c*). The concentration maximum of the sum (19′ BF + 19′ HF) found at the AD station was less pronounced than the maximum fucoxanthin concentrations. In general, fucoxanthin distribution paralleled that of Chl*a* (*see* Fig. 4*a* and 4*c*). Variations of the F_p-ratio with latitude indicated a north-south gradient (Fig. 5). Stations with a F_p-ratio higher than 0.5 were located south beyond 57° S, in the SIZ and in the CCSZ, while Fp-ratios lower than 0.5 were found in the POOZ and PFZ. The F_p-ratio was minimal (0.27) at station A15 (in the high POOZ) and maximal (0.65) at station A08 (Antarctic Divergence). Comparison between stations A01 and A16, sampled at a one-month interval, showed the F_p-ratio to differ by 10 %, due to a higher contribution of nanoflagellates at the end of summer (station A16). A significant relationship was observed between the F_p-ratio and the latitudinal variations of surface $Si(OH)_4$ concentrations (r = 0.88, $p < 0.001$) (Fig. 5*a*) and of the Z_e per $Z_m$ratio (r = 0.94, $p < 0.001$) (Fig. 5*b*). In conclusion, high values of F_p-ratio corresponded to oceanic areas where $Si(OH)_4$ was the most abundant and where the euphotic zone was deeper than the mixing zone.

The variations throughout the euphotic zone of the (Diadinoxanthin + Diatoxanthin) per Chl*a* [(DD + DT)/Chl*a*] ratio are presented at some representative stations along the transect (Fig. 6). At the southernmost stations (CCSZ and southern part of the SIZ), in a diatom-dominated system and where the euphotic zone was deeper than the wind-mixed layer, the vertical profile of (DD + DT)/Chl*a* paralleled that of surface light penetration. For the SIZ, such profiles showed a subsurface maximum with values ranging from 0.20 to 0.25; values decreased to 0.05 at about 100 m. At the northernmost stations, and particularly in the PFZ, where nanoflagellates dominated and where euphotic and wind-mixed layers were equal,

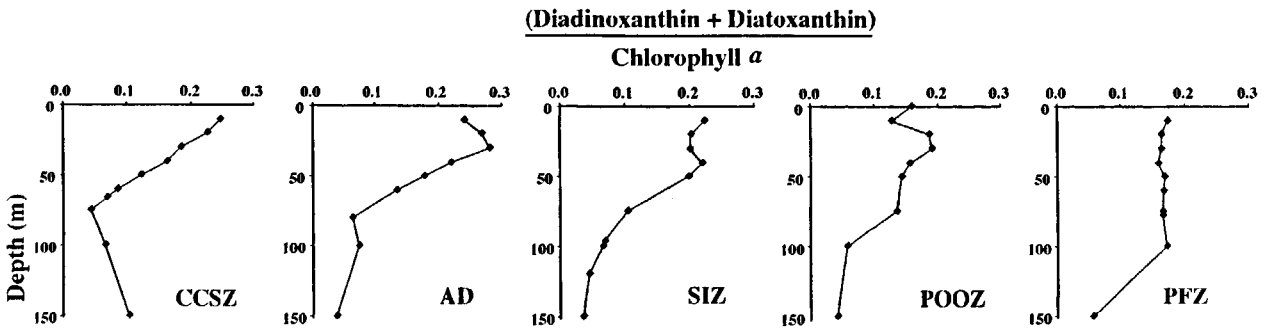

Figure 6

Vertical distribution of the (Diadinoxanthin + Diatoxanthin) per Chla ratio [(DD + DT)/Chla] for different stations along the transect.

Distribution verticale du rapport (Diadinoxanthine + Diatoxanthine) sur Chl*a* [(DD+DT)/Chl*a*] pour quelques stations de la radiale.

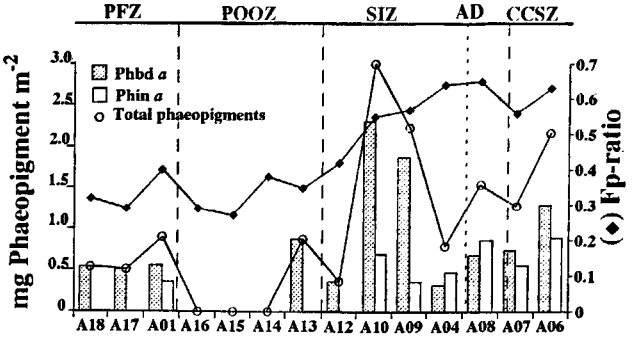

Figure 7

Latitudinal variations of the integrated (0-200 m) phaeophytin a (ΣPhina) and phaeophorbide a (ΣPhbda) concentrations. The latitudinal variations of the total phaeopigment concentrations (○) and of the F_p-ratio (♦) are also shown.

