

Some Environmental Factors Influencing Phytoplankton in the Southern Ocean Around South Georgia

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Summary. Data on phytoplankton and zooplankton biomass, and physical and chemical variables, are combined with a published multivariate description of diatom species composition to interpret variation within an area around South Georgia surveyed during an austral summer. Large-scale species distributions could be equated to the different water masses which reflected the interaction of the Antarctic Circumpolar Current with the island and the Scotia Ridge. Small-scale factors were found to act at an interstation scale and imposed local variation on the biogeographic pattern. Nutrient depletion could be related to phytoplankton biomass but no single inorganic nutrient of those measured ($\text{NO}_3\text{-N}$, $\text{PO}_4\text{-P}$ and silica) could be identified as important. The ratio Si:P appeared to be more important as an ecological factor. The impact of grazing by krill and other zooplankton could only be resolved as differences in phytoplankton biomass and phaeopigment content. Diatom species composition showed a relation to local krill abundance very different from that suggested by published studies, but could be explained as the effect of earlier grazing outside the study area. The effects of vertical mixing could not account for interstation differences as pycnocline depth was uniformly greater than euphotic depth, and vertical stability very low. Some comparison was made with data collected in 1926–31 by the Discovery Investigations. Significant differences in the distribution of certain taxa such as *Chaetoceros criophilum* and *C. socialis* were traced to major differences in hydrology.

Introduction

The plankton diatom species composition around South Georgia during three weeks of an austral summer have been described by Theriot and Fryxell (1985). Five distinct sectors were identified from analysis of diatom

abundance data from 64 stations forming a 240×180 nautical mile grid (Fig. 1). There was considerable heterogeneity within this simple overall pattern. This patchiness in community structure (and biomass) recorded around South Georgia reflects in a microcosm the distribution of phytoplankton throughout the Southern Ocean (El-Sayed 1984, Heywood and Whitaker 1984, Holm-Hansen 1985).

Hart (1934) was the first to identify some of the possible factors limiting the activities of phytoplankton in the Southern Ocean. He thought that physical features of the

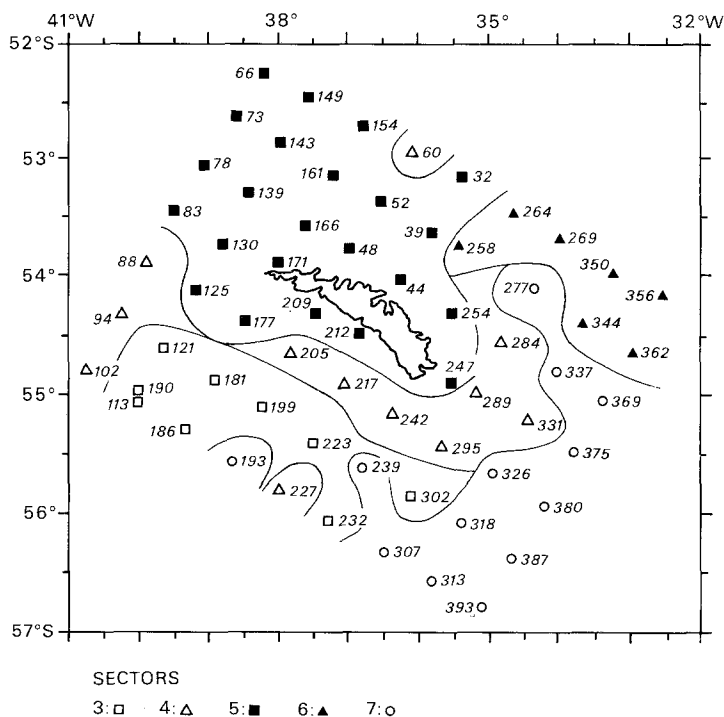


Fig. 1. Map of the stations of the South Georgia Zone Survey 1981, showing the division into five sectors on the basis of diatom species composition (Theriot and Fryxell 1985). The symbols used to identify the sectors are used in the other figures where relevant

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environment (light intensity and duration, ice, surface water stability and currents) exerted the strongest influence. Concentrations of the major nutrients are generally high throughout the Southern Ocean. Hart concluded that only silicate was likely to be limiting and then only in a few areas. Grazing and settling rates have since been added to Hart's list and there has been a considerable increase in knowledge of plant physiology and ecology in general. However little field experimental work has been carried out on Antarctic marine species (Heywood and Whitaker 1984, Holm-Hansen 1985). The high spatial variability in phytoplankton biomass relative to the distribution pattern of nutrient elements has been emphasized by Holm-Hansen (1985). The plants do not achieve the high growth rates suggested by the nutrient levels. Biomass is usually equal to only a few percent of the potential. Holm-Hansen pointed out that the understanding of interactions between biological, physical and geochemical processes in Antarctic waters was meagre in comparison with that for low latitudes.

Ecological factors can be studied in two different but complementary ways: by the experimental manipulation of individual environmental factors in the laboratory, and by the analysis of extensive sets of field data obtained under a wide variety of recorded environmental conditions. We have used the second approach in an attempt to relate the distribution of diatom communities and dominant species around South Georgia described by Theriot and Fryxell (1985) to corresponding environmental data sets available for the same period, 24 November–19 December, 1981. These range in scale from mesoscale water circulation to concentrations of dissolved nutrients and zooplankton abundance.

Environmental factors act synergistically. One variable may also act in several ways to influence overall variation in phytoplankton species composition and biomass. Consequently no single factor is likely to be identified as ecologically important from a subjective comparison of species and environmental data, even though this method may be effective over larger time- and space-scales (e.g. Hart 1942). Simple statistical comparisons produce equivocal results at best under these circumstances. We have therefore used multivariate analyses to reduce the interstation variability to a low dimensional, and therefore comprehensible, level before discussing the biological relationships (Allen and Skagen 1973, Jeffers 1978, Gauch 1982, Grieg-Smith 1983). Many permutations of the data sets were analyzed but only those which we believe informative are reported here.

Methods

Temperature and salinity were measured against pressure (depth) using a Plessey 9041 STD-SV telemetering underwater unit and data logger, interfaced with a dedicated microcomputer system. Calibration data were obtained from reversing thermometer readings and the laboratory estimation of salinity using an inductive salinometer (Guildline Autosal). Water samples were obtained using Niskin bottles on a General Oceanics rosette system attached to the STD unit. Species composition

of plankton diatoms for each station was based on multivariate analysis of counts from vertical net haul samples (Theriot and Fryxell 1985 – see also below). Chlorophyll and phaeopigment concentrations in water samples were estimated following filtration of one litre subsamples onto fine glass fibre filters (Whatman GF/C) under slight vacuum and extraction of the filters in 90% acetone in the dark at 0 °C for 24 h. Fluorescence of the extract was measured before and after acidification (UNESCO 1980) using a Turner-Amsco model 111 fluorometer. Dissolved reactive 'silica' (molybdate-reactive silicon), nitrate-nitrogen and phosphate-phosphorus were estimated using standard autoanalytical techniques (Technicon 1976, Stainton 1974, Treguer and Le Corre 1975, respectively). The abundance of the Antarctic krill, *Euphausia superba* Dana, and other zooplankton was estimated hydro-acoustically using a Simrad EKS120 (120 kHz) echosounder with a QM Mk II echointegrator. A crude index of zooplankton abundance, scored from one to seven, was assigned to each station from a map of acoustic data (Fig. 7) supplied by Dr. I. Everson (DAS). Multivariate analysis of environmental and species data was carried out using the SAS statistical package (SAS Institute Inc. 1982). Principal components were calculated from the product-moment correlation matrix. Details of principal components analysis (PCA) and canonical correlation analysis (CCA) are given in standard textbooks on multivariate statistics and their applications such as Kendal (1975) and Gauch (1982).

Description of the Study Area

Water Masses and Circulation in the Scotia Sea

South Georgia lies in the Antarctic Circumpolar Current, 2000 km east of Cape Horn. On entering the Scotia Sea the Antarctic Circumpolar Current is deflected north and west by the submerged ridge of the Scotia Arc, before it turns east again to flow around South Georgia and across the Atlantic Ocean sector of the Southern Ocean (Fig. 2) (Deacon 1933, 1937, Gordon and Goldberg 1970). It consists of sub-Antarctic and Antarctic Surface Waters from the Pacific Ocean sector of the Southern Ocean and the Bellingshausen Sea (Clowes 1934, Nowlin and Clifford 1982). Some mixing with Weddell Sea Surface Water occurs in the Scotia Sea. However the southern arm of the Scotia Ridge effectively restricts the flow of water out of the Weddell Sea (Carmack and Foster 1975) and most enters the Scotia Sea across the Weddell-Scotia Confluence east of the South Orkney Islands (Gordon 1966, 1967). Consequently there is a marked gradient of mixing across the Scotia Sea with the influence of Weddell Sea Surface Water being greatest to the south and east of South Georgia. The geographic positions of the boundaries (fronts) between sub-Antarctic, Antarctic and Weddell Sea Surface Waters vary almost continuously under the influence of a series of atmospheric depressions that drive the water circulation. The maximum displacement is limited by the bottom topography (Gordon and Goldberg 1970) but may be as much as 100 nautical miles (186 km). This is sufficient to affect the composition of the water flowing around South Georgia. Fortunately the core characteristics of the original waters mixing in the Antarctic Circumpolar

