Distribution and abundance of phytoplankton taxa in the eastern Scotia Sea
by Paul Robert Wade

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences
Montana State University

Abstract:
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Principal component analysis was calculated on the log-transformed biomasses of the fifteen phytoplankton taxa with the greatest variance that occurred in at least five observations on each of the two legs of the cruise. A canonical correlation analysis was calculated between the 15 phytoplankton taxa and the physical variables of temperature and salinity.

Two assemblages of phytoplankton correlated with different bodies of water were resolved. An assemblage of mainly large centric diatoms occurred with high biomass in the Weddell Sea to the south. An assemblage of more mixed taxa with lower biomasses occurred in Antarctic Circumpolar Current waters to the north. The distribution of the two phytoplankton assemblages reflect the dynamics of the physical oceanography of the area, showing a distinct frontal structure to the west, with mixing from meso-scale eddys down-current to the east.

The phytoplankton taxa sampled during a large and dense Euphausia superba swarm north of Elephant Island were similar in composition to the Weddell assemblage, although at lower biomasses, and showed evidence of preferential grazing of larger size classes during the nine days the swarm was sampled.

Large biomass observations showed moderate correlation with the magnitude of density difference between 100 meters and the surface, suggesting that physical mechanisms imparting vertical structure to the water column, such as the melting of the seasonal ice-pack, are important to phytoplankton dynamics in the Scotia Sea.

DISTRIBUTION AND ABUNDANCE OF PHYTOPLANKTON TAXA IN THE EASTERN SCOTIA SEA

by

Paul Robert Wade

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APPROVAL

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Paul Robert Wade

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

9/19/87 — Date

David Goodman — Chairperson, Graduate Committee

Approved for the Major Department

21 September 1987 — Date

Peter F. Brussard — Head, Major Department

Approved for the College of Graduate Studies

13 October 1987 — Date

M. Malone — Graduate Dean

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ABSTRACT

The dynamics of Antarctic phytoplankton communities are highly variable, both spatially and temporally. This paper examines a sampling of the phytoplankton communities in the eastern Scotia Sea and in the area between the Antarctic Peninsula and the South Shetland Islands. This analysis attempts to describe the distribution of the phytoplankton community, and to establish a statistical relationship between spatially coherent phytoplankton assemblages and the physical measurements of the water masses. The causal mechanisms that could account for the community structure and dynamics of the phytoplankton in the eastern Scotia Sea are also explored.

Principal component analysis was calculated on the log-transformed biomasses of the fifteen phytoplankton taxa with the greatest variance that occurred in at least five observations on each of the two legs of the cruise. A canonical correlation analysis was calculated between the 15 phytoplankton taxa and the physical variables of temperature and salinity.

Two assemblages of phytoplankton correlated with different bodies of water were resolved. An assemblage of mainly large centric diatoms occurred with high biomass in the Weddell Sea to the south. An assemblage of more mixed taxa with lower biomasses occurred in Antarctic Circumpolar Current waters to the north. The distribution of the two phytoplankton assemblages reflect the dynamics of the physical oceanography of the area, showing a distinct frontal structure to the west, with mixing from meso-scale eddys down-current to the east.

The phytoplankton taxa sampled during a large and dense <u>Euphausia superba</u> swarm north of Elephant Island were similar in composition to the Weddell assemblage, although at lower biomasses, and showed evidence of preferential grazing of larger size classes during the nine days the swarm was sampled.

Large biomass observations showed moderate correlation with the magnitude of density difference between 100 meters and the surface, suggesting that physical mechanisms imparting vertical structure to the water column, such as the melting of the seasonal ice-pack, are important to phytoplankton dynamics in the Scotia Sea.

INTRODUCTION

The dynamics of Antarctic phytoplankton communities are highly variable, both spatially and temporally (Hempel, 1985, Heywood and Whitaker, 1984). Although some sampled events indicate phytoplankton abundances or production rates in the Southern ocean to be equal to the greatest found in any ocean in the world, it is apparent that these events are not uniformally distributed throughout the Southern ocean or throughout the year (El-Sayed, 1985). Temporally, high biomass events are restricted to the short austral summer of the Antarctic. Spatial patterns are not as clear. Historical accounts indicate large blooms are consistently found in the vicinity of Antarctic Peninsula, and in the shelf areas of the islands in the vicinity of the Scotia Sea (Elephant Island, South Orkneys, South Georgia) (Heywood and Whitaker, 1984, Sakshaug and Holm-Hansen, 1985). Blooms have also been consistently found near the ice edge associated with the melting of the seasonal ice-pack in the austral spring and summer (Holm-Hansen et al, 1977).

This paper examines a quasi-synoptic sampling of the phytoplankton communities in the eastern Scotia Sea and in the area between the Antarctic Peninsula and the South Shetland Islands. The cruise was undertaken in the austral summer of 1981 on the ship R.V. Melville, with chief scientists T. D. Foster (leg 1) and O. Holm-Hansen (leg 2) (Holm-Hansen and Foster, 1981). This analysis attempts to describe the distribution of the phytoplankton community, and to establish a statistical relationship between spatially coherent phytoplankton assemblages and the physical measurements of the water masses. The causal mechanisms that could account for the community structure and dynamics of the phytoplankton in the eastern Scotia Sea are also explored.

Phytoplankton are not believed to be generally limited by nutrients in the Southern ocean (Heywood and Whitaker, 1984). The upwelling nature of the entire system confers consistently high nutrient levels with the exception of silicate, which may occasionally be limiting to diatoms, especially to the north in the vicinity of the Antarctic Convergence (Holm-Hansen et al, 1977). Physical, as distinct from chemical, environmental variables may be of more importance to phytoplankton production and standing stock. Those variables that affect the stability of the water column, keeping phytoplankton in the euphotic zone, may be of great importance (Sakshaug and Holm-Hansen, 1984).

The primary grazers of the Southern ocean are Euphausiids, which are very patchy in distribution. Euphausia superba is an integral link in the food chain of the Southern ocean, which, by some reports, supports a surprisingly large biomass at higher trophic levels (Hempel, 1985). Little is known about the dynamics between the patchy distributions of both grazer and primary producers, but it is indisputable that phytoplankton represent an important resource for krill production. A better understanding of the dynamics of phytoplankton communities may help explain krill distribution and abundance.

Physical and Chemical Oceanography of the Cruise

The physical oceanography of this cruise is discussed in Foster and Middleton (1984). The primary focus of the leg 1 cruise was to examine the confluence between the Weddell Sea and the Antarctic Circumpolar current flowing out of the Drake Passage. The Weddell gyre brings water clockwise from the Weddell Sea to flow parallel with waters flowing from the Drake Passage. They meet east of the South Orkneys in the vicinity of 48 degrees W. longitude, although the zone of first contact is thought to vary considerably seasonally and from year to year. Both currents flow to the east, with the Antarctic Circumpolar Current moving at approximately twice the speed (.2 m s^{-1}) of the Weddell Sea current (.1 m s^{-1}). They describe a spreading zone of meso-scale eddy-like structures downstream of the point of first contact between the two waters.

In this study, the clearest frontal structure exists on line 2 (Figure 1), which is near where the two waters first met at the time of the cruise. Downstream of this, on lines 3, 4, and 5, the boundary is not as distinctly defined, but there is an apparent progression from Weddell Sea water to the south to Antarctic Circumpolar Current water to the north, with some intermixing from eddy-like structures. Line 1, the eastern-most line at 50 degrees W. longitude, is not as clear-cut in the origin of its water. Weddell Sea water appears only at the southernmost point of the line, and the middle of the line shows evidence of vertical mixing in the region of the Scotia ridge.

Michel (1984) describes the chemical oceanography of this cruise. He indicates that silicate and temperature can be used as a signal to

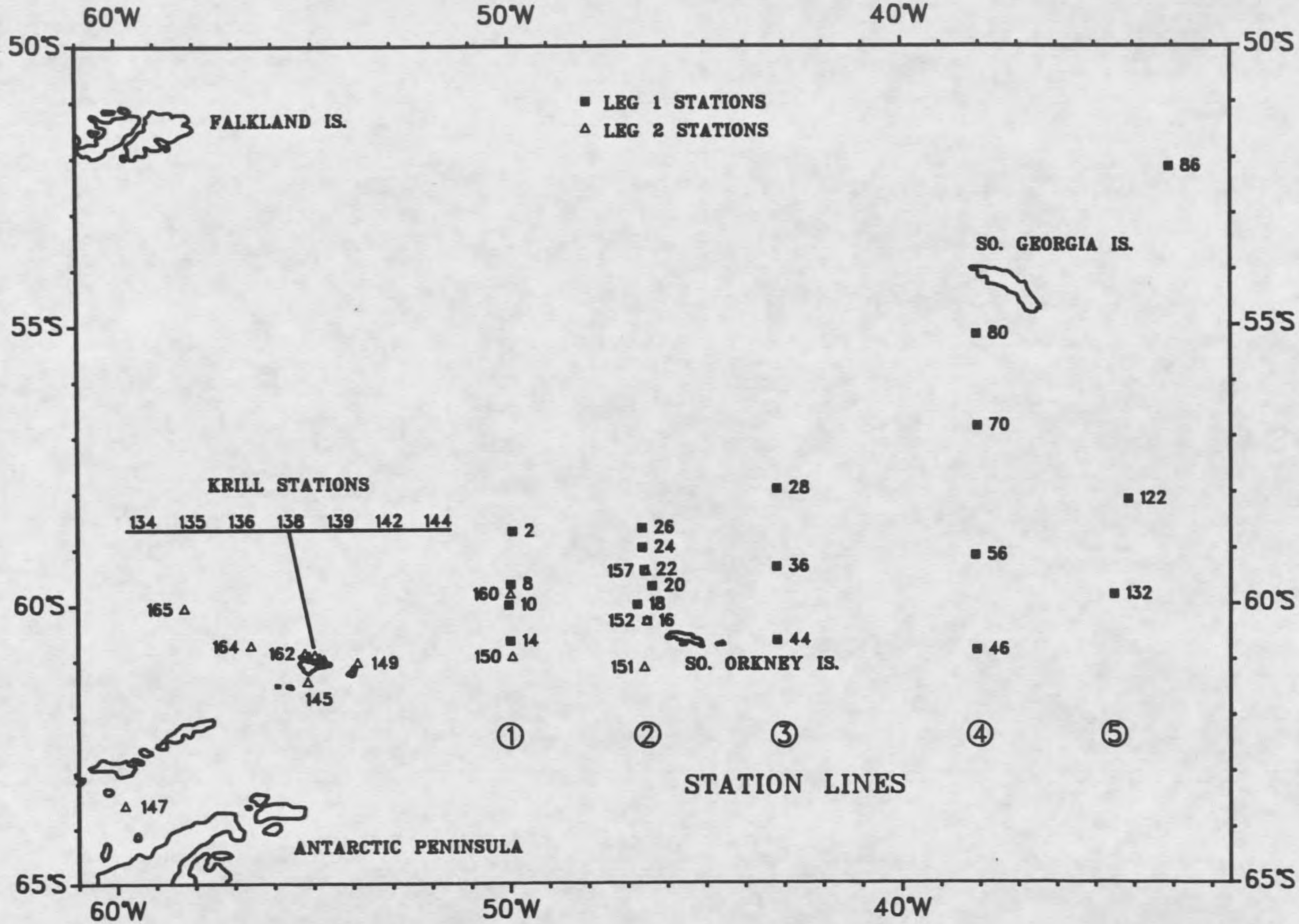


Figure 1. Position and number of phytoplankton stations.

distinguish circumpolar waters from Weddell Sea waters in the Scotia Sea, with higher silicate values and colder temperatures occurring in Weddell Sea water. Michel and Linick (1985) indicate a sharp gradient in carbon-14 concentration between Circumpolar Current waters and Weddell Sea waters. Low carbon-14 values are associated with low temperatures and clearly define Weddell Sea waters. The sharpest gradient in silicate, carbon-14, and temperature occurs on line 2 in the vicinity of stations 19 to 21. Lines 3, 4, and 5 exhibit gradients from north to south, but do not have as clearly defined a frontal structure as line 2.

METHODS

The Data Set

Leg 1 of the cruise consisted of five north-south transects (station lines 1 to 5, numbered west to East in Figure 1) of the Scotia Sea across the boundary between Weddell Sea waters and Antarctic Circumpolar Current waters, carried out from 24 January to 13 February. Leg 2 of the cruise consisted of further sampling carried out from 28 February to 23 March from the vicinity of Elephant Island and the South Shetland Islands off the tip of the Antarctic Peninsula eastward to the South Orkney Islands. A very dense and large krill swarm was sampled intensively just north of Elephant Island, and lines 1 and 2 from leg 1 were partially repeated.

Phytoplankton samples were collected by Dr. Ozzie Holm-Hansen of Scripps Institute of Oceanography. Fourty-three phytoplankton samples were collected at several depths from a total of 20 stations on leg 1. Fifty-five samples were collected from 18 stations on leg 2. There were 98 observations at 38 stations (stations are numbered in Figure 1). Phytoplankton samples were identified to the extent possible and individuals were counted by Freda M. H. Reid and Egil Sakshaug of Scripps Institue of Oceanography. Phytoplankton abundance was estimated using the Uterm"ohl technique with subsequent calculation of biomass by the method described in Reid et al. (1970).

Temperature, salinity, and density measurements were made at two meter intervals from the surface to 100 meters at all stations.

In this paper, leg 1 stations identified by Michel (1984) as being north of the confluence of the two bodies of water are referred to as Antarctic Circumpolar Current (ACC) stations. Leg 1 stations identified as being south of the confluence are referred to as Weddell Sea (WS) stations. On leg 2, the 7 stations north of Elephant Island sampled during the krill swarm (stations 134-144) are referred to as krill stations.

Statistical Treatment

A total of 92 taxa of phytoplankton were identified from the entire data set. The taxa used in the analysis were chosen by selecting the 15 taxa with the greatest variance in biomass, subject to the further constraint of occurring in more than five observations on each of the legs of the cruise.

Principal component analysis (Harris, 1975) was calculated on the 98 observations using the 15 selected phytoplankton taxa as variables. Spatially coherent assemblages of phytoplankton were identified. Coefficients of correlation were calculated between all 92 taxa and the principal components to reveal community-wide patterns.

Distinct masses of water were identified through principal component analysis of the surface temperature and salinity at each station. A canonical correlation analysis (Pielou, 1977) was calculated between the 15 phytoplankton taxa and the physical variables of temperature and salinity. This identified correlations between phytoplankton assemblages and physical characteristics of the water masses. Coefficients of correlation were calculated between all 92 taxa and the physical canonical variates, again to reveal community-wide patterns.

All the statistics were calculated on an IBM PC AT, using in-house software written in Microsoft Fortran version 4.0. Some of the Fortran subroutines used were modified from routines found in the SSP fortran library.

RESULTS

Total Biomass

Total biomass (sum of all 92 taxa) for each observation is plotted in Figure 2. The greatest biomasses occur at stations 16, 56, 20, and 36. On leg 1, there is a north-south trend, with lower biomasses to the north and higher biomasses to the south. Line 1 does not follow this pattern. Biomasses on leg 2 are generally less than on leg 1, with the maximum biomass on leg 2 (station 145) being approximately an order of magnitude less than the maximum biomass on leg 1. Stations on lines 1 and 2 of leg 1 that were re-sampled on leg 2 one month later show a decline in biomass of approximately one order of magnitude.

Spatial Resolution of Phytoplankton Assemblages

Phytoplankton Taxa

Most of the 92 taxa ranged through several orders of magnitude in biomass abundance. For the purposes of the multivariate analysis, the 15 selected taxa were therefore transformed by taking the natural logarithm of the biomass, augmented by one, to reduce the influence of the very large values (and to achieve more normal distributions).

Although the 15 taxa were selected by the magnitude of their variances, it is informative to note that selecting those taxa with the 15 highest mean biomass abundances would have only changed the list by

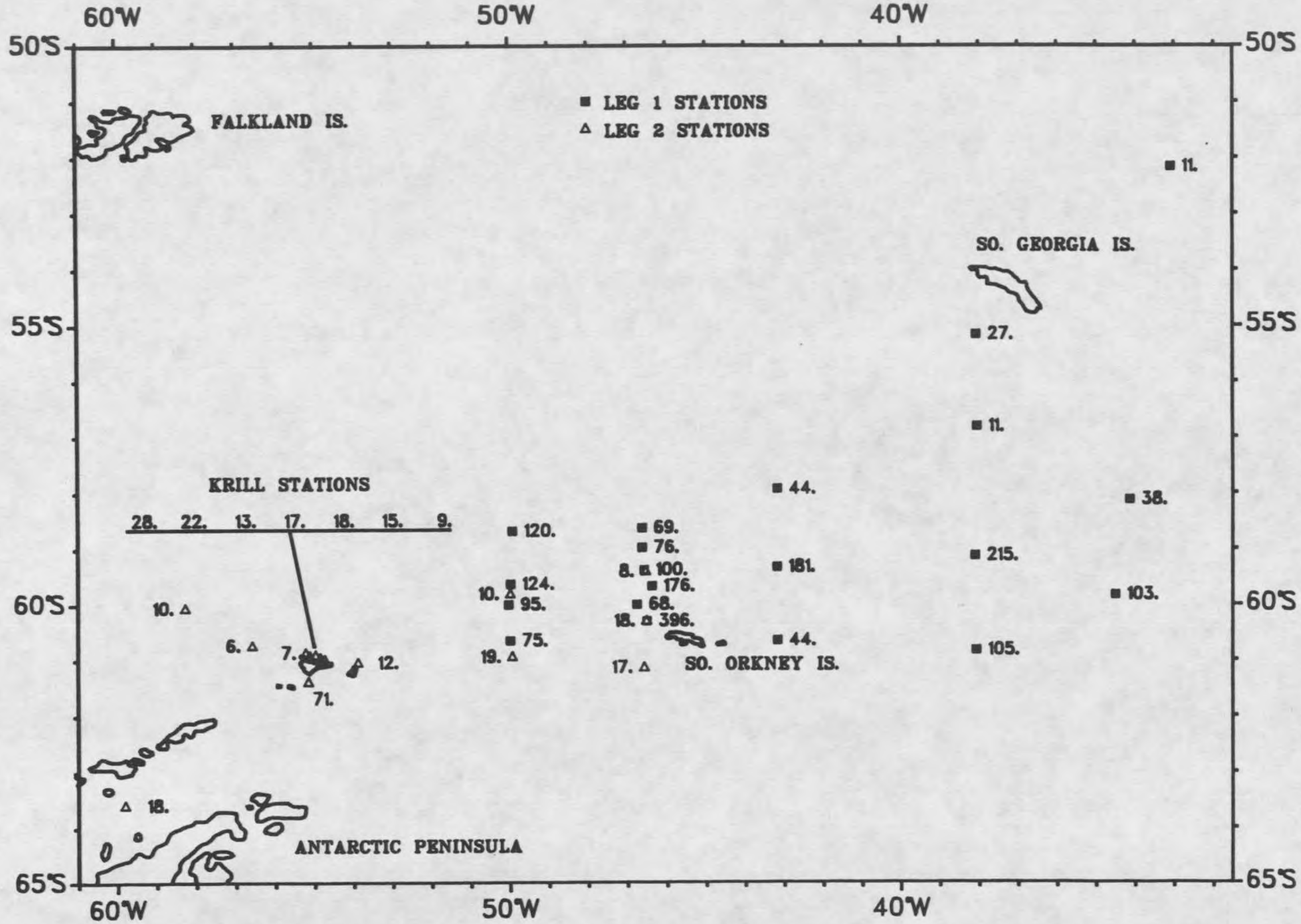


Figure 2. Total biomass (micrograms carbon per liter)

one taxon. Of the fifteen taxa, three are not identified to species. These three are thecate dinoflagellates, non-thecate dinoflagellates,and monads and flagellates. The identified species are eight centric diatoms, three pennate diatoms and one non-thecate dinoflagellate. Using the taxa with the highest variances insures that the major forms of variance within the entire data set are involved (unless there are small differences in variance between the highest variances and the lowest, or unless there is an inordinate amount of intercorrelation between the taxa not among the 15 greatest variances, neither of which is the case here).

