

Multivariate Statistical Analysis of Net Diatom Species Distributions in the Southwestern Atlantic and Indian Ocean

E. Theriot* and G. Fryxell

Department of Oceanography, Texas A&M University, College Station, TX 77843, USA

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Summary. Vertical net haul diatom assemblages from near South Georgia, and from between Africa and Antarctica, were examined and compared. Variation among South Georgia stations was examined by principal component, cluster and canonical discriminant analyses. Diatom distributions provide evidence for at least two distinct water masses. The region north of the island is characterized by neritic, temperate diatoms and by an assemblage with low species diversity. The region south of the island is characterized by oceanic, antarctic species and relatively high species diversity. The regions are most distinct to the west of the island, intergrading east of the island. Within the north-south division, five station groupings were detected on the basis of distribution of dominant net diatoms. By comparing classical species ecological categorizations to results of principal component analysis, a “neritic-oceanic” factor was identified from net diatom distributions. This factor was common to both areas in spite of the fact that *Biscoe* and *Agulhas* collections were from different seasons.

Introduction

Most phytoplankton studies of the antarctic region have been based on samples taken from an array of stations widespread in time and space (e.g. Karsten 1906, Mangin 1922; Hendey 1937; Hart 1942; Hustedt 1958; Frenguelli and Orlando 1958; Kozlova 1966; Hasle 1969; Van de Spoel et al. 1973). However, Hardy and Gunther (1935) focused on the net plankton assemblage of transects radiating from South Georgia (S. Georgia). Hendey's (1937) and Hart's (1942) reports were also derived in part from stations near S. Georgia.

Hardy and Gunther (1935) reported that Weddell Sea water and Bellingshausen Sea water were mixing in the

vicinity of S. Georgia. Hardy (1967) suggested that the high phytoplankton standing stock at S. Georgia resulted from each water mass contributing trace substances in which the other was deficient. Perhaps as a consequence of this area's productivity and apparently dynamic habitat, the island's waters reportedly have an unusual net diatom assemblage. Hart (1942) classified antarctic diatoms on the basis of their temporal and spatial distribution. He considered certain taxa, especially those with neritic distributions, to be characteristic of S. Georgia waters. However, all ecological groups reached their greatest abundance in the S. Georgia area (Hart 1942).

This study compares net diatom assemblages from samples taken during a three week survey of a grid of stations centered on S. Georgia during the austral spring of 1981. Species distributions near S. Georgia are compared with samples taken later in the same year in the southwestern Indian Ocean, facilitating characterization of the S. Georgia assemblage independent of literature ecological classifications. Hart's (1942) finding that the S. Georgia zone assemblage has both neritic and oceanic elements is confirmed, and comments are made on attempted ecological grouping of antarctic diatoms.

Materials and Methods

The grid around South Georgia of Fig. 1 was sampled during the first leg of the *RRS John Biscoe* cruise 3, 24 November–19 December 1981, by the British Antarctic Survey (stations and samples hereafter referred to as *Biscoe*). Thirty-five μm mesh vertical net hauls were made from a depth of 100 m, water depth and weather conditions permitting. Additional 35 μm mesh vertical net hauls, from 200 m to the surface, were analyzed from selected stations sampled during 16 February–5 March 1981 between South Africa and Antarctica by the South African vessel *Agulhas* (Fig. 2).

All net samples reported in this paper were cleaned by the method of Simonsen (1974) and mounted on permanent glass slides in Hyrax. At least 300 valves were tallied from each slide. If 20 species were not recorded after 300 valves then counting was continued until either 20 species or 500 valves were tallied. Species abundances were calculated

* Current address: Great Lakes Research Division, University of Michigan, Ann Arbor, MI 48109, USA

Table 1. Species occurring in half or more of either the *Biscoe* or *Agulhas* stations in order of frequency of occurrence in *Biscoe* samples. List compiled from cleaned net tows