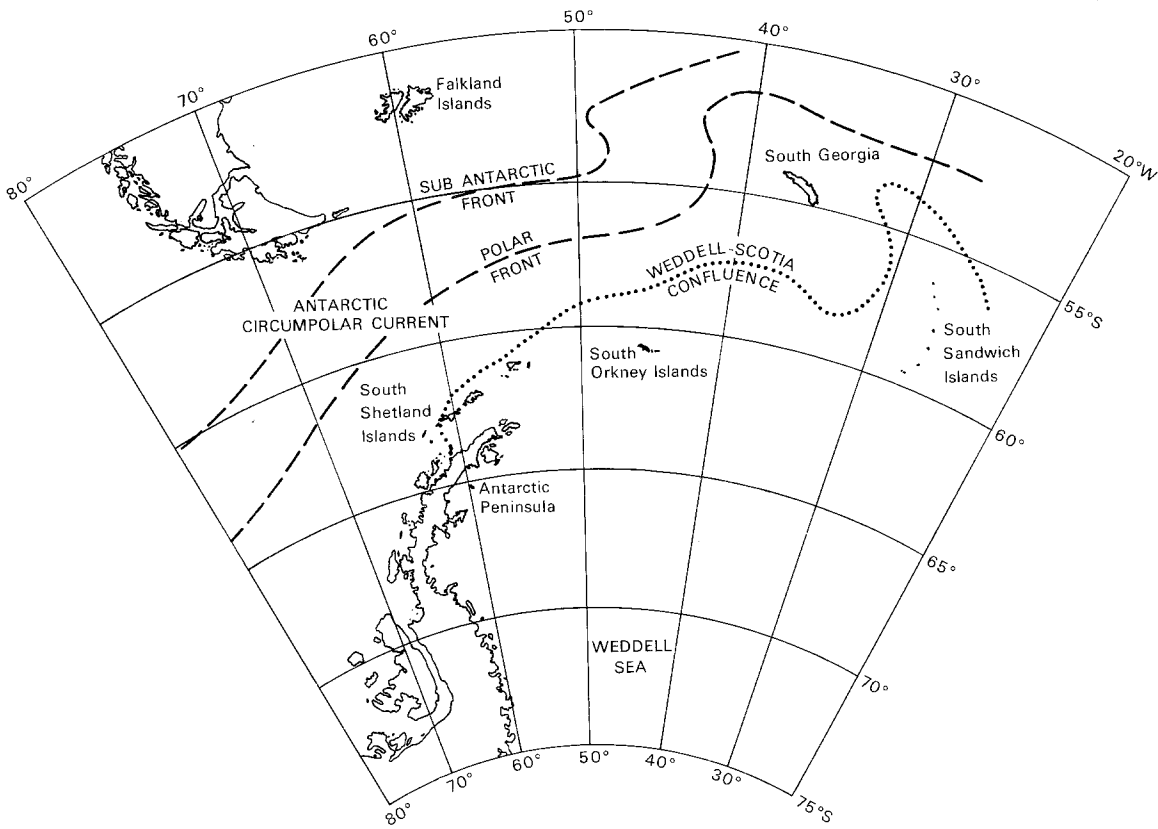


Fig. 2. Map of the Southern Ocean between 20°W and 80°W showing the Scotia Ridge and the Antarctic Circumpolar Current (after Gordon 1967). The Scotia Ridge (mentioned in the text) is a submarine ridge joining South America to the Antarctic Peninsula via South Georgia and the South Sandwich and South Orkney Islands

Current are very distinctive and permit the identification of their relative influence at any station. The potential-temperature and salinity of the Surface Water at a station in the southern Drake Passage was -1.06°C and 34.07‰ below the depth of seasonal warming in February 1982 (Fig. 3). Equivalent values recorded in the same month for the Weddell Sea were -1.72°C and 34.40‰ . Temperatures in the Scotia Sea were warmer due to the greater influence of the Warm Deep Water (-0.56°C) but a salinity of 34.36‰ clearly indicated that the contribution of water from the southern Drake Passage and the Weddell Sea were almost equal south of the South Georgia zone. However a core salinity of around 34.00‰ recorded for the Antarctic Surface Water at all 63 stations within the South Georgia zone indicated that water of Weddell Sea origin was not present during the period of study. The relatively low silica concentrations recorded of 20 to 50 mmol m^{-3} support this conclusion.

Water Masses and Circulation Around South Georgia

Analysis of individual potential-temperature-salinity profiles indicated that at least six distinct water masses were present within the South Georgia zone (Fig. 4). Their origin can be described in conjunction with the chart of geopotential topography (Fig. 5 b). The isolines indicate current flow and relative velocity. The pattern

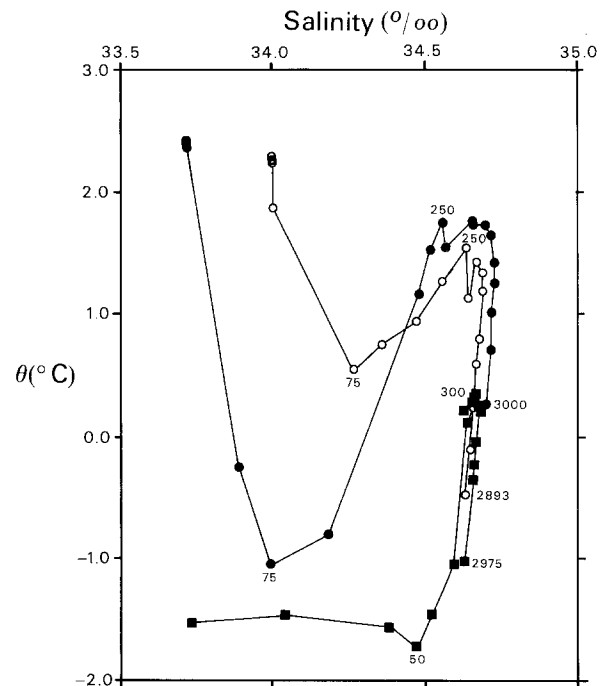


Fig. 3. Potential-temperature-salinity relationships at three stations. (●) southern Drake Passage ($62^{\circ}59.8'S$, $66^{\circ}34.9'W$) 13 February 1982; (■) Weddell Sea ($63^{\circ}58.0'S$, $49^{\circ}57.2'W$) 24 February 1982; (○) Scotia Sea ($57^{\circ}59.9'S$, $43^{\circ}05.5'W$) 1 March 1982

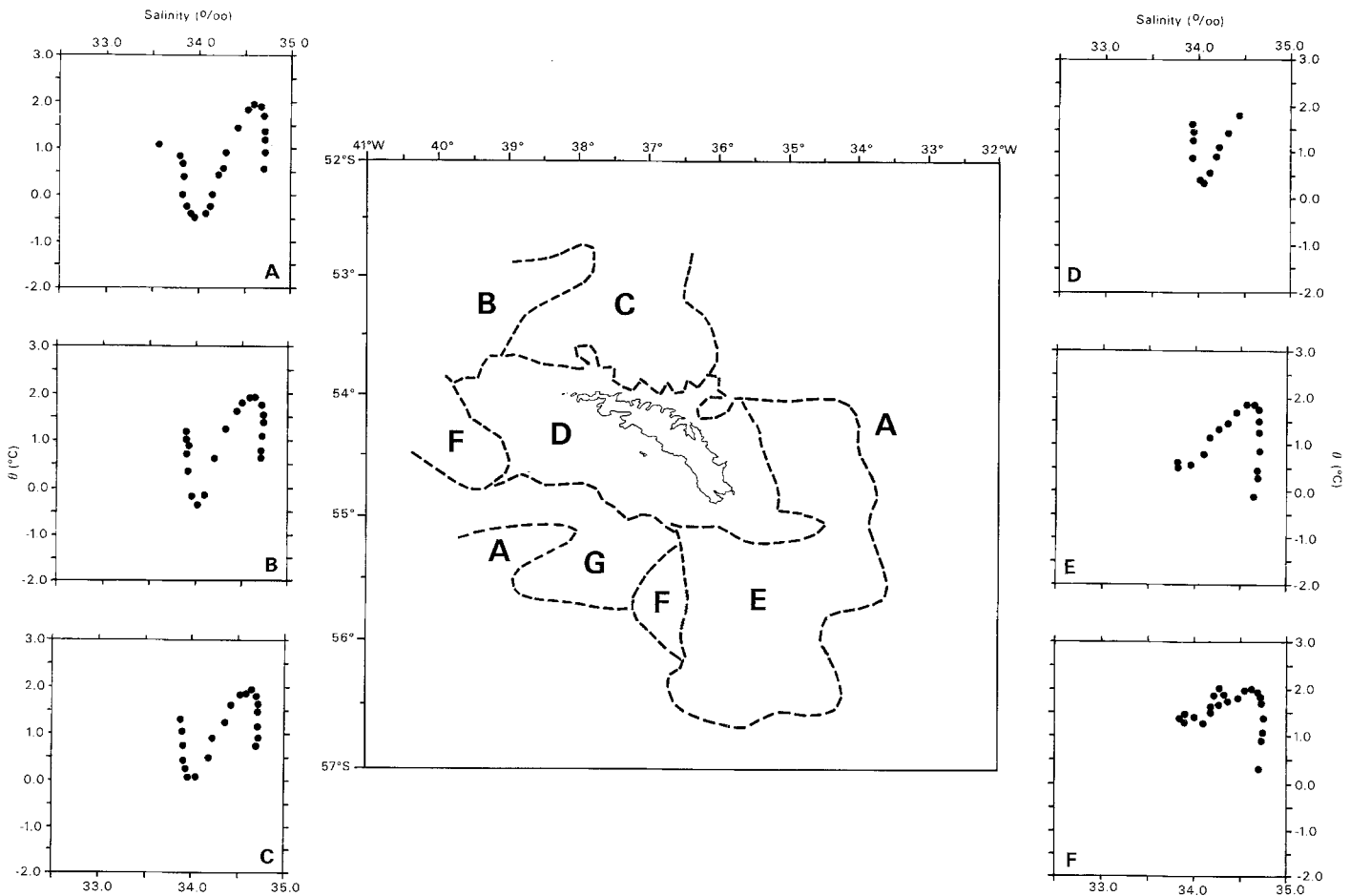


Fig. 4. The distribution of the different water masses found around South Georgia in November-December 1981 (central panel), based on the potential-temperature-salinity relationship detailed in A–F. The complex Water Mass G is described in the text