Principal component analysis (PCA) was carried out on the covariance matrix of the data set, rather than the correlation matrix, as it was desired to let the variances of the individual taxa influence their importance in the components (generally the more abundant taxa also showed the greatest variances in abundance).

Orthogonal Components

The eigenvectors defining the first five principal components are presented in Table 1. These five components account for over 71% of the total variance in the data.

The first principal component accounts for 31.5% of the variance in the data set, and contains large positive contributions from a number of taxa, with no taxa making large negative contributions. As one might expect, this component tracks total biomass fairly closely. The composition of the component is mostly centric diatoms, *Odontella weissflogii*, *Eucampia balaustium*, *Rhizolenia alata f.inermis*, and

Chaetoceros dichaeta, with one pennate, Synedra reinboldii, being the exception.

Table 1. Principal component analysis (on the covariance matrix) of the natural log-transform of the biomass of fifteen phytoplankton taxa.

	Eigenvectors				
Phytoplankton taxa	I	II	III	IV	V
Odontella weissflogii	.44	-.40	-.18	-.01	.21
Eucampia balaustium	.43	-.15	.01	-.09	-.10
Synedra reinboldii	.40	.17	.02	-.07	-.48
Rhizosolenia alata f. inermis	.37	-.14	-.19	-.01	-.01
Chaetoceros dichaeta	.36	.23	.08	-.21	-.07
Chaetoceros flexuosus	.26	.19	-.06	-.04	.11
Thecate dinoflagellates 10-79	.26	.33	.12	.85	.09
Gyrodinium lachryma	.18	-.07	.80	-.24	.32
Dactyliosolen antarcticus	.10	.40	-.45	-.23	.48
Nitzschia cf. heimii	.09	.21	.04	-.03	.05
Monads and Flagellates <2-20	.02	.07	.02	-.03	.00
Nitzschia cf. pseudonana	.00	.26	-.08	-.28	-.02
Corethron criophilum	-.01	.12	.07	.04	.52
Naked dinoflagellates 5-109	-.01	.14	.11	-.06	.10
Chaetoceros atlanticus S	-.07	.50	.16	-.14	-.27
Percent variance accounted for by component	31.5	16.2	9.8	7.3	6.5
Cumulative percent variance	31.5	47.7	57.5	64.8	71.3

The second principal component accounts for 16.2% of the variance in the data, and is dominated by positive contributions from two centrics, Chaetoceros atlanticus S, and Dactyliosolen antarcticus, and unidentified thecate dinoflagellates, contrasted against one large negative contribution from O. weissflogii.

The third principal component accounts for 9.8% of the variance in the data, and is dominated by a positive contribution from one species, the naked dinoflagellate Gyrodinium lachryma, with a negative contribution (although much less in magnitude) from the centric diatom, Dactylioselen antarcticus.

The fourth principal component accounts for 7.3 % of the variance in the data, and is dominated by a large positive contribution from thecate dinoflagellates.

The fifth principal component accounts for 6.5 % of the variance in the data, and has a large positive contribution from Corethron criophilum and a smaller positive contribution from D. antarcticus, and one large negative contribution from S. reinboldii.

Components I and II thus account for nearly one half of the total variance in the data set. Components III, IV, and V account for such similar amounts of variance that they cannot be considered distinct, and are each mostly dominated by one taxon. The rest of the components show little change in variance accounted for from one to the next.

The difference in variance in biomass between individual species decreases on the order of one magnitude between the first and last taxa of the fifteen taxa used in the analysis. Thus, adding additional taxa to the list of species included in the principal component analysis could not add significantly to the total variance of the data set, and the first two eigenvectors, at least, should be stable to the inclusion of additional taxa.

It can thus be concluded that the first two components account for the major community trends in the distribution and abundance of phytoplankton in the data set.

Coherent Spatial Patterns

Principal Component I. Component I scores exhibit a clear north-south trend on the leg 1 transects, with positive scores to the south and negative scores to the north (Figure 3). The highest scores occur at stations 16 and 18 on line 2, 44 and 36 on line 3, 46 and 56 on line 4, and 132 on line 5. Line 1 diverges from this trend, as its scores are all negative or near zero. The most negative scores occur for the most part at the north-most stations, and those stations with scores near zero tend to be intermediate.

Component I identifies a phytoplankton assemblage that occurs on the southern end of lines 2, 3, 4, and 5 of leg 1. On the leg 2 stations, there are positive scores at five of the seven krill stations, at the station just south of Elephant Island (145), at the station just to the east of Elephant and Clarence Islands (149), and, to a lesser extent, the two southern stations at 46 degrees longitude, what was line 2 on leg 1.

Except for station 145 south of Elephant Island (whose scores and biomass are high), all the leg 2 scores are positive but lower in magnitude than the leg 1 southern scores. This reflects the order of magnitude difference in total biomass from leg 1 to leg 2, and also the diminished coherence on leg 2 of the phytoplankton assemblage defined by the component (which is a result of the individual taxa which are part of the assemblage not occurring as consistently at every station identified by positive scores).

Principal Component II. Component II scores also have a north-south trend, with positive scores to the north and negative scores to

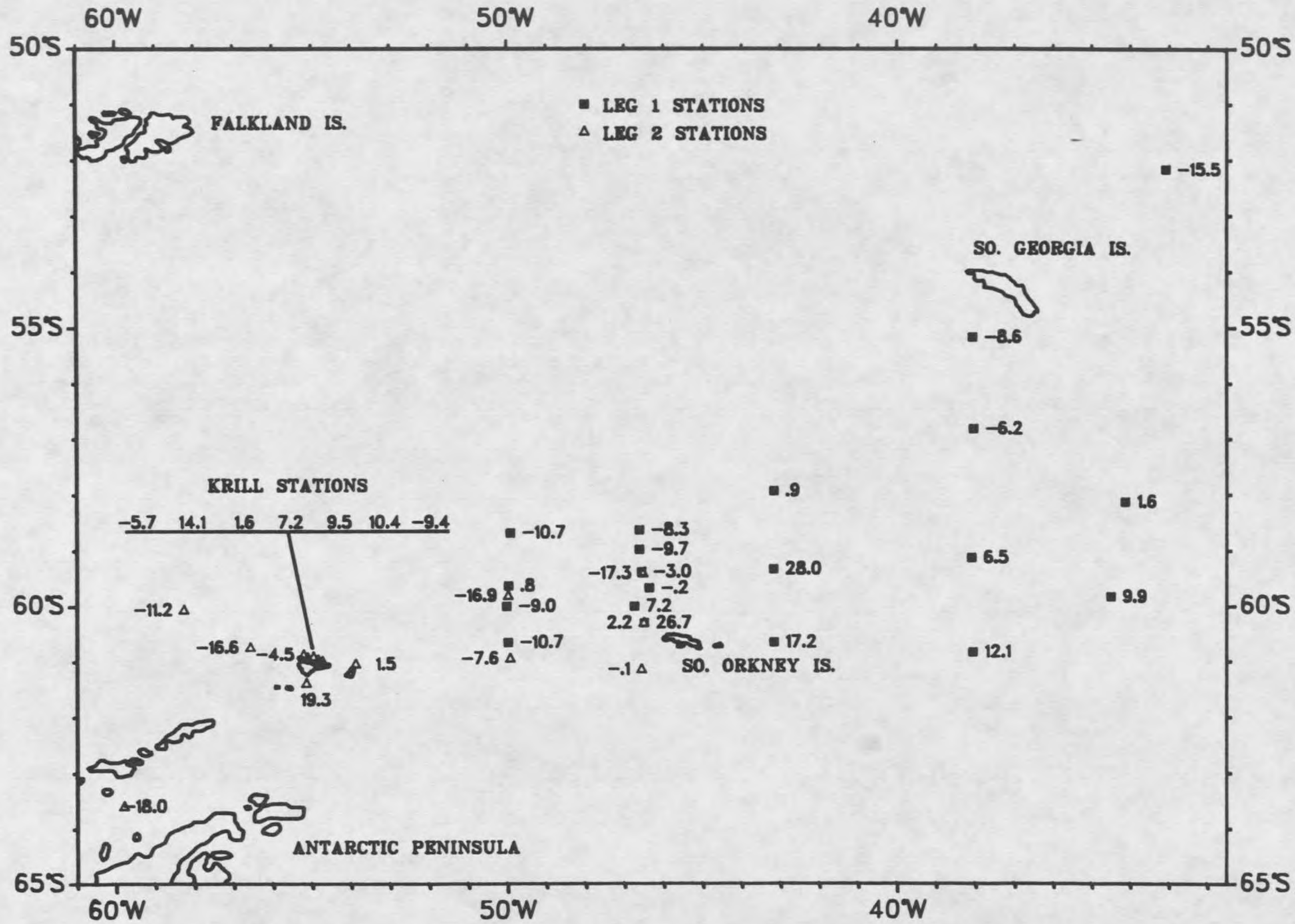


Figure 3. Principal component score I

the south (Figure 4). This holds for all the lines in leg 1 except for line 4, which has a positive score at its southern-most station (46). Component II shows a north-south trend on line 1, which the first component did not. The same general pattern as in component I exists on the leg 2 stations for component II. The krill stations have negative scores, as do the southern stations on leg 1. Station 149 to the east of Clarence Island also has negative scores, but station 145 south of Elephant Island differs in that it has positive scores. Of the three stations on line 2 that are repeated, the two stations to the south have similar scores to the leg 1 stations in the vicinity, but station 157 to the north has negative scores that are slightly smaller in magnitude.

Thus, principal component II identifies a phytoplankton assemblage that mostly occurs on the northern stations of leg 1. This assemblage is not present to the south on lines 1, 2, and 3 of leg 1, and only occurs at a few spots in leg 2, and does not occur at the krill stations.

There is only one taxon (O. weissflogii) with a strong negative loading in Component II, and most of the stations with large negative scores reflect the high abundance of that taxon (in addition to the low abundances of the northern assemblage). This taxa also had the largest positive contribution in component I, and two other taxa strongly positive from component I, E. balaustium and R. alata f. inermis, also show up as weakly negative in component II. Thus, the assemblage of negative taxa on component II partially recapitulates the positive taxa assemblage of component I, minus the presence of S. reinboldii and

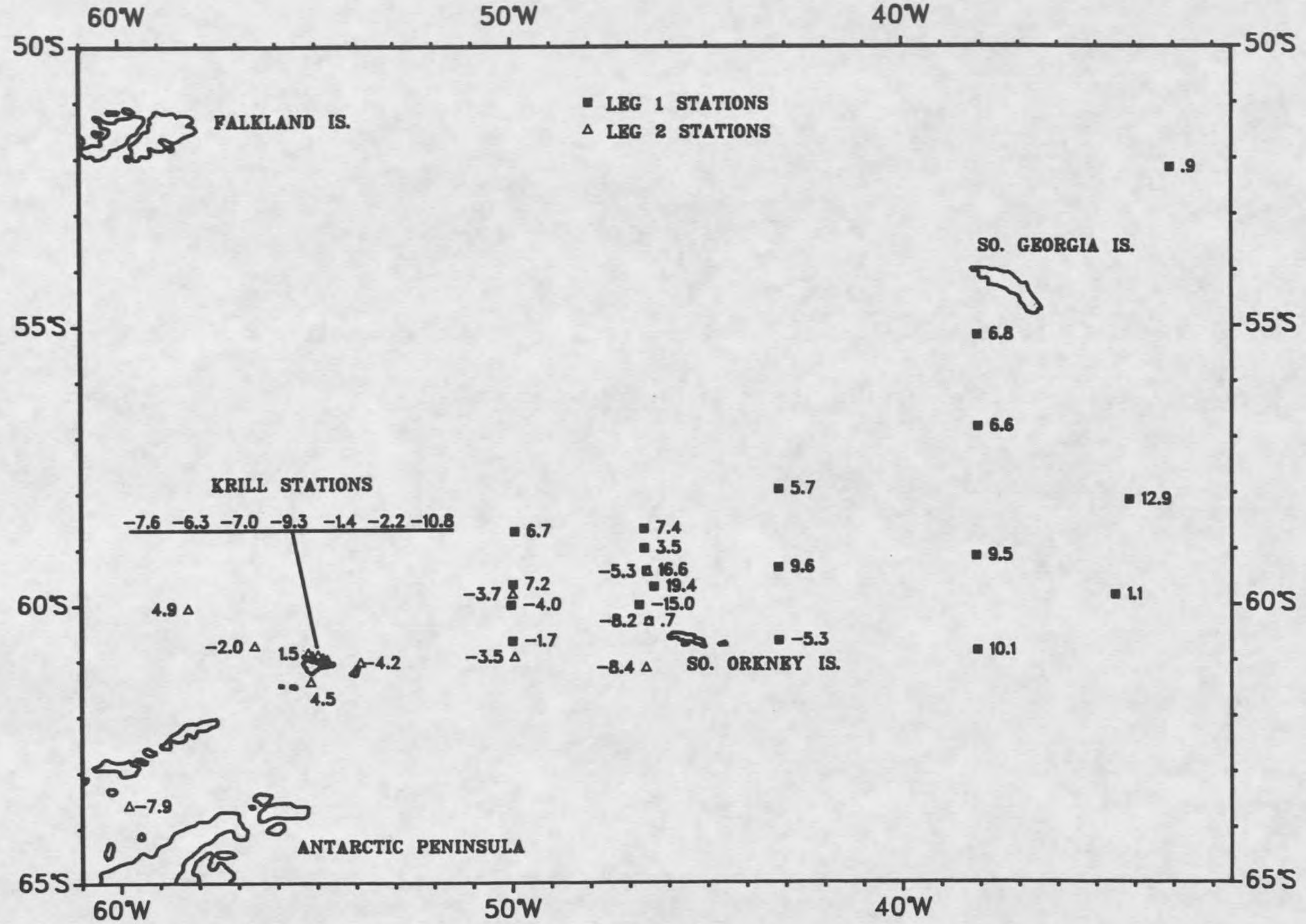


Figure 4. Principal component score II

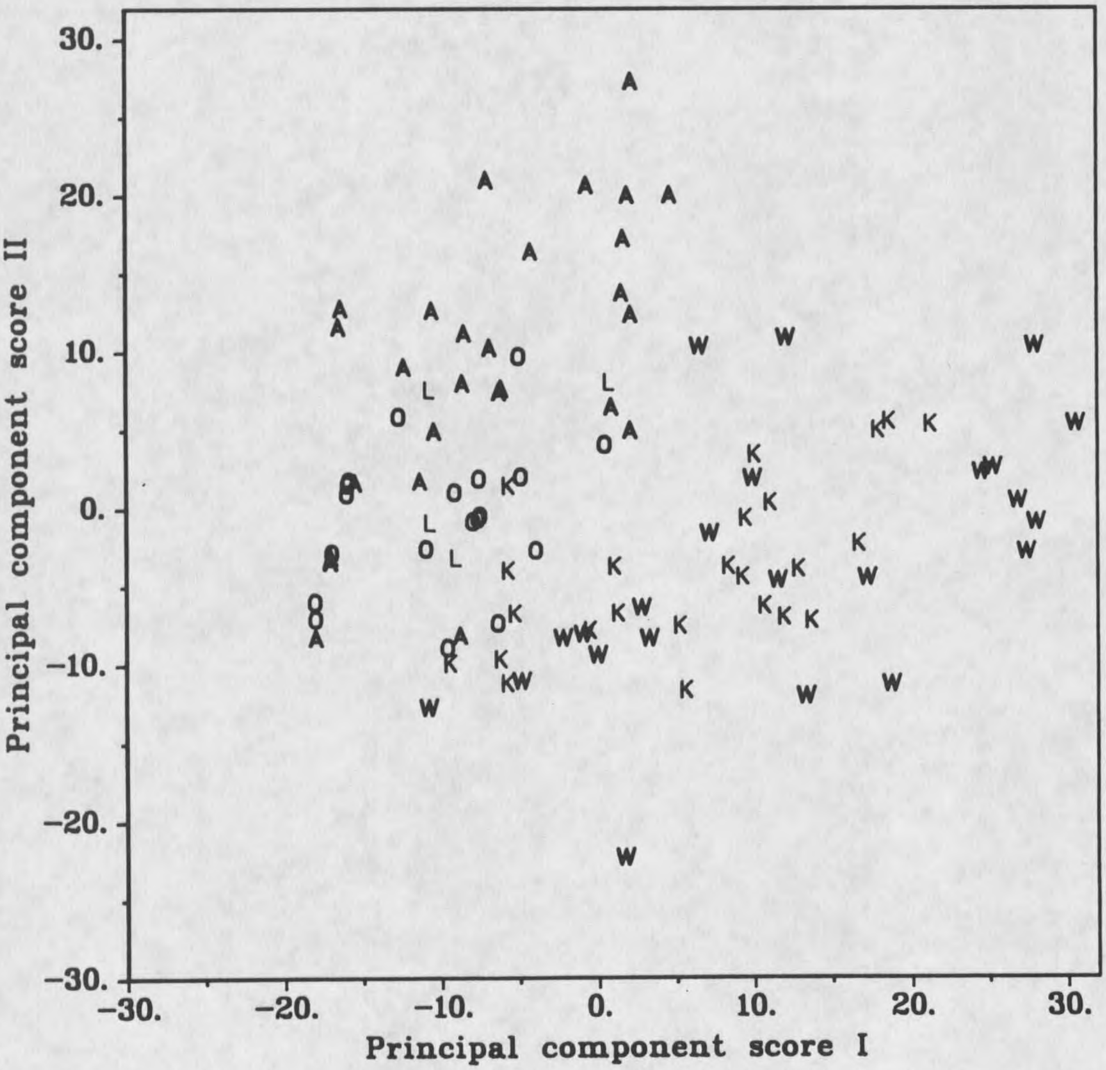
C.dichaeta. In other words, principal component II has identified (through positive contributions) an assemblage of phytoplankton species that generally occurs where the assemblage identified in component I does not occur, at the northern stations of leg I. A plot of component I scores versus component II scores shows that Leg 1 Weddell stations are clearly separated from Leg 1 ACC stations by the first two components (Figure 5). However, the two assemblages are not completely disjunct in their spatial distribution, otherwise both assemblages would have been identified in component I with opposite signs.