Code	Species	% frequency of occurrence	
		<i>Biscoe</i>	<i>Agulhas</i>
CRCRI	<i>Corethron criophilum</i>	100.0	100.0
NIKER	<i>Nitzschia kerguelensis</i>	93.8	100.0
CHCUR	<i>Chaetoceros curvisetum</i>	85.9	50.0
DSSPE	<i>Distephanus speculum</i>	84.4	91.7
THLEN	<i>Thalassiosira lentiginosa</i>	84.4	50.0
NICYL	<i>Nitzschia cylindrus</i>	81.2	100.0
RHHEBSEM	<i>Rhizosolenia hebetata</i> fo. <i>semispina</i>	81.2	25.0
NILIN	<i>Nitzschia lineola</i>	79.7	91.7
THTUM	<i>Thalassiosira tumida</i>	76.6	33.3
THGRA	<i>Thalassiosira gravida</i>	75.0	0.0
NISUB	<i>Nitzschia sublineata</i>	73.4	25.0
TXLON	<i>Thalassiothrix longissima</i>	71.9	91.7
CHCRI	<i>Chaetoceros criophilum</i>	71.9	66.7
CHATL	<i>Chaetoceros atlanticum</i>	70.3	58.3
NIPSE	<i>Nitzschia pseudonana</i>	68.8	100.0
NIANG	<i>Nitzschia angulata</i>	64.1	66.7
NICUR	<i>Nitzschia curta</i>	59.4	91.7
ODWEI	<i>Odontella weissflogii</i>	57.8	0.0
THSCO	<i>Thalassiosira scotia</i>	56.2	8.3
EUANT	<i>Eucampia balaustium</i>	54.7	50.0
CDOCU	<i>Coscinodiscus oculus-iridis</i>	54.7	16.7
PLDIR	<i>Pleurosigma directum</i>	54.7	0.0
NIRIT	<i>Nitzschia ritscheri</i>	53.1	41.7
NIHEI	<i>Nitzschia heimii</i>	51.6	25.0
CHCON	<i>Chaetoceros convolutum</i>	46.9	58.3
POPSE	<i>Porosira pseudodenticulata</i>	39.1	75.0
CHCAS	<i>Chaetoceros castracanei</i>	39.1	50.0
CHDIC	<i>Chaetoceros dichactum</i>	37.5	66.7
THGRCVEX	<i>Thalassiosira gracilis</i> var. <i>expecta</i>	14.1	75.0

as percentages (proportionate abundance) of the total valves enumerated. Two small *Nitzschia* species (*N. cylindrus* (Grunow) Hasle and *N. pseudonana* (Hasle) Hasle) were found incorporated into tintinnid loricas at several *Agulhas* stations. The two species were omitted, and proportionate abundances adjusted accordingly, only for comparison of *Biscoe* and *Agulhas* stations.

Relationships among stations' net diatom assemblages were assessed by principal component analysis (PCA) of the species correlation matrix, cluster analysis using an agglomerative averaging algorithm, nearest neighbor discriminant analysis and canonical discriminant analysis procedures (SAS Institute Inc. 1982). Principal component analysis performs best on relatively homogenous data sets with few rare species (Gauch 1982), and was the only procedure available to us for ordination without "a priori" station classification. Thus only those species occurring in 50% or more of the samples from at least one cruise were retained for analysis (Table 1). Two other editing protocols, selecting the most abundant and selecting the most variable species, produced nearly identical lists, and the resultant data matrices differ little from the one used. Distributions of locally abundant taxa not in multivariate analyses are individually noted.

Results

Characterization of the *Biscoe* Net Diatom Assemblage

Cluster analysis and nearest neighbor discriminant analysis identified five station groupings (Fig. 1). The northern sectors (5 and 6) are separated from the south-

