SURFACE DISTRIBUTION OF MICROPHYTOPLANKTON OF THE SOUTH-WEST INDIAN OCEAN ALONG A REPEAT TRANSECT BETWEEN CAPE TOWN AND THE PRINCE EDWARD ISLANDS

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Investigates the surface chlorophyll-a concentrations, microphytoplankton species composition and distribution along repeat transect between Cape Town and the Prince Edward Islands in early austral autumn 1996. Results of numerical and ordination analyses; Average abundances of microphytoplankton and the eight most important species.

Surface chlorophyll-a (chl-a) concentrations, microphytoplankton (>20 µm) species composition and distribution along a repeat transect between Cape Town and the Prince Edward Islands were investigated in early austral autumn (April/May) 1996. Samples were collected at approximately 30 nautical mile intervals for the analysis of size-fractionated chl-a and the identification and enumeration of microphytoplankton species. Peaks in total chl-a (>1 µg 1^{-1}) were recorded at the Subtropical Convergence (STC), at the Sub-Antarctic Front (SAF) and in the waters surrounding the Prince Edward Islands. In addition, a minor peak in chl-a concentration was recorded in the continental shelf waters. At stations where elevated chl-a concentrations were recorded, microphytoplankton generally formed a substantial contribution (-10%) to total chlorophyll. Outside these regions, total chlorophyll concentrations were lower (<0.9 µg 1^{-1}) and almost entirely dominated by nano- and picophytoplankton, which contributed >95% of the total. Microphytoplankton species composition along both transects were dominated by chain-forming species of the genera Chaetoceros (mainly C. neglectum, C. peruvianus and C. constrictus), Nitzschia spp. and Pseudoeunotia doliolus. Cluster and ordination analysis based on species composition identified five distinct microphytoplankton assemblages, which were closely associated with the different water masses in the region between Cape Town and the Prince Edward Islands. The microphytoplankton species composition and biogeographic zones identified during this investigation are in general agreement with similar studies conducted in the south-west Indian Ocean during the austral summer, which suggests that there are little seasonal trends in both the microphytoplankton species composition and biogeographic zonation.

The Southern Ocean is a non-uniform water mass separated into several thermohalines by major circumpolar fronts.[1-3] South of Africa in the region between Cape Town and the Prince Edward Islands, two major oceanic fronts are recognised, the Subtropical Convergence (STC) and the Sub-Antarctic Front (SAF).[1,3] The STC is the northern boundary of the Southern Ocean and, as a consequence, represents the southernmost distribution of many warm water subtropical planktonic species.[4-6] The SAF, located at -45degrees20'S, is a less prominent front than the STC. Most recently, however, the SAF has also been shown to represent an important biogeographic boundary to the distribution of Antarctic fauna and flora.[5-7]

In the vicinity of both fronts, elevated phyto- and zooplankton biomasses have been recorded.[6,7] The accumulation of phytoplankton cells, water column stability and the availability of essential nutrients such as iron, particularly in the vicinity of the STC, have been suggested as mechanisms to account for elevated phytoplankton in the vicinity of the fronts.[8-12] The increase in zooplankton biomass at the fronts is the consequence of high chlorophyll-a concentrations usually recorded in the region.[13,14]

Biogeographic studies conducted in the waters south of Africa during the austral summer have shown that the distribution of phytoplankton species is closely associated with specific water masses.[5,6.15] The differences in phytoplankton community structure are thought to reflect the specific physiological requirements of the phytoplankton species.[6,16-19] Although studies on the distribution of microphytoplankton during the austral summer in waters south of Africa are relatively well documented,[5,6,15] few such studies have been conducted in the austral winter. Most recently, a study conducted by Froneman et al.[17] in the vicinity of the STC and across a warm-core eddy during the austral winter suggested that there were no seasonal trends in microphytoplankton biogeography. This study was, however, restricted to the region of the front and as a consequence little is known of the seasonal variability of the microphytoplankton zones south of Africa.

In this paper we examine the species composition and distribution of microphytoplankton in the region south of Africa during the austral autumn and compare these results with previous studies conducted in summer.

Materials and methods

Data were collected at approximately 30 nautical mile intervals along a repeat transect between Cape Town and the Prince Edward Islands during voyage 81 of the S.A. Agulhas, conducted in early austral autumn (April/May) 1996 (Fig. 1). The southern transect to the islands was occupied from 25 to 29 April, whereas the return leg covered over the period 17-20 May.