The northern and southern assemblages are most disjunct on line 2, as the north-south boundary occurs at the same spot for components I and II. Though the north-south boundary of each assemblage continues to the east, there is a widening zone of overlap between them. The boundary of the southern assemblage from component I is farther north as one moves east, and the boundary of the northern assemblage from component II is farther south as one moves to the east. There is thus an apparent inter-mixing of the two assemblages to the east.

Principal Component III. Component III scores (Figure 6) mostly reflect the distribution of G. lachryma, with some perturbation from occurrences of D. antarcticus. G. lachryma has a widespread distribution on both legs, occurring nearly everywhere on leg 1 except stations 20 and 22 on line 2, and occurring nearly everywhere on leg 2 except at stations 159, 160, 162, and 164. There does not appear to be a readily interpretable spatial pattern in the component.

Principal Component IV. Component IV scores (Figure 7) mostly reflect the distribution of the taxon of unidentified thecate

Figure 5. Principal component scores from analysis on log biomass of 15 taxa of phytoplankton (n=98). Stations identified by letter (A=ACC, W=Weddell, L=Line 1, K=Krill,145,149, O=other).



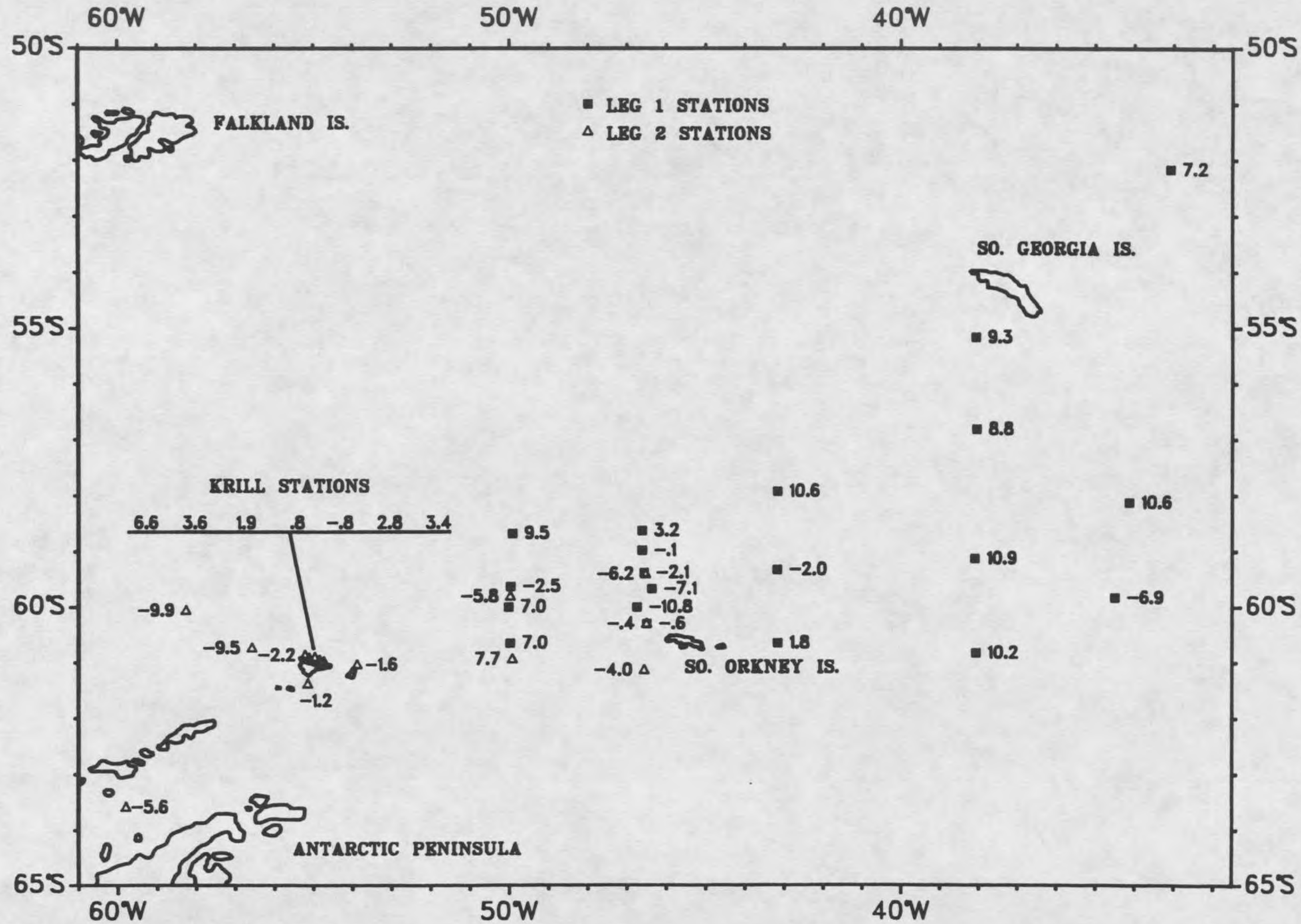


Figure 6. Principal component score III

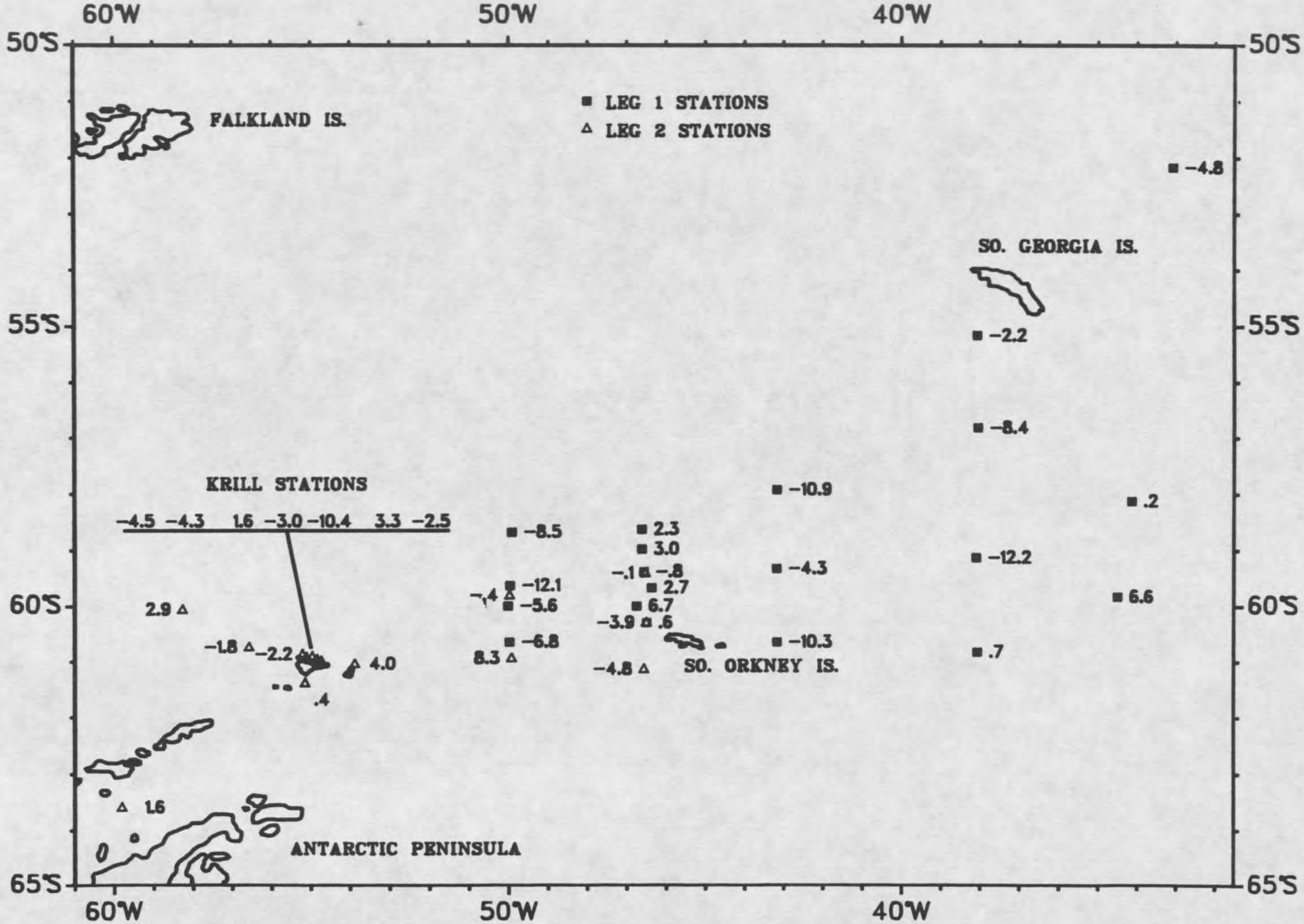


Figure 7. Principal component score IV

dinoflagellates 10-79. On leg 1, the taxon's distribution is similar to the distribution of the southern assemblage, but there are small differences that do not have a clear spatial pattern. On leg 2 thecate dinoflagellates 10-79 appear at only some of the observations at the krill stations, and do not appear at stations 151 or 152, whereas they do appear at stations 150, 162, and 164. These are all differences from the distribution of component I on leg 2. Therefore, with some exceptions, the distribution of thecate dinoflagellates is similar to the distribution of component I on leg 1, but differs enough on leg 2 to become a distinct component. It is possible that the distribution of the taxon does not have as coherent a spatial pattern as component 1 due to the fact that it may include many species.

Principal Component V. Component V (Figure 8) has a trend in scores of negative in the east and positive in the west, but the distribution of scores is not completely disjunct. This is due to the positive influence of *C. criophilum*, which appears at only 2 observations east of line 2 on leg 1 and at nearly every observation on leg 2, and the weaker negative influence of *S. reinboldii*, which appears on leg 1 at the two southern-most stations of line 2 and at stations to the east, and on leg 2 sporadically at the Elephant Island stations and the two stations (151 and 154) near the S. Orkneys. This component essentially identifies the unique and significantly large distribution of *C. criophilum*.

Correlation of Other Taxa with Principal Components

Due to a low number of observations relative to the number of variables, it was not reasonable to include all of the variables in the

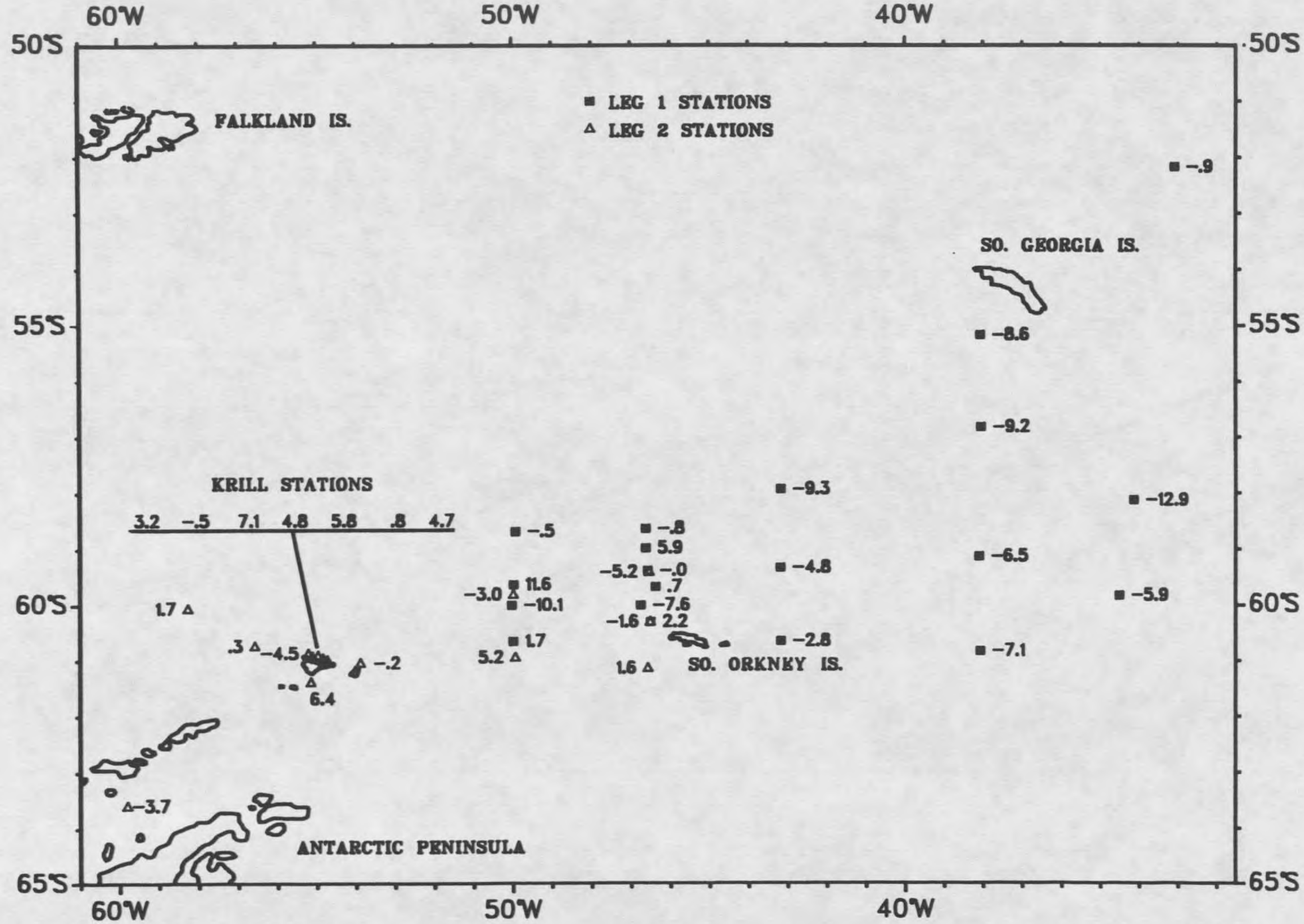


Figure 8. Principal component score V

principal component analysis. To incorporate all 92 taxa into the description of the distribution of the flora, simple coefficients of correlation between each taxon's log-biomass and the principal component scores were calculated (Table 2). The resulting correlations of component scores with taxa that were part of the principal components analysis will not be new information, as their roles in the components have already been described by their eigenvector values, which is their contribution to the component. However, the correlations of taxa not a part of the PCA will be new information.

Many of the taxa only occurred on leg 1. As their non-occurrences on leg 2 would lead to low correlations, and as there is a clear spatial interpretation to the principal components on legs 1 and 2 separately, these species had correlations calculated just over the 43 leg 1 observations. These correlations were used to describe the affinity of these species to the north and south assemblages.

A correlation in the range of the correlations of taxa that are significant contributors to the components indicates that the taxon in question has a distribution very similar to the component, ie. it is part of the same assemblage. However, it must be remembered that these are correlations, and so do not indicate the magnitude of the taxon's role (which was not true in the principal component analysis). Thus, a taxon identified as part of an assemblage in this way may account for a negligible part of the total biomass of the assemblage. What has been learned is that it has the same trend in distribution and relative abundance as the other taxa in the assemblage.

Table 2. Correlations between natural log-transformed biomass of all 92 individual taxa and principal component scores (PC) and physical canonical variate scores (CV).