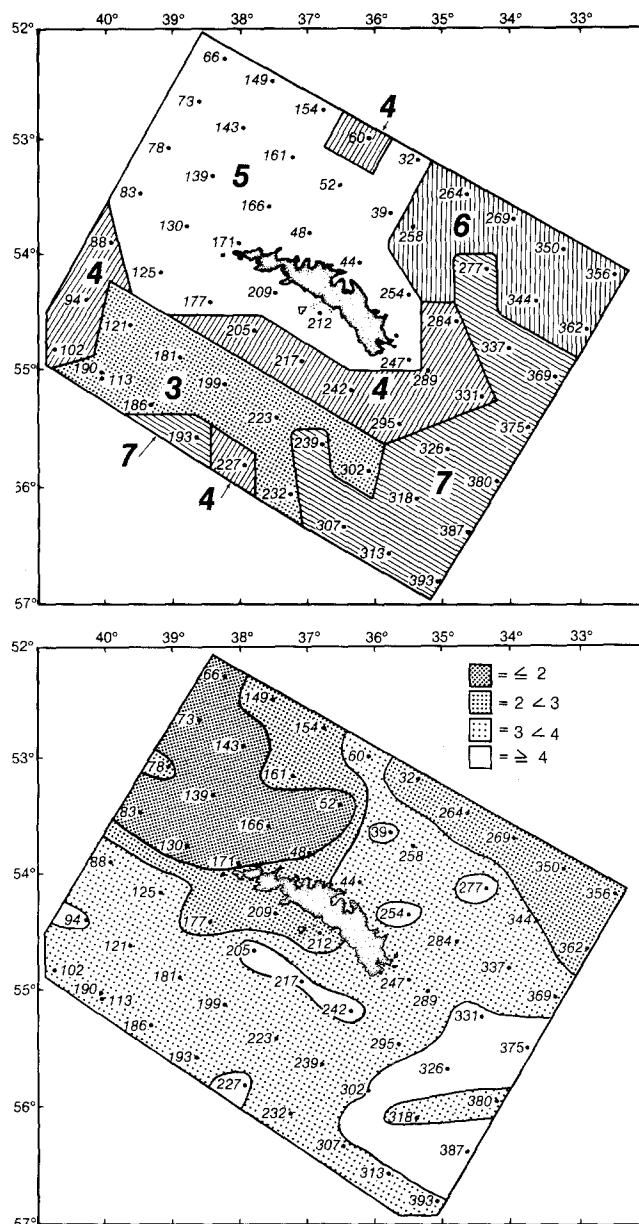


Fig. 1. Station grid near South Georgia sampled by the *R.R.S. John Biscoe* during November and December 1981. Above, *Biscoe* sectors 3-7 as determined by cluster and nearest neighbor discriminant analysis of species occurring in more than half of the *Biscoe* net tows. Below, Shannon species diversity index values. Contour intervals are given in the top right of the figure

ern (3, 4, and 7) along the first principal component axis (JBPCA1); within each of the north and south regions, sectors are arranged along JBPCA2 (Fig. 3). Individual sectors can be resolved in species space by canonical discriminant analysis (Fig. 4). The sectors can each be characterized by one or a few diatom species (Fig. 3), although any species may not be entirely restricted to one sector or, conversely, a characteristic species may not occupy all stations within its sector.

Beginning from the north, sector 5 is a diverse group of stations tied together by overlapping ranges of four

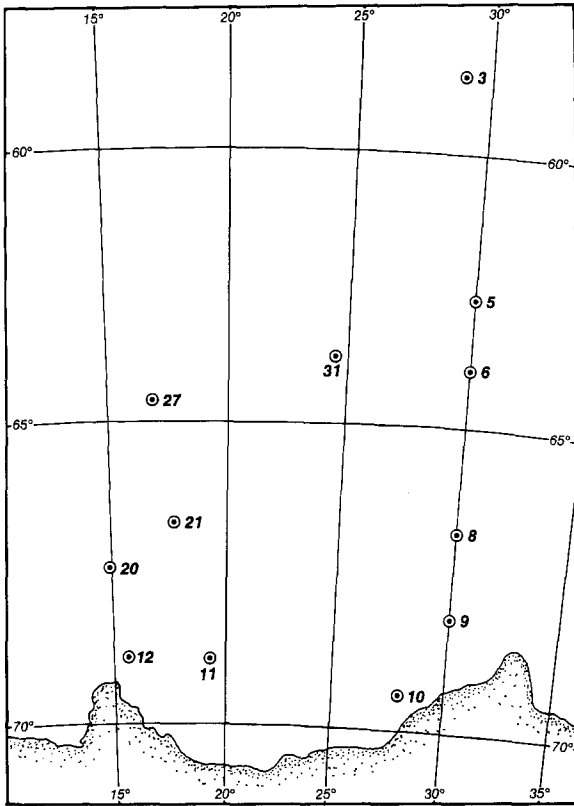


Fig. 2. Selected stations north of Antarctica sampled by the S.A. *Agulhas* during February and March 1981

so-called neritic species. It is an area of low to moderate species diversity (Fig. 1), and species distributions within 5 can be related to variation in diversity within the sector.

Thalassiosira scotia G. Fryxell and Hoban is proportionately most abundant in areas of 5 with higher species diversity (Figs. 1 and 5). This species was described from S. Georgia waters from areas of high total cell density (Fryxell et al. 1979), and occurs in abundance in a sample with high cell density in this study (over 2,000,000 c/l at station 209). Resting spore valves, rudimentary valves and vegetative valves (Fryxell et al. 1979) of this species were observed. Resting spores were generally few except at stations 209 and 212. Because these stations were sampled about two weeks later than those with the first occurrence of *T. scotia*, it is tempting to believe that stations 209 and 212 represent the end of growth of this species for the season in this sector. Alternatively, an abundance of resting spores may indicate conditions of the spatial and ecological limit of this species.

Hart (1942) reported the presence of *T. antarctica* Comber at S. Georgia. This species and *T. scotia* are highly similar in morphology (Fryxell et al. 1979, 1981), and it is likely that Hart (1942) and we are referring to the same taxon considering that *T. scotia* was found in abundance in the same region in different years.