Water samples for the identification and enumeration of microphytoplankton were taken using a shipboard pump (Iwaki Magnet pump), made from polyvinylidene fluoride and ceramic materials, and operated at a flow rate of -41 min^{-1}. The pump outlet was -5 m below the sea surface and the seawater supplied to the laboratory through PVC piping. Previous studies have shown that the collection of water samples using the shipboard pump does not significantly alter microphytoplankton community structure as a result of diatom cell rupture or breakage.[20] For the taxonomic analysis of the microphytoplankton standing stock, a 20-µm mesh filtration unit[21] was connected to the pump outlet and a constant volume of 20 litres of seawater was filtered at each station. The phytoplankton retained by the filter was preserved in 2% buffered formalin and enumerated and identified using a Nikon TMS inverted microscope operated at 400x magnification. A minimum of 500 cells or 100 fields was counted for each sample. Densities were then expressed as cells per litre. The microphytoplankton were identified using the works of Priddle and Fryxell[22] and Boden and Reid.[16]

In addition to the microphytoplankton sample, chlorophyll-a concentrations were determined at each station. A 250-ml aliquot seawater sample obtained from the shipboard pump was gently filtered (<5 cm Hg) through a serial filtration unit and fractionated into the pico-(<2.0 µm), nano- (2.0-20.0 µm) and microphytoplankton (>20 µm) size fractions. Chl-a concentrations were then determined fluorometrically after extraction in 90% acetone for 24 h.[23]

Numerical analysis

All data collected along the transect were log-transformed[24] before comparing stations using the Bray-Curtis measure of similarity. The analysis was carried out employing the Plymouth Routines in Multivariate Ecological Research computer package[25] according to the procedure described by Field et al.[26] Groupings in the dendrogram were not attempted below the 50% similarity level. Significance levels and sources of error

between the groupings identified were tested using the similarity programs SIMPER and ANOSIM.[25] Ordination analysis was then applied to the data set in an attempt to determine the dissimilarity between the association identified.[26] Groupings identified with the dendrogram were superimposed on the ordination analysis results.

To normalise distribution and eliminate zero values, numerical abundances and chl-a concentrations were converted using logtransformation.[24] Relationships between chl-a, temperature and microphytoplankton along the transects were tested using Pearson and 5th-order partial correlation analysis. The correlation analysis is a particularly useful tool for uncovering hidden or intervening variables and detecting false relationships.[24] The analyses were carried out using the computer package Stargraphics Version 5.0.

Results

Chlorophyll distribution. Along both transects, elevated chlorophyll-a concentrations (>0.5 µg 1^{-1}) were recorded in the waters surrounding the Prince Edward Islands, in the vicinity of the Subtropical Convergence and in the neritic waters of the African continent (Figs 2A and B). In addition, along the return transect, elevated chl-a concentrations were also associated with the Sub-Antarctic Front (Fig. 2B). At stations where elevated chl-a concentrations were recorded, microphytoplankton represented an important contributor (-10%) to total chlorophyll concentrations (Figs 3A and B). In particular, at stations located in the vicinity of the islands during the return leg, microphytoplankton contributed >50% of the total. An exception was along the return transect, where elevated chlorophyll concentrations in the vicinity of the STC were dominated by nanophytoplankton (Fig. 2B). Outside the regions of the elevated chl-a concentrations, total chlorophyll concentrations were always dominated by the nano- and picophytoplankton size fractions, which contributed >95% of the total (Figs 3A and B).

A preliminary test with Pearson and 5th-order partial correlation analysis showed no significant relationships between seasurface temperature, total chlorophyll-a concentrations and microphytoplankton abundance along either of the transects ($P > 0.05$).

Species richness. Species richness along both transects showed similar spatial pattern (Figs 4A and B). Generally, the highest number of microphytoplankton species was recorded in the vicinity of the STC, 34 along the Cape Town-Prince Edward Island transect and 38 along the return transect. The lowest number of species, generally less than 20, was consistently recorded in the waters between the STC and SAF (Figs 4A and B). South of the SAF along both transects, the total number of microphytoplankton species recorded increased.

