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PART I

# Sea-surface distribution of coccolithophores, diatoms, silicoflagellates and dinoflagellates in the South Atlantic Ocean during the late austral summer 1995

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**Abstract**

The sea-surface distribution of four selected fossilizable phytoplankton groups (coccolithophores, diatoms, silicoflagellates and dinoflagellates) has been studied along a transect from Cape Town (34°S) to South Sandwich Islands (57°S) during the late austral summer. The observed distribution of these groups shows that their biogeographical distribution is significantly constrained by the water masses and associated frontal systems of the Southern Ocean. Coccolithophores are the dominant group and show cell abundances up to $51 \times 10^3$ cells/l down to 57°S. Three restricted areas are marked by particularly high cell densities: the continental shelf of South Africa, the area between the Sub-Tropical Convergence and the Sub-Antarctic Front, and the southern border of the Antarctic Polar Front, where the highest abundances are recorded ($> 650 \times 10^3$ cells/l). The species composition of the various assemblages representative of the four groups defines distinct biogeographical zones bounded by marked sea-surface temperature gradients. This biogeographical distribution is confirmed by factor analysis of the coccolithophore (5 factors, 85% of the total variance) and diatom and silicoflagellate (7 factors, 87.5% of the total variance) populations. When compared with the distribution pattern of siliceous fossil assemblages in surface sediments, our data show a more accurate coupling between the various water-masses of the South Atlantic Ocean and the living siliceous population. 

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## 1. Introduction

The Southern Ocean is the most extended HNLC region (High Nutrient-Low Chlorophyll) of the world ocean, with phytoplankton standing stocks well below the level expected from the exceptional nutrient richness of the area. The biological forcing on atmospheric $CO_2$ draw-down, as indicated from measurements of partial pressure of $CO_2$ in surface waters (Jeandel, 1996), modulates the seasonal variations of this sink, which is primarily constrained by thermodynamics (Tréguer, 1996).

The geostrophic circulation patterns of the Southern Ocean produce extended zones with relatively uniform hydrographic characteristics. Furthermore, frontal boundaries are believed to influence biological dispersal between and containment within these zones. The phytoplankton of this ocean has been studied for more than 50 years. In the microplankton and nanoplankton size-groups (2–200 μm), diatoms and coccolithophores are among the most studied. Diatoms are usually considered to be dominant in the Southern Ocean (Hasle, 1969; Fenner et al., 1976; Jacques, 1981; Pichon, 1985). These organisms are particularly well adapted to Antarctic waters, where light, temperature and nutrient availability are thought to be favourable to their growth. Northward, in the Subantarctic zone, coccolithophores become the major group (Hasle, 1969). Their biogeographical extent is thought to be limited to the South by the 2°C isotherm (McIntyre and Bé, 1967; Verbeek, 1989). The fossil records of phytoplankton organisms constitute, together with geochemical proxies, some of the most important tools for reconstructing past changes in surface ocean conditions. Actualistic approaches, based on the biogeographic interpretation of large-scale phytoplankton distribution patterns, are essential for constraining paleo-oceanographic interpretations based on thanatocoenoses (Samtleben et al., 1995). The goal of the present study was to investigate, along a NE–SW transect of the South Atlantic Ocean, the abundances and species distribution of four phytoplankton groups selected for their fossilization potential: coccolithophores, diatoms, silicoflagellates and dinoflagellates.

## 2. Materials and methods

The data presented here were gathered aboard the R.R.S. *James Clark Ross* (JCR). Samples for the estimation of phytoplankton taxonomic composition and distribution were collected between 22 February and 01 March 1995, between Cape Town (34°S) and the South Sandwich Islands (57°S), during the JCR09/B cruise. A total of forty surface water samples were taken (Fig. 1; Table 1), at 0–5 m water depth, every half-degree of latitude between Capetown and 52°S, then every degree to 57°S. The water samples were obtained using the ship's uncontaminated sea-water supply. Temperature data were recorded every 5 min by the Seabird thermosalinograph of the Ocean logger at the sea water inlet. Additionally samples were taken in the vicinity of sharp temperature changes. The sampling follows the procedure described by Kleijne (1991) and Giraudeau and Bailey (1995), among others. Aboard ship, 3 to 10 l sea-water samples were prefiltered through a 150 μm sieve to screen out the large zooplankton,

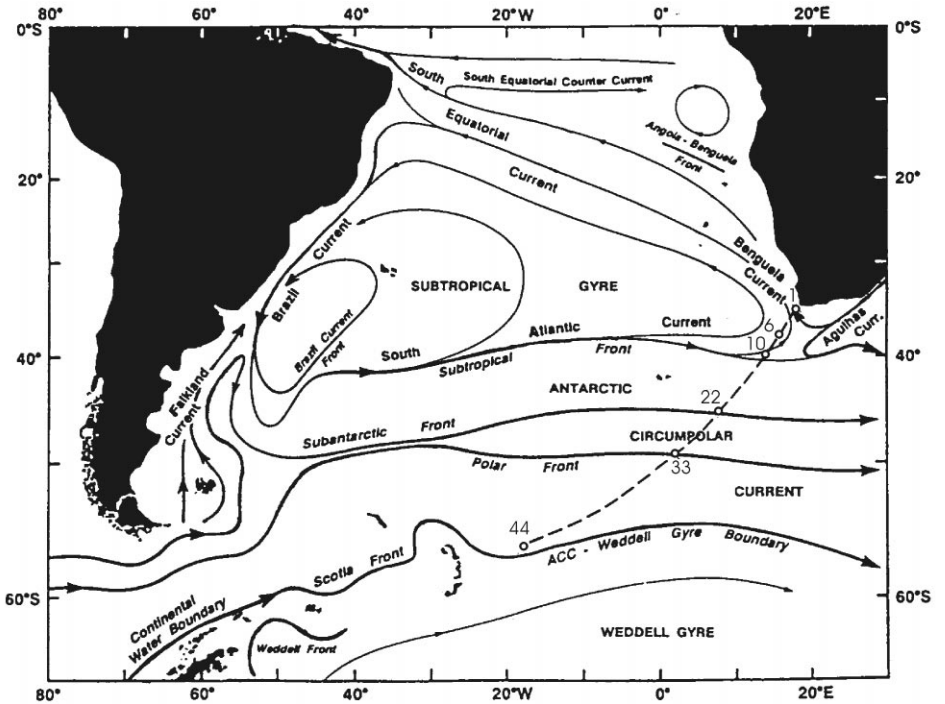


Fig. 1. Schematic representation of the large-scale, upper level geostrophic currents and fronts in the Atlantic Southern Ocean (after Peterson and Stramma, 1991). Dotted line shows the sampling transect. Selected stations at front locations are also plotted.

then vacuum filtered through Metricel Membrane filters (47 mm diameter, 0.8 μm pore size). This procedure allows for an homogeneous distribution of the particulate matter over the entire surface of the filter (Knappertsbuch and Brummer, 1995). Filters were then air-dried before being stored in plastic petri dishes.

The standing abundances of the phytoplankton groups (coccolithophores, diatoms, silicoflagellates and dinoflagellates) were determined by light microscopy. For this purpose, a small piece of the filter (20 $mm^2$) was mounted between slide and coverslip with Canada balsam. Counting was conducted at $\times 500$ magnification on a minimum of 10 fields of view (from a minimum of 200 cells to more than 5000 cells for the richest samples). The abundances were then expressed in cells/l, considering the volume of the sample and the average number of cells per field of view extrapolated to the entire sample, using the following formula:

$$N = (n \times S/s)/V,$$

where $N$ is the number of cells per liter, $n$ the number of cells per field of view, $S$ the effective filtration area ($mm^2$)-diameter 35 mm; $s$ the surface of a field of view at $\times 500$ magnification ($mm^2$)-diameter 330 μm; $V$ the volume filtered (l).

Table 1
Sample position, measured temperatures and volume of filtered sea-water (volume $< 10$ l when filter clogged)

| Sample | Lat. S | Long. | Temperature (°C) | Volume filtered (l) |
|---|---|---|---|---|
| 1 | 34°10′S | 18°06′E | 21.0 | 3.9 |
| 2 | 35°00′S | 17°26′E | 21.1 | 10.0 |
| 3 | 35°53′S | 16°51′E | 21.5 | 7.0 |
| 4 | 36°26′S | 16°20′E | 20.7 | 8.5 |
| 5 | 37°00′S | 15°55′E | 21.4 | 7.0 |
| 6 | 37°46′S | 15°27′E | 21.4 | 10.0 |
| 7 | 38°00′S | 15°19′E | 17.7 | 3.0 |
| 8 | 38°30′S | 15°01′E | 19.9 | 5.0 |
| 9 | 39°00′S | 14°39′E | 19.5 | 10.0 |
| 10 | 39°30′S | 14°17′E | 18.2 | 3.5 |
| 11 | 40°00′S | 13°55′E | 14.6 | 4.2 |
| 12 | 40°30′S | 13°32′E | 14.2 | 4.6 |
| 13 | 41°00′S | 13°11′E | 13.9 | 3.9 |
| 14 | 41°30′S | 12°51′E | 13.5 | 3.9 |
| 15 | 42°00′S | 12°30′E | 13.0 | 4.5 |
| 16 | 42°30′S | 12°00′E | 11.7 | 6.0 |
| 17 | 43°00′S | 11°17′E | 11.7 | 6.7 |
| 18 | 43°30′S | 10°37′E | 12.0 | 6.0 |
| 19 | 44°00′S | 9°52′E | 11.0 | 5.9 |
| 20 | 44°20′S | 9°21′E | 9.8 | 6.0 |
| 21 | 44°40′S | 8°49′E | 9.7 | 6.0 |
| 22 | 45°00′S | 8°13′E | 10.3 | 5.8 |
| 23 | 45°24′S | 7°30′E | 7.4 | 5.9 |
| 24 | 46°00′S | 6°34′E | 8.3 | 10.0 |
| 25 | 46°30′S | 5°46′E | 8.1 | 8.8 |
| 26 | 47°00′S | 5°00′E | 7.7 | 7.8 |
| 27 | 47°20′S | 4°27′E | 6.7 | 8.8 |
| 28 | 47°40′S | 3°54′E | 6.7 | 10.0 |
| 29 | 48°00′S | 3°19′E | 7.3 | 10.0 |
| 30 | 48°30′S | 2°29′E | 7.3 | 10.0 |
| 31 | 49°00′S | 1°40′E | 5.7 | 10.0 |
| 32 | 49°30′S | 0°46′E | 6.3 | 10.0 |
| 33 | 50°00′S | 0°02′W | 5.3 | 7.3 |
| 34 | 50°25′S | 0°47′W | 3.8 | 7.3 |
| 35 | 50°45′S | 1°24′W | 4.0 | 7.5 |
| 36 | 51°10′S | 2°06′W | 3.6 | 7.8 |
| 37 | 51°30′S | 2°43′W | 3.7 | 10.0 |
| 38 | 52°00′S | 3°36′W | 2.7 | 9.0 |
| 39 | 52°30′S | 4°47′W | 2.5 | 9.0 |
| 40 | 53°00′S | 6°11′W | 2.0 | 7.5 |
| 41 | 53°59′S | 9°04′W | 1.9 | 8.5 |
| 42 | 55°00′S | 12°06′W | 2.1 | 7.8 |
| 43 | 56°01′S | 15°12′W | 1.9 | 7.9 |
| 44 | 57°01′S | 18°15′W | 2.0 | 7.8 |

The species composition of the coccolithophore community was determined by light microscope examination at $\times 1250$ magnification on 50 fields of view (minimum of 250 cells). For each sample, relative frequencies (%) of individual species were estimated considering only the intact cells (coccospheres), as well as those showing evidence of disintegration during the filtration process. Species percentages were then converted into absolute abundances (cells/l), taking into account the total coccolithophore standing abundance for each sample. The coccolithophore species identification inferred from the LM study was subsequently validated by SEM examination of a few selected samples (see Kleijne, 1991, for the sample preparation technique).

Relative frequencies of individual genera of dinoflagellates were determined using the same counting procedure as for coccolithophores at $\times 500$ magnification on 20 fields of view.

A special sample preparation technique was required for diatom and silicoflagellate species determination. One half-section of the filter was dissolved by boiling it for 15 min in 50 ml concentrated $HNO_3$ solution. Acid and soluble salts were removed by successive washing in distilled water and four centrifugations at 1200 rpm for 7 min. As tested after several sets of centrifugations, this technique allows preservation of all valves (Pichon et al., 1987, 1992a, b). Splits of cleaned samples were allowed to settle on cover-glasses, which were then air-dried before being mounted with Naphrax. Diatom species were determined by light microscopy at $\times 1000$ magnification. The counts ($>300$ individuals per samples) on three random traverses (one on each slide) were used to calculate the valve abundances and percentages. The 300–400 individual counts per samples have been tested and used in various paleoecological investigations (Imbrie and Kipp, 1971; Schrader and Gersonde, 1978; Pichon et al., 1992a, b). Schrader and Gersonde (1978) demonstrated that only components constituting less than 2% of the total assemblage change in percentage from the 400 to cumulative test count up to 800 individuals. These minor fluctuations are of little importance for our biogeographical interpretations. The detailed data on individual species standing stocks and relative abundances are available upon request to the first author.

