

Diatom assemblages in surface sediments of the Ross Sea: relationship to present oceanographic conditions

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Abstract: Fifty four surface sediment samples from the western and central Ross Sea were examined to determine relationships between modern oceanographic conditions and surface sediment diatom assemblages. A centered R mode principal components analysis demonstrates four geographically distinct assemblages. The assemblage just north of the Ross Ice Shelf in the central Ross Sea is most closely associated with *Stephanopyxis* spp. (a heavily silicified diatom abundant during the Pliocene), and may result from a combination of winnowing/reworking, and modern flux of primarily non-siliceous algae. The algal assemblage in the western part of the central Ross Sea is most closely associated with *Thalassiosira gracilis* (an open water diatom), and reflects early seasonal pack ice break up during the late spring inception of the Ross Sea polynya. The algal assemblage north of Drygalski Ice Tongue, in the western Ross Sea, is most closely associated with *Fragilariopsis curta* (a diatom common in stratified ice edge zones), suggesting that water column seeding by species melting out of coastal sea ice is important in this area. The assemblage south of Drygalski Ice Tongue is most closely associated with resting spores of *Thalassiosira antarctica* (a diatom associated with coastal waters). Although the habitat of *T. antarctica* requires future research, we speculate that sea ice conditions unique to area B support an autumnal *T. antarctica* bloom.

Received 20 October 1997, accepted 30 March 1998

Key words: Antarctica, diatoms, Ross Sea, sea ice, surface sediments, *Thalassiosira antarctica*

Introduction

The use of diatom assemblages as proxies for environmental conditions has increased significantly in recent years as the demand for high resolution records of past climate change rises. Diatoms are sensitive to small changes in environmental parameters such as temperature, circulation, and sea ice cover. Although foraminifera, which are commonly used in paleoclimate studies, can be scarce at high latitudes, diatoms are abundant, diverse, and well preserved (Leventer & Dunbar 1996). The complexity of sea ice/ocean/atmosphere interactions in the Southern Ocean renders the use of diatoms essential to a well developed interpretation of present oceanographic conditions and past climate change.

Developing a detailed, accurate record of paleoceanographic conditions using diatoms requires an intricate knowledge of the modern system, including:

- a) the link between living assemblages and the environmental variables controlling their distribution,
- b) factors which alter the assemblage during transport through the water-column, and
- c) the spatial distribution of surface sediment assemblages as records of the overlying water-column structure.

The goal of this study is to link modern oceanographic conditions with diatom assemblages found in surface

sediments of the western and central Ross Sea, Antarctica. This study uses the results of a comprehensive study by Leventer & Dunbar (1996) of primary productivity in Ross Sea surface waters and factors altering the assemblage during transport through the water-column. Using the site-specific algal assemblage data provided by Leventer & Dunbar (1996) combined with more closely spaced surface sediment sampling, this study seeks to refine the conclusions of a previous Ross Sea surface sediment study by Truesdale & Kellogg (1979). Further, this study completes the link between upper water-column production, transport to the sediment, and surface sediment assemblage distribution, which will increase the accuracy and resolution with which future studies of past floral compositions in the Ross Sea may be interpreted.

Background

Physical setting

The Ross Sea floor is characterized by a series of north–north-east trending troughs, banks, and other features that have been interpreted as ice stream channels, till tongues, subglacial deltas, and morainal banks (Fig. 1) (Anderson *et al.* 1992). The shelf becomes deeper from the north to the south-western Ross Sea due to landward deepening from isostatic depression. The bathymetry of the Ross Sea partially controls circulation