	Coeffecients of correlation					
	PCA			CV		
Phtoplankton taxa	I	II	III	I	II	III
Nitzschia 'cylindrus'	.06	-.45	.13	.21	.63	.17
Nitzschia kerguelensis	-.37	-.00	-.39	-.32	-.11	-.01
Nitzschia cf. pseudonana	-.00	.55	-.12	-.45	-.33	.40
Nitzschia closterium	.22	.48	-.09	-.09	-.27	.10
Nitzschia cf. heimii	.30	.52	.07	-.12	-.09	-.00
Nitzschia angulata	-.13	.65	.18	-.45	-.37	.08
Nitzschia prolongatoides	.03	.62	.12	-.27	-.42	-.00
Nitzschia spp. 10->80	.21	.53	.00	-.05	-.57	-.09
Navicula sp.	.07	-.38	.18	.19	.63	.15
Pennates 5-299	.12	-.01	.17	.07	.30	.05
Pennate sp. AC	.17	.60	.03	-.19	-.33	-.06
Pennate sp. AH	.32	.52	-.02	-.04	-.36	.04
Synedra reinboldii	.74	.22	.02	.46	-.23	.18
Tropidoneis antarctica	.12	-.14	.02	.11	.40	.07
Asteromphalus hookeri	-.17	-.09	-.16	-.09	.09	-.10
Odontella weissflogii	.74	-.48	-.16	.84	.05	.27
Discoid Centrics spp. 100-259	.12	-.33	-.19	.26	.27	.08
Chaetoceros bulbosus	.32	.65	.04	-.17	-.25	.29
Chaetoceros chunii	.12	.16	-.04	.01	-.21	.12
Chaetoceros criophilus	.27	.40	.11	-.08	-.07	.26
Chaetoceros dichaeta	.70	.31	.08	.30	-.00	.12
Chaetoceros flexuosus	.56	.29	-.07	.13	-.02	.22
Chaetoceros neglectus	.23	.55	-.30	-.20	-.26	.16
Chaetoceros pendulus	-.03	.55	.00	-.30	-.29	.04
Chaetoceros peruvianus	-.04	-.25	.10	.10	.21	-.15
Chaetcoeros schimperianus	.15	.06	-.00	.05	.13	.09
Chaetoceros tortissimus	.43	-.20	.03	.35	.32	.38
Chaetoceros castracanei	-.09	.41	-.12	-.25	-.26	.05
Chaetoceros atlanticus S	-.14	.74	.18	-.47	-.50	.14
Chaetoceros curvatus	.25	.27	-.01	.06	-.21	.01
Chaetoceros sp. AM	.11	.69	-.01	-.27	-.44	.05
Chaetoceros spp.	.17	.53	.05	-.13	-.36	-.00
Charcotia sp. 80-89	-.09	.17	.20	-.13	.07	-.11
Corethron criophilum	-.02	.22	.10	-.16	.27	.23
Dactyliosolen antarcticus	.18	.55	-.49	-.20	-.26	.24
Eucampia balaustium	.80	-.19	.01	.68	-.10	.39
Porosira glacialis	.25	.00	-.06	.14	.16	.25
Rhizosolenia alata	.20	.16	.11	.02	.03	.30
Rhizosolenia alata f.indica	.03	.11	-.07	-.09	.01	.11
Rhizosolenia alata f.inermis	.70	-.18	-.20	.69	-.32	.08
Rhizosolenia antarctica	.07	.10	-.22	.02	-.18	-.02
Rhizosolenia chunii	-.14	.31	-.12	-.26	-.21	-.02
Rhizosolenia imbricata shrubsolei	.17	.45	.05	-.12	-.27	.22
Rhizosolenia truncata	.09	.47	-.10	-.20	-.33	.03

Table 2 (continued).

Rhizosolenia hebetata f.semispina	-.04	.44	-.18	-.27	-.20	-.10
Rhizosolenia simplex	.05	.23	.09	-.08	-.09	-.01
Rhizosolenia 'bidens'	-.01	.33	-.17	-.20	-.13	-.15
Rhizosolenia indica f.gracillima	.18	.17	-.12	.03	-.05	.08
Dinophysis contracta	-.06	-.01	.12	-.01	.19	-.17
Dinophysis punctata	.24	-.04	.03	.16	.05	.19
Dinophysis antarctica	-.00	.22	.08	-.10	-.05	-.00
Diplopeltopsis perlata	.17	-.23	.07	.18	.19	.27
Prorocentrum balticum	.08	-.13	.26	.07	.21	.18
Protoperidinium applanatum	.19	-.07	.24	.18	.32	.14
Protoperidinium archiovatum	.34	-.13	.11	.29	.15	.35
Protoperidinium cf. crassipes	.20	-.09	.03	.13	.10	.26
Protoperidinium defectum	-.06	.26	.08	-.20	.04	-.16
Protoperidinium macrapicatum	.16	-.21	.08	.19	.14	.27
Protoperidinium antarcticum	.10	-.12	.00	.11	.07	.17
Protoperidinium adeliense	-.05	.23	-.10	-.16	-.09	-.01
Protoperidinium turbinatum	.05	.10	.15	-.05	-.00	.07
Protoperidinium rosaceum	-.03	-.13	-.16	.05	-.07	-.01
Protoperidinium concavum	-.06	.11	-.16	-.14	-.02	-.05
Thecate dinoflagellates 10-79	.46	.42	.12	.18	-.06	-.01
Amphidinium hadai	.28	.19	.14	.07	.17	.13
Amphidinium sp. AX	.07	.44	.04	-.17	-.27	-.14
Amphidinium sp. AY	.33	.03	-.12	.23	-.06	.05
Gymnodinium flavum	.00	-.19	.18	.09	.23	.02
Gymnodinium frigidum	.08	-.08	.05	.10	.03	.15
Gyrodinium lachryma	.33	-.09	.83	.26	.52	.25
Gyrodinium rhabdomante	.31	-.06	-.05	.28	-.02	.07
Gyrodinium glaciale	-.00	.22	.08	-.10	-.05	-.00
Gyrodinium sp. AS	.24	.05	-.04	.15	.00	.09
Naked dinoflagellates 5-109	-.07	.53	.33	-.46	.34	.11
Emiliania huxleyi	-.24	.38	.01	-.36	-.17	-.02
Monads and Flagellates <2-20	.21	.50	.10	-.07	-.24	-.25
Flagellate AY	-.12	.58	-.12	-.40	-.34	-.10
Flagellate AC	-.05	.28	.12	-.18	-.17	.01
Distephanus speculum	-.02	.52	.11	-.34	-.23	.20
Thalassiothrix spp.	-.05	.23	-.10	-.16	-.09	-.01
Thalassiothrix antarctica	.47	.13	-.19	.34	-.34	-.18
Asteromphalus spp. 20-69	.30	.50	-.10	.01	-.46	-.05
Amphiprora spp.	.23	.10	-.01	.14	-.04	.02
Melosira sp. (chains)	-.11	.49	-.06	-.33	-.22	.03
Thalassiosira sp. AR	.41	-.22	-.17	.56	-.35	-.19
Thalassiosira spp. 5-79	.16	.64	.12	-.19	-.44	-.04
Mesodinium rubrum	.06	.19	.30	-.06	-.10	.07
Torodinium robustum (small)	-.08	.04	.11	-.10	-.03	-.04
Dactyliosolen antarcticus f.laevis	-.05	.23	-.10	-.16	-.09	-.01
Dinoflagellate cyst	.33	.07	-.15	.25	-.20	-.14
Dactyliosolen tenuijunctus	-.21	.41	-.08	-.39	-.22	-.05
Leptocylindrus sp.	-.02	.23	-.10	-.14	-.10	-.01

Correlations with Principal Component I. For component I, there are two taxa that have correlations within the range of the southern assemblage taxa on leg 1, and are thus added to the assemblage. Thalassiothrix antarctica was not included in the PCA because it did not occur on leg 2. On leg 1 it occurs at only 12 observations, all of them observations with positive scores for component I. Thalassiosira sp AR only occurs 6 times in the entire data set, and only at stations 16 and 18. These are species that occur only at stations on leg 1 that are part of the assemblage of component 1.

Two taxa correlate positively with component I over all observations. Chaetoceros tortissimus occurs only at station 16 on leg 1, and at all the stations on leg 2 that have positive scores on component 1. Gyrodinium rhabdomate occurs only at station 16 on leg 1 and at stations 138, 147, and 149 on leg 2.

Two taxa that correlate negatively with component I on leg 1 are Emiliania huxleyi and unidentified Flagellate AY. These only occur at the northern end of lines on leg 1, and thus are species that occur where the component I assemblage does not, but do not follow the trend of the component II assemblage (which extends to the southern end of lines 4 and 5).

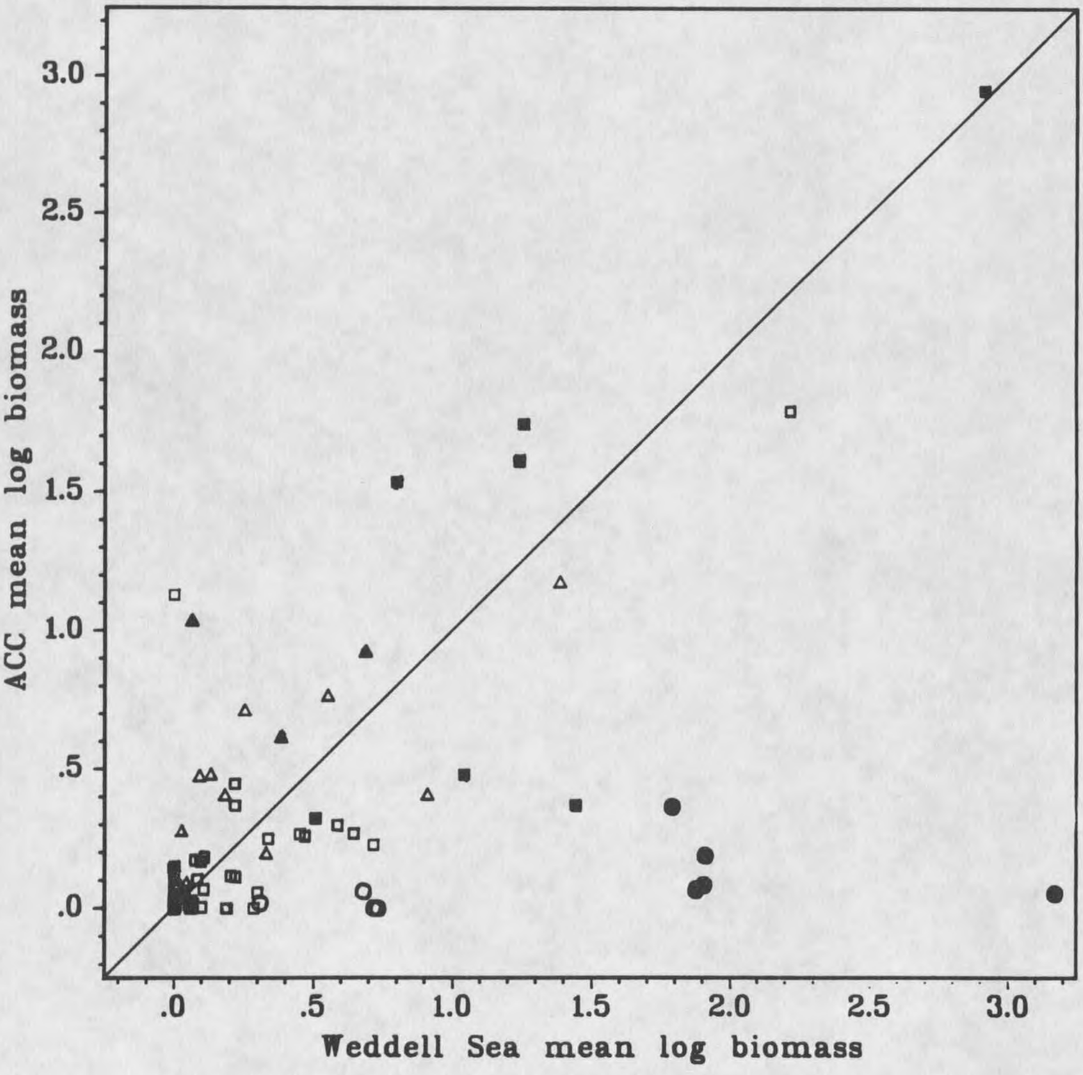
Correlations with Principal Component II. Although component II did not involve as many taxa out of the 15 used as component I, 7 additional taxa are associated with the northern assemblage through correlations with the component score over all observations. This shows that the component did involve an assemblage of many species, but that their means and variances in biomass were relatively low. In order of magnitude of the correlation, these taxa are: Chaetoceros sp. AM, Chaetoceros bulbosa, Nitzschia angulata, Thalassiosira spp 5-79, Nitzschia prolongatoides, Pennate sp. AC, and Chaetoceros neglectus.

Three more taxa are associated with the northern assemblage through correlations with component II over leg 1 observations. These are Nitzschia cf. heimii, Distephanus speculum, and Amphidinium hadii. All three of these species did occur on leg 2 in patterns other than the component score, thus their association with the northern assemblage only is revealed by the correlation with leg 1 only.

Correlations with Principal Component III. No taxon correlates positively with component III except for G. lachryma, reinforcing the interpretation that the component is dominated by only one taxon with a unique distribution and a large variance.

Conclusions from Correlations with All Taxa. Correlating additional taxa to the component scores clarifies interpretation of each component. A small number of additional taxa are identified through correlations with component I as being a part of the Weddell assemblage. Correlations with component II identifies a large number of additional taxa that are part of the ACC assemblage. This helps confirm that the pattern of component II is a community trend in a large number of taxa with lower abundances than those taxa in the Weddell assemblage, as can be seen from a comparison of mean log biomass at Weddell stations and at ACC stations (Figure 9). The Weddell Sea bloom is mainly composed of just five taxa that have very high abundances at Weddell Sea stations and occur at very low biomasses at ACC stations.

Figure 9. Mean log biomass at Leg 1 Weddell Sea stations plotted against mean log biomass at Leg 1 Antarctic Circumpolar Current stations, for all, 92 taxa. Circles represent taxa identified as part of Weddell assemblage, diamonds taxa identified as part of ACC assemblage, squares un-associated taxa. Filled symbols represent taxa used in PCA.



The ACC assemblage, on the other hand, tends to contain species with moderate abundances in both waters, with somewhat higher abundances at ACC stations. The lack of correlations with component III confirms that the pattern of component III is not acommunity-wide pattern, but is simply a pattern dominated by the distribution and abundance of one taxa, G. lachryma.

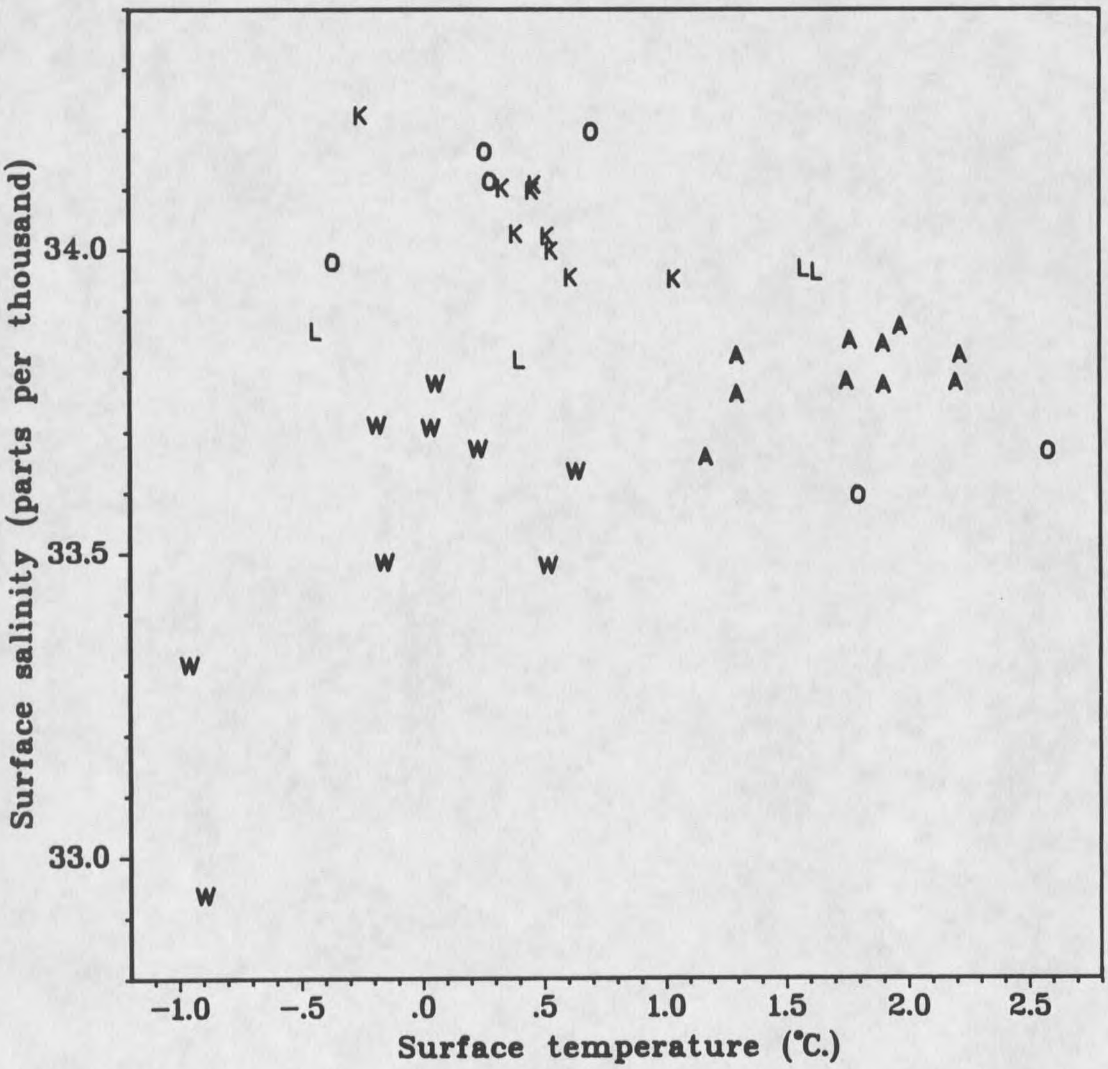
Physical Characteristics of the Water Masses

Temperature and Salinity

The plot of temperature against salinity for all surface observations (Figure 10) shows that there are several water masses that can be distinguished by their temperature/salinity signal. Maps showing the distribution of surface temperatures and salinities are presented in Figures 11 and 12. Weddell Sea water is cold and low in salinity due to the melting of the seasonal ice-pack. Two Weddell Sea stations (16 and 18) can be seen to be outliers in having very low temperature and salinity, most certainly reflecting their proximity to the melting ice-pack. ACC water is warmer and higher in salinity than the Weddell Sea water. Water in the vicinity of Elephant Island (on leg 2) is even higher in salinity, but is intermediate in temperature to Weddell and ACC water.