In order to synthesize the information given by the empirical counts of the two major groups (coccolithophores and diatoms), absolute abundances (cells/l) were analyzed by the Q-mode factor analysis program CABFAC (Imbrie and Kipp, 1971). Using the standard normalization options, this analysis transforms the occurrence of each taxon to a percentage of its total range in all water samples. This has the benefit of boosting the contribution to an analysis of the minor taxa. However, to limit the effects of counting error, taxa that never occurred in abundance above 2% were not included. A multilinear regression analysis (program REGRESS, Imbrie and Kipp, 1971) was conducted between the measured SST and calcareous nanoplankton (coccolithophores) and siliceous phytoplankton (diatoms and silicoflagellates) factors in order to assess quantitatively the relationship between the sea-surface physical and biogeographical patterns.

## 3. Results

### 3.1. Hydrography

The Sea Surface Temperature (SST) data recorded along the transect (2033 measurements) are shown as a temperature profile in Fig. 2. Several features, marked by high horizontal SST gradients, can be identified as characteristic of a front. According to Lutjeharms and Valentine (1984), the thermal surface characteristics of the major oceanic fronts south of Africa are sufficiently consistent and narrow to identify and locate their surface expressions by sea-surface temperature measurements alone. Using their definitions of the fronts, complemented by recent data from Belkin and Gordon (1996), four fronts were recognized (Table 2): the Agulhas Front (AF), the Sub-Tropical Convergence (STC), the Sub-Antarctic Front (SAF) and the Antarctic Polar Front (APF).

The AF is defined as the southern edge of the Agulhas return current (Lutjeharms, 1981; Lutjeharms and Emery, 1983). Our data show no merging of this front with the STC, as previously observed in several studies (Lutjeharms and Valentine, 1984; Lutjeharms, 1985; Lutjeharms et al.,1993; Belkin and Gordon, 1996, among others). The STC displayed the most prominent thermal shift along the transect (gradient of 0.34°C/km). The SAF and the APF show typical "Z"-like structure (Lutjeharms and Valentine, 1984), with small temperature inversions adjacent to the main thermal gradient. The surface expression of the APF, a front considered to be a major ecological boundary in the Southern Ocean, is defined by the sharpest horizontal SST gradient between 1 and 3°C in winter, and 3 and 6°C in summer (Tchernia, 1978). Our SST data, collected in late summer 1995, indicate that the surface expression of the APF at the Greenwich Meridian was found between 49°43′S and 50°40′S, an area marked by a gradient of 0.03°C/km between the isotherms 6.6 and 3.7°C.

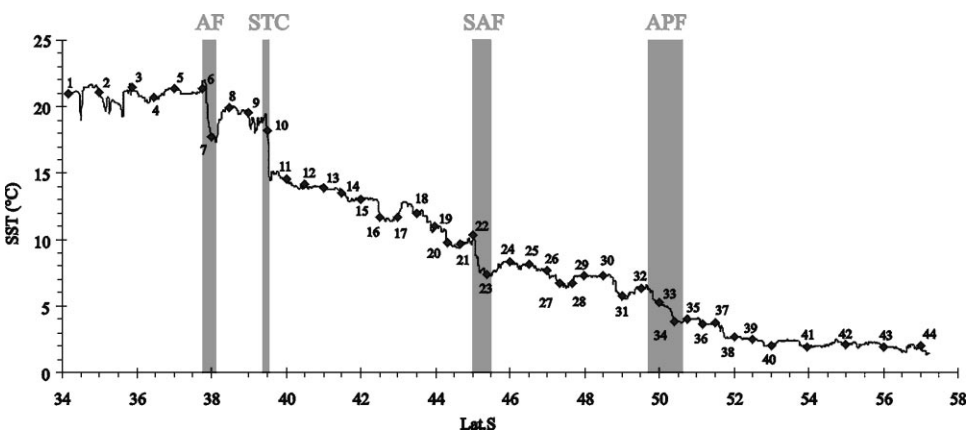


Fig. 2. In situ sea-surface temperature profile obtained along the transect JCR09/B with sampling station positions.

Table 2
Hydrological definitions of the fronts crossed by the transect JCR09/B

| | Lutjeharms and Valentine (1984) | | Belkin and Gordon (1996). | | Transect JCR09/B data (February 1995) | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Average latitudinal position °S | Temperature variation across the front | Average latitudinal position °S | Temperature variation across the front | Average latitudinal position °S | Temperature variation across the front | Axial temp. ( °C) | Width (km) | Gradient °C/km |
| AF | 39°37′ ± 1°14′ | 5.4°C ± 1.6°C | ? (front merging) | 3°C | 37°58′ | 4.7°C (from 22 to 17.3°C) | 19.65 | 34.5 | 0.14 |
| STC | 41°40′ ± 1°19′ | 7.3°C ± 1.9°C | North STC 35/36° between 0 and 10°E | 2.9°C | 39°31′ | 4.9°C (from 19.4 to 14.5°C) | 16.95 | 14.4 | 0.34 |
| | | | South STC 37°/40° | 4.8°C | | | | | |
| SAF | 46°23′ ± 1°04′ | 3.9°C ± 1.3°C | 45°/46° | 3.5°C | 45°16′ | 3.2°C (from 10.5 to 7.3°C) | 8.9 | 55 | 0.06 |
| APF | 50°18′ ± 1°20′ | 1.8°C ± 0.6°C | 49°/50° | 1.6°C | 50°08′ | 2.9°C (from 6.6 to 3.7°C) | 5.15 | 103.4 | 0.03 |

### 3.2. Phytoplankton cell densities

The living community (Fig. 3) showed peaks of abundance south of the APF ( $> 650 \times 10^3$ cells/l) and to a lesser extent in the northern part of the Subantarctic domain (between the STC and the SAF). Another peak in abundance was recorded near the continental margin of South-Africa, influenced by the Benguela upwelling system. Coccolithophores were the major component, averaging $120 \times 10^3$ cells/l and peaking at $493 \times 10^3$ cells/l. In general, diatoms were less numerous than coccolithophores (averaging $65 \times 10^3$ cells/l). However, between 45 and 47°S (south of the SAF), the abundance of diatoms was greater than that of coccolithophores. The maximum abundance of diatoms ($462 \times 10^3$ cells/l) was found south of the coccolithophore peak at 51°30 S. The remaining two groups, dinoflagellates and silicoflagellates, were poorly represented overall along the transect. Dinoflagellates reached a maximum of $84 \times 10^3$ cells/l at 52°30′S, whereas the silicoflagellate population did not exceed $2.6 \times 10^3$ cells/l in any given sample.

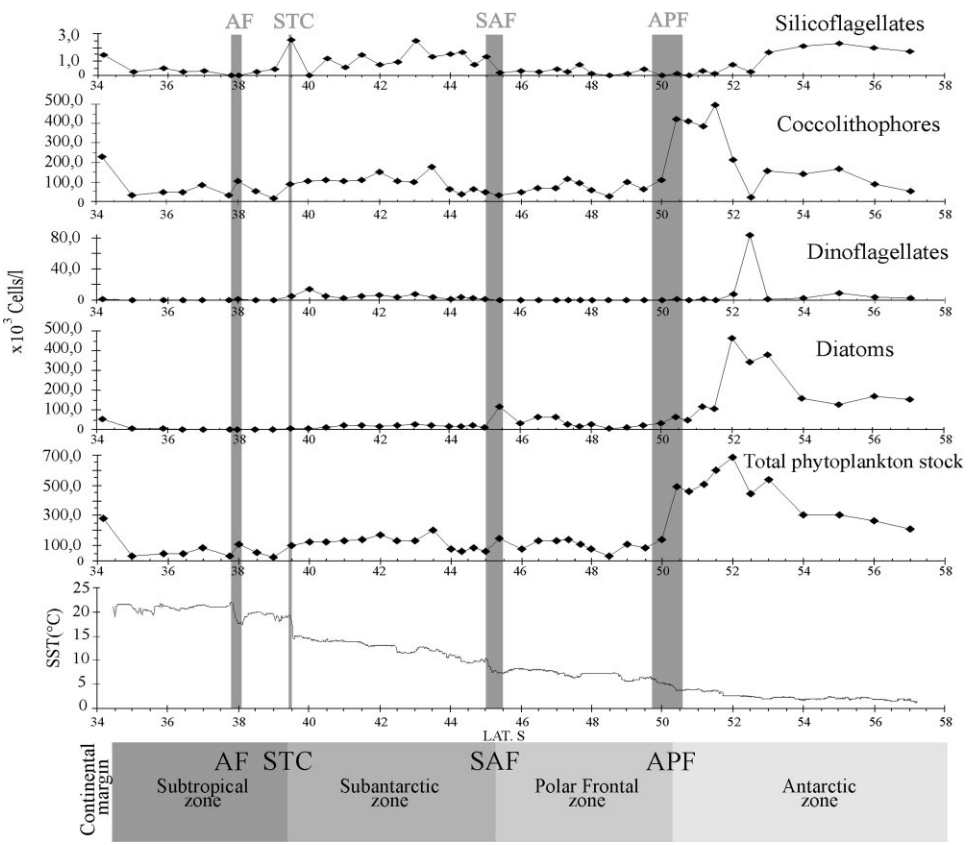


Fig. 3. Distribution of the total stocks (cells/l) along the transect and the in situ SST profile.

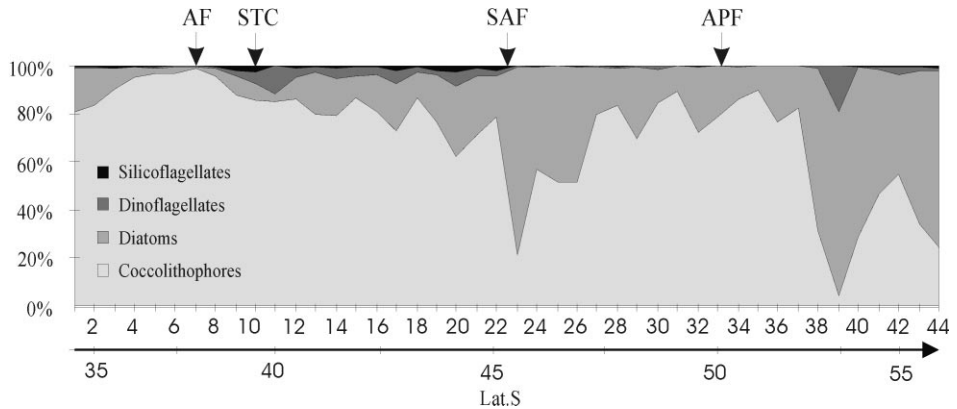


Fig. 4. Relative contribution (%) of the four studied groups (the data are plotted as equally spaced samples from 1 to 44 rather than linearly against latitude).

The area south of the APF was characterized by changing relative abundances between various groups: for example, between 50 and 52°S, the coccolithophore population peaked with an average value of $390 \times 10^3$ cells/l; at 52°30′S, a mixed community of diatoms and dinoflagellates dominated the flora, whereas further south, down to 54°S, the phytoplankton community was mainly composed of diatoms ($340 \times 10^3$ cells/l). Silicoflagellate abundances were also higher south of 53°S.

The cumulative relative percentages of the four groups are plotted in Fig. 4: diatoms and coccolithophores accounted for more than 80% of the total investigated population along the whole transect.

### 3.3. *Coccolithophore species diversity*

Twenty-three coccolithophore species were identified by light microscope examination (Appendix A). SEM analysis revealed 15 additional species that were present as rare or disintegrated cells or free coccoliths only.

*Emiliania huxleyi* was by far the dominant species, accounting for an average of 85% of the coccolithophore population. The coccolithophore assemblage collected at the AF is peculiar, with *Umbellosphaera tenuis* accounting for 37% of the coccolithophore population. South of the APF, the assemblage was monospecific (*E. huxleyi*). This area is also marked by the highest abundances of *E. huxleyi*, reaching a maximum of $493 \times 10^3$ cells/l between 50 and 52°S (Fig. 5). In contrast, minimum cell densities of *E. huxleyi* were located on the northern border of the STC ($13 \times 10^3$ cells/l) and to the south of their maximum density area ($17 \times 10^3$ cells/l at 52°30′S). The species diversity (number of species per sample) gradually decreases towards the Antarctic domain and peaks within the AF and north of the SAF.