The low diversity found in the northern most part of sector 5 is due to high proportionate abundance of *Chae-*

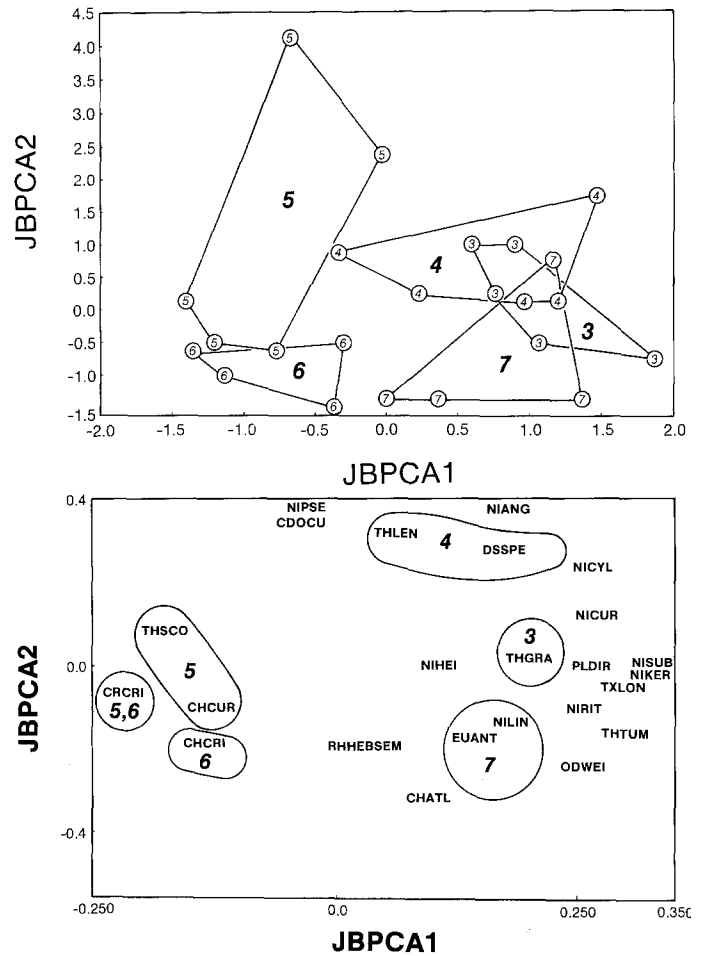


Fig. 3. Principal component analysis of correlation matrix of 24 most frequently occurring species at *Biscoe* stations. The first principal component axis, JBPCA1, accounts for 25%, and JBPCA2 for 15%, of the variance in the data set. Above, plot of station scores on JBPCA1 and JBPCA2. Only the outliers of each sector are identified and connected. Below, plot of *Biscoe* species coefficients on JBPCA1 and JBPCA2. Species circled are those judged most characteristic of particular sectors by individual species plots. Species codes are as in Table 1

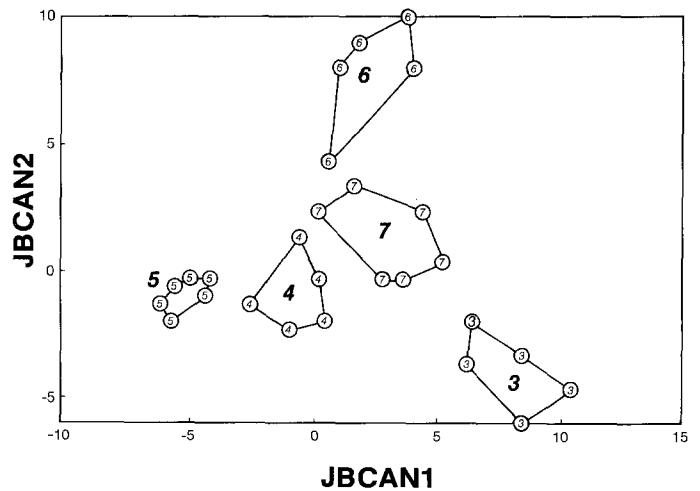


Fig. 4. Plot of *Biscoe* station scores on first two canonical discriminant axes derived from analysis of 24 most frequently occurring species at *Biscoe* stations (JBCAN1 and JBCAN2); only outliers of each sector are identified and connected