If just the leg 1 surface observations are considered in the plot of surface temperature versus salinity, there is a disjunct distribution between ACC water and Weddell Sea water. The temperature distribution between the two is disjunct, with Weddell Sea surface

Figure 10. Surface temperature plotted against surface salinity for all stations (n=38). Stations identified by letter (A=ACC, W=Weddell, L=Line 1, K=Krill,145,149, O=other Leg 2).



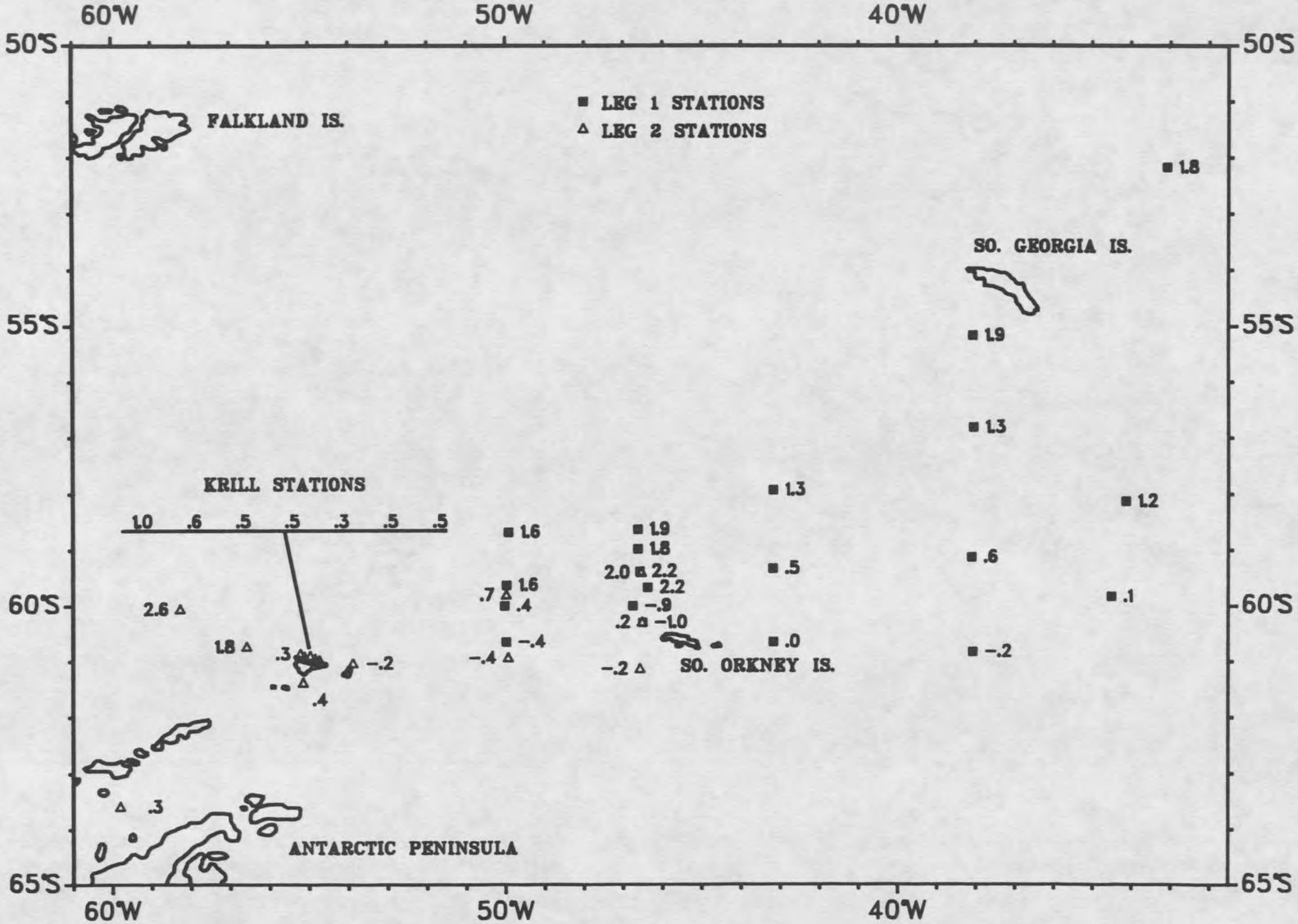


Figure 11. Surface temperature (°C.)

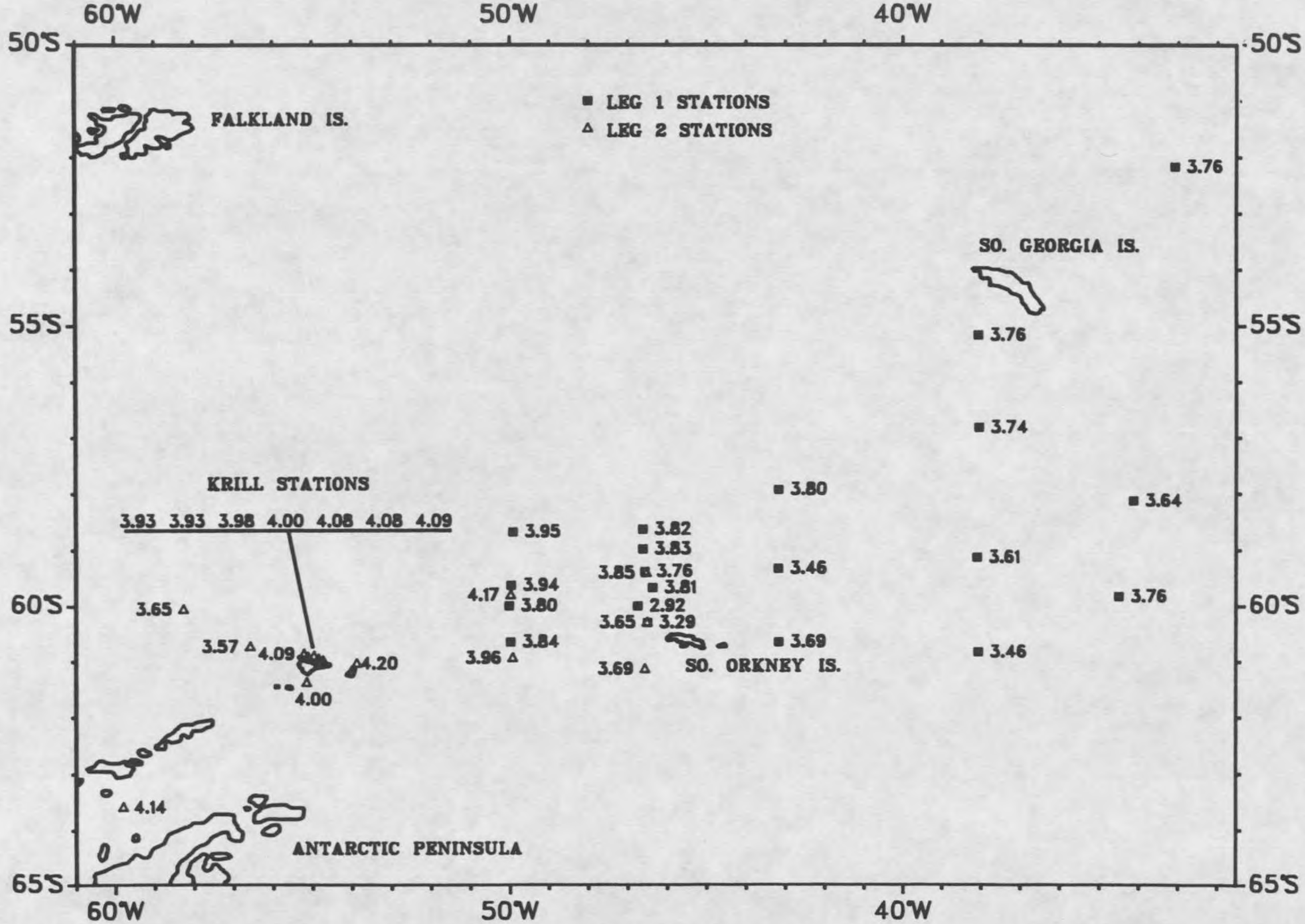


Figure 12. Surface salinity minus 30 (parts per thousand)

water less than 0.8 degrees Centigrade, while Drake Passage water is greater than 1.0 degrees Centigrade. Although the Weddell Sea water is less saline than the ACC water, there is more of a continuous distribution in salinities, with the boundary occurring around 33.7 parts per thousand. Thus, the two bodies of water can be distinguished by a combination of temperature and salinity of surface waters.

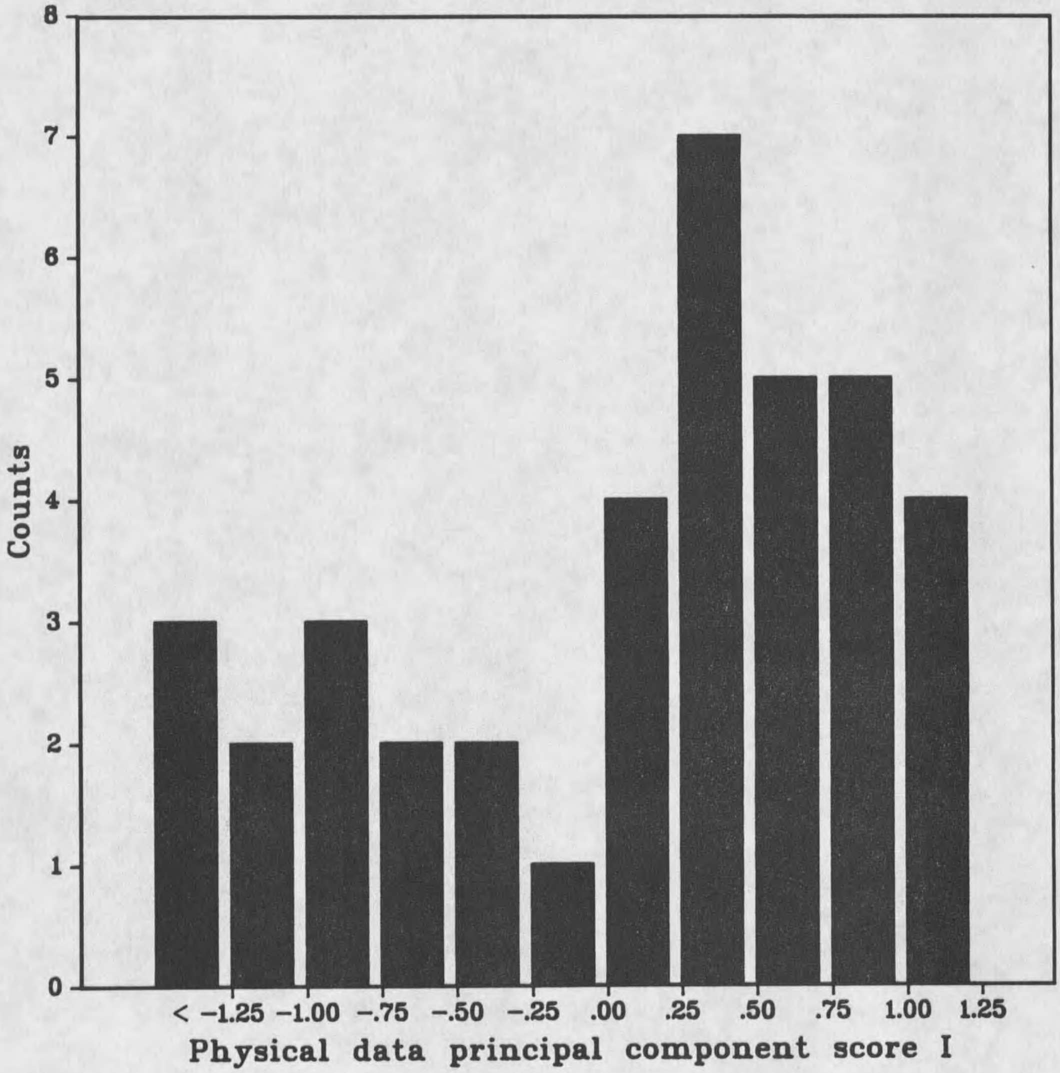
Principal Component

To form a single variable as a combination of temperature and salinity for the purpose of distinguishing the two bodies of water, a principal component analysis on the correlation matrix of surface temperature and salinity was performed. This amounts to a simple axis rotation to account for the most variance of the plot of surface temperature versus salinity (in the standardized space).

The results of this PCA give a first principal component that accounts for 57 % of the variance, with equal contributions from salinity and temperature. A histogram of the first component scores (Figure 13) shows a bi-modal distribution with the break between the two modes occurring around 0.0, with negative scores (low salinity and temperature) representing Weddell Sea stations, and positive scores (high salinity and temperature) representing Drake Passage stations and Krill stations.

If these scores are then plotted on a map (Figure 14), this gives a spatial representation of the boundary between Weddell Sea water and Drake Passage water. The boundary is sharpest between stations 18 and 20 on line 2, where Foster and Middleton (1984) suggest a frontal

Figure 13. Histogram of physical data principal component I scores showing bi-modal distribution with boundary at zero. Weddell Sea water is less than zero, ACC water is greater than zero.



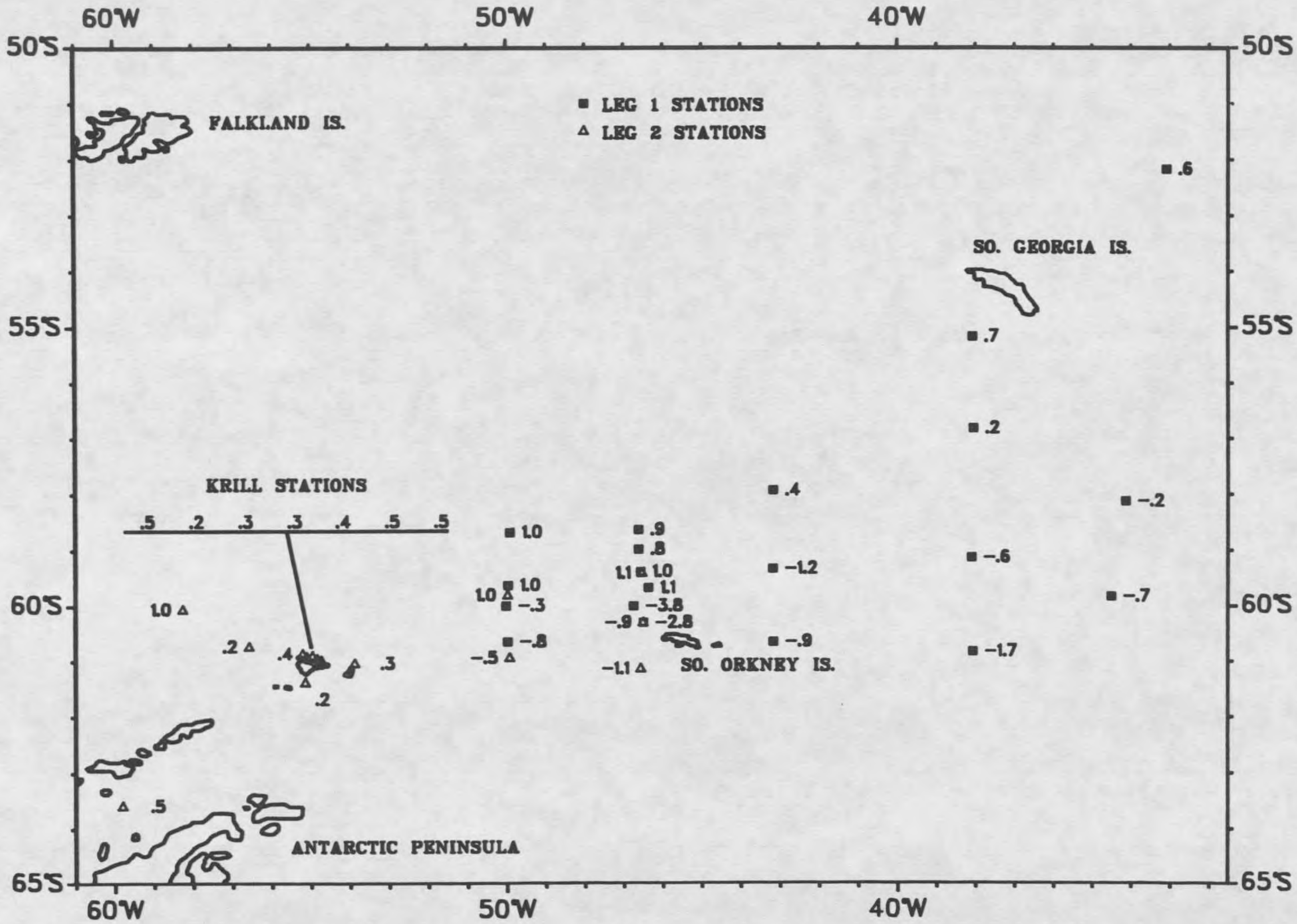


Figure 14. Physical data principal component score I

structure exists. This boundary is consistent with the boundary suggested by Michel (1984) and Michel and Linick (1985) from silicate and Carbon-14 data. We are thus confident that we have accurately identified Antarctic Circumpolar water and Weddell Sea water through their temperature and salinity signal.