Disregarding *E. huxleyi*, 5 species were distinguished as subordinate species, accounting for a maximum of 10–15% of the coccolithophore population. These species show latitudinal variations along the transect and define particular biogeographic zones bounded by frontal systems. *Gephyrocapsa oceanica* accounted for 13% of the

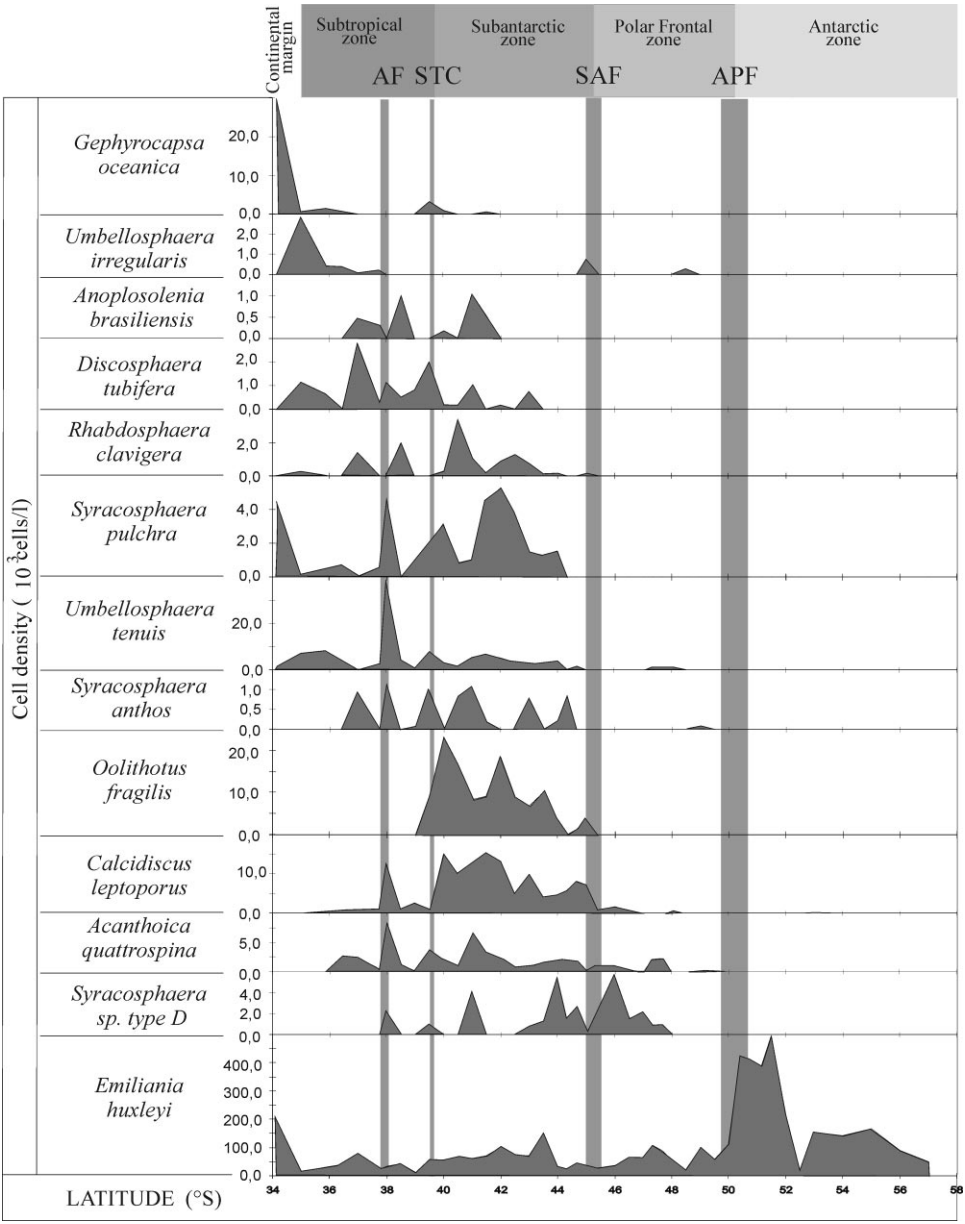


Fig. 5. Cell abundances of the major species of coccolithophores along the transect.

coccolithophore population at 34°10′S, near the continental margin of South Africa. *Umbellosphaera tenuis* reached 12% of the total assemblage in the Subtropical zone (between 35°S and 39°30′S), displaying the highest value (37%) at the AF. The relative abundance of this species falls abruptly in the Subantarctic zone (south of the

STC down to SAF). *Calcidiscus leptoporus* began to increase south of the AF, constituting an average of 10% of the population, and stayed in a range of 9–15% down to the SAF. *Oolithotus fragilis* accounted for 9% of the coccolithophore population within the Subantarctic zone but disappeared southward. Highest relative frequencies (5–12%) of *Syracosphaera* sp. type D (Kleijne, 1993) occurred in the area of the APF, between 44 and 46°S.

The Polar Frontal Zone (PFZ), from the SAF to the APF and the Antarctic domain, south of the APF, are characterized by the exclusive dominance of *E. huxleyi*, with rare occurrence of a few species that never exceed 3 to 4% of the coccolithophore assemblage (*Acanthoica quattrospina*, *Syracosphaera* sp. type D, *U. tenuis* and Holococcolithophores).

For the factor analysis, 18 species were considered according to their representation along the transect. As their individual trends were similar, Holococcolithophore species were lumped together. *Helicosphaera carteri* was excluded because of its commonly low occurrence (<2%). Given that the major taxon (*E. huxleyi*) has large variance, the multivariable analysis would essentially replicate its distribution. Therefore, it was also excluded from the statistical analysis. This choice was supported by a "test-factor analysis" including this species, where 41 out of the 44 samples were described by only one factor, largely dominated by *E. huxleyi*. Therefore, the eight samples characterized by a monospecifism of *E. huxleyi* were not considered in the factor analysis. Five factors accounting for 85% of the total variance were produced (Appendix B). Each of them supports the zonation established on empirical counts (Fig. 6). In addition, the statistical analysis shows that some species previously neglected on the basis of the counts, such as Holococcolithophore taxa and *A. quattrospina*, carry a significant environmental signature. Some samples, mostly situated in the vicinity of the fronts, show high statistical weights on several factors, an indication of mixed population within surface waters of frontal structures. The multilinear regression between the five factors and the JCR09/B SST has a multiple correlation coefficient ($r$) of 0.899, reflecting a good relationship between the near surface coccolithophore distribution and the surface water hydrology. The standard error of the estimate is $\pm 4.2$°C.

### 3.4. Diatom species

Fifty-five species of diatoms were identified (Appendix A). Three generic taxa (*Chaetoceros* sp., *Thalassiosira* sp., *Thalassiothrix* sp.) and 2 categories of resting spores (*Chaetoceros*, *Eucampia antarctica*) are included in this taxonomic list. Twenty-four species, each accounting for more than 10% of the diatom flora in at least one sample, are considered as the dominant elements of the diatom community. As with coccolithophores, the diatom populations displayed drastic changes in subordinate and dominant species along the transect (Fig. 7).

In the Subtropical zone, the major components of the diatom population were, in order of decreasing abundance, *Amphora* sp., *Fragilariopsis kerguelensis*, *Thalassionema nitzschioides*, *Thalassiothrix* sp. and *Chaetoceros* sp. Also common in this domain were *Coscinodiscus curvatulus*, *Fragilariopsis pseudonana*, *Nitzschia*

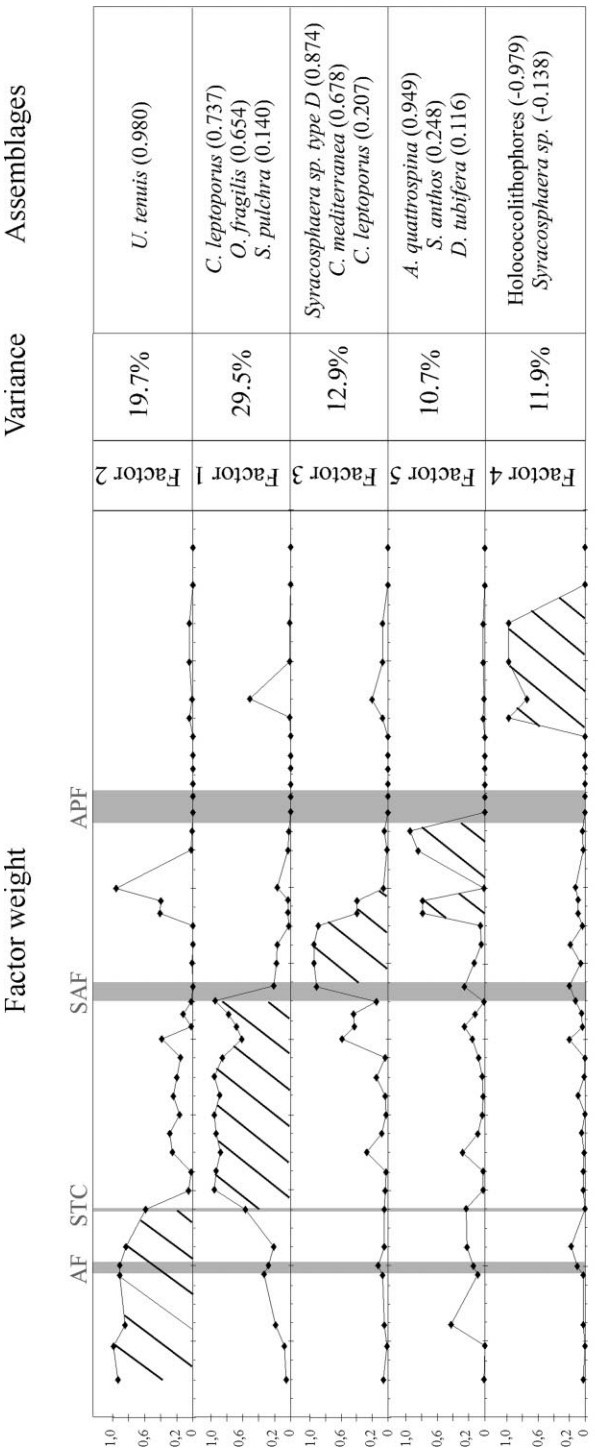


Fig. 6. Biogeographic factors produced by the Q-mode analysis of coccolithophores. Contributing species (factor weights) are given on the right-hand side.

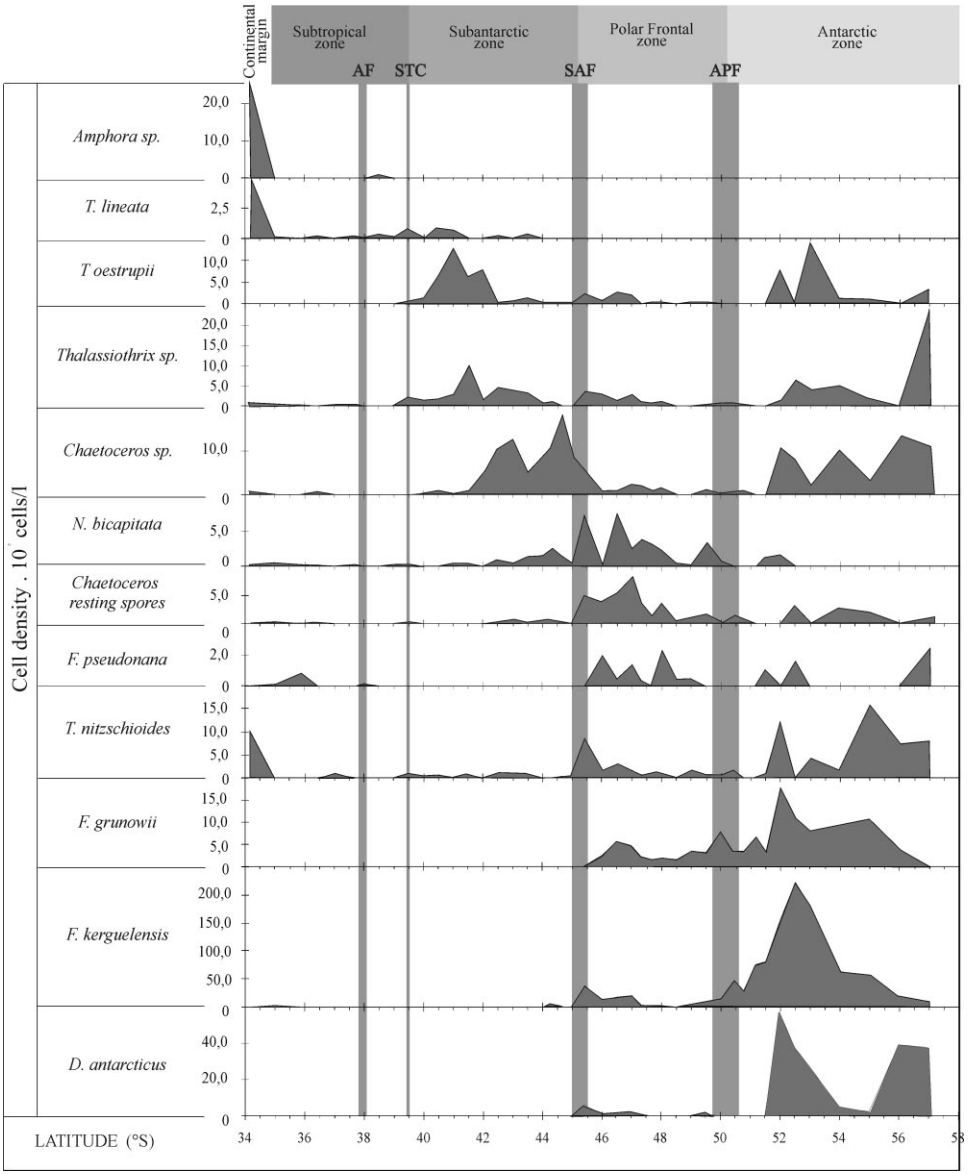


Fig. 7. Valve abundances of the major species of diatoms along the transect.