obtained was similar assuming a horizontal surface at any level below 75 m. Absolute values for the geostrophic currents could not be calculated because a level of ‘no motion’ could not be defined for the area. However approximate current speeds were calculated for the outer stations using 3000 dbar as the reference level. Values of 15.4 to 22.6 cm s^{-1} were obtained for the main flow off the southern shelf, and 5.1 to 12.3 cm s^{-1} for the mixed currents off the northern shelf of the island.

It would appear that the main flow of Antarctic Surface Water was from the west. The Scotia Ridge deflected most of this water eastwards along the southern edge of the South Georgia slope. The origin of Water Mass A appeared to be Antarctic Surface Water from the Pacific sector of the Southern Ocean and from the Bellingshausen Sea. The large anticyclonic gyre off the south-east corner of the island turned some of this water north and then west along the north coast, where it gradually lost its original identity to become Water Mass C after mixing with the locally modified shelf water – Water Mass D – and with Water Mass B. The latter was the remainder of the main inflow of water from the west which had been deflected along the northern edge of the Scotia Ridge.

The potential-temperature-salinity characteristics are very similar to Water Mass A. The near-surface layers (0–100 m) were slightly more saline which could indicate some mixing with sub-Antarctic water carried in eddies across the sub-Antarctic Front. Some of the Water Mass A water remained in the circulation of the gyre to mix with Water Mass D and Water Mass F waters to form Water Mass E. The origins of Water Mass D could have been in both Water Mass A and Water Mass B. The very distinctive Water Mass F was formed from the mixing of Antarctic Surface Water and Warm Deep Water by turbulent flow, down-current of underwater mounts. The potential-temperature-salinity profile for each station in Water Mass G was unique, and presumably reflected a complex mixing of Water Masses A, D, E and F.

Surface Water Stability and Radiation Climate

For this study it has been assumed that the pycnocline started where the density increased by 0.03 kg m^{-3} within 10 m. The depth of this layer differed considerably from station to station, ranging from 60 to 160 m (Fig. 5c). The nature of the pycnocline also differed, the

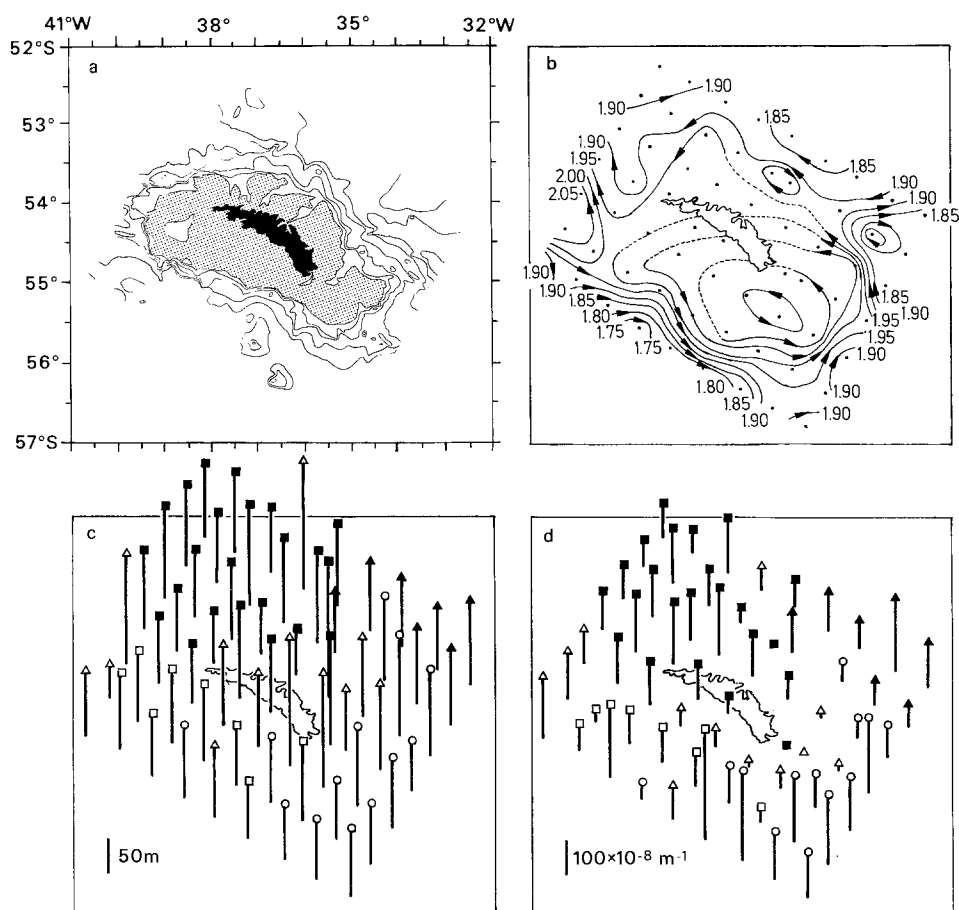


Fig. 5a–d. Physical features of the study area in November–December 1981. **a** Bathymetry. The shelf, shown by the stippled area, is bounded by the 250 m isobath. Remaining contours are 500 m, 1000 m, 2000 m, 3000 m, 4000 m, 5000 m (modified from Heywood and Allen 1984); **b** Geopotential topography of the sea surface drawn from dynamic heights calculated for the 250 dbar level; **c** Values for pycnocline depth ('flags' correspond to diatom sector symbols used in Fig. 1); **d** Stability, E over the top 100 m of the water column

changes in density varying in intensity and regularity. There was also wide variation in the stability (E) calculated for the top 100 m of the water column but all the values were low (Fig. 5d), reflecting variation in depth of pycnocline and homogeneity of the Surface Water layer. No obvious correlation of pycnocline depth or stability with bathymetry, water mass or preceding weather could be discerned. The weather records maintained by the Deck Officers indicate a mean wind speed of around 20 knots for the study period. The frequent strong winds must have caused considerable vertical and horizontal mixing in these waters of neutral or low stability. Lateral movement of the surface water layer may have carried phytoplankton communities across the intergrading boundaries between water masses.

Information on the penetration of photosynthetically active radiation (PAR) is available for only 23 of the stations (Dr. T. M. Whitaker, personal communication). The depth to which 1% of incident PAR penetrated (the usual definition of the euphotic zone) varied from 20 to 90 m. Corresponding values for 0.1% of incident PAR were 30 to 130 m. These data agree with published values for euphotic depth in the Scotia Sea (Walsh 1971, Table 3, Glibert et al. 1982). It is clear, therefore, that most if not all of the euphotic zone must have been within the mixed water layer at each station. Analysis of variance showed no significant differences in either pycnocline

depth or E for comparisons between water masses or diatom sectors. Effects of vertical mixing on the radiation environment of the phytoplankton could not therefore have contributed significantly to biomass variability or species distributions.

Inorganic Nutrients

Data on three inorganic nutrients – nitrate-nitrogen, phosphate-phosphorus and silica – were available for the stations in the study area. Each nutrient showed a complex pattern of variability in distribution of amount integrated for the top 100 m of the water column (Fig. 6a–c). However the stations forming the northern group of diatom sectors (Fig. 1) had higher mean concentrations than stations forming the southern group of diatom sectors (Table 1). Analysis of variance also revealed some significant differences between single sectors. Sector 6 had higher silica levels than any other sector ($P < 0.01$ for all values of F), and Sector 5 had higher levels of all nutrients than Sector 3 ($P < 0.05$ for all values of F).