Variations selon la latitude des concentrations intégrées (0-200 m) en phaeophytine a (ΣPhin*a*) et en phaeophorbide *a* (Σphbd*a*). Les variations selon la latitude des concentrations en phacopigments totaux (○) et du F_p-ratio (♦) sont également indiquées.

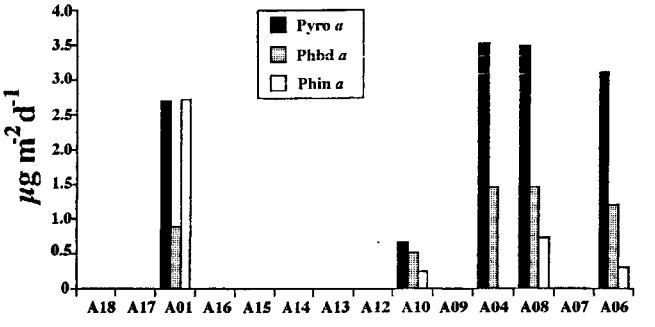

Figure 8

Downward daily vertical fluxes of phaeopigments (µg m^{-2} j^{-1}) as estimated from sediment traps at different stations of the transect.

Flux journaliers des phaeopigments (µg m^{-2} j^{-1}) estimés à partir des trappes à sédiments à différentes stations de la radiale.

values of the (DD + DT)/Chl*a* ratio were constant in the upper layer corresponding to the mixed layer (values ranging from 0.15 to 0.20).

In general, integrated concentrations (down to 200 m) of phaeopigments, mainly composed of Phbd*a* and Phin*a*, were higher in the diatom-dominaned south than in the nanoflagellate-dominated north (Fig. 7). No close relationship existed between phaeopigment and total biomass concentrations. No phaeopigments were found in the POOZ, and the highest phaeopigment concentrations were found in the SIZ, at stations A09 and A10, with values ranging between 2.2 to 2.9 mg (Phbd*a* + Phin*a*) m^{-2}. Phbd*a* was the dominant phaeopigment, except at stations situated at the Antarctic Divergence (A08 and A04) where Phin*a* dominated (Fig. 7). Concentrations of Pyro*a* in the water column were very low all along the transect (Fig. 7).

The contribution of phaeopigments to particulate organic material fluxes did not reflect the concentrations found in the water column (Fig. 8). Pyro*a* dominated except at the PFZ, where Phin*a* was as important as Pyro*a*. Total phaeopigment ((Phaeo) vertical fluxes, as estimated from sediment trap data, varied between 1.5 (at A10), 5.8 (at A08) and 6.2 (at A01) µg ΣPhaeo m^{-2} d^{-1} (Fig. 8).

Export rates were estimated by comparing pigments and phaeopigments found at the base of the euphotic zone and in the water column. If we assume that one molecule of Phin*a*, Phbd*a* or Pyro*a* is obtained from the degradation of one Chl*a* molecule, the measured phaeopigment concentrations can be converted to their "Chl*a* equivalent" ("Chl*a*-Eq") by using conversion factors derived from molecular weights. The average particulate organic material export percentage (d^{-1}) was estimated from pigments and the "Chl*a*-Eq" flux (mg m^{-2} d^{-1}) derived from sediment trap data, and divided by the integrated pigments and "Chl*a*-Eq" concentrations (mg m^{-2}) as measured in the water column. The resulting average percentage of pigments exported out of the photic layer was low, nowhere exceeding 0.3 % (Fig. 9). Export rates as estimated from non-degraded pigments always exceeded "Chl*a*-Eq" export rates. In general, export rates decreased south to north, being maximum in the CCSZ and at the Antarctic Divergence. At station A04, the estimated export rates showed extreme variability, ranging between near zero and 0.5 % of pigments exported per day (Fig. 9).