*bicapitata*, *Thalassiosira lineata* and *Fragilariopsis angulata*. The Subantarctic zone was marked by two biogeographic assemblages, with the predominance of two taxa (*Thalassiosira oestrupii* and *Thalassiothrix* sp.) in the northern part and one taxon (*Chaetoeros* sp.) in the southern part. *Corethron criophilum*, *N. bicapitata*, *Pseudoeunotia doliolus* and *F. kerguelensis* constituted the subordinate species. The diatom species diversity was maximum in the Polar Frontal Zone. *Fragilariopsis kerguelensis*

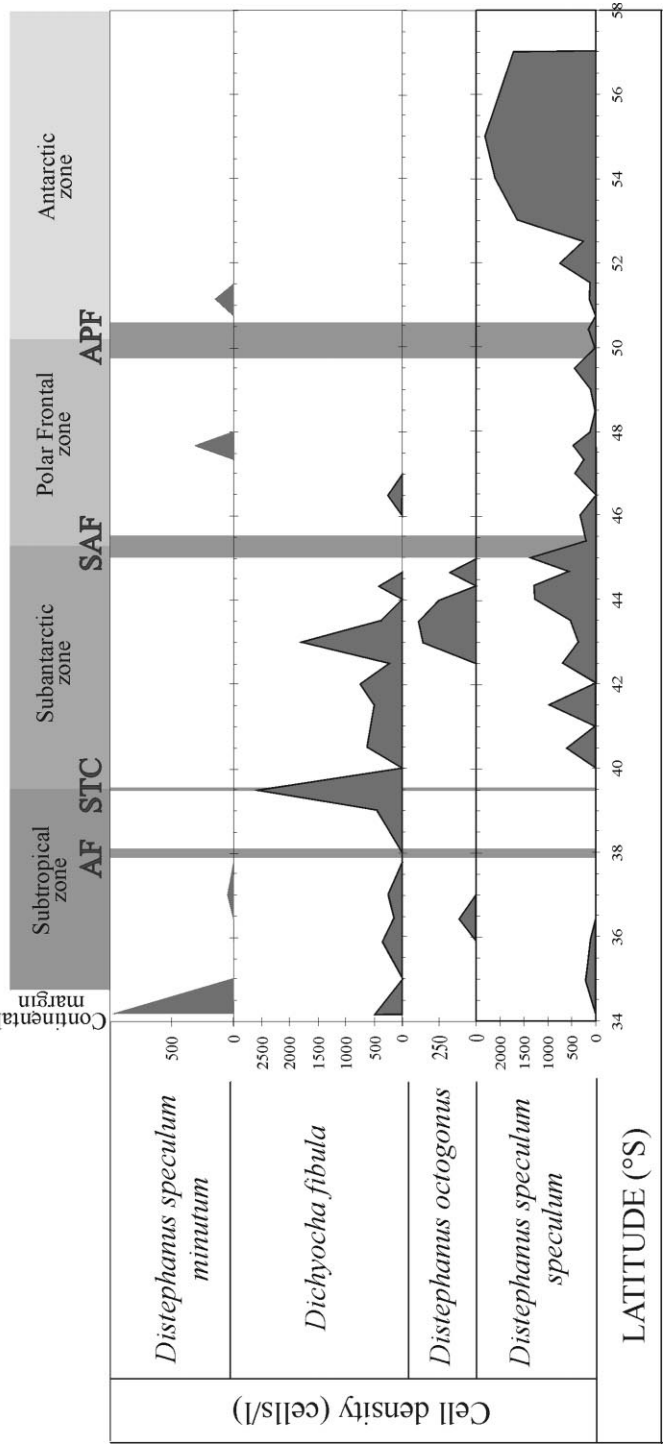


Fig. 8. Cell abundances of the 4 species of silicoflagellates along the transect.

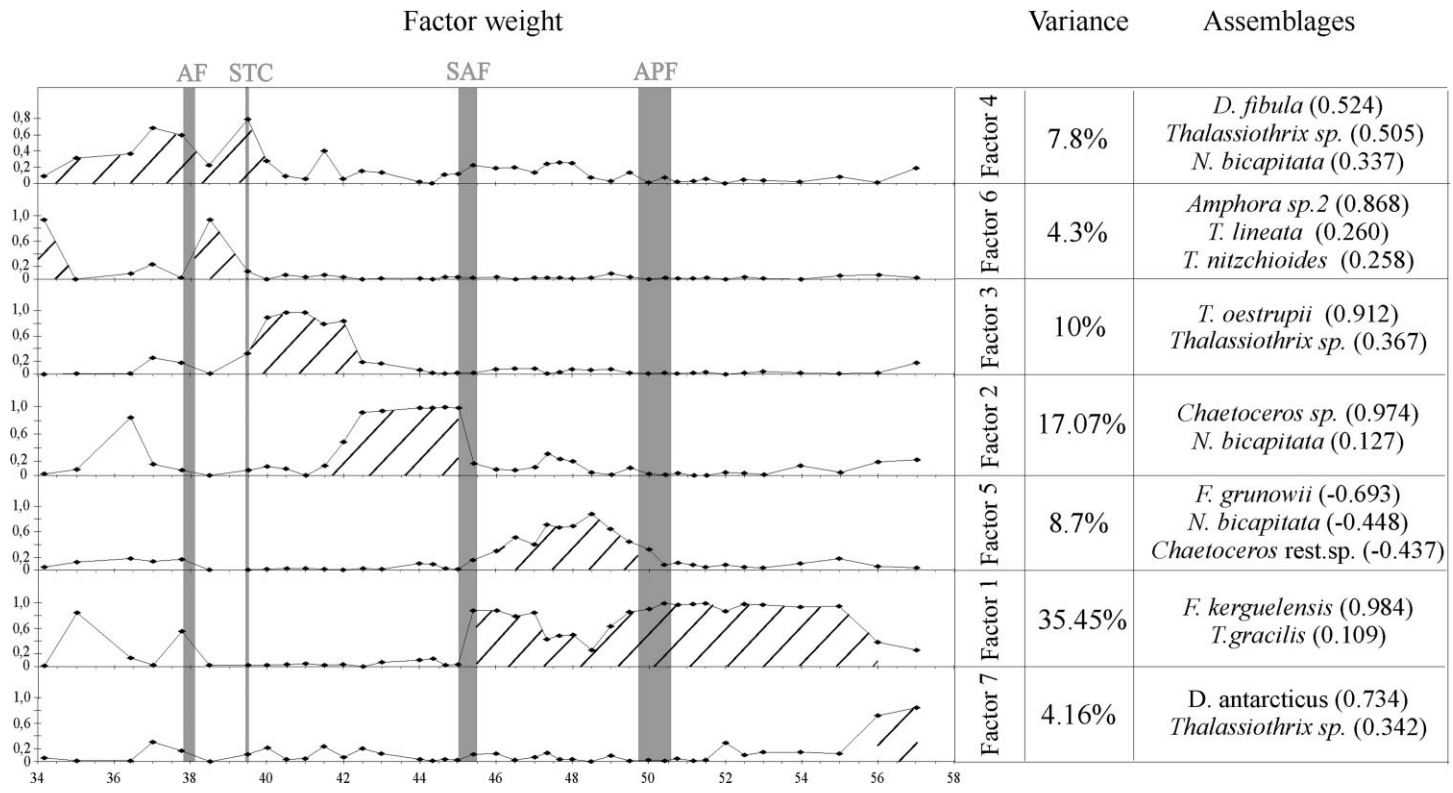


Fig. 9. Biogeographic distribution of factors produced by the Q-mode analysis of the siliceous phytoplankton (diatoms and silicoflagellates). Contributing species (factor weights) are given on the right-hand side.

became here the dominant species and accounted for an average of 24% of the diatom population. The subordinate species were *F. grunowii*, *Chaetoceros* resting spores and *N. bicapitata*. South of the APF, in the Antarctic domain, *F. kerguelensis* accounted for 47% of the diatom flora. *Fragilariopsis grunowii*, *Thalassiosira gracilis*, *Azpeita tabularis*, *Fragilariopsis curta* were the subordinate species most commonly associated with *F. kerguelensis*. The Antarctic domain is also marked by the highest diatom standing crop (mean values of $300 \times 10^3$ cells/l). This affects the distributional scheme of subordinate or rare species, which show higher abundances in this region than in the sector where they were found as dominant. This is the case for *Chaetoceros* sp. and *T. oestrupii*, which consequently display a bimodal pattern of distribution along the transect.

Four silicoflagellate species were identified along the transect (Fig. 8): *Dictyocha fibula*, *Distephanus speculum minutum*, *Distephanus speculum speculum* and *Distephanus octogonus*. The species *D. fibula* and *D. speculum speculum* were the most abundant species, with cell densities up to $2.5 \times 10^3$ cells/l. *Distephanus speculum speculum* was the most cosmopolitan species along the transect, reaching an average of $2 \times 10^3$ cells/l south of the APF. The species *D. fibula* seems well adapted to the region north of the SAF and showed a maximum abundance within the STC. The two species *D. speculum minutum* and *D. octogonus* were poorly represented in the samples, showing local peaks of abundance within the subtropical domain. Species diversity was maximum in the subantarctic zone between the STC and the SAF.

Diatoms constitute the second most important of the four phytoplankton groups that were studied. According to the procedure used in paleoclimatological work (Pichon et al., 1987, 1992), silicoflagellate abundance data were lumped with diatom data for the factor analysis in order to allow further investigations and comparisons of living and fossil assemblages. Fifty-three of the 60 diatom taxa were considered for this quantitative analysis (the seven species excluded on the ground of their low representativeness, $<2\%$, are: *Coscinodiscus marginatus*, *C. oculoides*, *C. oculus-iridis*, *Eucampia antarctica*, *Pseudonitzschia fraudulenta*, *Thalassiosira poroseriata* and *T. tumida*). Seven independent factors/assemblages were produced (Appendix C and D). These factors explain 87.5% of the total variance. As with coccolithophores, they are strictly constrained by the hydrological scheme but display sub-domains within the hydrological realms (Fig. 9). The boundaries of these sub-domains are associated with small temperature shifts on the in situ SST profile, probably due to the presence of filaments or eddies. The SAF was characterized by high weight of factor 5 (*F. grunowii* $= -0.693$), between, northward, high weight of factor 2 (*Chaetoceros* sp. $= 0.974$), and southward, high weight of factor 1 (*F. kerguelensis* $= 0.984$). The multinear regression between the seven factors and the JCR09/B SST produced a multiple correlation coefficient ($r$) of 0.954, reflecting the very close relationship between the near surface diatom distribution and the surface water hydrology. The standard error of the estimate is $\pm 4.5^{\circ}$C.