Correlation Between Assemblages and Water Masses

Canonical Correlation

In order to describe the degree of association between the phytoplankton assemblages and the water masses, the two data sets (biological and physical) were analyzed together, by means of a canonical correlation analysis. This analysis searches for the greatest degree of correlation between pairs of linear combinations of the two data sets, and gives the amount of contribution of each of the original variables to the canonical variate. Goodman, et al (1984) provides a brief description of the use of canonical correlation analysis in analyzing the association between phytoplankton assemblages and environmental variables.

The same data as the principal component analysis was used for the biological data set, the fifteen taxa with the greatest variance in biomass that occurred on both legs of the cruise. For the physical data, the temperature and salinity at 0 meters and 100 meters at each station were used. Eigenvectors representing the first three canonical variates are presented in Table 3.

Since the canonical correlation is searching for the greatest degree of correlation between linear combinations of the two data sets, the result does not necessarily account for the most variance within each data set (as a principal components analysis does).

Table 3. Canonical correlation analysis between the natural log-transform of the biomass of fifteen phytoplankton taxa and four physical variable (surface and 100 meter temperature and salinity).

	Canonical Variates			
	I	II	III	IV
Canonical correlation	.881	.730	.602	.493
Percent variance accounted for in phytoplankton data set	19.0	7.8	5.2	6.2
Percent variance accounted for in physical data set	36.5	18.5	29.2	15.8
Phytoplankton taxa		Eigenvectors		
Odontella weissflogii	.304	.106	.182	-.170
Rhizosolenia alata f. inermis	.223	-.307	-.069	.151
Monads and Flagellates <-20	.153	-.146	-.603	-.362
Synedra reinboldii	.135	-.123	.030	.266
Eucampia balaustium	.130	-.106	.332	-.222
Gyrodinium lachryma	.046	.287	.173	-.109
Thecate dinoflagellates 10-79	.030	-.009	-.032	-.116
Chaetoceros dichaeta	-.025	.173	-.091	.127
Corethron criophilum	-.034	.119	.234	.227
Naked dinoflagellates 5-109	-.054	.318	.047	-.048
Dactyliosolen antarcticus	-.075	-.092	.068	-.080
Chaetoceros flexuosus	-.085	.067	.081	.136
Chaetoceros atlanticus S	-.087	-.391	.250	.170
Nitzschia cf. heimii	-.098	.054	-.070	-.030
Nitzschia cf. pseudonana	-.207	-.172	.503	-.241
Physical variables				
Temperature 0M	-.888	-.119	-.505	-.445
Temperature 100M	.314	-.477	.712	.765
Salinity 0M	-.308	.860	-.042	-.132
Salinity 100M	-.130	-.138	-.486	.447

Canonical Variate I. In fact, the first canonical variate identified the same assemblage of species that was identified in the first principal component, those taxa that were abundant in Weddell Sea waters and at the krill stations. These taxa were correlated most strongly with the colder water found at 0 meters at these stations. They were also correlated with the lower salinities found at 0 meters at these stations, and with warmer water at 100 meters.

The canonical correlation coefficient, the correlation between the two sets of scores, was .881, a significant correlation ($p<.005$). This accounted for 19% of the variance in the biological data set, and 37% of the variance in the physical data set (note that the variance accounted for in the biological data cannot be directly compared to the variance accounted for in the principal components analysis, as the canonical correlation analysis is working on standardized data).

In order of magnitude of positive contribution, the taxa identified as part of the Weddell/krill assemblage were Odontella weissflogii, Rhizolenia alata f. inermis, Synedra reinboldii, and Eucampia balaustium. O. weissflogii dominates the positive contributions. The only difference between the PCA assemblage and the canonical assemblage identified was the inclusion of a taxon that was not a part of the PCA assemblage, Monads and Flagellates <2-20, in the canonical assemblage, and the exclusion of a taxon, Chaetoceros dichaeta, that was a part of the assemblage.

The negatively weighted taxa identified the same taxa that were identified by the second principal component, those taxa that were abundant in ACC water and not in Weddell Sea water on leg 1. In order of magnitude of negative contribution, those taxa are: Nitzschia cf. pseudonana, Chaetoceros atlanticus S, and Dactyliosolen antarcticus.

N. cf. pseudonana dominates the contributions. The only difference between the PCA assemblage and the canonical assemblage was the inclusion of Chaetoceros flexuosus in the canonical assemblage. Nitzschia cf. heimii also weakly contributes to the canonical assemblage, as it does to the PCA assemblage.

This resulted in first canonical variate scores (Figure 15) that were generally negative at the Weddell Sea stations, the krill stations, and the stations in the vicinity of Elephant Island, and positive at ACC stations.

The physical data contributions were dominated by a large negative contribution from surface temperature, with a weak but negative contribution from surface salinity, and a positive contribution from 100 meter temperature. This also resulted in positive canonical variate scores at the Weddell Sea stations, krill stations, and Elephant Island stations, and negative scores at the Drake Passage stations. This identifies the cold water found at the Weddell Sea stations, and indicates that, although warmer than the Weddell stations, the krill stations are also colder than the Drake Passage stations. Thus, surface water temperature is most correlated with this biological assemblage, as surface water temperature is the physical variable (in this data set) that best distinguishes Weddell Sea and krill station water from ACC water.

Surface salinity has a weaker positive contribution than surface temperature because, although the biological component occurs at both Weddell and krill stations, the krill stations have higher salinities, while the Weddell stations have low salinities. Thus the surface

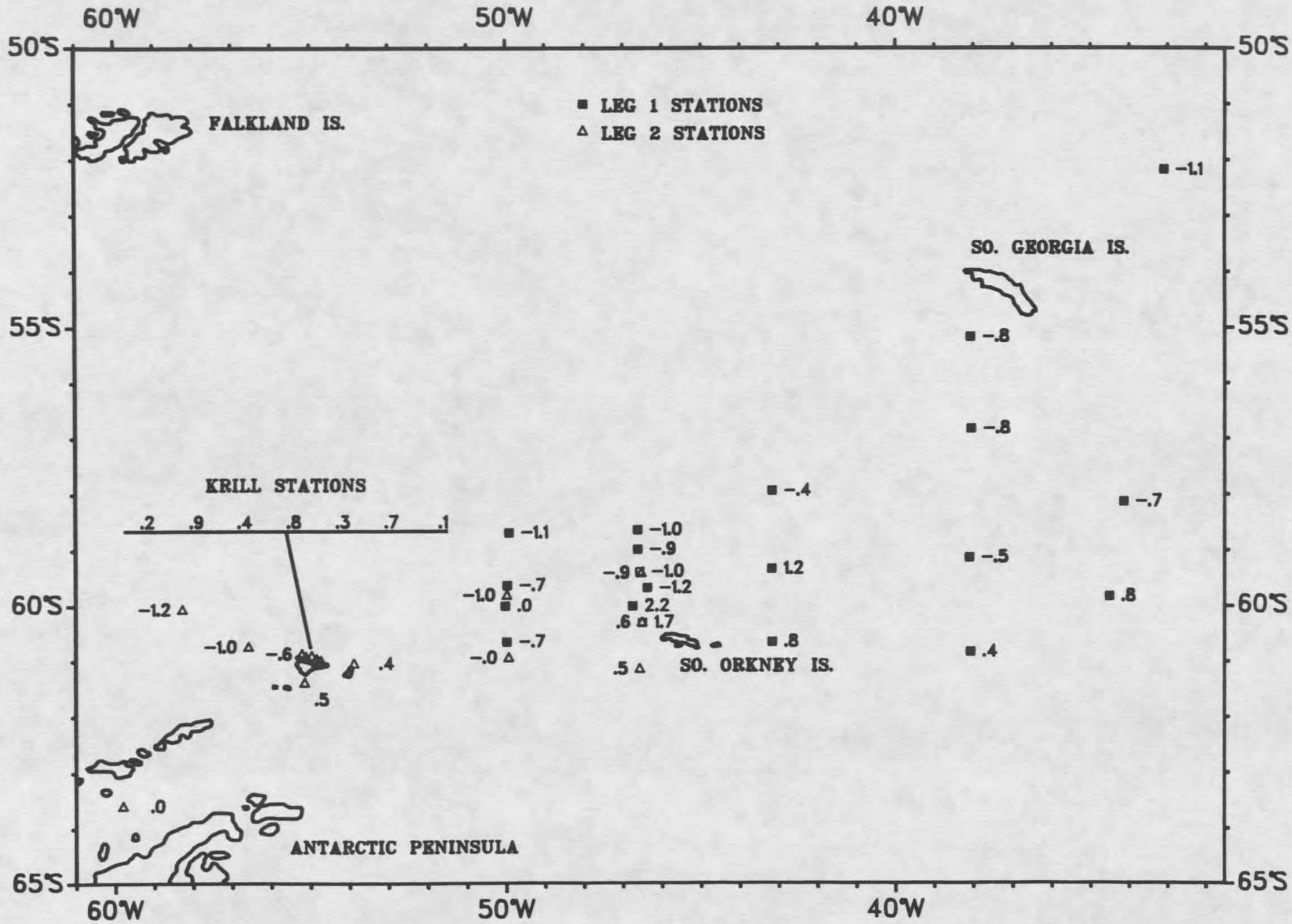


Figure 15. Canonical variate score I

salinity contribution is indicating the low salinities of the Weddell stations being correlated with the biological component.

Similarly, the positive contribution from 100 meter temperature indicates the warmer water found at 100 meters at the krill stations. This is a weak contribution as the 100 meter water at the Weddell stations is colder than the krill and Drake 100 meter water.

Additional taxa weakly associated with the WS assemblage through moderate negative correlations with this physical canonical variate are Chaetoceros tortissimus, Amphidinium sp AY, Gyrodinium rhabdomate, and Thalassiothrix antarctica. Additional taxa associated with the ACC assemblage through positive correlations with this physical canonical variate are Distephanus speculum, Nitzschia angulata, Dactyliosolen tenuijunctus, Flagellate AY, and Nitzschia kerguelensis (Table 2).

Canonical Variate II. The second canonical variate had a canonical correlation coefficient of .730 (significant at $p<.005$), and accounted for 8% of the variance in the biological data and 19% of the variance in the physical data. This component correlated those taxa abundant at many of the leg 2 stations, including the krill stations and associated stations near Elephant Island (145 and 149), and stations east of Elephant Island (150, 151, 152), with the greater salinities found at the surface at those stations, creating positive scores at these stations (Figure 16).

Those taxa identified as being a positive part of the component are, in order of contribution: Naked dinoflagellates, Gyrodinium lachryma, C. dichaeta, Corethron criophilum, and O. weissflogii. These were taxa that were as or nearly as abundant at the krill stations and

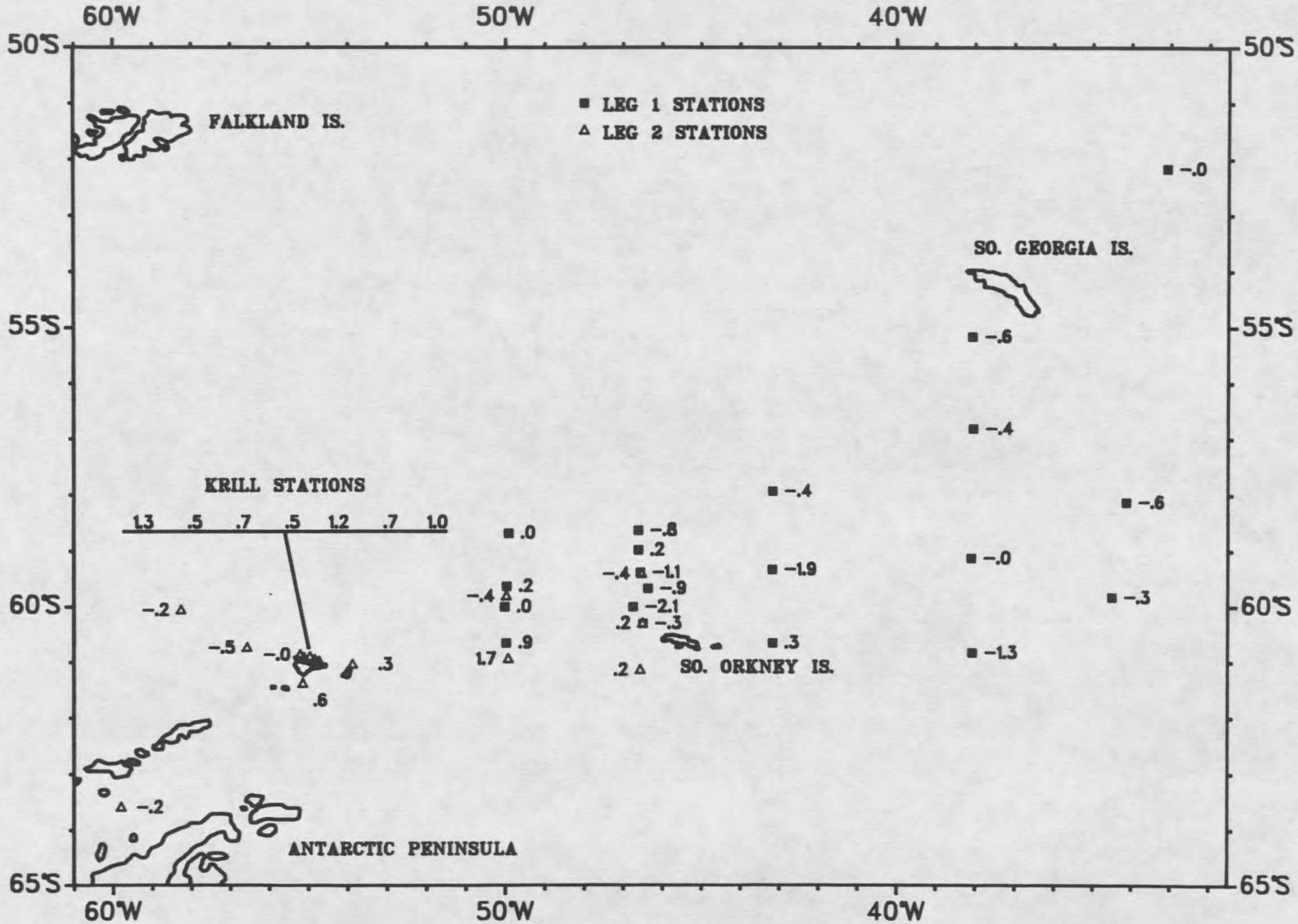


Figure 16. Canonical variate score II

also at stations 145, 149 and 150 as they were on leg 1 stations. Those taxa with large negative contributions to the canonical correlate, which are not as relatively abundant at the krill stations, are Chaetoceros atlanticus S and Rhizolenia alata f. inermis. Although these taxa appear at these stations, they do so with abundances far less than on leg 1. This is part of what prevents the Weddell Sea assemblage identified by principal component I, which had affinity with the krill stations, from being completely recapitulated. Those taxa whose abundances at the leg 2 stations identified are far less than on leg 1 are excluded, as the water mass being correlated with is the water at the krill and Elephant Island stations, not the water at WS stations. This explains why R. alata f. inermis, S. reinboldii, and E. balaustium are not associated with the canonical variate.

Additional taxa associated through correlations with this physical canonical variate are Navicula spp., Nitzschia 'cylindrus', and Tropedoneis antarcticus (Table 2).

Canonical variate III. The third canonical variate identified just the krill and Elephant Island stations (145 and 149) by correlating taxa abundant at just those stations on leg 2 with the warmer water found at 100 meters at those stations, creating positive scores at those stations (Figure 17). The two taxa showing this pattern most were Nitzschia pseudonana and E. balaustium, while Monads and Flagellates <2-20 contributed negatively to this pattern. Whereas variate II identified taxa occurring through many of the leg 2 stations, including the krill stations, variate III identifies taxa that occur on leg 2 just at the krill stations and in the vicinity of Elephant Island.

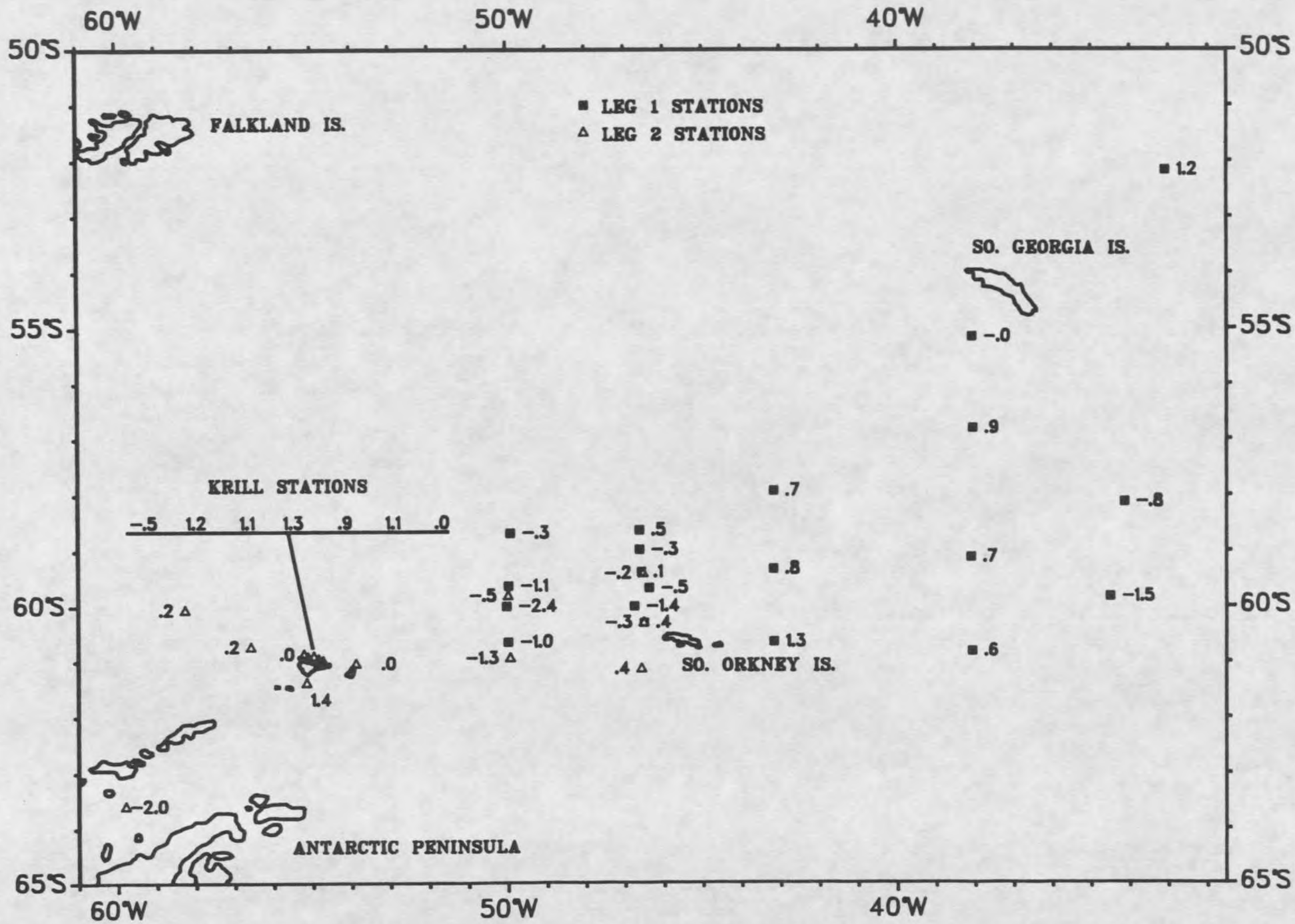


Figure 17. Canonical variate score III

Additional taxa associated with this physical canonical variate through correlations are Chaetoceros tortissimus, Diplopeltopsis perlata, Protoperidinium archioratus, Protoperidinium macrapicatum, and Protoperidinium cf. crassipes (Table 2).