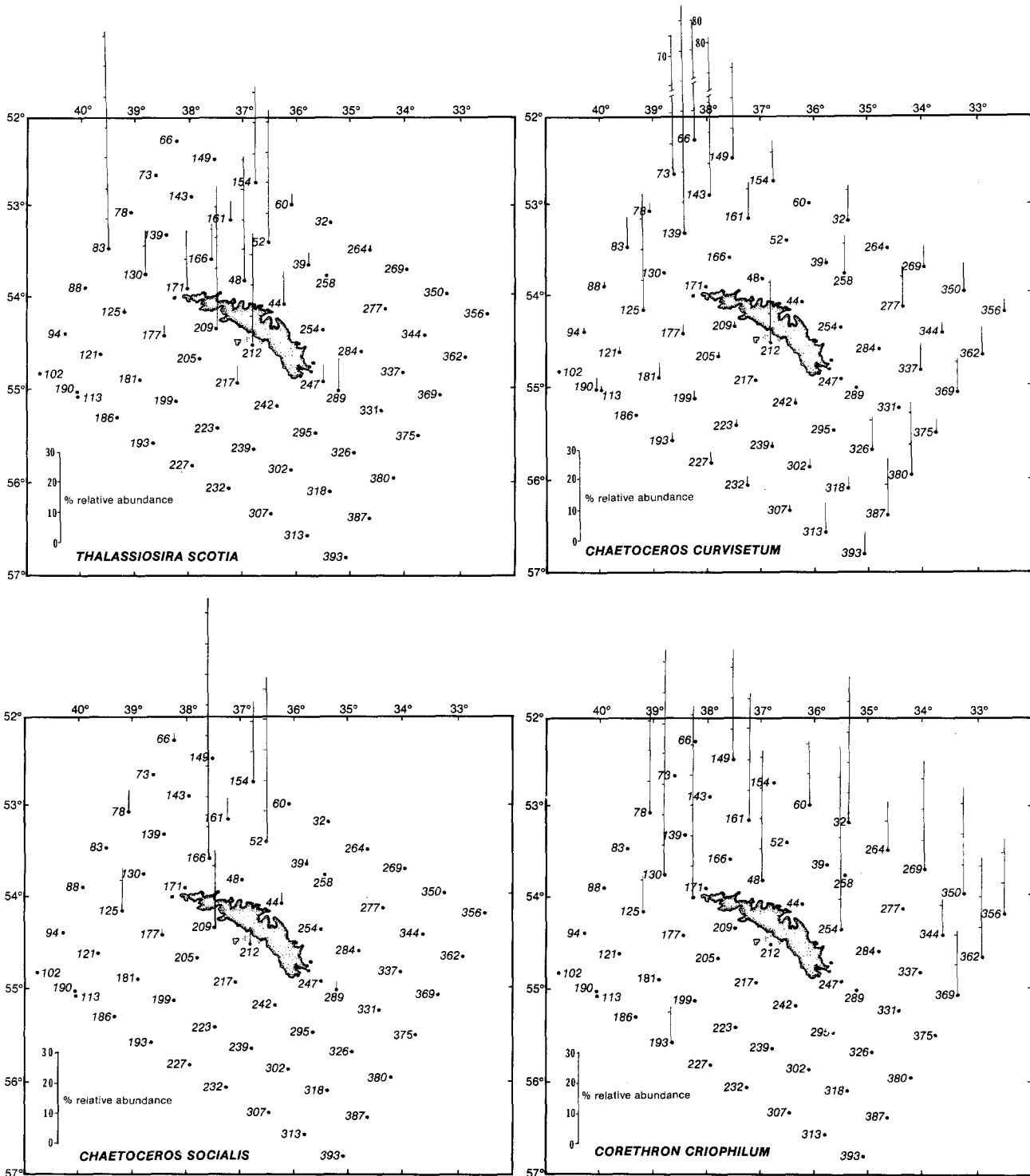


Fig. 5. Distribution of selected diatoms characteristic of waters north of South Georgia, November – December 1981. Occurrences greater than 10% are plotted for *Corethron criophilum*; occurrences greater than 1% are plotted for other species

taetoceros curvisetum Cleve (Fig. 5). This species also occurs in moderate abundance at many *Biscoe* offshore stations outside of sector 5. *Chaetoceros socialis* Lauder was not used in the multivariate analysis (only 28% frequency of occurrence over all *Biscoe* stations). As is *T. scotia*, *C. socialis* is proportionately abundant at stations

of moderate overall diversity (Figs. 1 and 5). Both *C. curvisetum* and *C. socialis* are considered neritic, temperate species (Cupp 1943; Hendeny 1964; Drebes 1974). *Corethron criophilum* Castracane is abundant at several stations in 5, but is also proportionately abundant in sector 6 (Fig. 5).