### 3.5. Dinoflagellate genera

A total of eight genera were recognized: *Amphisolenia*, *Ceratium*, *Dinophysis*, *Gonyaulax*, *Oxytoxum*, *Podolampas*, *Prorocentrum* and *Protoperidinium*. These taxa

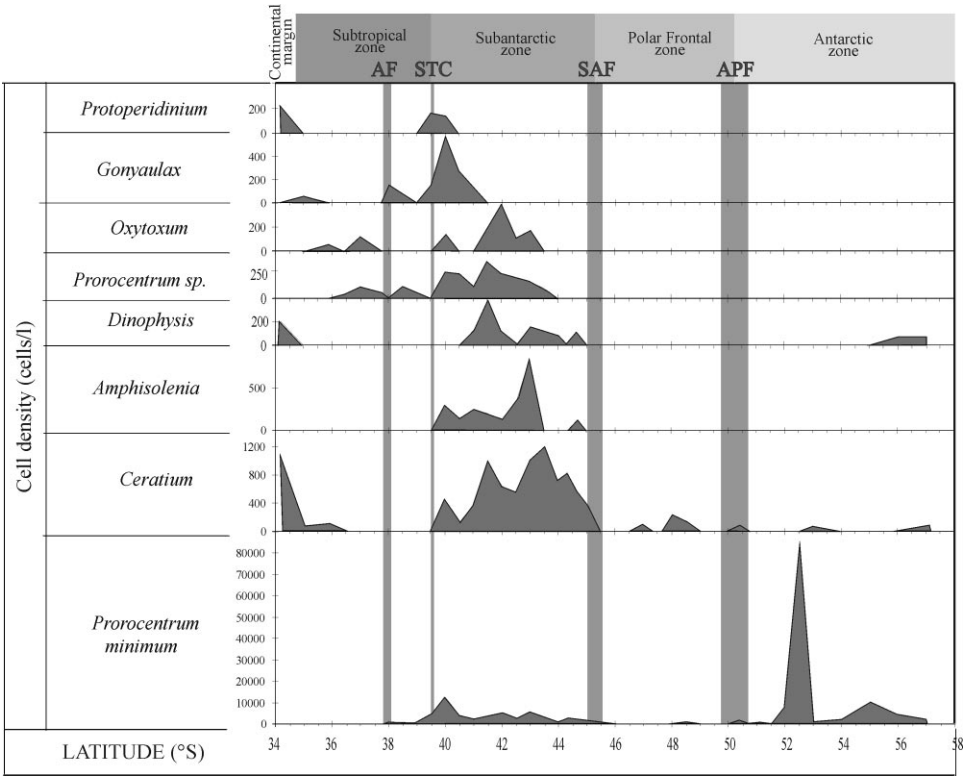


Fig. 10. Cell abundances of the 8 genera of dinoflagellates along the transect.

were minor contributors to the total community (100–500 cells/l) and preferentially thrived in the northern part of the Subantarctic zone between the STC and the SAF, and near the African coast (Fig. 10). *Ceratium* and *Prorocentrum* dominated the dinoflagellate population, with maximum percentages of 67 and 100%, respectively. *Prorocentrum minimum*, the only taxon identified at the species level, constituted the major component of the dinoflagellate assemblage along the transect. This species reached $84 \times 10^3$ cells/l south of the APF and also showed a peak of abundance south of the STC ($12 \times 10^3$ cells/l at 40°S). The dinoflagellate species diversity is maximum between the STC and the SAF and decreases toward the south.

## 4. Discussion

### 4.1. Total cell densities and the hydrographical scheme

Three different areas on the transect were identified as peculiar environments of high phytoplankton concentrations (according to the four groups studied). They are,

from north to south, the water masses near the African coast, the subantarctic waters between the STC and SAF, and the southern border of the APF, where highest phytoplankton cell abundances were recorded.

The high densities ($300 \times 10^3$ cells/l) observed at the northern station (34°10 S) may be explained by the presence of nutrient-rich waters over the continental margin of South Africa, a phenomenon associated with the Benguela upwelling (Lutjeharms and Meeuwis, 1987; Brown et al., 1991; Painting et al., 1993). Coccolithophores accounted for 80% of the total phytoplankton recorded at this northern location. As this phytoplankton group is known to thrive preferentially in stratified and oligotrophic water (Winter et al., 1994), their dominance here can be interpreted as an aged upwelled water signal.

The part of the Subantarctic zone between the STC and the SAF is characterized by relatively high cell densities ($200 \times 10^3$ cells/l), which contrast with the low abundances observed in the adjacent Subtropical zone. Population increase at the STC has previously been documented in the Atlantic (Allanson et al., 1981; Weeks and Shillington, 1994) and Indian (Jacques and Minas, 1981) sectors of the Southern Ocean. Allanson et al. (1981) have shown that the STC, and the northern border of this front, are characterized by a high *chlorophyll a* signal. A similar observation was made by Weeks and Shillington (1994) on the basis of CZCS imagery integrated over 3 years (1978–1981). Chlorophyll concentrations, 10 times higher than the typical values measured in the pelagic environment of the Southern Ocean, have been reported by them at the northern border of the STC. According to them, this enhanced productivity signal is due to a stratification in the surface waters induced by the mixing of the subtropical and subantarctic waters at the STC. In contrast, our study did not record high cell abundances at the northern border of the STC, but did to the south. Furthermore, our data showed that the flora sampled within the STC is dominated by coccolithophores, whereas a high chlorophyll signal, as recorded by Allanson et al. (1981) and Weeks and Shillington (1994), usually marks, according to the last authors, a phytoplankton biomass dominated by diatoms and dinoflagellates. As no measurements of *chlorophyll a* were carried out during this study, and as we concentrated only on 4 phytoplankton groups, it is not possible to exclude a similar chlorophyll pattern at the STC. The use of cell abundances only, as an indicator of the biological activity, is here not possible. A more synoptic study of the region, recording the total living phytoplankton community and *chlorophyll a* levels is needed to reconcile the two sets of observations.

As previously mentioned, our results showed a strong contrast between the Subtropical zone, where phytoplankton organisms were scarce, and the northern Subantarctic zone, which displays high cell abundances. This contrast implies a significant change in nutrient concentrations across the STC, from nutrient-poor Agulhas current waters to nutrient-rich subantarctic surface waters.

The southern border of the APF (50°S to 54°S) displayed the highest cell abundances measured along the transect, with a total density exceeding $5 \times 10^6$ cells/l. Enhanced biological activity is a common feature of the southern border of the APF, as reported by Fenner (1976), Jacques (1980), Jacques and Minas (1981) and Allanson et al. (1981), among others. According to Jacques and Minas (1981), this phenomenon

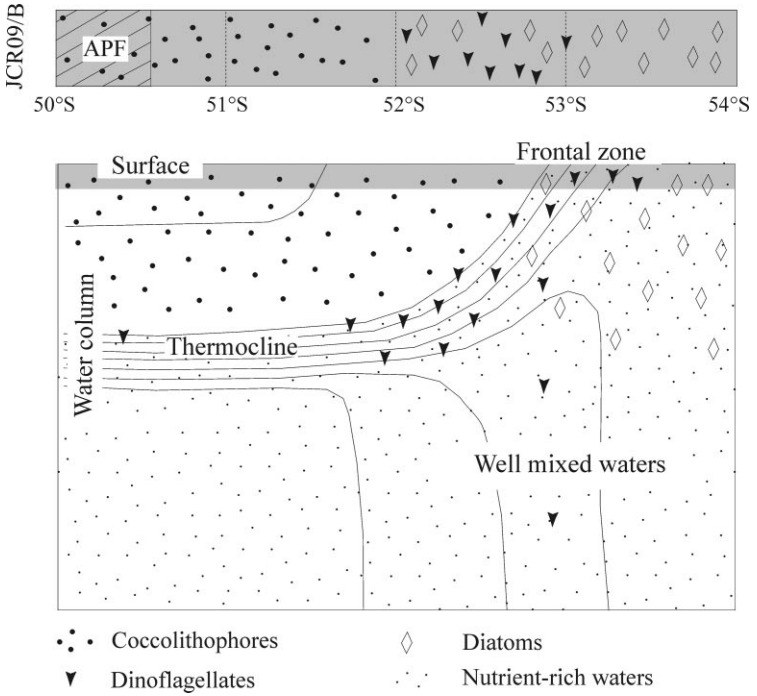


Fig. 11. Schematic representation of the spatial changes in phytoplankton communities across a hydrological front (after Houghton, 1988) and comparison with the situation at (shaded block) and south of the APF (surface transect JCR09/B).

can be explained by nutrient-rich waters moving northward from the Antarctic Divergence. Allanson et al. (1981) consider that such a high productivity signal on the southern border of the APF may be the reflection of upwelling in surface waters. This area is also characterized by successive changes in the dominances between the phytoplankton groups: from a coccolithophore dominated population between 50 and 52°S, to a mixed community of diatoms and dinoflagellates between 52 and 52°30′S, and ultimately to a population consisting only of diatoms south of 52°30′S. This distributional pattern reflects the physical properties of the associated water masses and fronts expressed in phytoplankton communities (Fig. 11; Pingree et al., 1988; Houghton, 1988; Legendre and Lefèvre, 1989). It may be explained by a different adaptation of the various groups to the change in light, temperature and nutrients, associated with physical changes of the hydrology. This distribution pattern identifies a "biological front" located at the latitude of the observed dinoflagellate peak (52°30′S). However, the position of this "biological front" does not coincide with the axial position of the hydrological surface expression of the APF, located at 50°S on the basis of the SST profile. A 2° difference in latitude separate the two signatures. This observation suggests the existence of upwelling at the southern boundary of the APF, as indicated by Allanson et al. (1981).

### 4.2. Southern occurrence of coccolithophores and coccolithophore assemblages

Coccolithophores are the major components of the flora recorded along the transect, with cell densities up to $51 \times 10^3$ cells/l down to 57°S. Although these organisms are known to be one of the major phytoplankton groups within the world ocean, their occurrence in such abundances in the Austral ocean is quite unusual, as this ocean is normally reported to be dominated by diatoms (Hasle, 1969; Fenner, 1976; Winter et al., 1994).

The coccolithophore abundances reported on the transect JCR09/B fluctuate around $120 \times 10^3$ cells/l. This figure is consistent with that observed in the open ocean environments (maximum of $170 \times 10^3$ cells/l in the NW Pacific, Okada and Honjo, 1973). The maximum cell density ($493 \times 10^3$ cells/l) recorded south of the APF is within the range of values measured in bloom conditions in the Southern Atlantic (from 3 to $2340 \times 10^3$ cells/l in upwelled waters off the Cape Peninsula, Mitchell-Innes and Winter, 1987) but considerably less than the bloom concentrations reported in the North Atlantic ($20 \times 10^6$ cells/l -Holligan et al., 1993). The APF is considered to be the southern boundary of coccolithophore occurence. South of this front, only rare and malformed coccolithophores have been observed, all probably brought by surficial currents (Verbeek, 1989; Winter et al., 1994). Nevertheless, in the South Pacific coccolithophore abundances up to $86 \times 10^3$ cells/l have been reported south of 62°S by Hasle (1960). Our observations showed that coccolithophores can successfully colonize Antarctic waters at least to 57°S in the Southern Summer (SST $< 5$°C).

The biogeographical distribution of the factors/assemblages confirms the importance of frontal features and their associated water masses on the coccolithophore population. The assemblage composition agrees well with the known environmental optima of the species that constitute these assemblages. The occurrence of *G. oceanica* in the sector of the Benguela upwelling system (station no.1, Table 1) is consistent with its ecological preferences as described by several authors (Mitchell-Innnes and Winter, 1987; Kleijne et al., 1989; Okada, 1992; Kleijne, 1993). *U. tenuis* which is adapted to subtropical waters (McIntyre and Bé, 1967; McIntyre et al., 1970; Okada and Honjo,1973; Okada and McIntyre, 1977; Winter et al., 1994) is found north of the STC on the transect. The species *C. leptoporus*, usually abundant in oligotrophic and temperate waters (McIntyre and Bé, 1967; Brand, 1994), characterizes the part of the Subantarctic zone between the STC and the SAF. In the Southern Hemisphere, this species preferentially occurs in the subpolar belt (McIntyre et al., 1970; McIntyre and Bé, 1967), as does *Coccolithus pelagicus* in the northern hemisphere (a species absent from the austral flora). The present study also documents the distributional pattern of some scarcely reported species such as *Syracosphaera* sp. type D (Kleijne, 1993), *A. quattrospina* and the Holococcolithophore species, which characterize the southern half of the transect. A comparison between these results on coccolithophore living assemblages and their occurrence in marine sediments woud have been of great interest in this study. So far, however, there are no synoptic studies of fossil coccolithophore assemblages in this sector of the Atlantic ocean to allow such a comparison.

### 4.3. Diatom assemblages

The environmental optima of the observed diatom species are consistent with the previously documented biogeographical distribution of extant diatoms in the Southern Ocean (Hargraves, 1968; Fenner et al., 1976). This is the case for *Amphora* sp., found only in the warmest subtropical waters; *T. oestrupi*, which is frequently observed in the Subantarctic domain; *F. kerguelensis*, which is the dominant taxon of the Austral waters; and *D. antarcticus*, which characterizes the southern limit of the studied transect. The cosmopolitan species *N. bicapitata* is found at the northern edge of the APF, as previously reported by Fenner et al. (1976). The maximum diatom species diversity and abundances are recorded south of the SAF.

Diatoms are the major component of the surficial biogenic sediments of the Southern Ocean. Pichon et al. (1987, 1992b) have shown that the biogeographic distribution of Antarctic flora (diatoms and silicoflagellates) in modern core top samples from the Southern Ocean coincides with present-day sea-surface parameters, particularly the summer SST (Levitus, 1982). Therefore, they have been sucessfully used as proxy indicators for paleoceanographic research. We propose here to compare our data with those published by Pichon et al. (1987, 1992b), who studied the surficial sediments of the Atlantic sector of Southern Ocean and their associated diatom and silicoflagellate fossil assemblages. They showed that the modern asssemblages of these siliceous phytoplankton groups in surface sediments situated under the overlying Subantarctic and Antarctic waters produce only two factors, corresponding to two biogeographic zones: the "Subantarctic" (variance = 12.6%) and "open-ocean Antarctic" (variance = 34%) assemblages. The 0.6 factor loading boundary of the "open-ocean Antarctic" assemblage falls between the 4° and 6°C summer isotherms to the north, a few degrees north of the APF. In comparison, the living diatom distribution produced five different factors/assemblages within the same domains (Fig. 12). This discrepancy can be explained by the difference between an instantaneous signal obtained from a single sample of living organisms and a sedimentary signal resulting from an integrated productivity over many years, combined with the effects of transport and dissolution, which can modify the biogenic material during and after its deposition (Pichon et al., 1992a).