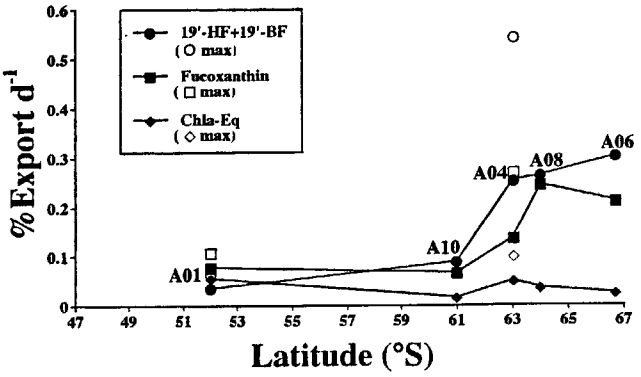

Figure 9

Export rates of particulate organic material (% d^{-1}) as calculated from the comparison of the amounts of fucoxanthin, (19' BF + 19' HF), and "Chla-Eq" found in the water column with those harvested in the sediment traps (200 m). At stations A01 and A04, maximal values of export rates are shown (open symbols).
Flux d'exportation de la matière organique particulaire (% j^{-1}) calculés à partir des données pigmentaires (fucoxanthine, 19' BF + 19' HF, « Chla-eq ») de la colonne d'eau et des trappes à sédiments (200 m). Aux stations A01 et A04, les valeurs maximales des flux d'exportation sont indiquées (symboles ouverts).

DISCUSSION

Phytoplankton distribution and the different sub-systems

In this study, algal composition and abundance were examined, together with a series of sub-systems in the Indian sector of the Southern Ocean, during the late austral summer period. The phytoplankton biomass, expressed as Chl*a* concentrations, was low (< 0.45 mg m^{-3}), particularly in the POOZ. This is consistent with previous studies which characterized the Southern Ocean as essentially oligotrophic (Jacques, 1989; Cullen, 1991; Smith, 1991; Cota *et al.*, 1992). Two zones of enhanced autotrophic biomass were found along our transect, at the Antarctic Divergence and in the PFZ. Some recent data concerning the Polar Front Zone present this region as photosynthetically productive (Tréguer and van Bennekom, 1991; Tréguer and Jacques, 1992). But, if local enhancement of Chl*a* levels was evident, it has been shown to display strong temporal variability (Laubscher *et al.*, 1993). Our data confirmed this variablity. Comparison between stations A01 and A16, geographically identical but sampled in the middle and at the end of the austral summer, respectively, showed total phytoplankton biomass at the end of the summer period to be 40 % lower than during summer. The taxonomic phytoplankton composition varied along the transect, with an inversion of species dominance at the northern limit of the SIZ (57° S). Diatoms dominated in the south (CCSZ and SIZ) and nanoflagellates dominated in the north (POOZ and PFZ). The vertical distribution of phytoplankton varied from south to north along the transect, with a geographical transition at about 57° S. South of this latitude, the SIZ was characterized by the presence of a deep Chl*a* maximum; while to the north, the POOZ was characterized by a uniform Chl*a* distribution in the upper layer. Vertically, the dominance of nanoflagellates relative to diatoms was constant in the POOZ and in the PFZ. In contrast, the relative dominance of diatoms versus nanoflagellates in the SIZ and CCSZ was more variable, probably indicating microstructures in the water column in these areas.

Environmental control on phytoplankton distribution

What limits the enhancement and maintenance of the Antarctic phytoplankton is still a matter of debate (Nelson and Tréguer 1992; Laubscher *et al.*, 1993). In this study, we focused on the influence of nutrient concentrations, vertical mixing and grazing pressure on specific phytoplankton distribution, being aware that other factors and processes may also influence the qualitative and quantitative distribution of the autotrophic biomass. Such is the case, in particular, of iron, which is supposed to be an important limiting factor for phytoplankton growth, especially in the offshore environment (Martin *et al.*, 1990; De Baar *et al.*, 1990; Buma *et al.*, 1991*a*; Martin *et al.*, 1991).

From one end to the other of the transect, nitrate was always present in concentrations far in excess (~ 28 μM) of phytoplankton demands, and thus nitrate was supposed here not to be a limiting-factor. In contrast to the distribution of nitrate, the concentration of silicic acid [$Si(OH)_4$] increased in a gradient from north to south. High $Si(OH)_4$ concentrations (40-50 μM) were found in the SIZ; in the permanently ice-free waters, near the Polar Front Zone, concentrations were up to five times lower (< 10 μM). This distribution of silicic acid concentration is consistent with previous studies conducted in different parts of the Southern Ocean (Jacques, 1983; Le Jehan and Tréguer, 1983; Sommer, 1986; Tréguer and Jacques, 1992). Moreover, the significant correlation (r = 0.88, $p < 0.001$) which we found along the transect between the amount of silicic acid in the surface layer (0-40 m) and the F_p-ratio (Fig. 5*a*) suggests that diatom abundance may be strongly linked to silicic acid concentrations. High $Si(OH)_4$ concentrations have been previously demonstrated to be required for maximum growth of Antarctic diatoms (Jacques, 1983; Jacques, 1989). On the basis of different culture experiments, Antarctic diatoms were assumed to exhibit a much lower affinity for $Si(OH)_4$ than diatoms from other world oceanic sectors (Jacques, 1983; Sommer, 1986; Sommer, 1991; Nelson and Tréguer, 1992). From these and our results, a limitation of diatom growth by $Si(OH)_4$ deficiency is assumed to occur at the northernmost stations in this sector of the Southern Ocean, although these $Si(OH)_4$ concentrations are thought to be saturating in other oceanic areas (Nelson and Tréguer, 1992). Nevertheless, the importance of $Si(OH)_4$ concentrations in limiting diatom growth remains to be precisely defined, since other factors (*e.g.* light limitation, grazing) might also play determinant roles in phytoplankton distribution (Sommer, 1986; Sommer, 1991).