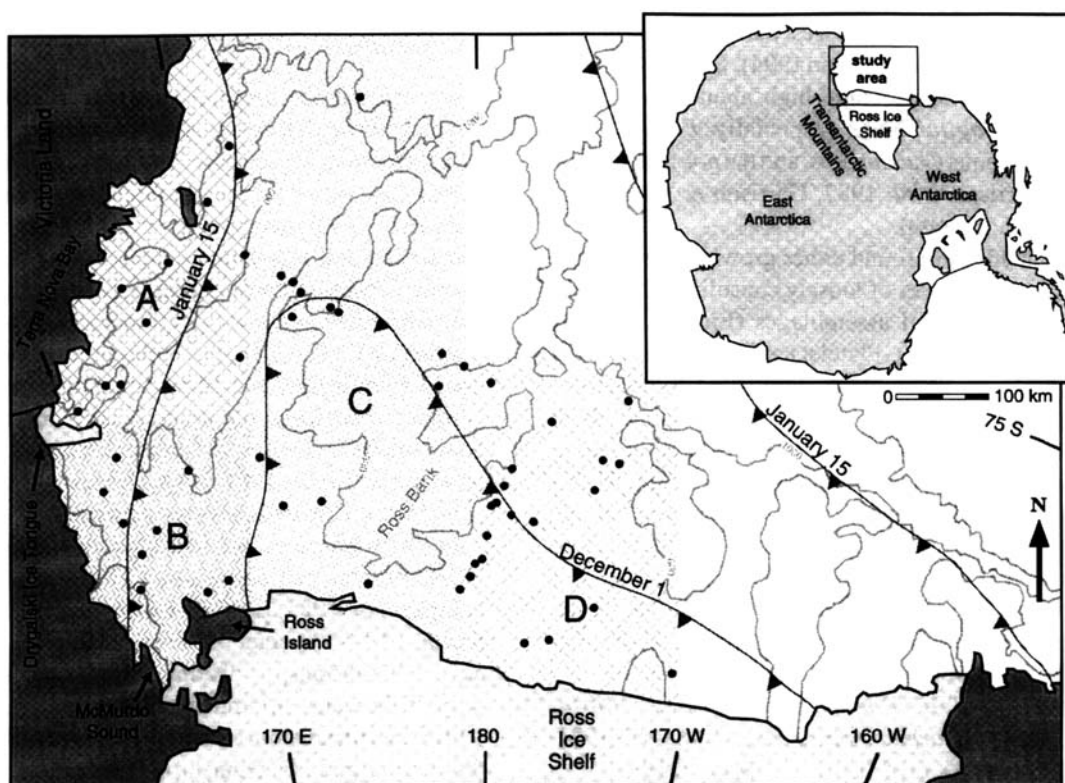


Fig. 1. Bathymetry, ice edge, and location map of 54 surface sediment samples used in this study. Surface assemblage data was previously published for six samples by Leventer & Dunbar (1996). Patterns delineate areas A, B, C, and D discussed in text. Lines with arrows show a generalized pattern of sea ice recession in the Ross Sea (based on figures prepared by the Naval Polar Oceanography Center; modified from Leventer *et al.* 1993). The arrows point toward the position of open water for 1 December (late spring/early summer) and 15 January (mid summer).

and sedimentation on the shelf (Hayes & Davey 1975, Anderson *et al.* 1984, Dunbar *et al.* 1985). Currents enter the Ross Sea from the east and exit west along a narrow strip of the Victoria Land coast. The salinity of waters entering the Ross Sea increases from east to west due to increased brine production from sea ice formation along the west coast, especially in the Terra Nova Bay polynya, just north of Drygalski Ice Tongue (Jacobs *et al.* 1970, Zwally *et al.* 1985). The winter salinity increase in combination with strong surface winds creates a cyclonic (clockwise) gyre along the west coast, which increases the residence time of waters on the shelf (Anderson *et al.* 1984, Dunbar *et al.* 1985, Kurtz & Bromwich 1985).

Factors affecting diatom distribution in the photic zone

Modern diatom distributions are controlled by a variety of interrelated environmental parameters, including light, salinity, temperature, nutrient availability, water-column stability, and sea ice (Dunbar *et al.* 1985, Leventer & Harwood 1993). On the Antarctic continental shelf, sea ice exerts considerable control over other environmental variables. Therefore, sea ice formation, type, extent, and breakout patterns (melt-out versus break-up by wind) give rise to

several distinct diatom assemblages (Grossi & Sullivan 1985, Smith & Nelson 1985, Garrison *et al.* 1986, 1987, Krebs *et al.* 1987, Garrison & Buck 1985, 1989, Fryxell 1989, 1991, Kang & Fryxell 1991, 1992, 1993, Kang *et al.* 1993; Leventer *et al.* 1993, Moisan & Fryxell 1993, McMinn 1994, Leventer & Dunbar 1987, 1988, 1996, Bidigare *et al.* 1996, Gleitz *et al.* 1996, in press).

Sea ice serves as a temporary winter habitat for several species of diatoms (Garrison & Buck 1985). Different species are incorporated into various types of sea ice due to the nature of sea ice formation (Garrison *et al.* 1986, 1989). Fast ice, which is composed primarily of congelation ice with a columnar texture (Garrison *et al.* 1986, Jeffries & Adolphs 1997, Gleitz *et al.* in press), supports an algal assemblage of primarily bottom layer and algal strand pennates (Krebs *et al.* 1987, Leventer & Dunbar 1987, McMinn 1994). With the exception of *Fragilariopsis curta* and *F. cylindrus*, which are also common in pack ice and the marginal ice-edge zone, fast ice diatoms are rare in sediments (Truesdale & Kellogg 1979, Leventer & Dunbar 1987, 1988, Leventer 1992).

Pack ice, which is composed of frazil ice with a granular texture (Garrison *et al.* 1986, Jeffries & Adolphs 1997, Gleitz *et al.* in press), supports an assemblage of planktonic diatoms that have been non-selectively concentrated throughout the

sea ice body by physical processes during ice formation (Garrison *et al.* 1983, 1989, McMinn 1994). Species common to pack ice communities include high abundances of the pennate genus *Fragilariopsis* (especially *F. curta* and *F. cylindrus*), the genus *Chaetoceros*, and the prymnesiophyte *Phaeocystis* (Garrison *et al.* 1987, Garrison & Buck 1985, 1989, Gleitz *et al.* in press).