Numerical analyses. The stations along the return transects between the Cape Town and Prince Edward Islands were divided into five distinct microphytoplankton groups (Fig. 5). The average microphytoplankton abundances and the eight most abundant species accounting for >80% of similarity within each assemblage are listed in Table 1. Since each microphytoplankton group identified with the numerical analysis was associated with a specific water mass or feature, the groups are designated by the name of the feature or water mass with which it is associated. The water masses are identified after Hofmann[27] and Boden et al.[15]

The major groups of stations common to both transects were from north to south: the Agulhas Return Group (ARG), the Subtropical Convergence Group (STCG), the Sub-Antarctic Zone Group (SAZG) and the Polar Front Zone Group (PFZG). In addition to

these groups, along the Cape Town-Prince Edward Island transect, a distinct group of stations, designated the Subtropical Zone Group (STZG), was identified (Fig 5). ANOSIM and SIMPER programs identified all these groups as being significantly different from one another ($P < 0.05$ in all cases). Stations 113 and 129 were identified as outliers in the numerical analysis (Fig. 5). At these stations the lowest microphytoplankton abundances along the entire transect were recorded.

Ordination analysis. The results of the ordination analysis with the microphytoplankton groups identified with the dendrogram essentially give similar results (Fig. 6). An exception were the two Agulhas Return groups, which were identified as being separate according to the hierarchial cluster analysis but were grouped together in the ordination analysis (Fig. 6).

Discussion

The numerical analyses employed during this investigation identified five distinct microphytoplankton groupings closely associated with various water masses along the transects (Figs 3 and 4). This result broadly corresponds to a previous study conducted in the austral summer in the region between Cape Town and the Prince Edward Islands.[15] Although Boden et al.[15] identified a Frontal Zone Group in their study, it appears to correspond to the Sub-Antarctic Zone Group during this investigation. A major difference in the results of this study from previous ones conducted in austral summer is that the STC did not appear to represent an important biogeographic barrier,[5] possibly reflecting seasonal variability (Fig. 5). Temperature has been shown to play an important role in regulating shifts in microphytoplankton community structure.[6] During this investigation, however, microphytoplankton distribution was not significantly correlated with temperature ($P > 0.05$), suggesting that other factors are responsible for biogeographic zonation. Unfortunately, as no physicochemical data were collected, it is impossible to speculate on reasons for shifts in microphytoplankton community in the different water masses. It should be noted, however, that oceanographic processes such as eddies shed from the Agulhas Retroflection which subsequently migrate across the STC, cross-frontal mixing and meridional shifts in the position of oceanic fronts may facilitate the transfer of species between the different biogeographic zones identified during this investigation and previous studies.[17,28]

Along both transects, the highest number of microphytoplankton species was found at stations in the vicinity of the STC (Figs 3A and B), which can probably be related to both circulation patterns and the convergent nature of the STC that results in cross-frontal mixing.[28-30] Boden et al.[15] suggested that tropical species may be transported to the vicinity of the front by the Agulhas Current. The presence of Planktoniella sol, a species restricted to Agulhas waters,[15] in the microphytoplankton assemblages of the STC during this investigation provides evidence of the importance of the Agulhas Current in transporting warmer water species to the frontal region. Also, the presence of the common Sub-Antarctic species, Chaetoceros messanensis, in the waters of the STC group suggests that crossfrontal mixing of subtropical and sub-Antarctic waters due to the convergent nature of the front may also account for the high species richness recorded in the vicinity of the front during this investigation. Overall, the microphytoplankton species composition during this study was similar to previous studies conducted in summer.[5,6,15,16] These facts suggest that there are little seasonal trends in both the microphytoplankton species composition and biogeographic zonation.

During the entire investigation total chlorophyll concentrations were generally dominated by nano- and picophytoplankton (Figs 3A and B). This is also evident in the low

abundances of microphytoplankton generally recorded during the study (Table 1). A shift in phytoplankton size composition from a community dominated by large microphytoplankton cells in early summer to one dominated by small phytoplankton cells in winter has been documented in a previous study south of Africa.[31] Indeed, this shift appears to occur throughout the Southern Ocean during winter.[32] Increased turbulence and unfavourable light environment have been suggested as possible mechanisms to account for the shift in phytoplankton size structure.[12] The predominance of small phytoplankton cells has important implications for energy dynamics of the region. Grazing studies conducted in the Southern Ocean have shown that, where small phytoplankton cells dominate total chl-a, microzooplankton generally represent the most important grazers of phytoplankton production.[31,32] This result has important implications for the biologically mediated carbon flux, the so-called biological pump.[33,34]