Previous studies have emphasized the important role of water- column stability in promoting phytoplankton growth by maintaining it in the euphotic zone (Veth *et al.*, 1992;

Schloss and Estrada, 1994). In the case of strong vertical mixing of the water column, phytoplankton may not remain in a light regime favourable to photosynthesis; thus, they have to photoadapt (Lewis *et al.*, 1984). In the CCSZ and SIZ, where the euphotic layer was 70 % deeper than the wind-mixed layer, we found vertical profiles of the (DD + DT)/Chl*a* ratio which paralleled profiles of light penetration, indicating that phytoplankton could initiate photoadaptation processes in the context of an adequate hydrological regime (Claustre *et al.*, 1994). The uniform profiles of the (DD + DT)/Chl*a* ratio observed in the POOZ and PFZ indicated that the mixing processes were faster than the photoadaptation processes of phytoplankton (Claustre *et al.*, 1994). Thus, the capacity of phytoplankton to photoadapt in the northern and in the southern parts of the transected area appeared to be very different. But considering only the abundance of the autotrophic biomass as expressed in terms of integrated Chl*a* concentrations, the differences were observed between the south, characterized by a relatively shallow wind-mixed layer, and the north, characterized by a much deeper wind- mixed layer, were minimal. It is clear, however, when considering the very close relationship that exists between the Fp-ratio and the variations of the euphotic: wind-mixed layer depths ratio (Fig. 5*b*, $r = 0.94$ and $p < 0.001$), that light conditions strongly influence specific phytoplankton development. While diatoms were dominant in the southernmost stations of the transect, characterized by an euphotic layer 70 % deeper than the wind-mixed layer, the PFZ – characterized by strong vertical mixing - was essentially populated by nanoflagellates. Thus, diatoms appeared to grow under quite stratified waters, in a hydrological regime allowing phytoplankton to remain in favourable light conditions for growth. Nevertheless, the deep pigment maximum we observed in the SIZ, and particularly at the Antarctic Divergence, could hardly have been related to favourable light conditions for phytoplankton growth, since at this depth the percentage of the Photosynthetically Available Radiation (PAR) was no more than 1.3 (data not shown). Thus, the deep pigment maximum was here assumed to be related to accumulation of biomass (sedimentation), rather than to growth processes occurring at this depth. In contrast, nanoflagellates appear to be able to grow under less favourable light conditions due to vertical mixing of the water column, and this, without being photoadapted as revealed from the general uniform trends of the (DD + DT)/Chl*a* profiles. Recent studies carried out in other oceanic areas have already established the presence of nanoflagellates at very low light levels, in association with high nitrate availability (Claustre *et al.*, 1994; Claustre and Marty, 1995). Sverdrup (1953) has defined the "critical depth" for phytoplankton as the depth below which respiratory rates exceed photosynthesis rates. This approach was originally established for Norwegian Sea data and has been shown to be adequate for determining phytoplankton blooming conditions in temperate waters; its application in Antarctic waters, however, has been a matter of debate (Smetacek and Passow, 1990; Nelson and Smith, 1991; Mitchell and Holm-Hansen, 1991*a*). A reformulation of Sverdrup's "critical depth" calculation from recent optical and physiological data has been developed and applied to the Southern Ocean (Nelson and Smith, 1991). However, the accurate determination of "critical depth" is certainly species-specific (Smetacek and Passow, 1990). Indeed, our results clearly demonstrate the necessity of considering the taxonomic composition of the phytoplankton compartment before attempting to determine the precise role of light conditions as a factor limiting phytoplankton growth.