Globally, the species composition of living (this study) and of fossil factors/assemblages (Pichon et al., 1987, 1992a, b) are similar. However, differences in the dominant species were observed, probably due to selective dissolution in the water column on at the water-sediment interface. This is particularly apparent in the Subantarctic zone, where the fossil assemblage is dominated by *T. nitzschioides* (0.497) and *Coscinodiscus tabularis* (0.486), whereas the JCR09/B data show successive dominance from north to south of *T. oestrupii* (0.912), *Chaetoceros* sp. (0.974), *F. kerguelensis* (0.507) and *F. grunowii* (−0.693). In the Antarctic zone, the differences are less obvious. The species *Thalassiothrix* sp. (0.530), *F. kerguelensis* (0.507) and *T. gracilis* (0.373) are the dominant species of the antarctic fossil assemblage, whereas *F. kerguelensis* (0.984) and *T. gracilis* (0.109) dominate the living assemblage. The surficial origin of the samples (collected between 0 and 5 m for the purpose of this study) should also be taken into account to further explain this discrepancy between the fossil and living records.

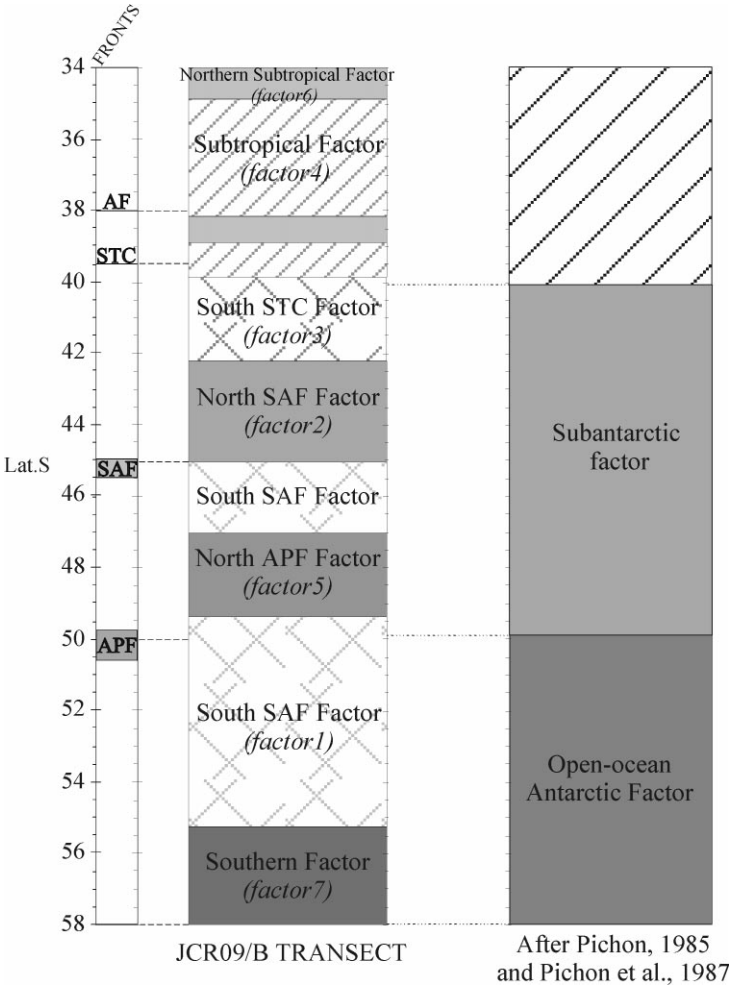


Fig. 12. Schematic comparison of the geographical distribution of factors produced by the *Q*-mode analysis of living and fossil assemblages of siliceous phytoplankon.

Indeed, recent work in the Southern Ocean (Tréguer, 1996) has shown that the chlorophyll maximum south of the APF is at the base of the photic zone (around 100 m deep) and not in the surficial layers. Seasonal changes in species diversity are a supplementary factor of discrepancy, as shown for instance from a time-series study in the Open Ocean Antarctic Zone (KERFIX station, 50°40′S −68°25′E, Pichon, in preparation).

### *4.4. Silicoflagellate assemblages*

Silicoflagellate species are also constrained by the surface hydrology of the Atlantic sector of the Southern Ocean. The Q-mode factor analysis showed that

the species *D. fibula* is an excellent proxy indicator of the subtropical water masses, whereas *D. speculum speculum* is strongly associated with Antarctic waters south of the APF.

### 4.5. Dinoflagellate assemblages

Dinoflagellates are preferentially found in the northern part of the Subantarctic zone, between the STC and the SAF. The species *Prorocentrum minimum* is the only species recorded with "near-bloom" abundances south of the APF. Although this species has been observed in the Indian Ocean north of the STC (Taylor, 1976; Sournia et al., 1979), it has never been reported at the APF latitudes, neither in the Indian nor in the Southern oceans. Among the eight dinoflagellate genera identified along the transect, only cysts of *Protoperidinium* and *Gonyaulax* are likely to be preserved in the sediments. Besides, these taxa are among the less abundant along the studied transect.

## 5. Conclusions

The present study has shown that the distribution of the four studied phytoplankton groups was strictly constrained by the surficial hydrological scheme of the Atlantic sector of the Southern Ocean. Each water mass can be associated with a specific biological signature, as supported by the phytoplankton cell abundance variations, which give rise to characteristic assemblages. The multilinear regression between the calcareous and siliceous phytoplankton factors and the measured SST values at the time of sampling (February 1995) reflects the close relationship between the near surface distribution of the various populations and the surface water hydrology (multiple correlation coefficients of 0.899 and 0.959 respectively). Both the calcareous and the siliceous phytoplankton groups are particularly abundant in near-coastal waters off Southern Africa and in the Subantarctic zone. Highest cell abundances were recorded on the APF southern border, therefore confirming that this frontal system is not representative of the "poor productivity–high nutrient concentrations" model that usually characterizes the Southern Ocean.

Our data show that the biological expression of the APF (documented by a horizontal succession of phytoplankton groups – Fig. 11) does not mirror its hydrological expression (deduced from the in situ temperature profile – Fig. 2). Indeed, 2° of latitude separates these two signatures. The hypothesis of a divergence occurring in the surficial water layers on the southern border of the APF may explain this discrepancy.

Coccolithophores, in terms of cell density, are the major component of the studied phytoplankton community. Only two sectors along the transect, the northern part of the Polar Frontal Zone and the Antarctic zone south of 51°30′S, are dominated by diatoms. Consequently, coccolithophore production in the Austral sector of the Atlantic Ocean might play a role, with regard to the carbon biogeochemical cycle (photosynthesis and calcification processes – Westbroek et al., 1993), as important as

in the Subarctic regions (Fernandez et al., 1993; Robertson et al., 1994; Brown and Yoder, 1994).

In order to complement and validate the results obtained in this study, further investigations in this region are obviously needed: these include not only whole water column sampling and assessment of seasonal variability, but also measurements of additional physical/chemical/biological parameters (salinity, nutrients, *cholorophyll a*, picoplankton concentrations). The synoptic study of Samtleben et al. (1995) in the Norwegian-Greenland Sea, as well as the analyses conducted in the Pacific Ocean by Andreasen and Ravelo (1997) and Watkins and Mix (1998), offer a good methodological framework for a thorough study of South Atlantic phytoplankton dynamics and the use of this information in paleoceanographic reconstructions.

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Appendix A

Mean and maximum values (punctual maxima) of the various phytoplankton groups and species stocks

| | Mean (cells/l) | Max (cells/l) |
|---|---|---|
| **Phytoplankton total stock** | **187 828** | **686 375** |
| | Mean | Max |
| **Coccolithophore total stock** | **118 612** | **492 750** |
| *Acanthoïca quattrospina* | 908 | 6 750 |
| *Algirosphaera robusta* | 17 | 319 |
| *Anoplosolenia brasiliensis* | 80 | 1 039 |
| *Calciosolenia murrayi* | 22 | 835 |
| *Calcidiscus leptoporus* | 3 029 | 15 394 |
| *Coronosphaera mediterranea* | 257 | 2 190 |
| *Discosphaera tubifera* | 264 | 2 805 |
| *Emiliania huxleyi* | 104 712 | 492 750 |
| *Gephyrocapsa oceanica* | 818 | 29 601 |
| *Helicosphaera carteri* | 22 | 249 |
| *Oolithotus fragilis* | 2 695 | 22 988 |
| *Rhabdosphaera clavigera* | 267 | 3 338 |
| *Syracosphaera sp.* | 161 | 1 555 |
| *Syracosphaera sp.type D* | 742 | 5 595 |
| *S. anthos* | 160 | 1 125 |
| *S. lamina* | 62 | 1 039 |
| *S. pulchra* | 830 | 5287 |
| *Umbellosphaera tenuis* | 2 544 | 38 250 |
| *U. irregularis* | 109 | 2 794 |
| *U. sibogae* | 22 | 637 |
| *Undetermined Holococcolithophores* | 463 | 4 500 |
| *Corisphaera sp.* | 45 | 997 |
| *Poritectolithus maximus* | 2 | 80 |

| | Mean | Max |
|---|---|---|
| **Diatom total stock** | **64 274** | **462 500** |
| *Actinocyclus curvatulus* | 19 | 706 |
| *Amphora bicuarta* | 38 | 728 |
| *Amphora sp. 2* | 595 | 25 283 |
| *Asteromphalus hookeri* | 50 | 1 870 |
| *A. parvulus* | 115 | 3 561 |
| *A. heptactis* | 183 | 5 610 |
| *A. hyalinus* | 301 | 4 008 |
| *Azpeitia tabularis* | 1 946 | 23 871 |
| *Chaetoceros atlanticum* | 354 | 12 636 |
| *Chaetoceros sp.* | 3 527 | 17 954 |
| *C. resting spores* | 1 033 | 8 010 |
| *Corethron criophilum* | 1 123 | 27 462 |
| *Coscinodiscus curvatulus* | 142 | 1 820 |
| *C. marginatus* | 5 | 127 |
| *C. oculoides* | 4 | 164 |
| *C. oculus-iridis* | 2 | 68 |
| *Dactyliosolen antarcticus* | 4 954 | 56 694 |
| *Eucampia antarctica (veg)* | 2 | 68 |
| *E. antarctica (resting spore)* | 132 | 3 159 |
| *Fragilariopsis angulata* | 274 | 9 495 |
| *F. curta* | 1 312 | 19 616 |
| *F. grunowii* | 2 535 | 17 903 |
| *F. kerguelensis* | 24 280 | 222 709 |
| *F. pseudonana* | 302 | 2 282 |
| *F. ritscheri* | 569 | 3 530 |
| *F. separanda* | 2 401 | 52 218 |
| *Melosira sol* | 23 | 840 |
| *Navicula directa* | 645 | 12 826 |
| *Nitzschia bicapitata* | 1 008 | 7 284 |
| *N. kolaczeckii* | 48 | 1 550 |

(*continued on next page*)