Plankton Biomass

Highest values of phytoplankton biomass, as particulate chlorophyll *a*, were associated with stations in the north-west of the study area, although distribution was patchy

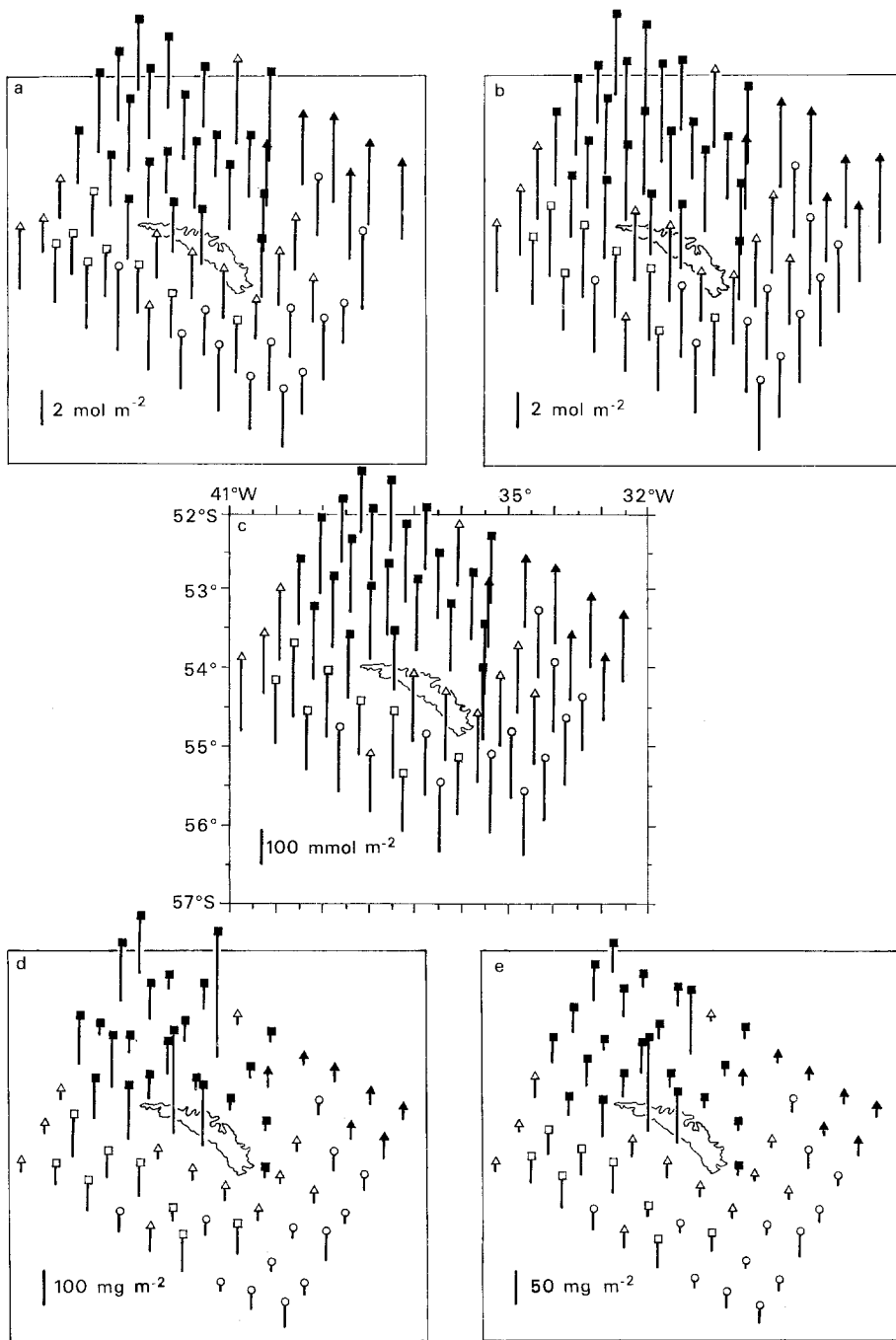


Fig. 6a–e. Distribution of inorganic nutrients and plant pigments, integrated over 100 m depth, November–December 1981. **a** silica; **b** $\text{NO}_3\text{-N}$; **c** $\text{PO}_4\text{-P}$; **d** particulate chlorophyll *a*; **e** particulate phaeopigments

here (Fig. 6d). A second area with high levels of chlorophyll *a* was present along the southern edge of the study area. Overall distribution was markedly heterogeneous and could not be associated subjectively with any feature of the physical or chemical environment. Distribution of phaeopigments was also patchy (Fig. 6e) but followed closely that of chlorophyll *a*.

The regions of highest zooplankton biomass were in the northeastern quadrant of the study area (Fig. 7). Zooplankton abundance appeared to have no congruence with the pattern of water masses (Fig. 4) or with the distribution of phytoplankton biomass (Fig. 6d).

Diatom Community Distribution

The five diatom sectors defined by Theriot and Fryxell (1985) are reviewed briefly here as biogeographic boundaries within the study area (Fig. 1). We believe the spatial pattern of species distribution did not change significantly during the 23 day period of the study. If temporal change were more significant than spatial variation, the sectors would reflect the chronology of sampling, indicated by station numbers in Fig. 1, and might also exhibit a strong correlation with phytoplankton biomass as the populations changed over time. Neither trend is evident.

Table 1. Simple statistics of environmental data, all variables integrated to 100 m depth except krill abundance which was integrated to 200 m. Note that 63 stations formed the complete grid of the South Georgia Zone Survey for environmental data, but one of these stations was duplicated for the phytoplankton net hauls giving the 64 stations analysed by Theriot and Fryxell (1985). Samples are pooled for all stations, and separately for the northern diatom sectors (5+2) and for the southern sectors (3+4+7). Differences between mean values of each inorganic nutrient for northern and southern stations were all significant at $P < 0.05$ according to analysis of variance F -test for equal means. N is the number of observations. Zooplankton abundance ('krill') scores are derived from Fig. 7

Variable	N	Minimum	Mean	Maximum	Units
All sectors pooled					
Chlorophyll a	63	14.11	59.62	363.03	mg m^{-2}
Phaeopigment	63	3.51	22.36	133.15	mg m^{-2}
Silica	61	1.98	3.25	5.07	mol m^{-2}
$\text{NO}_3 - \text{N}$	62	2.61	3.97	5.53	mol m^{-2}
$\text{PO}_4 - \text{P}$	59	151.92	185.09	218.79	mmol m^{-2}
Krill score	63	1	3.4	7	score
Northern sectors pooled					
Silica	29	2.31	3.67	5.07	mol m^{-2}
$\text{NO}_3 - \text{N}$	30	3.11	4.15	5.53	mol m^{-2}
$\text{PO}_4 - \text{P}$	29	170.35	189.55	213.89	mmol m^{-2}
Southern sectors pooled					
Silica	32	1.98	2.94	4.78	mol m^{-2}
$\text{NO}_3 - \text{N}$	32	2.61	3.80	4.45	mol m^{-2}
$\text{PO}_4 - \text{P}$	30	151.92	180.78	218.79	mmol m^{-2}

The diatom sectors were defined in the context of a selection of the most widespread taxa and the principal components on which these sectors were distinguished are linear combinations of all the taxa used. However Theriot and Fryxell (1985) list certain taxa which typify sectors or groups of sectors and these can be equated with the 'indicator species' of classical community ecology. Authorities for species names are given by Theriot and Fryxell (1985). *Chaetoceros curvisetum*, *Chaetoceros socialis* and *Thalassiosira scotia* characterize the large number of stations forming Sector 5 in the north of the study area (Fig. 1). *Chaetoceros criophilum* was most abundant in Sector 6. The centric diatom *Corethron criophilum* occurred at all stations but was more abundant in Sectors 5 and 6. Southern sector stations shared a high incidence of *Nitzschia kerguelensis*. Sector 4 stations also had high abundances of *Thalassiosira lentiginosa* and the silicoflagellate *Distephanus speculum*. Sector 3 was further characterized by *Thalassiosira gravida*. The southeastern stations forming Sector 7 were dominated by *Nitzschia lineola* and *Eucampia balaustium*.

Differentiation in diatom populations was most marked between 'northern' stations (Sectors 5 and 6) and 'southern' stations (Sectors 3, 4 and 7). This appeared to correspond to water mass distribution (Fig. 4). The most pronounced difference between diatom sectors occurred at the western end of the study area, where eastward flowing water first impinged on the island shelf. Both cir-