We do not have any primary production data to identify the causes of the elevated chl-a concentrations recorded in the vicinity of the STC along both transects and in the vicinity of the SAF along the return transect (Figs 2A and B). Biological enhancement in the vicinity of these fronts is, however, well documented.[5,6,12,17] Increased in situ primary production rates primarily resulting from increased water column stability are thought to account for the elevated chl-a concentrations in the vicinity of the fronts. In the vicinity of the STC, cross-frontal mixing with nutrient-rich sub-Antarctic waters and the availability of dissolved iron re-suspended from the nearby shelf sediments have also been suggested as mechanisms to account for elevated phytoplankton biomass.[11,12,28] It is also possible that the elevated chlorophyll concentrations recorded at the STC may be due to the accumulation of phytoplankton cells by converging surface waters in the vicinity of the front.[10] Indeed, during this investigation, the highest abundances of microphytoplankton were recorded at stations in the vicinity of the STC (Table 1).

The elevated chl-a concentrations recorded in the waters surrounding the Prince Edward Islands during this investigation are consistent with previous studies conducted in the region.[35,37] Several hypotheses have been advanced to account for the enhanced phytoplankton biomass found in the vicinity of the islands. Perissinotto and Duncombe Rae[36] suggested that the elevated chlorophyll concentrations were the result of increase in situ production rates resulting from water column stability imparted by anticyclonic eddies found in the vicinity of the islands. Water column stability would further be promoted by the high levels of freshwater run-off from the islands.[37] Coupled with the water column stability, the high nutrient concentrations largely derived from the islands[35,38] would further promote phytoplankton growth. Indeed, the preliminary results from size-fractionated primary production studies conducted in the vicinity of the islands suggest that the highest phytoplankton growth rates were recorded in the waters around the islands (R.K. Laubscher, pets. comm.).

In conclusion, the microphytoplankton species composition and results of numerical analyses from our study agree closely with previous studies conducted during summer in the waters of the south-western Indian Ocean.[5,6,15,16] This result suggests that there are few seasonal trends in either microphytoplankton species composition or distribution south of Africa. A seasonal shift in the size composition of the phytoplankton is, however, evident. This shift may have important implications for the subsequent partitioning of carbon between the various size classes of herbivorous zooplankton.[31-34]

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Table 1.
Average abundances of microphytoplankton and the eight most important microphytoplankton species, accounting for >80% of the similarity between stations in each microphytoplankton group identified according to hierarchial cluster analysis.

Values in parenthesis are standard deviations.

The following chart reads as follows:

Row 1: Microphytoplankton group

Row 2: Average abundances (cells 1^{-1})

Row 3: Microphytoplankton species

Agulhas Retroflection Group

262 (+/=194)

Pseudoeunotia doliolus; Chaetoceros peruvianus; Rhizosolenia stolterfothii; Cylindrotheca closterium; Nitzschia chains; Thalassiosira spp.; Thalassiothrix spp.

Subtropical Zone Group

1084(+/=898)

Bacteriastrum criophilum; Chaetoceros constrictus; C. didymus; Dactyliosolen antarcticus; Rhizosolenia stolterfothii; Nitzschia spp.; Thalassionema spp.

Subtropical Convergence Group

3639 (+/=2209)

Chaetoceros constrictus; C. peruvianus; Cylindrotheca closterium; Pseudoeunotia doliolus; Corethron criophilum; Rhizosolenia stolterfothii; Thalassiosira spp.; Thalassionema spp.

Sub-Antarctic Zone Group

1307 (+/=1163)

Nitzschia chains; Rhizosolenia stolterforthii; Chaetoceros constrictus; Cylindrotheca closterium; Bacteriastrum criophilum; Pseudoeunotia doliolus;

Thalassiosira spp.

Polar Front Zone Group

301(+/=126)

Chaetoceros neglectum; Dactyliosolen antarcticus; Nitzschia chains; N. serata group; Chaetoceros peruvianus; C. atlanticus; Cylindrotheca closterium; Thalassiothrix spp.