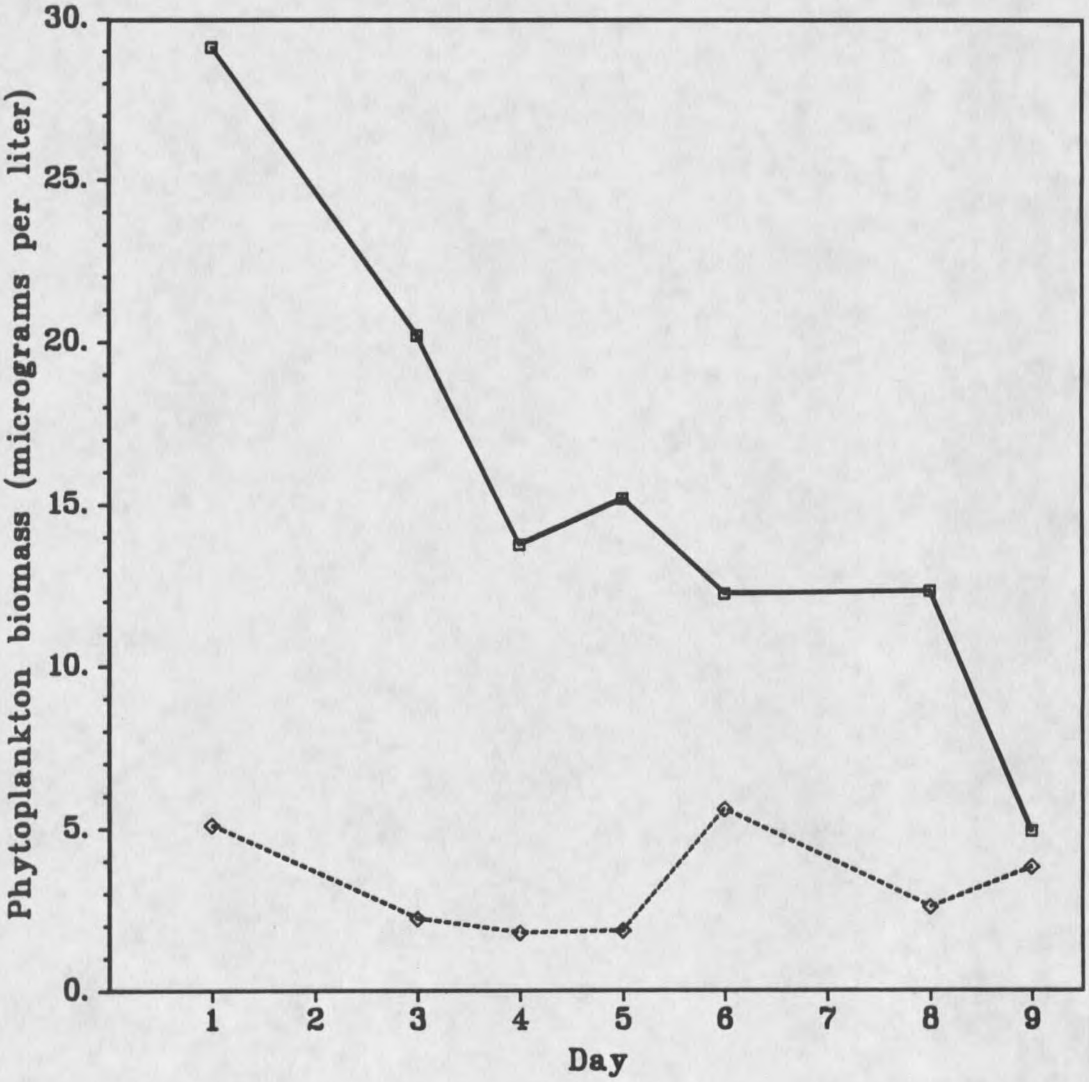
Size Distribution at the Krill Stations

For nine days (February 28 to March 8), samples were taken in the krill swarm discovered north of Elephant Island. This swarm has been described as a super-swarm (El-Sayed, 1985). Phytoplankton data from 7 stations occupied in the krill swarm are part of the data set being analyzed. These seven stations represent a short term time-series that perhaps show the effects of the intense grazing pressure that was probably occurring. These stations were analyzed as a time-series.

Antezana and Ray (1984) reported that this krill swarm drastically reduced the standing crop of phytoplankton in the water column. It has been suggested that Euphausia superba are much more efficient grazers on microplankton (greater than 10 microns) than they are on nanoplankton (less than 10 microns) (Hewes, 1984), and thus might significantly shift the size distribution of the phytoplankton standing stock. Quetin and Ross (1985) have shown in laboratory experiments that clearance rates of Euphausia superba feeding on phytoplankton are directly related to cell size (on phytoplankton 4 to 40 microns in Equivalent Spherical Diameter (ESD)), with larger cells taken at higher rates.

The summed biomass of all taxa greater than 10 microns ESD and all taxa less than 10 microns ESD are plotted against time in Figure 18.

Figure 18. Total phytoplankton biomass at 7 stations sampled over 9 days (Febuary 28 to March 8) during krill swarm north of Elephant Island. Solid line is sum of all taxa > 10 microns Equivalant Spherical Diameter (ESD), dashed line is sum of all taxa <10 microns ESD.



The summed biomass of taxa less than 10 microns ESD did not show a great change, whereas the sum biomass of all taxa greater than 10 microns did show a steep decline over the nine days of the sample. Therefore, this can be cautiously interpreted as indicating that taxa greater than 10 microns ESD are being grazed by E. superba, while the nanoplankton remained relatively unchanged.

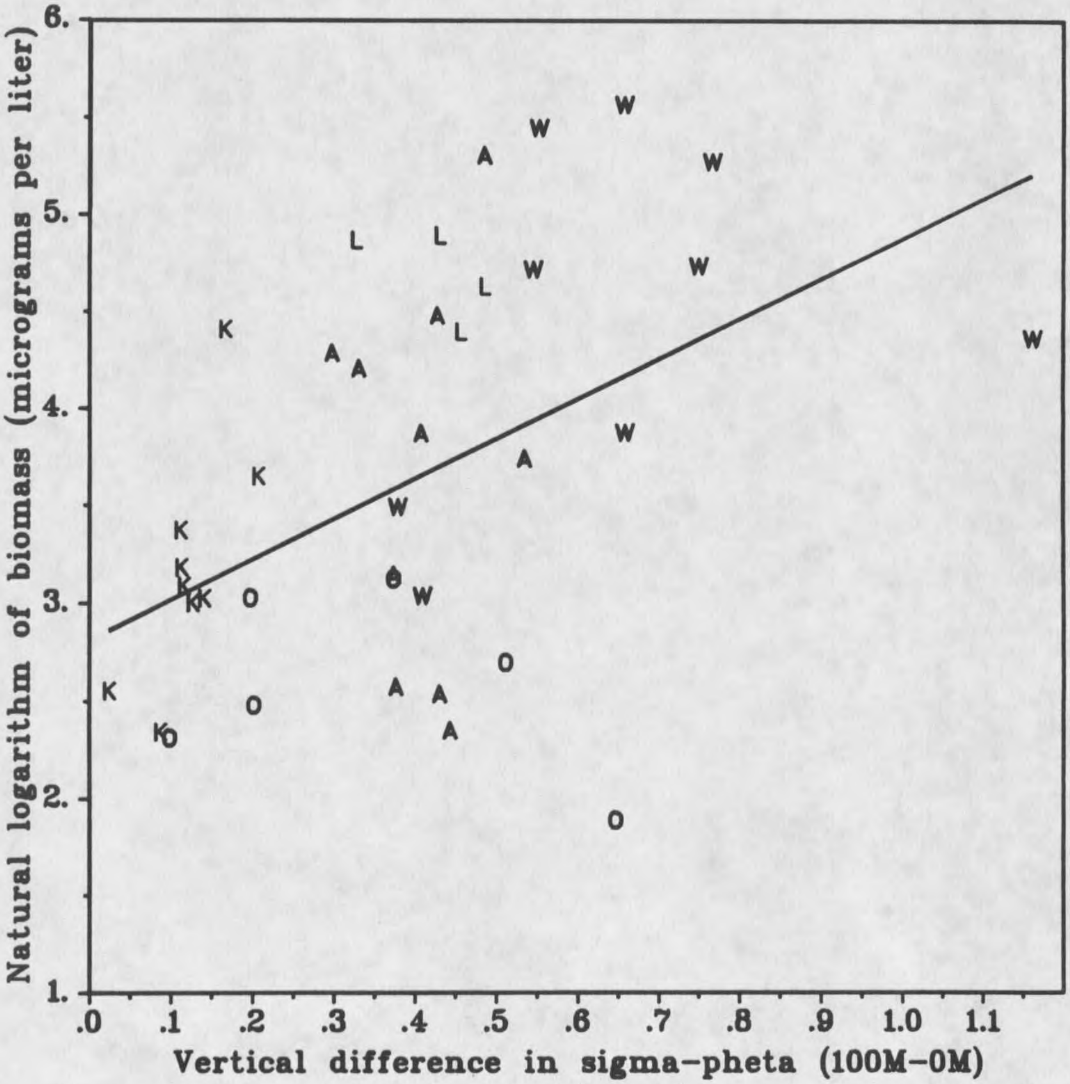
This cannot be considered a definitive proof of the grazing effects of krill, as this was not a controlled experiment. However, the result is suggestive of the effects of grazing of krill on the size distribution of phytoplankton standing stocks, and indicates that E. superba may have significant influence on the species composition of standing stocks of phytoplankton in the Antarctic.

Correlation Between Biomass and Vertical Density Difference

Since it has been suggested that greater vertical stability contributes to higher biomasses, the natural logarithm of total biomass (augmented by one) is plotted against the difference in density (sigma-pheta) between 0 meters and 100 meters in Figure 19. This was done using the biomass of the surface observation at each of the 38 stations on legs I and II. There is a reasonably clear trend of greater biomass with greater vertical stability, with only one troubling outlier, which is a Drake Passage station (164), sampled at the end of the study very late in the season (March 23).

There is a considerable amount of variance in the trend, which contributes to the medium correlation ($r=.47$, significant at $p<.005$). This is expected, as it is not assumed that vertical structure is the

Figure 19. Natural logarithm of total biomass at surface observation of each station regressed on difference in density (sigma-pheta) between 100 meters and 0 meters at each station ($r=.47, p<.005$). Letter codes are identified in Figure 10.



only factor controlling biomass, but simply one of many factors contributing to it.

Test for Temporal Confounding of the Data

Although this analysis is concerned with the spatial distributions of phytoplankton taxa, space and time are confounded in the study by the sampling procedure. This was unavoidable given the spatial scale of the study (and the limitation of one ship).

To test that phytoplankton distributions were not changing over time rather than over space, two coefficients of correlation were calculated, the correlation between the phytoplankton assemblage distance and spatial distance, and the correlation between phytoplankton assemblage distance and temporal distance (defined as days between samples), over all possible pairs of observations. The phytoplankton assemblage distance was defined as the euclidean distance between the first three principal component scores of the two observations. This gives a measure of the degree of similarity between the phytoplankton assemblages at the two observations.

This was done over all leg 1 observations. The correlation between phytoplankton distance and spatial distance ($r=-.05$, $p>.05$) was not greatly different from the correlation between phytoplankton distance and temporal distance ($r=-.09$, $p\cong.1$). This was also repeated over all observations, yielding another spatial correlation ($r=.04$, $p>.05$) and temporal correlation ($r=.20$, $p<<.01$).

As there is no evident east-west structure to the phytoplankton data and there is a north-south boundary to the phytoplankton distribution, one would expect only a small amount of correlation between spatial distance and phytoplankton distance. In both trials, there was less than the expected correlation, as the spatial correlation is not significantly different from zero in either case.

If the data were not confounded by the length of time between samples, the correlation between phytoplankton distance and temporal distance should be close to zero. Over the leg 1 observations, this is the case, as the correlation between temporal distance and phytoplankton distance is not significantly different from zero. However, for the entire data set, there is a small degree of positive correlation between temporal distance and phytoplankton distance, which is significantly different from zero. There are two nodes along the temporal scale, 0 to 15 days difference between observations (which are within leg 1 and within leg 2) and 33 to 57 days (which are between leg 1 and leg 2). The between leg 1 and leg 2 node is slightly higher on the phytoplankton distance scale, implying that phytoplankton distances are greater between leg 1 and leg 2 than they are within leg 1 and within leg 2.

Therefore, there does not appear to be any serious temporal confounding of the data within leg 1. There is a small amount of temporal confounding between the legs; therefore the time lag between sampling leg 1 and leg 2 must be borne in mind when interpretations are drawn from the data.

DISCUSSION

Factors Influencing Production and Standing Stocks of Phytoplankton in the Antarctic

The distribution of phytoplankton biomass in the Antarctic is known to vary considerably, both in space and in time (Hempel, 1985). Bodungen et al (1986) distinguish between factors controlling rates of growth and those controlling the accumulation of cells. Since nutrients are rarely if ever found to be limiting in the Southern ocean , other factors must be considered to understand what controls rates of growth, although the role of micro-nutrients has not been fully explored (Holm-Hansen et al, 1977).

The main remaining limits to physiological growth are light and temperature. There is a large scale correlation between daily insolation and production going from waters far north of the Antarctic Convergence to waters close to the Antarctic continent, but meso-scale differences in production cannot be fully accounted for by the variation in light at that scale (Holm-Hansen, et al, 1977). Temperature has been found to be limiting to antarctic phytoplankton (Neori and Holm-Hansen, 1982), with 7 °C found to produce the maximum rate of growth in populations used to waters from -1. °C to 2. °C. Again, though, meso-scale differences in factors (such as temperature) within regions of the Antarctic are generally not great enough for differential growth rates to account for the large variation in biomass that is found (Bodungen, 1986). In sum, Holm-Hansen, et al (1977) report much variation in growth rates from waters with similar conditions of light, inorganic nutrients, and temperature.

Factors controlling the accumulation of cells, such as water column stability or density structure, grazing, and the initial seed population, can vary greatly between adjacent water masses. Antarctic waters are often unstable and deeply mixed to over 100 meters (Hempel, 1985). Meltwaters from the receding ice-edge in the austral spring enhance the vertical stability of the water column, contributing to spring blooms that follow the ice-edge and are thought to be regular phenomena (Smith and Nelson, 1985; Smith and Nelson, 1986; El-Sayed and Taguchi, 1981). Entrainment in a shallower mixed-layer would lead to a higher concentration of cells above the pycnocline, but not necessarily a higher biomass integrated over the entire water column. However, there is a certain amount of time necessary for a given cell in dark conditions to adapt to a high light regime. Thus, overall production rates in water frequently circulated from high to low light regimes would be lower than production rates in water maintained in high light regimes. Therefore, increased vertical stability could increase overall production rates by consistently keeping a greater number of cells in the euphotic zone, where they could take advantage of the long Antarctic austral summer days.

Grazing, especially by dense swarms of <u>Euphausia superba</u>, can reduce standing stocks of phytoplankton in the Antarctic severely. However, it is not clear that all blooms are heavily grazed. Long-lived blooms probably receive heavy grazing pressure eventually, but many of the phytoplankton blooms in the Antarctic seem to be short-lived, so it is not clear that they are always "found" by a krill swarm, and hence controlled by krill grazing pressure. Many researchers report a negative correlation between chlorophyll A and krill abundance (Weber and El-Sayed, 1985, El-Sayed, 1984), which could indicate that krill do regularly graze phytoplankton stocks in the locations where the krill occur in significant numbers.

For most of the year in the Antarctic, light is clearly limiting to growth. The high light regime of summer does not last for very long, suggesting the possibility that maximum standing stocks are limited by the end of the growing season. If this is the case, the size of the initial seeding of a water mass in the austral spring may be of great importance to the eventual maximum size of the standing stocks. This may be of especial importance to ice-edge blooms, as the density structure from the melting ice-pack is a short-lived phenomena that breaks down as the season progresses. Therefore, the release of high standing stocks of epontic algae into the water column in some parts of the Antarctic may be one factor contributing to the attainment of higher standing stocks in those areas (Ackley et al, 1979).