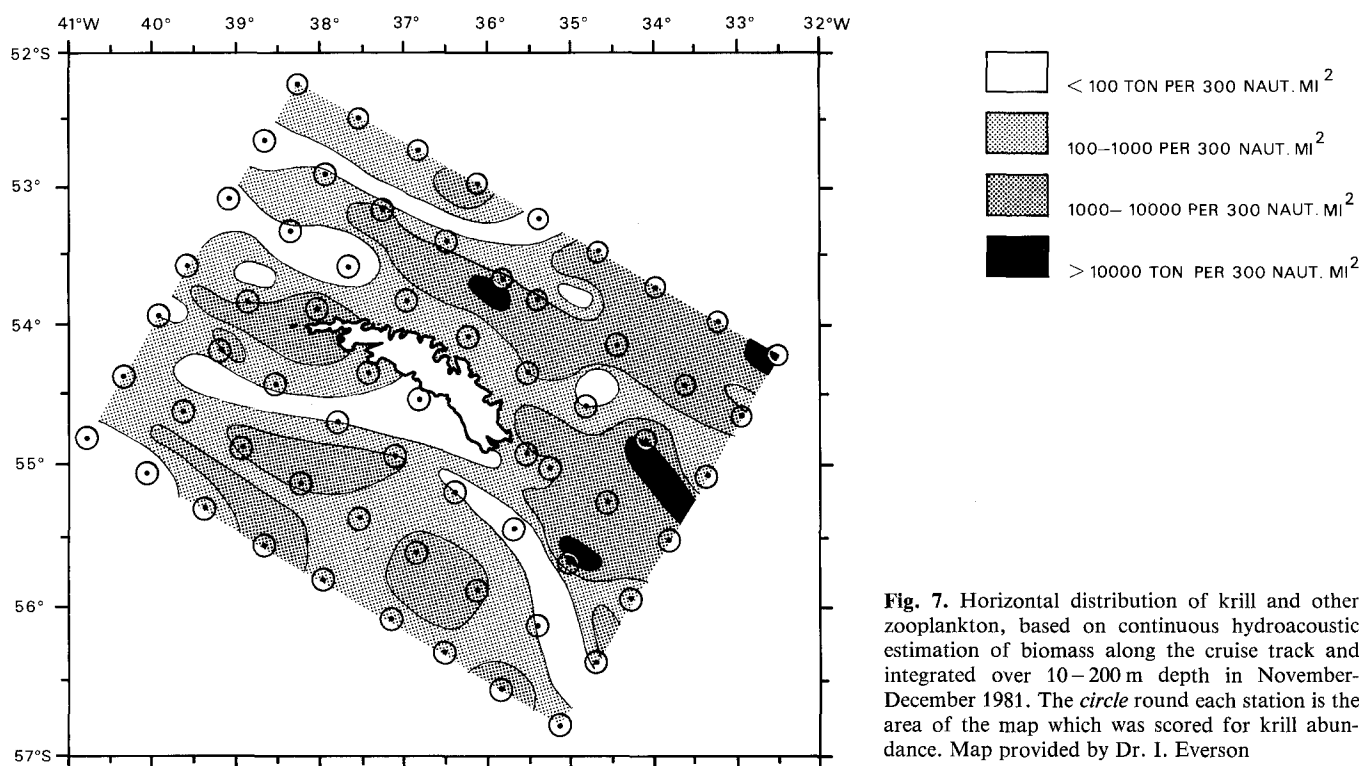


Fig. 7. Horizontal distribution of krill and other zooplankton, based on continuous hydroacoustic estimation of biomass along the cruise track and integrated over 10–200 m depth in November–December 1981. The circle round each station is the area of the map which was scored for krill abundance. Map provided by Dr. I. Everson

ulation and boundaries between sectors were less discrete in the eastern (down-current) half of the study area. The convoluted boundaries between southern sectors may reflect the meandering flow of the currents along the southern edge of the South Georgia shelf.

Multivariate Analysis of Data

This series of multivariate analyses explores variability across the entire study area. In each case, the composition of principal components or canonical variates is presented in tabular form with a brief interpretation in the text. Identification of processes associated with components or variates is suggested by the different loadings and coefficients of the variables. Ordination of stations in relation to the variables is presented. A simple overview of the relationship between phytoplankton biomass, nutrients and grazing is developed to incorporate biogeographic patterns. Reference is made in a few cases to analyses not presented explicitly in this paper.

Phytoplankton Biomass and Environmental Variables

Principal components analysis (PCA) was carried out using five environmental variables and phytoplankton biomass (Table 2). Missing data reduced the numbers of stations analyzed to fifty-seven. Integrated phaeopigment amount was expressed as a proportion of the 'total plant pigment' because phaeopigment on its own was a redundant datum, being highly correlated with chlorophyll *a* amount ($r = 0.89$, $P < 0.01$). Pigment ratio ($PR = \text{phaeopigments} : \text{chlorophyll } a + \text{phaeopigments}$) was only slightly correlated with chlorophyll *a* ($r = -0.25$) and represents a more useful index of pigment degradation in the particulate material sampled. However acid-shift of fluorescence provides only a crude index of phaeopigment amount and does not distinguish between pigment degradation through senescence and through grazing (Gowen et al. 1983). The variable, 'krill score' ($\equiv \text{ZOO}$ -

plankton abundance) was taken to represent grazing pressure.

The process accounting for most variability between stations (Table 2, axis 1) appears to have been a decrease in all nutrients associated with high phytoplankton biomass. No single inorganic nutrient of the three analyzed emerged as being of overwhelming importance, although nitrate-nitrogen showed a stronger negative correlation with chlorophyll *a* than either phosphate-phosphorus or silica. Bivariate correlations had also shown no significant relationship between chlorophyll *a* amount and any of the three inorganic nutrients.

Grazing was implicated as an important process by the second axis of this PCA. An inverse relationship between 'krill score' and pigment ratio indicated an effect of grazing on the 'quality' of the phytoplankton cells. We explain this by assuming that heavy grazing pressure would produce a low PR where phaeopigment was lost rapidly from the upper water column in faecal material (Lorenzen and Welschmeyer 1983) and the remainder of the population contained few senescent cells (Pennington 1941, Gliwicz 1975). High silica and low phosphate-phosphorus were associated with this interaction, reflecting in part the coincidence of high zooplankton abundance and high silica in the northeast quadrant of the study area.

A second effect of grazing was evident from the composition of the third axis (Table 2). Some stations could be identified at which high phytoplankton biomass and phosphorus amount coincided with low PR and grazing pressure. The low PR suggests heavy grazing had occurred recently at these stations. Phosphate-phosphorus and silica were again negatively related: the ratio Si:P may be an important chemical variable in the study. This and the remaining axes segregate mainly outliers among the stations, rather than identify trends common to all.

Ordination of stations for this PCA has been carried out using scores from the first two axes. A scatter plot shows that neither of the ecological processes implicated in interstation variability (nutrient uptake and grazing) can be identified with a particular diatom sector (Fig. 8). Stations from most sectors scatter uniformly across the plot, indicating that the processes are common to all sectors. The few stations forming Sector 6 are an exception to this in that they all have positive scores on the first axis and negative scores on the second axis. This reflects the uniformly high krill abundance and silica amounts in the northeast quadrant of the study area.

Species Composition and Environmental Variables

Species composition was first introduced into the range of variables examined by using canonical correlation analysis (CCA). CCA differs from PCA in that relationships are not examined in the context of all the variables together. Species variables are summarized as a set of canonical variates (linear combinations of variables) and a second set, of environmental variates, is similarly gener-

Table 2. Loadings of plankton biomass and inorganic nutrient variables (standardized to zero mean and unit variance) on axes of a principal components analysis. Axis loadings exceeding ± 0.25 , arbitrarily considered high, are shown italicized

Axis	Eigenvalue	Proportion of total variance		
PC1	1.8183	0.30		
PC2	1.2919	0.22		
PC3	1.0210	0.17		
		0.69		
Variable	Loadings (eigenvectors)			
	PC1	PC2	PC3	
Chlorophyll <i>a</i>	-0.48	0.11	0.48	
Pigment ratio	0.16	-0.65	-0.48	
Silica	0.38	0.32	-0.16	
NO ₃ -N	0.61	0.09	0.21	
PO ₄ -P	0.48	-0.17	0.57	
Krill score	0.09	0.65	-0.36	

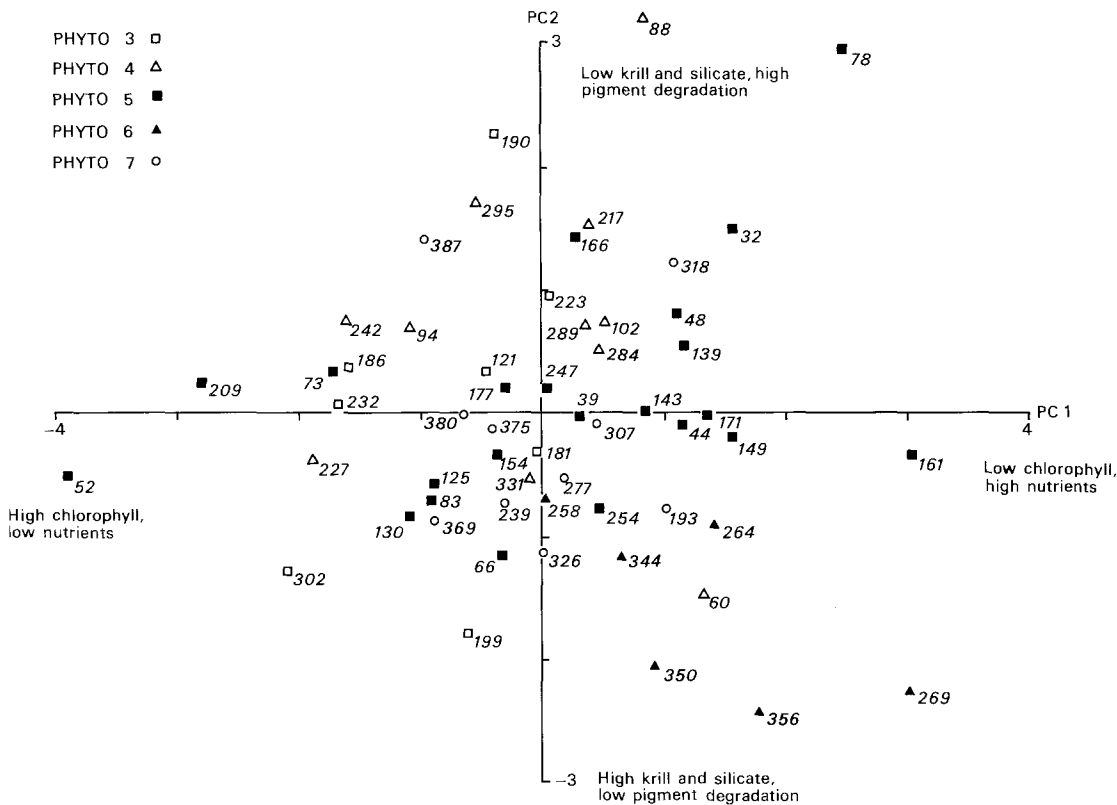


Fig. 8. Scatter plot of 57 stations around South Georgia with respect to axes 1 and 2 of PCA using environmental data and phytoplankton and krill abundance (Table 2)

ated. The species variates are then manipulated to maximize their correlation with the environmental variates (Gauch 1982, Carleton 1984). The proportionate abundances of 13 species were used in the analysis rather than the 27 taxa used by Theriot and Fryxell (1985) to define the diatom sectors. The criterion for the selection of species was the possession of significant correlations ($P < 0.05$) with at least three of the variables in the environmental variate. These consisted of the six variables used in the PCA plus the distance offshore.