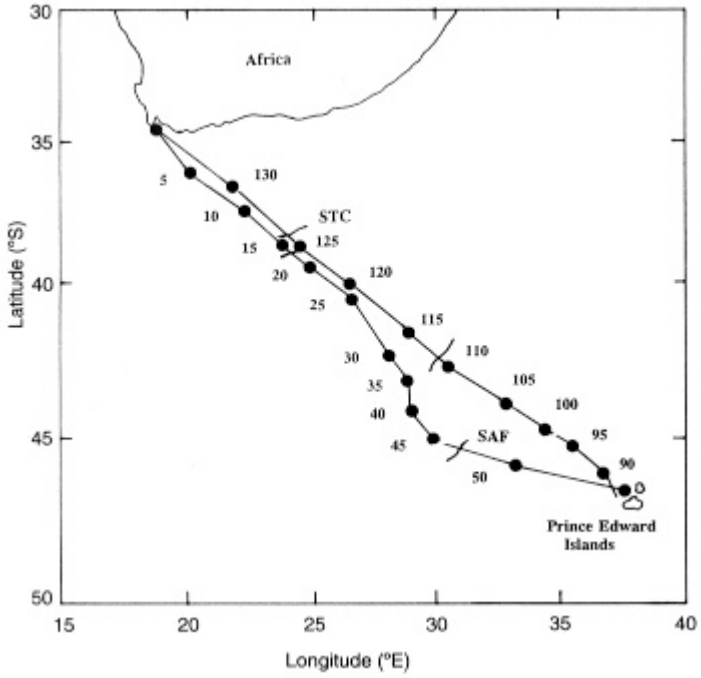
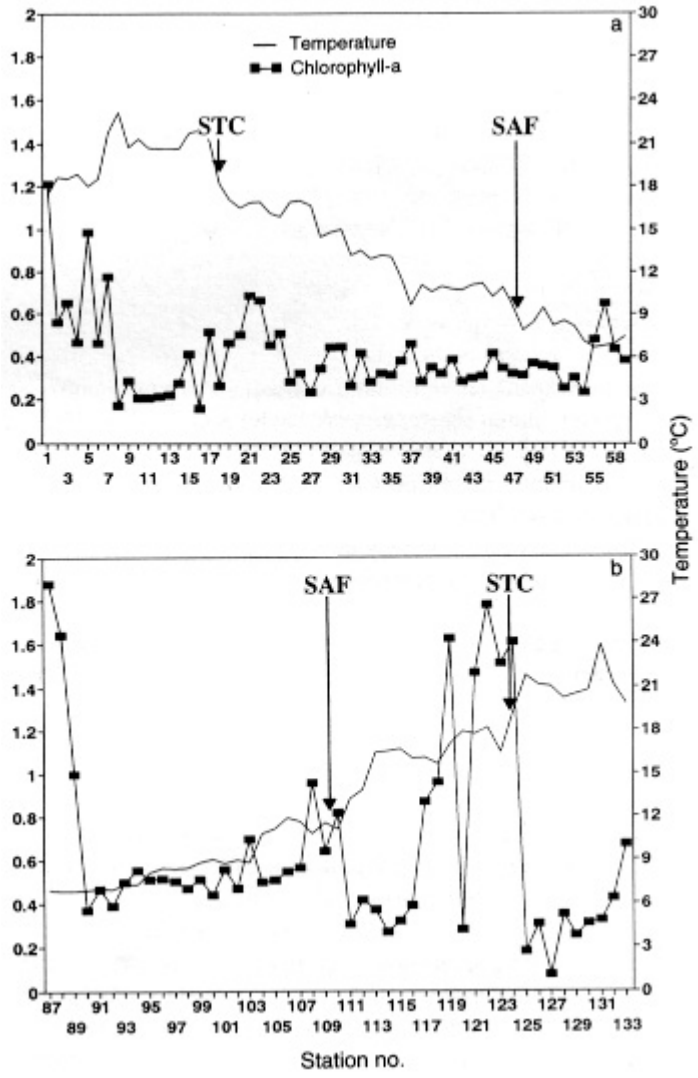
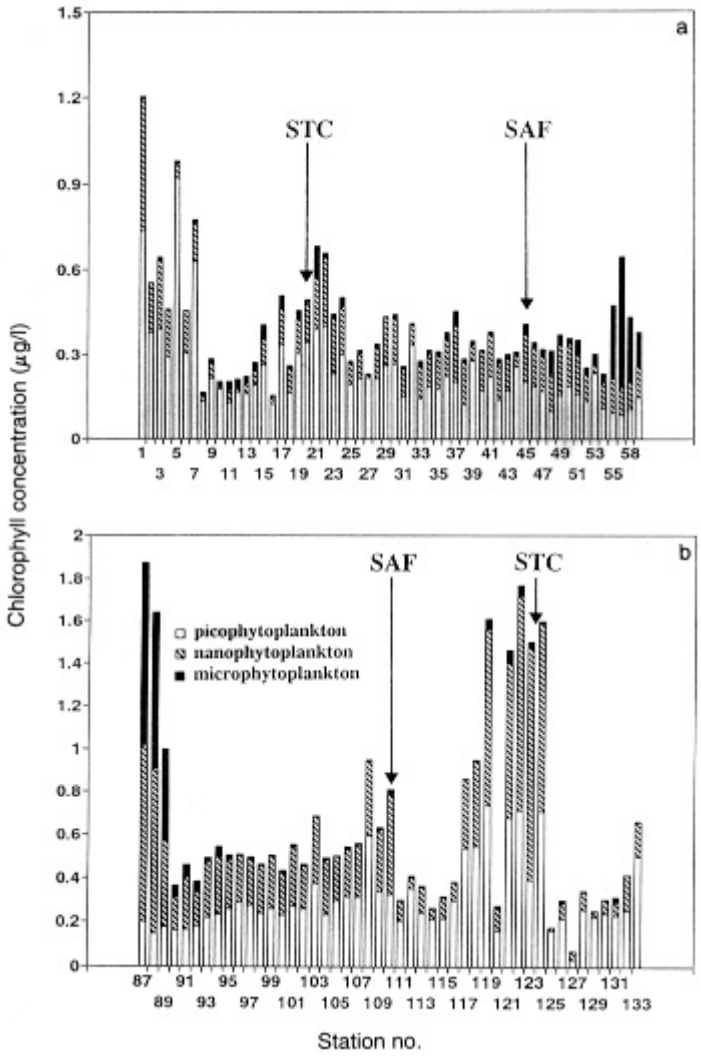