Export rates and phytoplankton structure community

Grazing pressure is assumed to be an important factor controlling biomass loss of phytoplankton (Bidigare *et al.*, 1986; Tréguer and Jacques, 1992). The sinking flux of particulate organic material depends on the community structure of the producers, which determines the community structure of consumers and may vary significantly for different food webs (Welschmeyer and Lorenzen, 1985; Michaels and Silver, 1988; Legendre and Le Fèvre, 1989). Thus, the question of diatom versus nanoflagellate dominance is of interest not only theoretically, but also because the size structure of phytoplankton may have important consequences on carbon fluxes through the water column (Bodungen *et al.*, 1986; Jacques and Panouse, 1991)

In systems characterized by the dominance of flagellates, the main consumers are the heterotrophs of the microbial loop (Jacques, 1989; Lancelot *et al.*, 1989). Small phytoplankton cells sink slowly, and are supposed to promote high grazing rates (Michaels and Silver, 1988). In such systems, phaeopigments remain in the photic layer and are then transformed into colourless products through photo-oxidation (SooHoo and Kiefer, 1982*a*; SooHoo and Kiefer, 1982*b*; Welschmeyer and Lorenzen, 1985). These colourless products are undetectable by HPLC. Moreover, microzooplankton, due to their efficient digestive systems, are also expected to degrade phaeopigments into colourless products (Klein *et al.*, 1986; Barlow *et al.*, 1988). It is consequently to be expected that only trace amounts of phaeopigments, if any, would be detected in systems dominated by the "microbial loop". Our phaeopigment data support these hypotheses. In the POOZ and PFZ, *i.e.* oceanic areas characterized by nanoflagellate dominance, low phaeopigment concentrations were found in the water column (Fig. 7).

In systems dominated by diatoms, the main consumers are generally copepods and euphausiids, which, unlike nanoflagellates, produce large fecal pellets that are supposed to sink rapidly (Komar *et al.*, 1981), preventing their phaeopigment content from being photo-oxidized. In this study, high levels of phaeopigments (essentially composed of Phin*a* and Phbd*a*) were found in the SIZ and CCSZ, in comparison with the amounts measured in the POOZ and PFZ.

Our results suggest that grazing processes, although their quantitative influence on phytoplankton distribution was not easily measured, exhibited different pressures according to the different phytoplankton groups encountered in each oceanic sub-system. The quantitative and qualitative description of particulate organic material fluxes out of the photic zone was further analysed in typical nanoflagellate

(station A01) and diatom (station A04) dominated systems from four-day sediment traps. The quantitative importance of non-degraded Chl*a* (data not shown) and Phin*a* found in the traps at station A01 indicated that flux of the particulate organic material out of the photic zone was due not only to grazing, but also to repackaging of particles and physical transport (*e.g.* downwelling) (Michaels and Silver, 1988; Legendre and Le Fèvre, 1989). In contrast, material found in sediment traps at station A04 was relatively more degraded than at station A01, indicating that at this station, grazing pressure was probably the essential process responsible for material removal out of the euphotic zone.

Export fluxes calculated in the PFZ (station A01) and from 67 to 60° S (stations A10 to A05) were extremely low (less than 0.3 % of organic material exported per day). The export rate was related to the phytoplankton community structure in the photic zone as described by the F_p-ratio. The southernmost stations were characterized by the highest export rate mean values of the transect, and by a high F_p-ratio (0.5-0.7), particularly at the Antarctic Divergence (0.65). In contrast, the Polar Front Zone was characterized by a low F_p-ratio and a relatively low export flux, as reported previously (Jacques, 1991; Bak *et al.*, 1992). Thus the F_p-ratio variations appeared to be closely related to the export rate mean variations in the different sub-systems. However, the high variability of flux rates at station A04 (data not shown) showed that on a short time scale, export rates and phytoplankton composition may be largely uncorrelated. Furthermore, preliminary comparison of the F_p-ratio with true measurements of the *f*-ratio during the same cruise (Goeyens *et al.*, unpublished results) suggests a significant correlation between these two parameters. High values of the f-ratio previously found in the SIZ (f-ratios of 0.8-0.9 reported by Collos and Slawyck, 1986) are consistent with our results. The F_p-ratio has already been proposed as an adequate alternative tool to the traditional f-ratio (Eppley and Peterson, 1979) to describe the trophic status (new *vs* regenerated production) of various oceanic areas (Claustre, 1994). However, spatial and temporal scales must be taken into account before concluding from these results that export rates are directly related to the type of production (new or regenerated) in this system (Legendre and Gosselin, 1989). Some authors have already placed restrictions on the direct association between export rates and new or regenerated systems, which refers to the nature of nutrients used by primary producers, whereas export rates concern pathways in the food web (Legendre and Le Fèvre, 1989). Thus, accurate physical data defining watermass circulation, as well as accurate temporal and spatial scales of observations, are necessary before export rates and the structure of phytoplankton communities can be correlated.

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