The scatter of stations with respect to the first canonical variates separates the 'northern' and 'southern' groups of diatom sectors (Fig. 9). *Chaetoceros criophilum* was again shown to be the characteristic taxon of the 'northern' Sector 6. The widespread *Nitzschia kerguelensis* and the two *Thalassiosira* species, *T. tumida* and *T. gravida* distinguish the sectors of the 'southern' group. Silica, nitrate-nitrogen and grazing pressure determined the environmental variation.

The second canonical variates separate the diverse group of stations forming Sector 5 from the remainder (Fig. 9), on the basis of a population increase in two diatoms – *Chaetoceros socialis* and *Thalassiosira scotia*. These species had produced the high chlorophyll abundance at some stations in the sector, mainly over the shelf. The importance of *Chaetoceros criophilum* and krill abundance to these variates highlights the stations at Sector 6 at the opposite end of this cline.

Different species community information was used in another PCA, the final analysis of the series. Data for individual species could not be incorporated into a PCA because their greater variability would swamp the analysis, and consequently no relationship with environmental variables would be revealed. Instead we have used summary variables describing species composition derived from a PCA of the species correlation matrix carried out by Theriot and Fryxell (1985). These principal components are linear combinations of weighted proportionate abundances of selected species, the loadings of which reflect the importance of individual taxa in interstation variability. The taxa with high loadings are analogous to indicator species in subjective assessments of vegetation communities (Gauch 1982, Grieg-Smith 1983) but here may appear in more than one component. For convenience we refer to these principal components as 'species associations'. Details of the important species in each can be found in Theriot and Fryxell (1985) and will be highlighted below. Note that the character of these principal components encompasses variation between stations, but does not necessarily correspond to individual diatom sectors which are distinguished by using more than one principal component.

The loadings of environmental data on axes of this PCA correspond well with the results of the first analysis which dealt with environmental data alone (compare Tables 2 and 4). The addition of information on species

Table 3. Results of canonical correlation analysis for selected species and environmental variables, based on data for the 57 stations around South Georgia which had no missing environmental data. An asterisk indicates a product-moment correlation between values of the individual variable and values of the canonical variate of greater than or equal to ± 0.5 . Variables with such a correlation and a coefficient of greater than or equal to ± 0.25 (*italicized*) on an axis are considered to be 'associated' with the axis in the text. Only the first two canonical correlations (**Rc**) between corresponding species and environmental axes were significant ($P < 0.05$)

a Species variables	Coefficients	
	Var 1	Var 2
<i>Chaetoceros criophilum</i> Castracane	0.37*	0.58*
<i>Chaetoceros socialis</i> Lauder	-0.20	-0.31*
<i>Corethron criophilum</i> Castracane	0.09	0.02
<i>Distephanus speculum</i> (Ehrenberg) Haeckel ^a	-0.24	0.01
<i>Nitzschia angulata</i> (O'Meara) Hasle	-0.04	0.14
<i>Nitzschia kerguelensis</i> (O'Meara) Hasle	-0.35*	0.23
<i>Odontella weissflogii</i> (Janisch) Grunow	0.22	0.13
<i>Rhizosolenia hebetata</i> fo. <i>semispina</i> (Hensen) Gran	-0.03	-0.02
<i>Thalassiosira gravida</i> Cleve	-0.31	-0.06
<i>Thalassiosira lentiginosa</i> (Janisch) Fryxell	0.15	-0.02
<i>Thalassiosira scotia</i> Fryxell et Hoban	-0.07	-0.29*
<i>Thalassiosira tumida</i> (Janisch) Hasle	-0.52*	0.05
<i>Thalassiothrix longissima</i> Cleve et Grunow	0.08	0.17
b Environmental variables		
Chlorophyll <i>a</i>	0.23	-0.70*
Pigment ratio	-0.12	-0.04
Silica	0.80*	0.05
NO ₃ -N	0.30*	-0.35
PO ₄ -P	0.15	0.10
Krill score	0.26	0.39*
Distance offshore	-0.21	0.44*
c Canonical correlations (Rc)		
Rc	0.91	0.84

^a *Distephanus* is a silicoflagellate; all other taxa are diatoms

composition provides a spatial context for the processes identified by the first PCA of this study. This was not obvious from the earlier ordination of stations (Fig. 8). **Species Association 1** indicates a north-south cline in nutrient depletion correlated with high phytoplankton biomass on the first axis. **Species Association 3** on the same axis suggest there is a subsidiary west-east gradient. This is consistent with the high phytoplankton biomass present at some stations in **Sector 5** and agrees with the pattern indicated by the second canonical variates (Table 3, Fig. 9).

A group of southern and western stations with low phytoplankton biomass and moderate grazing pressure were identified by the second axis. Processes taking place at these stations probably correspond to the second grazing interaction identified earlier. Chemical nutrients had

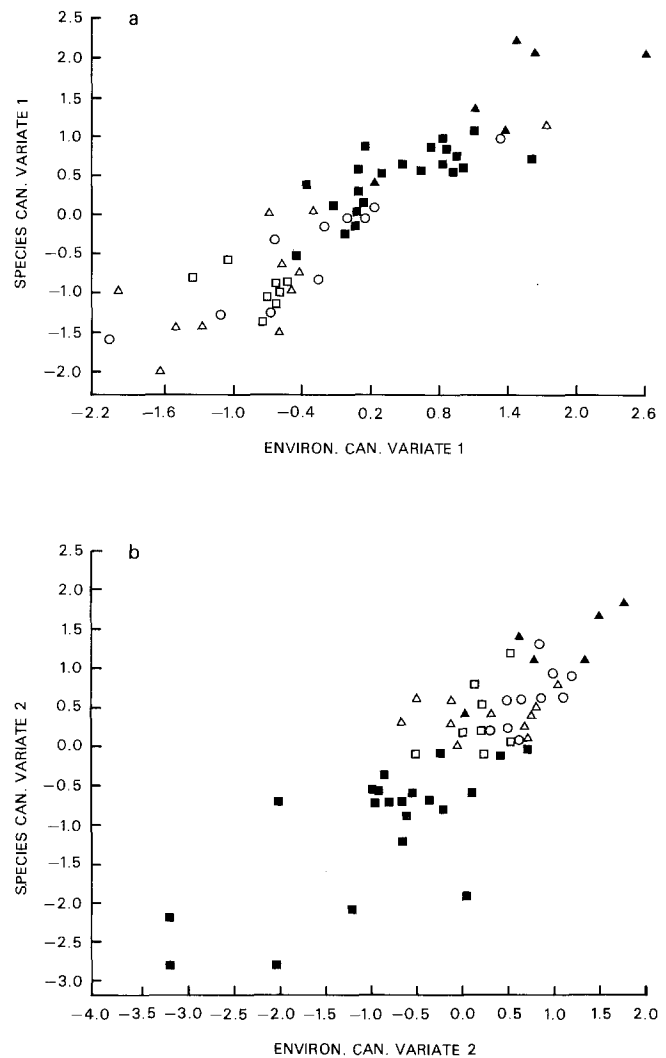


Fig. 9a, b. Scatter plots of stations around South Georgia with respect to species and corresponding environmental-canonical variates (ordinate and abscissa, respectively). **a** First canonical variates; **b** Second canonical variates. Note particularly that *filled symbols* represent the two northerly sectors (5 and 6)

low loadings on the axis but behaved in the same way as chlorophyll *a*, suggesting a gradient of total nutrient concentration where chlorophyll *a* indicated the particulate fraction of the nutrient pool rather than the dynamic capacity of the phytoplankton for nutrient uptake. This facet of phytoplankton-nutrient interactions was seen more clearly in the first PCA.

Species Association 2, important in the third axis of this analysis, identified particularly the stations of **Sector 4**. The pattern of variable loadings suggests that these stations could be characterized by low grazing pressure, low Si:P ratio and high *PR*, suggesting the grazing interaction highlighted in the previous PCA. *Thalassiosira lentiginosa*, small *Nitzschia* species and the silicoflagellate *Distephanus speculum* distinguished stations in this group.