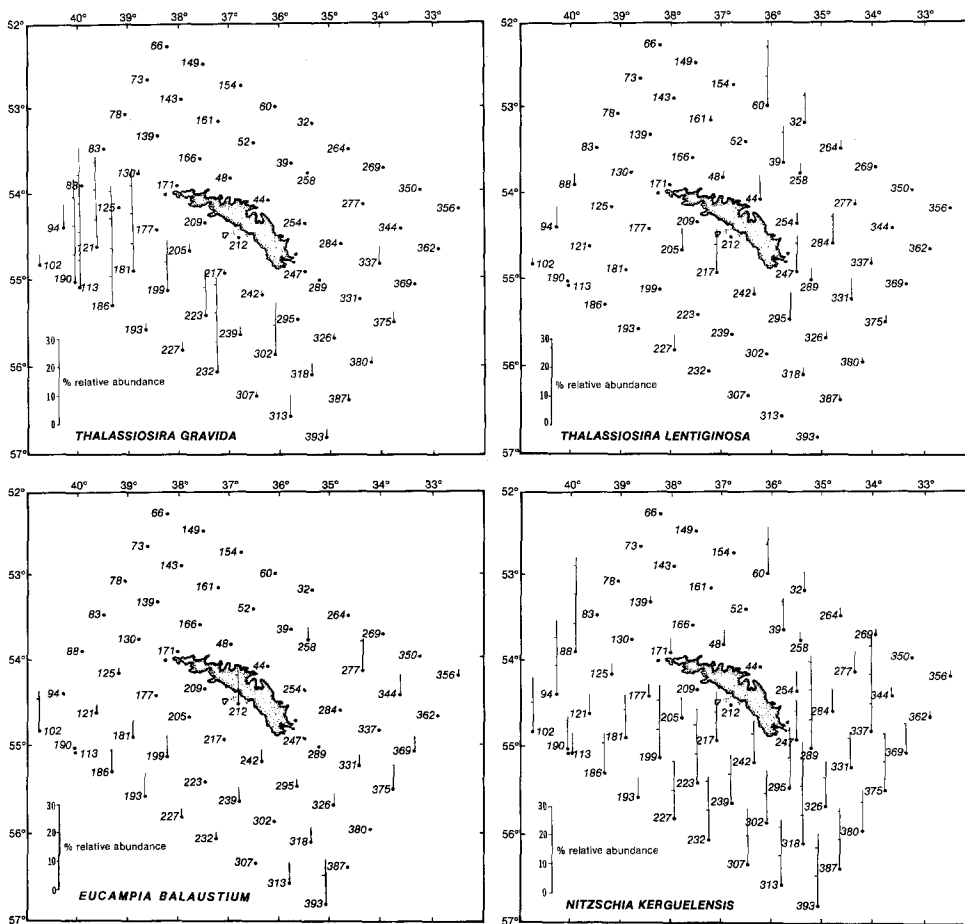


Fig. 6. Distribution of selected diatoms characteristic of waters south of South Georgia, November – December 1981. Occurrences greater than 1% are plotted

Sector 6 is characterized by the high average proportionate abundance (34%) of *Chaetoceros criophilum* Castracane; the species exceeds 10% proportionate abundance in only two stations outside of sector 6. There are conflicting views in the literature of its distribution, perhaps a result of wide tolerance of environmental conditions. However, another factor may be that the identification of *C. criophilum* and similar species is problematical (Fryxell and Medlin 1981). It reportedly tends to increase in importance southward (Hart 1942; Hasle 1969), although Kozlova (1966) regarded it as subantarctic. Manguin (1960) and Kozlova (1966) regarded this species as oceanic, but Frenguelli and Orlando (1958) consider it neritic, and found it to be especially abundant near S. Georgia.

Sector 3 is characterized by *Thalassiosira gravida* Cleve (Fig. 6). This species is distributed throughout 3, 4 and 7, but reaches its greatest average proportionate abundance in 3 (>30%). It is virtually absent from the strongly neritic assemblage dominating sector 5, even though it is considered a neritic species (Hasle 1976). However, one of us (GAF) has observed gelatinous colonies of this species in abundance south of S. Georgia in the Scotia Sea at and near the ice edge, far from land,

during the austral spring of 1983, suggesting that the S. Georgia population may be derived from oceanic waters north of the pack-ice. Its high proportionate abundance indicates it formed gelatinous colonies in our samples because its diameter (ca. 20–25 μm) is less than the mesh of our nets. Observation of living material (not performed) is necessary to confirm presence of such colonies.

Sector 4 is best characterized by *T. lentiginosa* (Janisch) G. Fryxell and the silicoflagellate, *Distephanus speculum* (Ehrenb.) Haeckel. These species connect the geographically outlying stations of sector 4 (station 60, 88, 94, 102 and 227) to the central part of the sector (Figs. 1 and 6). The former species is considered oceanic (Kozlova 1966). *D. speculum* is widespread in the world's oceans, but seems to occur in highest numbers in antarctic waters (Hasle 1969).

Sector 7 is best characterized by *Eucampia balaustium* Castracane and *Nitzschia lineola* Cleve (Fig. 6). Although the former species is considered neritic and antarctic in distribution by Kozlova (1966), it is widespread in antarctic waters (Hustedt 1958; Hasle 1969). The latter species was frequently abundant in the Pacific sector of the antarctic waters, except at the ice edge (Hasle 1965).

Sectors 3, 4 and 7 share several abundant so-called oceanic species, underscoring the division between north and south sectors along JBPCA1 (Fig. 3). Moreover, species distributions give the impression of a water mass curling around the eastern end of S. Georgia (e.g. *N. kerguelensis*) (O'Meara) Hasle; Fig. 6). This image is reinforced by other species with more restricted distributions and lower proportionate abundance (Fig. 6). The PCA also illustrates this. Sectors 3 and 5 are in geographic proximity but are far apart in species space. However, there is some intergradation of these sectors through 4 and 7 (Fig. 3).