Appendix A (*continued*)

| **Coccolithophore species** | | | **Diatom species** | | |
|---|---|---|---|---|---|
| *Periphyllophora mirabilis* | 26 | 1 125 | *N. closterium* | 41 | 425 |
| *Undetermined genus* | 357 | 3 338 | *N. linearis* | 214 | 1 962 |
| | | | *N. a polaris* | 1 379 | 59 677 |
| | | | *N. sicula var.* rostrata | 61 | 1 187 |
| | | | *Pleurosigma directum* | 102 | 2 984 |
| | | | *Pseudoeunotia doliolus* | 216 | 2 984 |
| | Mean | Max | *Pseudo-nitzschia fraudulenta* | 9 | 218 |
| **Silicoflagellate total stock** | **781** | **2 571** | *P. lineola* | 847 | 12 605 |
| *Dictyocha fibula* | 228 | 1 799 | *P. seriata* | 93 | 4 045 |
| *Distephanus speculum minutum* | 34 | 962 | *P. turgidula* | 169 | 2 374 |
| *D. speculum speculum* | 490 | 2 308 | *P. turgiduloides* | 135 | 3 561 |
| *D. octogonus* | 30 | 386 | *Proboscia alata* | 39 | 1 187 |
| | | | *Rhizosolenia styliformis* | 190 | 1 333 |
| | | | *Roperia tesselata* | 649 | 9 927 |
| | | | *Thalassionema nitzschioides* | 1 963 | 15 590 |
| | | | *T. nitzschioides var. parva* | 726 | 28 051 |
| | | | *Thalassiosira decipiens* | 15 | 327 |
| | Mean | Max | *T. delicatulata* | 38 | 607 |
| **Dinoflagellate total stock** | **4 161** | **84 125** | *T. gracilis* | 3 651 | 33 347 |
| *Amphisolenia* | 52 | 840 | *T. gravida* | 44 | 802 |
| *Ceratium* | 223 | 1 207 | *T. lentiginosa* | 379 | 5 610 |
| *Dinophysis* | 34 | 398 | *T. lineata* | 195 | 5 259 |
| *Gonyaulax* | 32 | 574 | *T. oestrupii* | 1 685 | 13 731 |
| *Oxytoxum* | 27 | 391 | *T. oliverana* | 176 | 1 870 |
| *Podolampas* | 3 | 110 | *T. poroseriata* | 8 | 338 |
| *Prorocentrum minimum* | 3 707 | 84 125 | *T. trifulta* | 209 | 4 747 |
| *Prorocentrum sp.* | 51 | 398 | *T. tumida* | 4 | 164 |
| *Protoperidinium* | 12 | 216 | *Thalassiosira sp.* | 89 | 1 870 |
| *Undetermined genus* | 22 | 220 | *Thalassiothrix sp.* | 2 147 | 24 049 |
| | | | *Tropidoneis antarctica* | 100 | 2 225 |

Appendix B

Varimax Factor Matrix and Varimax Factor Score Matrix produced by the *Q*-mode analysis of coccolithophores

| No. | Station | Comm. | Factor 1 | Factor 2 | Factor 3 | Factor 4 | Factor 5 | SST (°C) |
|---|---|---|---|---|---|---|---|---|
| *Varimax Factor Matrix* | | | | | | | | |
| (1 | *W1* | *0.024* | 0.024 | **0.148** | − 0.026 | 0.014 | − 0.014) | 21 |
| 2 | *W2* | 0.874 | 0.055 | **0.931** | 0.056 | − 0.017 | − 0.012 | 21.1 |
| 3 | *W3* | 0.986 | 0.076 | **0.990** | 0.006 | − 0.003 | − 0.004 | 21.5 |
| 4 | *W4* | 0.934 | 0.184 | **0.849** | 0.042 | 0.018 | 0.422 | 20.7 |
| (5 | *W5* | *0.467* | 0.236 | 0.081 | 0.004 | − 0.164 | **0.614**) | 21.4 |
| 6 | *W6* | 0.944 | 0.329 | **0.907** | 0.063 | 0.024 | 0.095 | 21.4 |
| 7 | *W7* | 0.963 | 0.283 | **0.914** | 0.124 | − 0.095 | 0.148 | 17.7 |
| 8 | *W8* | 0.819 | 0.215 | **0.828** | 0.045 | − 0.180 | 0.229 | 19.9 |
| 9 | *W9* | *0.631* | **0.701** | 0.311 | 0.161 | − 0.127 | 0.041) | 19.5 |
| 10 | *W10* | 0.715 | 0.562 | **0.586** | − 0.045 | 0.002 | 0.233 | 18.2 |

Appendix B (*continued*)

| No. | Station | Comm. | Factor 1 | Factor 2 | Factor 3 | Factor 4 | Factor 5 | SST (°C) |
|---|---|---|---|---|---|---|---|---|
| 11 | *W11* | 0.928 | **0.961** | 0.055 | − 0.038 | 0.018 | 0.021 | 14.6 |
| 12 | *W12* | 0.875 | **0.934** | 0.022 | − 0.021 | − 0.024 | 0.023 | 14.2 |
| 13 | *W13* | 0.985 | **0.874** | 0.254 | 0.275 | 0.009 | 0.284 | 13.9 |
| 14 | *W14* | 0.964 | **0.928** | 0.292 | 0.084 | − 0.048 | 0.093 | 13.5 |
| 15 | *W15* | 0.943 | **0.954** | 0.172 | − 0.027 | 0.001 | 0.038 | 13 |
| 16 | *W16* | 0.855 | **0.887** | 0.243 | − 0.034 | − 0.091 | 0.027 | 11.7 |
| 17 | *W17* | 0.981 | **0.959** | 0.195 | 0.151 | − 0.010 | 0.035 | 11.7 |
| 18 | *W18* | 0.762 | **0.854** | 0.159 | 0.034 | − 0.001 | 0.077 | 12 |
| 19 | *W19* | 0.933 | **0.613** | 0.391 | 0.581 | − 0.202 | 0.162 | 11 |
| 20 | *W20* | 0.712 | **0.682** | − 0.026 | 0.423 | − 0.031 | 0.258 | 9.8 |
| 21 | *W21* | 0.828 | **0.778** | 0.119 | 0.438 | − 0.044 | 0.120 | 9.7 |
| 22 | *W22* | 0.922 | **0.941** | − 0.024 | 0.149 | − 0.118 | − 0.012 | 10.3 |
| 23 | *W23* | 0.983 | 0.216 | − 0.005 | **0.911** | − 0.198 | 0.257 | 7.4 |
| 24 | *W24* | 0.935 | 0.176 | − 0.012 | **0.939** | − 0.061 | 0.138 | 8.3 |
| 25 | *W25* | 0.955 | 0.164 | − 0.001 | **0.945** | − 0.184 | 0.047 | 8.1 |
| 26 | *W26* | 0.793 | − 0.027 | − 0.003 | **0.888** | 0.028 | − 0.051 | 7.7 |
| 27 | *W27* | 0.944 | 0.031 | 0.407 | 0.394 | 0.085 | **0.784** | 6.7 |
| 28 | *W28* | 0.944 | 0.031 | 0.404 | 0.392 | 0.085 | **0.787** | 6.7 |
| 29 | *W29* | 0.961 | 0.170 | **0.955** | 0.054 | − 0.127 | − 0.011 | 7.3 |
| (30 | *W30* | 0.619 | − 0.005 | 0.060 | 0.034 | − **0.783** | 0.044) | 7.3 |
| 31 | *W31* | 0.719 | 0.038 | − 0.026 | − 0.014 | 0.017 | **0.846** | 5.7 |
| 32 | *W32* | 0.905 | 0.023 | 0.015 | 0.041 | 0.037 | **0.949** | 6.3 |
| 33 | *W39* | 0.966 | − 0.015 | 0.041 | 0.073 | − **0.979** | 0.020 | 2.5 |
| 34 | *W40* | 0.847 | 0.511 | 0.015 | 0.198 | − **0.739** | − 0.011 | 2 |
| 35 | *W41* | 0.966 | − 0.015 | 0.041 | 0.073 | − **0.979** | 0.020 | 1.9 |
| 36 | *W42* | 0.966 | − 0.015 | 0.041 | 0.073 | − **0.979** | 0.020 | 2.1 |
| Variance (%) | | | 29.554 | 19.738 | 12.942 | 11.944 | 10.686 | |
| Cum. Var (%) | | | 29.554 | 49.292 | 62.235 | 74.178 | 84.864 | |

*Varimax Factor Score Matrix*

| | Factor 1 | Factor 2 | Factor 3 | Factor 4 | Factor 5 |
|---|---|---|---|---|---|
| *Acanthoïca quattrospina* | 0.023 | 0.015 | 0.041 | 0.037 | **0.949** |
| *Algirosphaera robusta* | 0.000 | 0.006 | − 0.001 | 0.000 | 0.002 |
| *Anoplosolenia brasiliensis* | 0.005 | 0.035 | − 0.012 | − 0.008 | 0.025 |
| *Calciosolenia murrayi* | 0.004 | 0.001 | − 0.003 | 0.001 | 0.002 |
| *Calcidiscus leptoporus* | **0.737** | − 0.020 | 0.207 | − 0.066 | − 0.036 |
| *Coronosphaera mediterranea* | − 0.016 | 0.010 | 0.378 | 0.036 | − **0.109** |
| *Discosphaera tubifera* | 0.036 | 0.056 | − 0.052 | − 0.030 | **0.116** |
| *Gephyrocapsa oceanica* | 0.002 | 0.090 | − 0.021 | 0.010 | − 0.011 |
| *Oolithus fragilis* | **0.654** | − 0.073 | − **0.179** | 0.054 | − 0.014 |
| *Rhabdosphaera clavigera* | 0.045 | 0.031 | − 0.046 | − 0.027 | 0.071 |
| *Syracosphaera sp.* | 0.010 | 0.025 | − 0.024 | − **0.138** | 0.047 |
| *Syracosphaera sp. type D* | ÷ 0.021 | − 0.017 | **0.874** | 0.084 | 0.035 |
| *S. anthos* | 0.030 | − 0.052 | − 0.061 | − 0.013 | **0.248** |
| *S. lamina* | 0.015 | − 0.001 | − 0.004 | 0.001 | 0.002 |
| *S. pulchra* | **0.140** | 0.088 | − 0.039 | 0.011 | − 0.016 |
| *Umbellosphaera tenuis* | 0.049 | **0.980** | 0.006 | 0.051 | − 0.009 |
| *U. irregularis* | − 0.011 | 0.082 | − 0.003 | − 0.028 | − 0.020 |
| *Umbilicosphaera sibogae* | 0.007 | − 0.001 | − 0.002 | 0.001 | 0.000 |
| Holococcolithophores | − 0.015 | 0.041 | 0.073 | − **0.979** | 0.020 |

Appendix C
Varimax Factor Matrix produced by the *Q*-mode analysis of diatoms and silicoflagellates