Table 4. Loadings of variables on axes of principal components analysis of correlation matrix using both species and environmental data. Axis loadings exceeding ± 0.25 (*italicized*) are arbitrarily considered high loadings in text

Axis	Eigenvalue	Proportion of total variance
1	2.2732	0.21
2	1.7609	0.16
3	1.6107	0.15
		0.52

Variable	Loadings (eigenvectors)		
	Axis 1	Axis 2	Axis 3
Species Association 1	-0.37	0.55	0.08
Species Association 2	-0.00	0.05	0.38
Species Association 3	0.36	0.45	-0.06
Species Association 4	0.01	-0.11	0.23
Species Association 5	0.10	0.11	-0.32
Chlorophyll <i>a</i>	-0.30	-0.53	-0.24
Pigment ratio	0.00	0.24	0.37
Silica	0.44	-0.10	-0.27
NO ₃ -N	0.53	-0.14	0.10
PO ₄ -P	0.35	-0.18	0.45
Krill score	0.20	0.27	-0.45

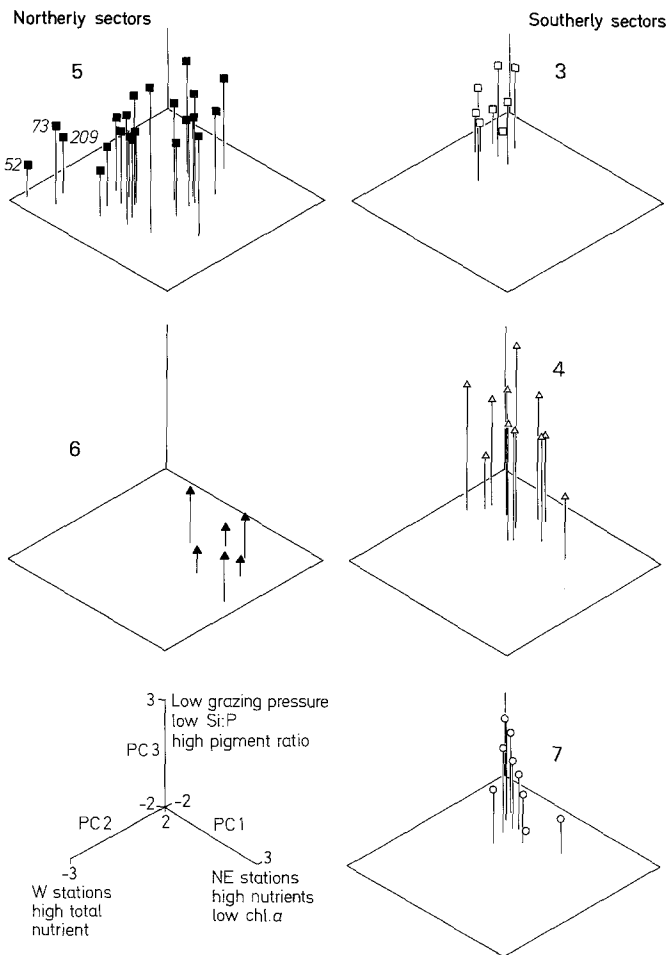


Fig. 10. Isometric diagrams of the scatter of stations from the five diatom sectors with respect to the first three axes of PCA using environmental and species data (Table 4). Three outlier stations of Sector 5 are identified

Intersector Variation

The first three axes of the last PCA account for just over half of the total interstation variation in the context of the 12 variables examined. Their value lies in the linking of biogeographic and environmental data. Scatter plots of the stations on any two of the axes still failed to separate individual sectors because no single ecological process could be ascribed to a sector. However, a description of each sector can be obtained from plots of the stations on the first three axes (Fig. 10).

Interstation variability in Sector 5 was large but a trend in the scatter could be detected. At one extreme stations with high phytoplankton biomass (e.g. 52, 73 and 209) had high total, but depleted dissolved, nutrient pools. Opposing stations were characterized by lower phytoplankton biomass and high *PR*. The impact of grazing was apparently low throughout this sector. High amounts of chlorophyll *a* and nitrate-nitrogen, and low grazing pressure had also served to separate Sector 5 stations from the remainder in the CCA.

Sector 6 stations formed a compact group in this ordination (Fig. 10). Heavy grazing pressure and high dissolved nutrient concentrations, especially silica, characterized all stations. Species composition of the diatoms was biased towards some large taxa such as *Chaetoceros criophilum* (virtually restricted to this sector) and *Corethron criophilum*, and some smaller-celled species were less common. The stations of Sector 6 had appeared as a distinct group in all the analyses carried out and were always easily distinguished from the neighbouring Sector 5.

Sector 4 was the most variable of the southern sectors. The cline in the station cluster was defined by a transition from high to low grazing pressure and nutrient content. Species associations with high loadings on the first axis of the last PCA are those reflecting the high variability of species composition in this sector. Low Si:P and slightly lower grazing impact separate most Sector 4 stations from those of Sector 5.

It is more difficult to characterize Sectors 3 and 7 with respect to other sectors using environmental criteria. Although both formed compact groups in ordinations involving species composition and environmental data (Figs. 9 and 10), they appeared to be subsets of the more variable Sector 4 and subject to the same environmental influences.

Discussion

The heterogeneity of the phytoplankton around South Georgia is typical of the Scotia Sea and most other areas of the Southern Ocean. A data set derived from a comparatively large number of stations sampled within a small area, and over a short period of time, allows the analysis of small-scale environmental interactions revealed as variation between stations. The data were not

obtained from an investigation into phytoplankton ecology and two potentially important variables were not measured. Data on ammonia are not available. It is present normally at much lower concentrations than nitrate in the Southern Ocean (Slawyk 1979, Glibert et al. 1982, M. J. Whitehouse and V. R. Woodley, BAS, personal communication) yet appears to be the preferred nitrogen source for Antarctic marine phytoplankton (Slawyk 1979, Biggs 1982, Glibert et al. 1982). Data on phytoplankton species composition is restricted to diatoms and therefore reflects only one facet of the community. Nanoplankton may form a significant fraction of the photoautotrophic biomass. Bröckel (1981) found 12 to 22% of the phytoplankton carbon occurring in the size fractions $\leq 20 \mu\text{m}$ at three stations near South Georgia. Other large-celled phytoplankters such as dinoflagellates were scarce in the samples used for the present data set. Large-scale variables such as the annual variation in radiation climate, and constant environmental features such as the low water temperatures, are also important in determining the character of Antarctic marine phytoplankton but fall outside the scope of this investigation.

Our analyses show that the species composition of the diatom communities in the study area reflected the previous history of the water masses, and boundaries between communities showed a high degree of congruence with divisions between water masses. Local changes were superimposed upon this pattern and these could be related to nutrient interactions and grazing pressure.

Water Masses and Phytoplankton Species Composition

The water masses and diatom sectors were defined using very different criteria yet the congruence between them suggests that much of the variation in species composition could be linked to the immediate history of the water masses. Physical and chemical characteristics of water around South Georgia reflected local modification of Antarctic Surface Water from the Pacific Ocean sector of the Southern Ocean, including the Bellingshausen Sea (Fig. 2). The pronounced distinction between the northern and southern diatom sectors in the west of the study area must reflect separation of the Antarctic Circumpolar Current into two streams flowing north and south of the Scotia Ridge. The pattern is disrupted by the island, and gyres and meanders on the eastern side were reflected in the convoluted boundaries between diatom sectors.

No evidence could be found for the presence of water of Weddell Sea origin in the study area. This contrasts with the results of the other major study in the area, undertaken during the Discovery Investigations in the 1920's and 1930's (Hart 1934, 1942, Hardy and Gunther 1936, Hendey 1937). The confluence between Scotia Sea and Weddell Sea waters was then situated very close to South Georgia (Deacon 1933). Mixing between the two water masses took place within the present study area in 1926–27 (Hardy and Gunther 1936, Fig. 6). This situ-

ation appeared consistent through the early 1930's (Hart 1934). There is now some evidence for considerable annual variation in the geographic position of the boundaries between the main water masses near South Georgia (Heywood et al. 1985). Deacon (1977) has demonstrated a correlation between mean water temperature of the 0–50 m layer and mean air temperature, and has shown an overall rise of about 1 degree Celsius in the annual mean air temperature between 1925 and 1975. Deacon's supposition of a corresponding rise in water temperature is supported by recorded water temperatures. The lowest and highest temperatures were in 1928 and 1963, respectively. The geographic positions of the polar fronts in Drake Passage and the Scotia Sea must be the major influence determining which phytoplankton species are present around South Georgia. The evidence for profound differences in circulation near the island between the period of the Discovery Investigations and the present investigation implies no a priori expectation of similarity between the two diatom species distributions. Comparison shows that some anomalies in the species distributions can be traced to differences in hydrology. *Chaetoceros criophilum* was widespread around the island during December–January 1926–27. However it predominated in Weddell Sea water and in the mixing zone with "Bellingshausen" water (Hardy and Gunther 1936, Fig. 26). In the present study this species characterized Sector 6 and was very restricted in its distribution outside it (although it is reported widespread in the Southern Ocean as a whole). Sector 6 is the closest sector to the likely position of the Weddell-Scotia Confluence (Fig. 2) but potential-temperature-salinity characteristics and silica concentrations at stations in this sector were within the ranges expected for Scotia Sea water. *Chaetoceros socialis* was very abundant during the 1926–27 summer survey but occurred almost exclusively to the south of the island (Hardy and Gunther 1936, Fig. 28). It was found in high abundance only at some stations in the northern Sector 5 during the present survey. However, another common diatom, *Nitzschia kerguelensis*, had similar distributions in both surveys (Hardy and Gunther 1936, Fig. 31, cited as *Fragilaria antarctica*). Comparison of major species distributions around South Georgia during the two surveys is summarized in Fig. 11. Although some differences can be ascribed to changes in the pattern of mesoscale circulation, some other features remain unexplained.

Interstation Variation Associated with Small-Scale Factors

The local pattern of species composition and biomass distribution was modified by ecological interactions. The involvement of two environmental influences was identified: availability of dissolved inorganic nutrients and grazing by zooplankton.