Comparison of *Biscoe* and *Agulhas* Assemblages

Principal component analysis of the frequently occurring species in both areas provides some separation of *Biscoe* and *Agulhas* samples (AGJBPCA; Fig. 7), while species coefficients reveal some patterns of species distributions common to both areas (Table 2). Whether *Biscoe* or *Agulhas*, stations to the right of Fig. 7 tend to have higher proportionate abundance of *Nitzschia kerguelensis* than those on the left, reflecting this species high positive loading on AGJBPCA1 (>0.25). Five other species, each also characterized as oceanic in distribution, share the same pattern of distribution and moderate to high (>0.10) positive coefficients on the first two PCA axes (Cupp 1943; Hendey 1964; Kozlova 1966; Hasle 1969).

A second group of eight species has moderate to high positive coefficients on the first axis, but negative coefficients on the second (Table 2). These taxa are higher in proportionate abundance at *Biscoe* stations. As a group they are difficult to classify, being a mixture of oceanic and neritic forms. Some individual species are likewise difficult to categorize (e.g. *E. balaustium*, see Hasle 1969).

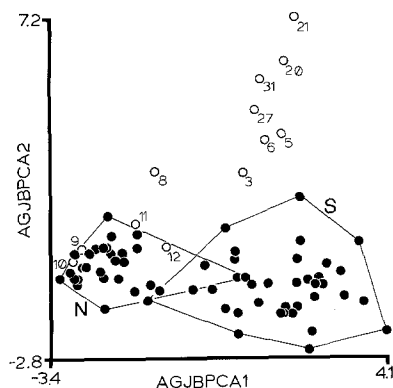


Fig. 7. *Biscoe* (●) and *Agulhas* (○) station scores plotted on first and second principal components derived from analysis of most frequently occurring species (AGJBPCA1 and AGJBPCA2). Each symbol represents at least one station. Individual pooled *Agulhas* stations are numbered according to Fig. 2. Outliers of pooled northern sectors (5+6) and southern sectors (3+4+7) of *Biscoe* stations are connected and identified respectively as (N) and (S)

Table 2. Principal component analysis of the *Biscoe* and *Agulhas* samples pooled. Species coefficients on first two principal component axes (AGJBPCA1 and AGJBPCA2). Based on species occurring in at least half of the samples from at least one cruise, except *Nitzschia cylindrus* and *N. pseudonana* are excluded. Species proportionate abundances are adjusted as a percentage of total assemblage minus these two *Nitzschia* species. Species groups are determined from coefficients on the first and second axes, respectively. Group 1 species' coefficients are positive, positive; Group 2 are positive, negative; Group 3 are negative, not loaded ($-0.1 < x < 0.1$).

Group	Species	% variance	
		AGJBPCA1 17	AGJBPCA2 12
1	<i>Nitzschia kerguelensis</i>	0.293	0.177
1	<i>Nitzschia lineola</i>	0.192	0.276
1	<i>Thalassiothrix longissima</i>	0.212	0.294
1	<i>Chaetoceros atlanticum</i>	0.218	0.282
1	<i>Chaetoceros convolutum</i>	0.128	0.293
1	<i>Chaetoceros dichaeum</i>	0.127	0.394
2	<i>Thalassiosira tumida</i>	0.342	-0.194
2	<i>Thalassiosira gravida</i>	0.152	-0.158
2	<i>Nitzschia sublineata</i>	0.315	-0.281
2	<i>Nitzschia angulata</i>	0.111	-0.133
2	<i>Eucampia balaustium</i>	0.182	-0.133
2	<i>Pleurosigma directum</i>	0.263	-0.228
2	<i>Nitzschia ritscheri</i>	0.246	-0.136
2	<i>Odontella weissflogii</i>	0.303	-0.184
3	<i>Corethron criophilum</i>	-0.268	0.006
3	<i>Chaetoceros curvisetum</i>	-0.110	0.078
3	<i>Thalassiosira scotia</i>	-0.224	-0.069
3	<i>Distephanus speculum</i>	0.133	0.087
3	<i>Thalassiosira lentiginosa</i>	0.011	-0.160
3	<i>Rhizosolenia hebetata</i> fo. <i>semispina</i>	0.086	-0.115
3	<i>Chaetoceros criophilum</i>	-0.078	0.009
3	<i>Nitzschia curta</i>	-0.020	0.058
3	<i>Coscinodiscus oculus-iridis</i>	-0.065	-0.069
3	<i>Nitzschia heimii</i>	0.136	-0.013
3	<i>Porosira pseudodenticulata</i>	0.007	0.088
3	<i>Chaetoceros castracanei</i>	0.228	0.087
3	<i>Thalassiosira gracilis</i> var. <i>expecta</i>	0.070	0.351