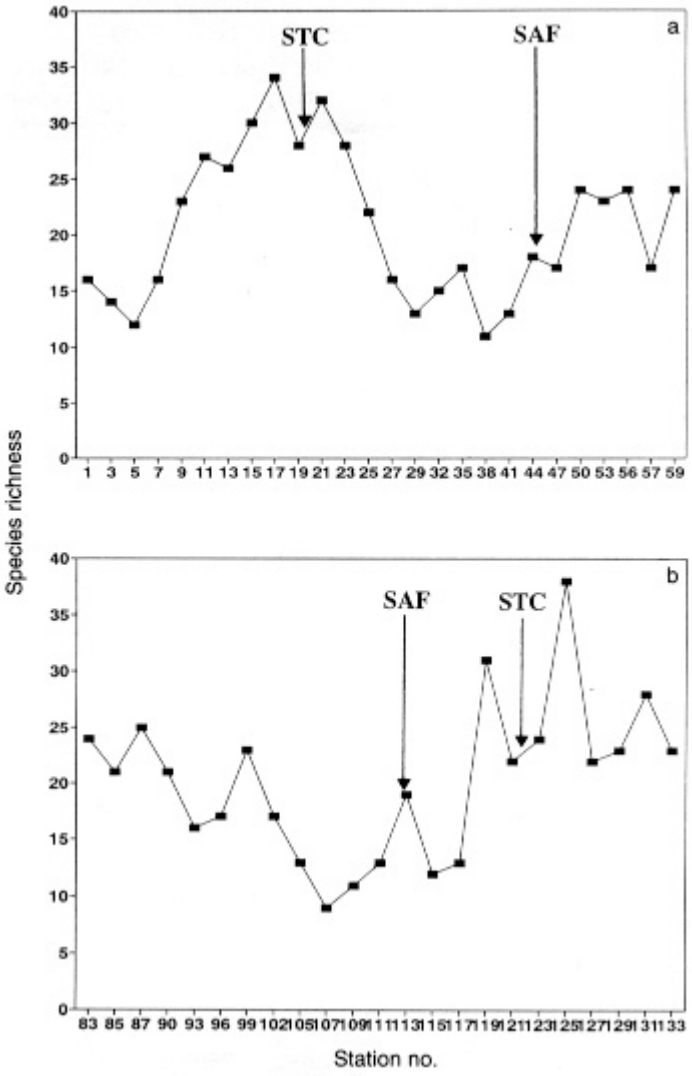
Fig. 1. Cruise track: spatial distribution of stations along the repeat grid between Cape Town and the Prince Edward Islands conducted in austral autumn (April/May) 1996. STC, Subtropical Convergence; SAF, Sub-Antarctic Front.