Association of Phytoplankton Assemblages with Water Masses on Leg 1

On leg 1, the analysis clearly defines two distinct phytoplankton assemblages, one occurring in Weddell Sea waters and the other occurring in Antarctic Circumpolar Current waters. The assemblages are highly correlated with the physical signal of the bodies of water. Additionally, total biomass is generally at least twice as great in

Weddell Sea water versus ACC water. Thus, the two bodies of water differ both in composition and abundance.

Leg 1 Abundance Differences

In regards to abundance, it does not appear that differential productivity rates at the time of sampling could account for the difference between the waters. Macro-nutrients are not limiting in either water mass. Daily insolation is not thought to vary on a scale great enough to account for the differences in biomass found within the study area. Temperature can effect productivity rates (Neori and Holm-Hansen, 1982), but rates increase with temperature up to 7°C., which would argue for higher potential rates in the northern waters, not in Weddell Sea waters. In this study, the variation in surface temperature is only from -1°C. in the Weddell Sea to 2°C in ACC water. Growth response of four arctic ice diatoms were unchanged over salinities ranging from 10 to 50 parts per thousand (Grant and Horner, 1976), indicating the salinity difference between the Weddell Sea water and ACC water (at most, 2 parts per thousand) could not account for the difference in abundance. Silicate concentrations are higher in the Weddell Sea, whose standing stocks are more diatom-dominated than the ACC waters, but it is not clear that silicate is limiting diatom production in the ACC waters, as concentrations are still high (Michel, 1984). The answer, therefore, is more likely to be due to factors controlling the observed standing stocks of phytoplankton rather than present production rates.

The Role of Epontic Algae. A major portion of the Weddell Sea is covered with ice during the austral winter, including portions of the study area. Epontic algae (ice-algae) are reported to attain standing stocks within the ice in the Weddell Sea high enough to constitute a phytoplankton bloom on their release into the water column, without any further growth (Ackley et al., 1979).

The fate of epontic algae once released into the water column is not certain, as they may simply settle out of the water column quickly, as perhaps suggested by the substantial diatom sediments in the Antarctic (DeMaster, 1981). However, it is also possible that epontic algae may serve as the inoculum for the spring ice-edge bloom. In a comparison in the Weddell Sea of ice-algae community composition with adjacent water column composition of phytoplankton, Garrison and Buck (1985) found that the taxonomic composition was similar. Their study was done one year previous to this study, and they found, both in the ice and in the adjacent water column (in what was thought to be a viable state), all the species identified in this study as the Weddell Sea assemblage . Two of the species in the WS assemblage, Odontella weissflogii and Eucampia balaustium, have been identified in the ice and in the adjacent water column in the form of resting spores (Hoban et al., 1980), suggesting they may over-winter in the ice and re-seed a bloom in the austral spring.

The Weddell Sea may therefore benefit from a release of phytoplankton, mainly centric diatoms, from the melting seasonal ice-pack that could serve as both a significant contribution to the standing stocks and as an inoculum of species well suited to the spring and summer bloom conditions that exist. Self-evidently, net production of a population is related to the size of the standing stocks. Under the constraints of a short growing season in the Antarctic, the release of ice-algae may constitute a significant "head-start" for the waters of the Weddell Sea, enabling them to achieve higher standing stocks than other waters. This assumes that maximum standing biomass is only limited by the declining light regime at the end of the short growing season.

Vertical Stability of the Water Column. Another related factor possibly contributing to the size of standing stocks is the enhanced vertical stability of the water column that exists near the melting seasonal ice-pack. Waters in the Southern ocean are often unstable to 100 meters or more, and are often mixed to great depths. In this study, there are much greater vertical differences in density in Weddell Sea waters than in ACC waters, due to lowered salinities and temperatures, indicating the influence of the melting ice-pack on Weddell Sea water. Ice-edge blooms in the density layer have been documented from the Weddell Sea (Smith and Nelson, 1986).

This study has shown an overall relationship between the magnitude of the density gradient over the first 100 meters of the water column and the phytoplankton biomass. It thus appears that physical processes relating to the vertical stability of the water column are important to phytoplankton dynamics in the Scotia Sea. The largest biomass stations in the Weddell Sea are particularly distinguished by considerably lower temperatures and salinities, indicating the proximate influence of the melt-waters of the seasonal ice-pack. There are only five stations with salinities less than 33.62 parts per thousand, all in the Weddell Sea on leg 1. These 5 stations (16, 56, 36, 46, and 18) are all high biomass stations, ranking as the first, second, third, seventh, and fourteenth greatest biomass stations, respectively. Therefore, the data suggests that ice-edge blooms have contributed to the high abundances found in the Weddell Sea.

Station 18 is slightly anomalous, having the fourteenth greatest biomass with the lowest salinity in the data set (32.92 parts per thousand). However, it also has the lowest temperature (-1.°C.), indicating that it is perhaps the most recently melted water, and has thus not had enough time since melting to accumulate higher standing stocks. The lower salinity melt-waters would be expected to heat quickly, since the mixed layer is so shallow. A few of the shallow pycnocline stations in the Weddell Sea have very low salinities with moderate temperatures, suggesting some warming of the surface waters has occurred.

In partial contrast to this trend, stations 20 and 22, just to the north of the frontal zone on line 2, have the fourth and ninth largest biomasses, but have relatively high salinities. They do have a moderately large density difference between 0 and 100 meters, due to relatively warm surface water. Similarly, stations 8 and 2, with the fifth and sixth largest biomasses, respectively, have relatively high surface salinities and temperatures. In conclusion, stations with greatly lowered salinities and temperatures appear to have conditions that allow for the accumulation of large biomasses, but are not the only stations or conditions at which large biomasses are found.

Grazing by Euphausia superba. Grazing pressure from krill could also effect standing stocks of phytoplankton. However, the distribution of euphausiid species during the cruise did not show any clear pattern of higher abundances in circumpolar water north of the confluence with Weddell waters (Brinton, 1985), which could have partially explained the lower biomasses in ACC water. Stations returned to during leg 2 had greatly reduced biomasses, which may have been due to grazing by krill, but leg 1 abundance differences do not appear to have been caused by grazing pressure.

Leg 1 Community Differences

In addition to a difference in total abundance between the two waters, there is also a distinct difference in community composition. One might expect different compositions as the two bodies of water come from different sources. However, most taxa in the Antarctic have circumpolar distributions, and the waters of the Antarctic Circumpolar Current mix with the waters of the Weddell gyre in the eastern Scotia Sea. One might then assume that every taxon in the ACC has the opportunity to occur in the Weddell Sea also, and thus it is necessary to think of causal explanations for the non-uniform distribution of taxa. Four possibilities, not mutually exclusive, are presented to account for the differences.

Circulation of Large Diatoms. The Weddell Sea assemblage is dominated by larger diatoms, while the ACC assemblage has a greater proportion of its total abundance in the smaller size phytoplankton (0-20 microns). A shallower mixed-layer should lead to greater turbulence per unit wind-stress than a deeper mixed-layer. Therefore, the shallower mixed-layer caused by ice melt at many of the Weddell stations could lead to enough turbulence to keep the larger diatoms entrained in the mixed-layer, whereas they may settle out of a less vigorously stirred deeper mixed-layer. This may account for the relative abundance of larger diatoms in the Weddell Sea assemblage.

Winter Survival in the Weddell Sea. The role of epontic algae in seeding the Weddell Sea assemblage, as previously mentioned, could contribute to species differences. It is possible that not all taxa are able to overwinter in the ice and/or survive the long period of little or no light and then once again become a part of the plankton community upon release into the water column. Studies have shown that the assemblage in the ice is very similar to the assemblage of viable cells in the adjacent water column (Garrison and Buck, 1985). If the ice-algae seed is of dominant importance in determining the Weddell Sea assemblage, this would prevent the possibility of any taxon participating in the assemblage if it was not able to survive overwintering in the ice pack of the Weddell Sea.

Neritic Assemblages. The ACC assemblage may be characterized as "oceanic", while the Weddell assemblage is "neritic". The largest bloom of the Weddell assemblage occur in water adjacent to the island shelf north of the South Orkney Islands. The only station near a shelf in ACC water was near South Georgia Island, which did not have a relatively high biomass of phytoplankton. Thus, the Weddell assemblage may consist of neritic species common to the island shelf areas of the Antarctic Peninsula and Scotia Sea. In fact, a majority of the Weddell Sea taxa species are described as neritic in Heywood and Whitaker (1984). The krill stations also occur on an island shelf (north of Elephant Island), and we have shown the similarity of species composition between the krill stations and the Weddell stations. It is then possible that this is a neritic assemblage, and that in the Weddell Sea the assemblage achieves high standing stocks on the shelf off the South Orkneys and is then carried downstream to the east into other parts of the Weddell Sea. This would account for the assemblage not occurring at the southern-most station (14) on line 1, as this is upstream from the South Orkney shelf. However, there is as yet insufficient information to definitively characterize many Antarctic phytoplankton species as neritic or oceanic, and give comprehensive causal explanations of their distributions. Species are characterized only on the basis of where they have been found in the past.

Large blooms of phytoplankton have consistently been reported from the shelf areas of the Antarctic Peninsula and Scotia Ridge islands. These shelves are generally shallow (100-200 meters) and may enhance phytoplankton standing stocks in the same way hypothesized for melt waters of the receding ice-edge -- by restricting circulation of surface waters to a depth shallower than they would otherwise obtain. Bodungen et al (1986) suggest that the neritic species form resting spores and sink as a strategy to remain on the shelf, as they are likely to be re-circulated if they settle at a depth of only 100 to 200 meters, whereas an oceanic species that sinks in 2000 meters of water is likely to have little chance of being recirculated. Two of the neritic species in our Weddell Assemblage are known to form resting spores (Hoban et al, 1980).

Silicate Distribution. The distribution of silicate could contribute to species differences. Although generally considered to be in amounts that are not limiting, silicate concentrations measured on this cruise (Michel, 1984) are higher in the Weddell waters than in the ACC waters. Within the short temporal blooms of the Antarctic, it remains possible that silicate, though not ultimately limiting to growth by being depleted to exhaustion, could be rate-limiting to the diatom blooms of the southern ocean, due to demand outstripping the maximum rate of uptake. It has been suggested that this is possible near the Antarctic Convergence (Heywood and Whitaker, 1984). This could also account for the greater diatom abundance in the Weddell assemblage than in the ACC assemblage.

Relationship of Community Structure to Physical Oceanographic Processes

The two assemblages are most disjunct at line 2, close to the area where the ACC waters first meet WS waters. On lines 3, 4, and 5, while the extremes of the lines are clearly one assemblage or the other, there is a zone of overlap of the assemblages that widens to the east. This zone of mixing between the assemblages corresponds to the zone of widening meso-scale eddys that Foster and Middleton (1984) propose to account for the physical oceanography of lines 3, 4, and 5. Thus, the phytoplankton assemblages appear to be partially mixed horizontally by meso-scale physical oceanographic processes.

This suggests that taxa in the ACC assemblage have had the opportunity to enter Weddell Sea water, but for some reason, do not get recirculated in the Weddell gyre or are not able to remain in the water column until the following spring, at least not in sufficient numbers to be a significant part of the phytoplankton biomass in the Weddell Sea. This may be related to the unique conditions of the seasonal ice-pack or the island shelf areas.

Temporal Changes in Lines 1 and 2

Leg II of the cruise was started on February 28, approximately two weeks after the end of leg I, and continued for 23 days. Though the analysis has been presented as a synoptic study, the entire cruise lasted 58 days. The statistical analyses treat all observations equally with no regard to temporal or spatial arrangement. The results have been interpreted spatially but it is interesting to consider the temporal aspects to the data when examining leg II. The large spatial scale of the sampling combined with the relative permanence of the frontal structure at the ACC-Weddell confluence ensures that re-sampling the same position one month later will likely mean sampling from the same general body of water, although the local conditions may have changed considerably. This appears to be the case on line 2, as the surface temperature and salinities of stations 151 and 152 are still indicative of WS water, while station 157 is still indicative of ACC water.

As the PCA and canonical correlation analysis were carried out over the entire data set (legs I and II), it is clear that the spatial distribution, coherence with water masses, and relative abundance of taxa were essentially the same on leg II as leg I. Total abundances were generally one order of magnitude less on leg II. Stations 151, 152, and 157 do show concordance with the phytoplankton distribution in the same area on leg 1 through similar principal component scores, although biomasses are considerably less. Two stations (150 and 160) were re-sampled from what had been line 1 of leg I. These two stations also have first principal component scores that are within the same range of scores from this area on leg I, although there is more variation in the scores in this area.

The general conclusion is that on the first two lines of leg 1 the same pattern in phytoplankton distribution exists approximately one month later, although abundances are much less. This probably reflects the breakup of vertical structure of the water column and subsequent dilution through deeper mixing, along with the considerable, though patchy, effects of grazing by krill. The physical data do show less vertical stability of the waters on leg II, and much of leg II was spent sampling a large *Euphausia superba* swarm, which was associated with a decline of biomass of phytoplankton (Antezana and Ray, 1984). Of course, the water that was there one month before has moved on, and the water replacing it may have had lower biomasses for some other reason.

Krill Stations

The physical and chemical analyses of Foster and Middleton (1984) and Michel (1984) were carried out only over leg I, so the characterization of the water around Elephant Island is uncertain. The krill stations carry their own unique temperature-salinity signal within this data set. There is little change from 0 meters to 100 meters, indicating the waters are well mixed to 100 meters. At 0 meters, temperatures are intermediate to ACC and WS water while salinities are higher than both ACC and WS water. At 100 meters, the krill stations are within the range of ACC water. Elephant Island is to the west of the zone of first contact between ACC and WSW, so the waters around Elephant Island are influenced mostly by either ACC water or Bransfield strait water. The one station sampled in the Bransfield strait (147) is identical to the krill stations in its surface temperature and salinity, but is very different at 100 meters. The temperature and salinity of the water around Elephant Island thus suggests that the water comes from either the Bransfield strait or the ACC, or some combination of both. The lack of vertical structure to the water around Elephant Island suggests that perhaps, most simply, 100 meter ACC water has been mixed to the surface.

It is clear that the Elephant Island (EI) water has no relationship to WS water, whereas the phytoplankton assemblage around Elephant Island has been identified as being similar to the Weddell assemblage. There is no evidence that the EI assemblage is related to ice-edge melting. The EI assemblage is in waters close to or over the island shelf, which would lend plausibility to a neritic assemblage, as was also suggested for the WS bloom north of the South Orkneys. The majority of taxa that form the WS assemblage are also present at the krill and Elephant Island stations, but they do not dominate the total biomass of the observations to the extent they did on leg 1. There are also a large number of additional taxa that appear at the krill and Elephant Island stations that were not a part of the WS assemblage on leg 1. Some of these only occur around Elephant Island, while others also occur at the other southern stations of leg 2. The krill assemblage appears to be loosely defined and variable.

Corethron criophilum is note-worthy in being as equally abundant (where it occurs) on leg 2 as on leg 1, and in not appearing east of line 2 on leg 1. It is possible that the prominence of C. criophilum on leg 2 is due to it favoring later season conditions, as has been suggested in Hempel (1985). Gyrodinium lachryma is also exceptional in being equally abundant on leg 2 as leg 1, although its distribution is more widespread.

Although the WS stations and the krill stations share a similar assemblage of phytoplankton, the total abundance of the WS assemblage is generally one order of magnitude greater than the total abundance of the EI assemblage. As mentioned, this is also the case for leg I stations that were re-sampled on leg II.

Abundances around EI may not have been greater earlier in the season than when they were sampled. It is not clear that the seasonal ice-pack has as great an influence those waters.

Alternatively, abundances around EI may have been as great as leg 1 abundances at the time leg 1 was sampled but had declined by the time of sampling on leg 2. This is suggested by the concrete evidence that on lines 1 and 2 of leg I, standing stocks did decrease substantially by the time they were re-sampled on leg II. There are three possible explanations to account for the suggestion of a decline in biomass around Elephant Island by the time it was sampled.

First, early season blooms may have been carried away from the area and production may have declined as the season progressed. Daily mean insolation declines by 50% between January 21 and March 21 at that latitude (Holm-Hansen et al, 1977). Second, the lack of vertical structure to the water suggests that if there had been any density structure to the water previously, by the time of sampling it had broken down, with the consequent deeper mixing and dilution of standing stocks. There is no direct evidence to suggest that either of these explanations actually occurred.

Third, the decrease in standing stocks may be due to grazing by krill or other zooplankton. There is direct evidence of this at the krill stations. Antezana and Ray (1984) document the decline in biomass during the krill swarm while this paper documents the change in community structure that also occurred. As the swarm existed before the ship arrived, an unknown amount of grazing occurred before the standing stock was sampled. The initial standing stocks are unknown, but it is conceivable that they were considerably greater than when first sampled.

Station 145 south of Elephant Island, not in the krill swarm, has a similar phytoplankton assemblage to the krill stations but biomasses twice as large. However, station 149 north-east of Clarence Island also has a similar distribution of phytoplankton, but with biomasses generally lower than the krill stations, perhaps suggesting that this water was grazed heavily as it moved past Elephant Island.

CONCLUSIONS

There were different assemblages of phytoplankton in the Antarctic Circumpolar Current water and in the Weddell Sea. Interactions with the shelf areas and with the seasonal ice-pack appear to be important to the dynamics of the Weddell Sea community, which achieved higher biomasses. The assemblage later in the season in the vicinity of Elephant Island was similar in composition to the Weddell assemblage, and may have been even more similar before it was subjected to the heavy grazing pressure by Euphausia superba that was ongoing at the time of sampling.

The largest phytoplankton blooms in the Weddell Sea may be restricted to ice-edges and shelf areas, creating a patchy mosaic of resources for Euphausia superba. Krill swarms are also associated with the ice-edges and shelf areas. It is unclear with what certainty a phytoplankton bloom will be "found" by a krill swarm, but if found, a swarm can significantly alter the phytoplankton standing stocks and the species compositions.

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