Coastal *Agulhas* stations (9–12) are plotted with northern sector *Biscoe* stations on the AGJBPCA axes. This is not an artefact of the reduced dimensionality of the PCA analysis. Discriminant analysis also places coastal *Agulhas* stations with northern sector *Biscoe* stations and the discriminant axis is highly significantly correlated with AGJBPCA2 ($r = 0.80$, d.f. = 74, $P < 0.01$). Taxa held in common by these stations include *Corethron criophilum* and *Chaetoceros curvisetum*. The latter species is classified as neritic (Cupp 1943; Hendey 1964); the former reaches its greatest proportionate and absolute abundance in neritic areas (Hart 1942; Frenguelli and Orlando 1958; Cassie 1963; Hasle 1969; Fryxell and Hasle 1971).

Discussion

Species characterizations and station groupings in the waters of S. Georgia support Hardy's (1967) concept of a

complex hydrography. Shifts in species assemblages over relatively short distances can approximate the magnitude, if not quality, of changes reported at the Antarctic Convergence zone (Hart 1942; Manguin 1960; Kozlova 1966; Hargraves 1968; Hasle 1969). Areas of precipitous change in the diatom assemblage may reflect abrupt changes in the environment, e.g., areas of contact of water masses with distinct origins containing already present and separately developing assemblages. This is probably especially true of the region just to the west of the island, at the border of sector 5 with the composite sector 3 plus 4 (3+4). The characteristic species of 5 are neritic, and two of them are considered temperate. Several of the dominants of 3+4 are reportedly oceanic and antarctic or subantarctic. There is a strong gradient of diversity values near the common border of 3+4 and 5. Less sharp change over an area might reflect mixing of water masses, contact of water masses of similar characteristics, and/or species in competition along ecological gradients within a single water mass. Species coefficients and ecological characterizations show a mixture of oceanic and neritic species in the *Biscoe* stations south of S. Georgia, perhaps indicating an interaction of ocean-derived populations with nearshore effects.

There was some congruence between Hart's (1942) species groupings and species associations in *Biscoe* samples. For example, many of Hart's group III species are dominants or subdominants in the southern sectors (3+4+7, e.g. *T. gravida*). However, *Chaetoceros socialis*, one of Hart's group III species, is limited to sector 5 in this study. Three of Hart's (1942) group II taxa were dominants in this study: *Corethron criophilum*, *Chaetoceros criophilum* and *Rhizosolenia hebetata* fo. *semispirina* (Hensen) Gran. However, their distributions were not completely congruent. The first taxon had a scattered distribution in sectors 5 and 6, the second was limited almost entirely to sector 6 and the last was moderately abundant throughout nearly the entire S. Georgia area.

A large portion of the literature on antarctic diatoms is devoted to grouping species with similar ecological distributions. Hart (1942) believed that such groups should accurately reflect the "space/time distribution" of the species, and included the season of greatest abundance as one criterion for his species groups. Hasle (1969) recognized a seasonal component to geographic distribution of certain widespread species (subgroups of her group 7), and showed how discrepancies in certain species characterizations could be explained by accounting for season. Season can be considered a set of associated ecological factors.

Similarly, we consider "neritic" or "oceanic" less as geographic locations and more as environmental phenomena consistent enough in their association to be viewed as distinct. Some assemblages at S. Georgia were dominated by so-called neritic species; others, by so-called oceanic species. Species distributions at *Agulhas* stations independently supported these ecological characterizations. The former species were characteristic of

the most landward *Agulhas* stations; the latter species, of open ocean stations. Our PCA of pooled *Agulhas-Biscoe* data revealed that this "neritic-oceanic" factor was common to both areas. These similarities occurred in spite of seasonal difference in sampling that may have resulted in differentiation of open ocean *Agulhas* stations from *Biscoe* stations. Other named and unnamed ecological factors exist (e.g. depth). Thus, it may be that Hasle's (1969) conclusions on the interplay of season and geography can be generalized to other factors in order to explain apparent discrepancies in species distributions.

Another factor, spatial scale, can also influence species groupings. The pertinent horizontal scale in antarctic waters has been addressed (e.g. Hasle 1969; Kopczynska 1980). Venrick (1982) found discrete assemblages over depths of less than 200 m in the north Pacific. However, examination of discrete whole water samples revealed no apparent differences in kinds of species with depth in our study areas (unpublished data).

Horizontal scale does have a significant effect on apparent species groupings. In the S. Georgia area, a mosaic of species distributions with varying degrees of overlap was the rule. It is evident that overlap among assemblages could have been less, resulting in more discrete (but more arbitrary) species groupings, had we examined fewer, more widely spaced, stations. This is not a criticism of Hart's groupings, but attempts to make species groupings that fulfill Hart's (1942) ideal of reflecting species "space/time distribution" would do well to recognize that scale in both space and time affects apparent species groupings.

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