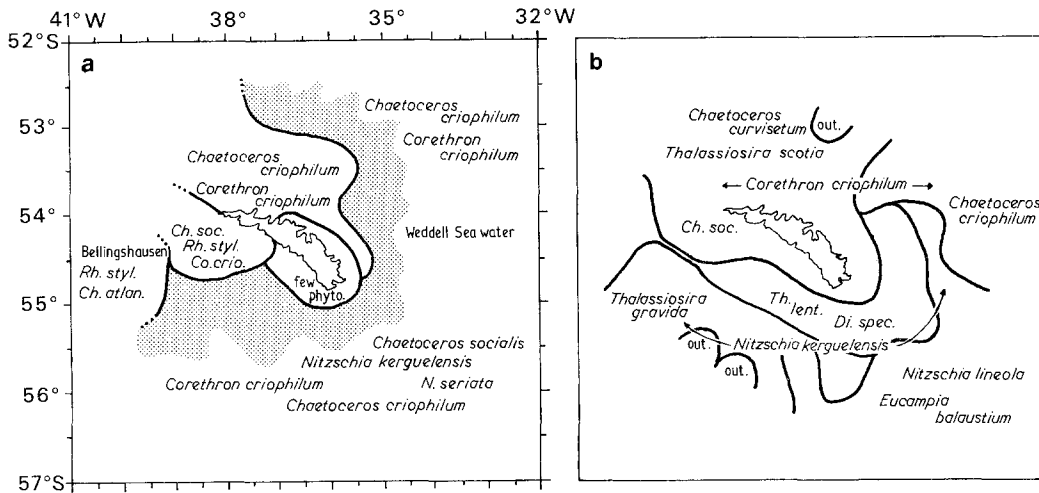


Fig. 11 a, b. Comparison of diatom species distributions around South Georgia. **a** Data from Discovery Investigations, showing the influence of Weddell Sea water (stippled area). Compiled from the data for 1926–31 from Hart (1934) and Hardy and Gunther (1936); **b** Data from November–December 1981, based on Theriot and Fryxell (1985). The narrow isthmus between the two parts of Sector 4 (south-west quadrant) reflects similarity of stations but does not imply physical continuity. Three outlier stations (out) are identified. Two species, *Corethron criophilum* and *Nitzschia kerguelensis*, were proportionately abundant in more than one sector. Abbreviations of species names are: *Ch. atlant.* = *Chaetoceros atlanticum*, *Ch. soc.* = *C. socialis*, *Co. crio.* = *Corethron criophilum*, *Di. spec.* = *Distephanus speculum*, *Rh. styl.* = *Rhizosolenia styliformis*, *Th. lent.* = *Thalassiosira lentiginosa*

The availability of inorganic nutrients can affect both species composition and production (hence biomass). However the concentrations of the major nutrients south of the Subantarctic Front appear to be greatly in excess of phytoplankton requirements (Hart 1942, Holm-Hansen et al. 1977, Slawyk 1979, Glibert et al. 1982, El-Sayed 1984, Heywood and Whitaker 1984, Holm-Hansen 1985). Ecological investigations of mesoscale phytoplankton variability (Walsh 1971) and culture enrichment and bioassay experiments (Hayes et al. 1984) support this. High levels of $\text{NO}_3\text{-N}$, $\text{PO}_4\text{-P}$ and silica were found around South Georgia during the period of this study. Only $\text{NO}_3\text{-N}$ showed a statistically significant, albeit weak, relationship to phytoplankton biomass. However, multivariate analysis of interstation variability showed that there was a stronger, inverse relationship between phytoplankton biomass (particulate chlorophyll *a*) and a combination of the dissolved nutrients measured. The diminution of the total nutrient pool by phytoplankton growth was clearly demonstrated although no single nutrient could be identified as being important in determining phytoplankton variation.

Another feature of the dissolved nutrient pool was implicated in interstation variability. An inverse relationship between silica and $\text{PO}_4\text{-P}$ appeared consistently in the analyses. Differences in ambient Si:P ratios were especially significant in the gradient between Sectors 5 and 6. The ratios between nutrients can be ecologically more important than absolute concentrations, and can be effective even when nutrient concentrations are high as in the Southern Ocean. Experimental work has shown that Si:P supply ratio can determine the outcome of competition between pairs of freshwater diatoms (Tilman and

Kilham 1976, Tilman 1977). Jacques (1983) has shown that some Antarctic marine *Nitzschia* species (including *N. kerguelensis*, cited as *Fragilariopsis kerguelensis*) have unusually high silicon requirements as indicated by uptake kinetics. Silicon concentrations at which uptake rate was half of the saturated rate (K_s) were $12\text{--}22\text{ mmol m}^{-3}$ for two Antarctic *Nitzschia* species grown in culture, which contrasts with published values of $K_s < 5\text{ mmol m}^{-3}$ for non-Antarctic marine plankton diatoms (Paasche 1980, Jacques 1983). Jacques cites the high Si:P and Si:N assimilation ratios of 88 and 6, respectively, calculated for some Southern Ocean phytoplankton by Le Jehan (1982). The importance of the Si:P ratio can be ascribed to the difference in the expected recycling dynamics of the two elements. Many phosphorus compounds are labile and remineralization may take place in the euphotic zone, possibly enhanced by zooplankton excretion (Hargrave and Geen 1968, Mullin et al. 1975, Lehman and Scavia 1982). By contrast, silica incorporated into particulate material such as diatom frustules is relatively insoluble, and will be lost from the euphotic zone by sedimentation. This effect is enhanced by low water temperature (Kamatami 1982) and when the frustules are in faecal material (Schrader 1971, Kamatami 1982, Lorenzen and Welschmeyer 1983). The silica pool in the Southern Ocean is regenerated by the influx of silica-rich water by eddy diffusion or advection (Copin-Montegut and Copin-Montegut 1978).

Grazing impact was a consistently important feature of interstation variability and implicated in variation in phytoplankton biomass and pigment ratio. The mean chlorophyll *a* biomass in the study area was probably adequate to sustain the mean krill biomass. This supposi-

tion is based on order-of-magnitude calculations using published values for krill abundance, estimated grazing rates (Clarke and Morris 1983, Morris et al. 1983) and the likely range of Antarctic phytoplankton cell division rates (Jacques 1983, Table 5). However, distribution of phytoplankton is normally patchy and krill form dense swarms. Local grazing impact in this heterogeneous system may be dramatically high.

Zooplankton, particularly krill, could have a significant impact on species composition of the diatom community through selective grazing. The retention efficiency of the filtering mechanism of krill is dependent on the size of food particles (McClatchie and Boyd 1983, Meyer and El-Sayed 1983), although particles as small as 1 μm maximum linear dimension (MLD) probably can be retained (Kils 1983). Kawamura (1981) and Kawamura and Ichikawa (1984) have compared species composition of diatoms in areas with and without local krill concentrations in the Pacific Ocean sector of the Southern Ocean. The overall picture is one of selective grazing of large-celled and chain-forming taxa, with a resultant enhancement of the abundance of some small-celled taxa such as small *Nitzschia* (*Fragilariopsis*) spp. and small *Chaetoceros* spp. This is consistent with the pattern observed by Meyer and El-Sayed (1983) during laboratory exclusion experiments carried out with krill feeding on phytoplankton from the Bransfield Strait. They found that grazing resulted in increased proportionate abundance of cells <20 μm MLD.

The species distributions of diatoms within our study area appear to contradict these published observations. The large-celled, chain-forming *Chaetoceros criophilum* dominated Sector 6 which also had the highest mean krill abundance. Some of the *Nitzschia* species which Kawamura (1981) and Kawamura and Ichikawa (1984) found to be typical of heavily grazed areas were characteristic taxa of the southern sectors around South Georgia where krill abundance was lower. If the difference in species composition between stations north and south of the island, already identified with mesoscale circulation pattern, is related to grazing then it is clear that the zooplankton distribution within the study area at the time of sampling cannot be implicated. The relationship would require that the grazing determining the diatom species composition occurred before the period of survey and, therefore by implication, outside the study area. It is feasible to suppose that krill were likely to have been more abundant in the more southerly waters of the Antarctic Circumpolar Current in the light of its known geographic distribution. The krill species *Euphausia superba* is essentially an animal of the Antarctic Coastal Current which is carried into the Antarctic Circumpolar Current by the Weddell Gyre. It is impossible to quantify the time scale of this interaction as we are unable to estimate the residence time of water in the study area. Meyer and El-Sayed (1983) obtained significant differences between the phytoplankton in grazed and ungrazed seawater after 2 to 27 h. However such a rapid change would not be ex-

pected in nature because grazing pressure would be intermittent and less intense. The krill densities used in their experiments (2–15 animals in 4.48 dm³ vessels) are attained only in swarms. Krill disperse to feed (Everson and Ward 1980, Morris et al. 1983).

Although low vertical stability is an important feature of the Southern Ocean as an environment for phytoplankton photosynthesis (Walsh 1971, Jacques 1983) it could not be implicated in phytoplankton variability around South Georgia. We calculate that most, if not all, of the euphotic zone was within the mixed layer at all of the stations.

Multivariate analyses show that differences in species composition between northern and southern stations around South Georgia can be identified with water masses and may have arisen from differences in grazing pressure before the waters reach South Georgia. Smaller-scale variation in phytoplankton was manifested by interstation variation in chlorophyll *a* biomass and in pigment ratio, and was associated with reduction of the total major nutrient pool, variation in Si:P ratio, and with local grazing pressure.

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