| No. | Station | Comm. | Factor 1 | Factor 2 | Factor 3 | Factor 4 | Factor 5 | Factor 6 | Factor 7 | SST (°C) |
|---|---|---|---|---|---|---|---|---|---|---|
| *Varimax Factor Matrix* | | | | | | | | | | |
| 1 | W1 | 0.891 | 0.016 | 0.019 | 0 | 0.087 | − 0.044 | **0.937** | 0.058 | 21 |
| 2 | W2 | 0.822 | **0.838** | 0.086 | 0.009 | 0.313 | − 0.119 | 0.005 | 0.013 | 21.1 |
| 3 | *W3* | *0.531* | **0.508** | 0.142 | − 0.006 | 0.492 | − 0.084 | 0 | − 0.058 | 21.5 |
| 4 | W4 | 0.898 | 0.133 | **0.842** | 0.007 | 0.363 | − 0.178 | 0.086 | 0.012 | 20.7 |
| 5 | W5 | 0.725 | − 0.022 | 0.162 | 0.257 | **0.682** | − 0.136 | 0.233 | 0.307 | 21.4 |
| 6 | W6 | 0.75 | 0.549 | 0.077 | 0.175 | **0.596** | − 0.164 | 0.02 | 0.172 | 21.4 |
| 7 | *W7* | *0.524* | 0.47 | 0.095 | − 0.102 | 0.321 | − 0.363 | − 0.063 | − 0.21 | 17.7 |
| 8 | W8 | 0.913 | 0.024 | 0.005 | − 0.007 | 0.22 | 0.002 | **0.93** | − 0.001 | 19.9 |
| 9 | *W9* | *0.684* | 0.255 | 0.094 | 0.133 | **0.735** | − 0.142 | 0.132 | − 0.122 | 19.5 |
| 10 | W10 | 0.77 | 0.021 | 0.077 | 0.329 | **0.792** | 0.001 | 0.119 | 0.115 | 18.2 |
| 11 | W11 | 0.935 | 0.025 | 0.131 | **0.891** | 0.278 | − 0.011 | 0 | 0.213 | 14.6 |
| 12 | W12 | 0.95 | 0.031 | 0.098 | **0.962** | 0.093 | − 0.02 | 0.064 | − 0.035 | 14.2 |
| 13 | W13 | 0.938 | 0.041 | 0.003 | **0.964** | 0.054 | − 0.022 | 0.037 | − 0.047 | 13.9 |
| 14 | W14 | 0.856 | 0.017 | 0.14 | **0.786** | 0.398 | − 0.012 | − 0.066 | 0.236 | 13.5 |
| 15 | W15 | 0.931 | 0.033 | 0.486 | **0.828** | − 0.055 | − 0.003 | 0.038 | − 0.063 | 13 |
| 16 | W16 | 0.942 | − 0.005 | **0.916** | 0.196 | 0.155 | − 0.025 | − 0.003 | 0.2 | 11.7 |
| 17 | W17 | 0.943 | 0.07 | **0.936** | 0.17 | 0.135 | 0.012 | 0.016 | 0.121 | 11.7 |
| 18 | *W18* | *0.654* | 0.02 | **0.693** | 0.273 | 0.283 | − 0.08 | − 0.002 | 0.111 | 12 |
| 19 | W19 | 0.987 | 0.101 | **0.98** | 0.067 | − 0.02 | − 0.096 | 0.008 | 0.038 | 11 |
| 20 | W20 | 0.985 | 0.121 | **0.98** | 0.028 | 0.002 | − 0.093 | 0.002 | 0.012 | 9.8 |
| 21 | W21 | 0.984 | 0.022 | **0.985** | 0.011 | − 0.106 | − 0.023 | 0.028 | 0.029 | 9.7 |
| 22 | W22 | 0.98 | 0.034 | **0.981** | 0.026 | − 0.115 | − 0.012 | 0.033 | 0.028 | 10.3 |
| 23 | W23 | 0.883 | **0.876** | 0.176 | 0.022 | 0.22 | − 0.152 | 0.017 | 0.114 | 7.4 |
| 24 | W24 | 0.927 | **0.878** | 0.086 | 0.078 | 0.185 | − 0.303 | − 0.033 | 0.125 | 8.3 |
| 25 | W25 | 0.925 | **0.783** | 0.078 | 0.093 | 0.193 | − 0.51 | 0.003 | 0.026 | 8.1 |
| 26 | W26 | 0.905 | **0.838** | 0.114 | 0.09 | 0.129 | − 0.401 | − 0.02 | 0.073 | 7.7 |
| 27 | W27 | 0.872 | 0.432 | 0.316 | − 0.006 | 0.242 | − **0.713** | − 0.027 | 0.132 | 6.7 |
| 28 | W28 | 0.808 | 0.483 | 0.238 | 0.036 | 0.257 | − **0.671** | − 0.021 | 0.033 | 6.7 |
| 29 | W29 | 0.829 | 0.498 | 0.206 | 0.075 | 0.248 | − **0.686** | − 0.016 | 0.037 | 7.3 |
| 30 | W30 | 0.856 | 0.261 | 0.045 | 0.062 | − 0.071 | − **0.881** | 0.022 | − 0.001 | 7.3 |
| 31 | W31 | 0.832 | 0.625 | − 0.015 | 0.078 | − 0.026 | − **0.647** | 0.084 | 0.091 | 5.7 |
| 32 | W32 | 0.966 | **0.858** | 0.111 | 0.02 | 0.131 | − 0.446 | − 0.029 | − 0.008 | 6.3 |
| 33 | W33 | 0.911 | **0.897** | − 0.017 | 0.008 | − 0.01 | − 0.326 | 0.003 | 0.026 | 5.3 |
| 34 | W34 | 0.982 | **0.985** | 0.013 | − 0.022 | 0.069 | − 0.081 | − 0.018 | − 0.014 | 3.8 |
| 35 | W35 | 0.955 | **0.97** | 0.028 | − 0.009 | 0.016 | − 0.108 | − 0.006 | 0.045 | 4 |
| 36 | W36 | 0.969 | **0.981** | − 0.005 | − 0.022 | 0.027 | − 0.08 | − 0.006 | 0.006 | 3.6 |
| 37 | W37 | 0.992 | **0.992** | 0.001 | − 0.031 | 0.055 | − 0.044 | − 0.023 | − 0.025 | 3.7 |
| 38 | W38 | 0.843 | **0.867** | 0.041 | 0.004 | 0.004 | − 0.083 | − 0.001 | 0.287 | 2.7 |
| 39 | W39 | 0.974 | **0.978** | 0.031 | − 0.027 | 0.043 | − 0.05 | − 0.031 | 0.102 | 2.5 |
| 40 | W40 | 0.965 | **0.969** | 0.016 | 0.041 | 0.032 | − 0.035 | − 0.016 | 0.147 | 2 |
| 41 | W41 | 0.931 | **0.937** | 0.139 | 0.021 | 0.014 | − 0.105 | − 0.002 | 0.146 | 1.9 |
| 42 | W42 | 0.941 | **0.94** | 0.041 | 0.013 | 0.082 | − 0.178 | 0.052 | 0.121 | 2.1 |
| 43 | W43 | 0.711 | 0.384 | 0.198 | − 0.02 | 0.013 | − 0.051 | 0.064 | **0.719** | 1.9 |
| 44 | W44 | 0.899 | 0.256 | 0.221 | 0.185 | 0.188 | − 0.038 | − 0.02 | **0.844** | 2 |
| Variance (%) | | | 35.452 | 17.067 | 10.028 | 7.762 | 8.7 | 4.258 | 4.158 | |
| Cum. Var (%) | | | 35.452 | 52.519 | 62.547 | 70.309 | 79.009 | 83.267 | **87.425** | |

Appendix D
Varimax Factor Score Matrix produced by the *Q*-mode analysis of diatoms and silicoflagellates

| | Factor 1 | Factor 2 | Factor 3 | Factor 4 | Factor 5 | Factor 6 | Factor 7 |
|---|---|---|---|---|---|---|---|
| *Varimax Factor Score Matrix* | | | | | | | |
| *Actinocyclus curvatulus* | 0.001 | 0.000 | 0.000 | 0.001 | −0.003 | −0.001 | −0.001 |
| *Amphora bicuarta* | −0.002 | 0.001 | −0.001 | 0.002 | −0.021 | −0.003 | 0.001 |
| *Amphora sp. 2* | 0.024 | −0.009 | −0.014 | −0.066 | 0.007 | **0.868** | −0.028 |
| *Asteromphalus hookeri* | −0.001 | 0.003 | −0.002 | −0.002 | 0.000 | 0.000 | 0.017 |
| *A. parvulus* | 0.004 | 0.001 | −0.003 | 0.005 | −0.014 | −0.003 | 0.003 |
| *A. heptactis* | −0.001 | −0.002 | −0.005 | −0.008 | 0.000 | 0.001 | 0.060 |
| *A. hyalinus* | 0.000 | −0.005 | −0.002 | 0.013 | −0.009 | 0.004 | 0.054 |
| *Azpeitia tabularis* | 0.048 | 0.000 | 0.016 | −0.030 | −0.045 | 0.016 | 0.063 |
| *Chaetoceros atlanticum* | 0.007 | 0.000 | 0.000 | −0.002 | 0.007 | 0.000 | 0.001 |
| *Chaetoceros sp.* | 0.008 | **0.974** | 0.007 | **−0.146** | 0.015 | 0.033 | 0.039 |
| *Chaetoceros resting spores* | −0.022 | 0.022 | −0.014 | 0.032 | **−0.437** | −0.027 | 0.034 |
| *Corethron criophilum* | 0.011 | 0.076 | −0.004 | 0.085 | 0.028 | −0.026 | 0.034 |
| *Coscinodiscus curvatulus* | −0.015 | 0.063 | −0.038 | **0.110** | −0.081 | 0.053 | −0.080 |
| *Dactyliosolen antarcticus* | 0.032 | −0.028 | −0.046 | −0.073 | −0.022 | −0.021 | **0.734** |
| *Eucampia antarctica* (*resting spore*) | 0.003 | −0.001 | 0.000 | 0.000 | 0.002 | −0.002 | 0.015 |
| *Fragilariopsis angulata* | 0.035 | 0.045 | −0.049 | **0.165** | 0.063 | −0.023 | −0.098 |
| *F. curta* | 0.025 | −0.005 | −0.007 | −0.025 | 0.006 | 0.003 | **0.131** |
| *F. grunowii* | 0.024 | −0.061 | 0.057 | **−0.231** | **−0.693** | 0.059 | 0.079 |
| *F. kerguelensis* | **0.984** | 0.002 | −0.034 | 0.060 | −0.004 | −0.032 | −0.051 |
| *F. pseudonana* | 0.001 | −0.001 | −0.041 | **0.135** | **−0.192** | −0.057 | **−0.108** |
| *F. ritsheri* | 0.029 | −0.012 | 0.004 | **0.181** | −0.075 | −0.032 | −0.015 |
| *F. separanda* | 0.054 | −0.006 | −0.004 | −0.033 | 0.036 | 0.003 | **0.137** |
| *Melosira sol* | 0.001 | 0.000 | 0.008 | −0.003 | 0.001 | 0.001 | −0.002 |
| *Navicula directa* | −0.012 | 0.010 | −0.031 | 0.052 | −0.006 | −0.008 | **0.179** |
| *Nitzschia bicapitata* | −0.030 | **0.127** | −0.091 | **0.337** | **−0.448** | −0.089 | **−0.182** |
| *N. kolaczeckii* | 0.003 | 0.015 | 0.034 | 0.016 | 0.004 | 0.006 | −0.042 |
| *N. closterium* | −0.009 | 0.003 | 0.008 | 0.019 | −0.031 | −0.007 | 0.007 |
| *N. linearis* | 0.007 | 0.000 | −0.001 | −0.005 | 0.003 | 0.001 | 0.014 |
| *N. a polaris* | 0.018 | −0.002 | −0.006 | 0.012 | 0.005 | −0.004 | 0.039 |
| *N. sicula var. rostrata* | 0.013 | 0.004 | −0.004 | 0.014 | 0.014 | −0.003 | −0.011 |
| *Pleurosigma directum* | −0.003 | −0.001 | −0.003 | −0.001 | −0.038 | 0.054 | 0.000 |
| *Pseudoeunotia doliolus* | −0.006 | 0.027 | 0.054 | 0.091 | 0.028 | −0.010 | −0.019 |
| *Pseudo–nitzschia lineola* | 0.033 | 0.014 | 0.002 | 0.027 | 0.037 | 0.003 | 0.010 |
| *P. seriata* | −0.004 | −0.003 | −0.002 | 0.009 | −0.004 | 0.079 | 0.016 |
| *P. turgidula* | −0.010 | 0.002 | −0.008 | 0.015 | **−0.100** | −0.014 | 0.001 |
| *P. turgiduloides* | 0.002 | 0.000 | −0.001 | 0.005 | −0.031 | −0.004 | −0.001 |
| *Proboscia alata* | 0.002 | 0.004 | 0.000 | 0.002 | 0.001 | −0.001 | −0.001 |
| *Rhizosolenia styliformis* | −0.002 | 0.021 | 0.060 | 0.018 | 0.009 | −0.013 | 0.015 |
| *Roperia tesselata* | 0.019 | −0.003 | 0.000 | 0.055 | **−0.125** | 0.052 | −0.059 |
| *Thalassionema nitzchioides* | −0.004 | −0.003 | 0.014 | **0.253** | **−0.118** | **0.258** | **0.245** |
| *T. nitzchioides var. parva* | 0.016 | −0.016 | 0.025 | **0.130** | 0.046 | 0.058 | **0.149** |
| *Thalassiosira decipiens* | 0.001 | 0.000 | 0.000 | 0.001 | −0.005 | −0.001 | 0.000 |
| *T. delicatulata* | −0.002 | −0.001 | −0.001 | −0.003 | −0.020 | 0.010 | 0.003 |
| *T. gracilis* | **0.109** | −0.005 | 0.029 | −0.078 | −0.005 | 0.059 | **0.228** |
| *T. gravida* | −0.004 | −0.002 | −0.002 | 0.021 | −0.003 | 0.004 | 0.021 |

(*continued on next page*)

Appendix D (*continued*)

| | Factor 1 | Factor 2 | Factor 3 | Factor 4 | Factor 5 | Factor 6 | Factor 7 |
|---|---|---|---|---|---|---|---|
| *T. lentiginosa* | − 0.010 | − 0.011 | 0.016 | 0.050 | − 0.039 | 0.054 | 0.064 |
| *T. lineata* | 0.001 | 0.004 | 0.015 | **0.163** | 0.032 | **0.260** | − 0.035 |
| *T. oestrupii* | 0.043 | − 0.019 | **0.912** | − **0.142** | − 0.028 | 0.041 | − **0.148** |
| *T. oliverana* | 0.005 | 0.001 | − 0.002 | − 0.003 | − 0.001 | 0.001 | 0.029 |
| *T. trifulta* | − 0.005 | − 0.005 | − 0.009 | **0.117** | 0.014 | **0.181** | 0.010 |
| *Thalassiosira sp.* | 0.003 | − 0.003 | 0.015 | 0.007 | − 0.003 | − 0.003 | 0.007 |
| *Thalassiothrix sp.* | − 0.032 | 0.074 | **0.367** | **0.505** | 0.026 | − **0.132** | **0.342** |
| *Tropidoneis antarctica* | − 0.011 | − 0.003 | − 0.001 | − 0.002 | − 0.083 | 0.034 | − 0.002 |
| *Dyctyocha fibula* | − 0.027 | 0.043 | − 0.012 | **0.524** | 0.094 | **0.110** | − **0.140** |
| *Disthephanus speculum speculum* | − 0.007 | − 0.002 | − 0.003 | 0.020 | − 0.014 | 0.020 | 0.014 |
| *D. speculum minutus* | 0.013 | 0.083 | 0.017 | − 0.007 | − 0.012 | − 0.007 | 0.006 |
| *D. sp. 8* | − 0.003 | 0.033 | − 0.011 | 0.018 | 0.003 | 0.000 | − 0.012 |