S: Fig. 2. Total chlorophyll-a and temperature profiles along the (A) Cape Town-Prince Edward Island transect and (B) Prince Edward Island-Cape Town transect. STC, Subtropical Convergence; SAF, Sub-Antarctic Front.



S: Fig. 3. Size-fractionated chlorophyll along the (A) Cape Town-Prince Edward transect and (B) Prince Edward-Cape Town transect. STC, Subtropical Convergence; SAF, Sub-Antarctic Front.



S: Fig. 4. Species richness along the (A) Cape Town-Prince Edward Island transect and (B) Prince Edward Island-Cape Town transect conducted in austral autumn (April/May) 1996. STC, Subtropical Convergence; SAF, Sub-Antarctic Front.

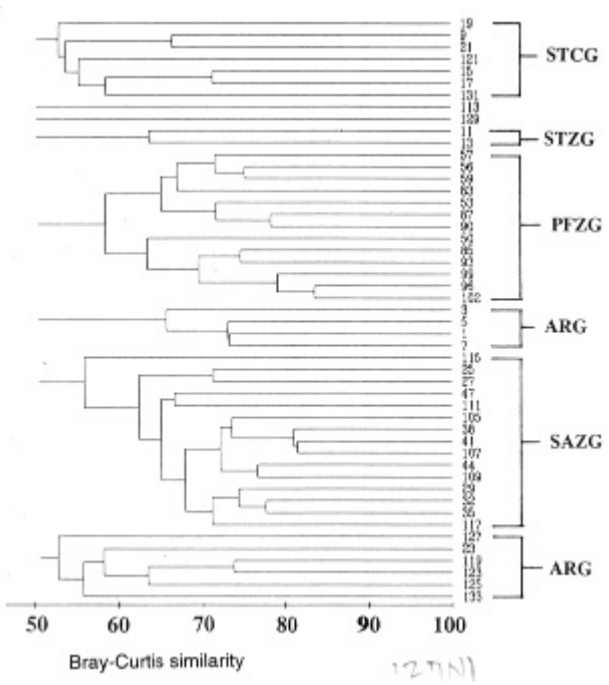


Fig. 5. Dendrogram showing the classification of stations based on microphytoplankton abundance and species composition along the repeat transect between Cape Town and Prince Edward Islands in austral autumn (April/May) 1996. ARG, Agulhas Return Group; STCG, Subtropical Convergence Group; SAZG, Sub-Antarctic Zone Group; PFZG, Polar Front Zone Group; STZG, Subtropical Zone Group.

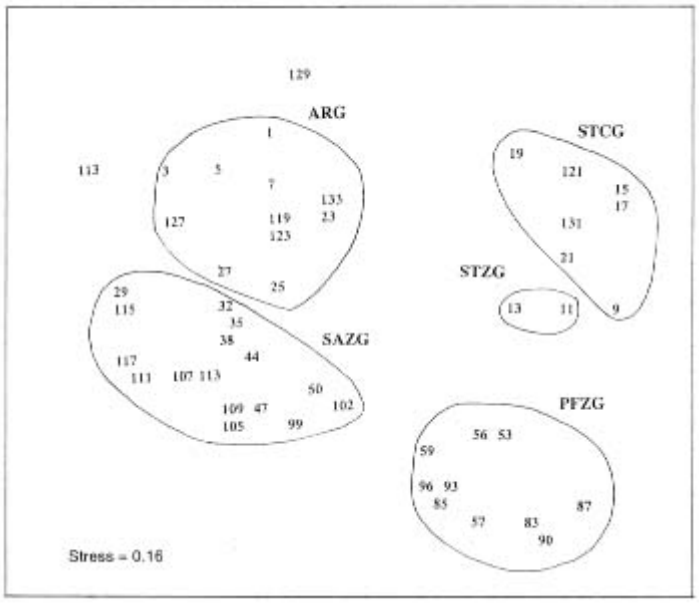


Fig. 6. Ordination analysis carried out on microphytoplankton abundance data collected during the repeat transects in austral autumn (April/May) 1996. Axes are arbitrary.

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