Ice platelets, which are found either growing *in situ* at the base of fast ice or as a layer of loosely consolidated crystals, also support distinct algal assemblages (Eicken & Lange 1989, Smetacek *et al.* 1992). Platelet ice formed *in situ* under fast ice supports an assemblage dominated by pennates (Smetacek *et al.* 1992). Layers of loosely consolidated platelets form when supercooled waters streaming out at depth from underneath an ice shelf rise and accumulate as a dense slush layer under near shore pack and fast ice (Dieckmann *et al.* 1986, Eicken & Lange 1989). These platelets can travel long distances and, as they rise, may trap planktonic organisms (Dieckmann *et al.* 1986). Therefore, this type of platelet ice supports quite a different assemblage dominated by planktonic centric diatoms (*Thalassiosira antarctica*, *T. tumida*, *Porosira pseudodenticulata*, *P. glacialis*, and *Stellarima microtrias*) (El-Sayed 1971, Horner 1985, Smetacek *et al.* 1992, Gleitz *et al.* 1996).

Just as different sea ice types support different assemblages, the process by which the ice breaks up in the spring (melting versus physical break out by wind stress) can affect the species observed in the water-column and sediments. Melt-out of pack and fast ice produces a low salinity melt lens that stratifies the upper water-column and supports a rich algal bloom. The bloom is seeded by melt-out of species such as *F. curta* and *F. cylindrus*, which are common in both sea ice and the marginal ice-edge zone (Garrison & Buck 1985, Smith & Nelson 1985, Garrison *et al.* 1987). Sea ice melt-out has been linked to the mode of summer primary productivity in the south-western Ross Sea (Smith & Nelson 1985, Nelson & Smith 1986, Leventer & Dunbar 1996). By contrast, in the wind-stressed southern central Ross Sea, Leventer & Dunbar (1996) noted:

- a) a more diverse diatom assemblage with high contributions of *Fragilariopsis* (*F. cylindrus*, *F. kerguelensis*, *F. obliquecostata*, and *F. ritscheri*) and *Thalassiosira gracilis*, which are associated with open water, ice marginal environments (Hasle 1965, Buck *et al.* 1985, Leventer & Dunbar 1987, Leventer *et al.* 1993),
- b) an increase in the prymnesiophyte *Phaeocystis*, and
- c) a decrease in *F. curta*.

Leventer & Dunbar (1996) propose that this summer assemblage results from the early spring break out of pack ice (Fig. 1) by winds blowing off the ice sheet during the late winter development of the Ross Sea polynya.

Factors affecting particle transport

Aside from environmental variables affecting assemblage composition and distribution in the photic zone, factors such as aggregation, dissolution, and advection alter the diatom assemblage on its journey through the water-column to the sediment. Cell aggregation resulting from faecal pellet production and cell entanglement during superblooms can greatly decrease transportation time from the photic zone to the sediments (Smayda 1970, Smetacek 1985, Alldredge & Gottschalk 1989, Jaeger *et al.* 1996). Assemblage composition can be significantly altered by dissolution of small or lightly silicified frustules in the water-column and at the sediment/water interface (Nelson & Gordon 1982, Dunbar *et al.* 1989, Leventer & Dunbar 1987, 1996, DeMaster *et al.* 1996, Nelson *et al.* 1996). However, several workers argue that dissolution contributes less to assemblage alteration than factors such as advection and cell aggregation (Nelson & Gordon 1982, Dunbar *et al.* 1985, Ledford-Hoffman *et al.* 1986, Nelson & Smith 1986, Leventer & Dunbar 1987, 1996). Lateral advection can transport diatoms large distances in their descent through the water-column (Burckle & Stanton 1975, Leventer 1991). Despite diatom assemblage alteration by aggregation, dissolution, and advection during transport through the water-column, changes in the mode and level of primary productivity in the upper water-column (although not the complete phytoplankton assemblage) appear to be faithfully recorded in the underlying surface sediments in the Ross Sea (Leventer & Dunbar 1987, 1996). Therefore, algal assemblages in surface samples may be used as proxies for sea ice type, distribution, and break out pattern in the overlying water-column.

Methods

Fifty four trigger, kasten, and box core tops were taken aboard the *Polar Duke* in 1992, and the *Nathaniel B. Palmer* in 1994, 1995, and 1996 (Fig. 1). Piston core tops were not considered in this study because they seldom preserve the sediment water interface. Biogenic silica analyses were completed as described by DeMaster (1981). Quantitative diatom slides were produced using a settling method (Scherer 1994); coverslips were mounted using Norland Optical Adhesive 61. The slides were counted using an Olympus microscope with an oil immersion lenses at 1000x magnification. Only specimens in which greater than half the diatom was preserved, or the middle of the diatom was preserved, were included in the count. When possible, 500 specimens were counted for each slide. When it was impossible to count 500, 200–300 specimens were counted. If it was not possible to count more than 90 specimens per slide due to low diatom concentrations, species data were not used in further analysis, although biogenic silica measurements were made. Twenty percent of the slides were recounted by each worker to test data reproducibility (for reproducibility results, see Cunningham 1997).

Statistical procedures

All statistical procedures used the program Multi-Variate Statistical Package (MVSP) (Kovach 1990). This provides the user with options to centre and transform data sets before running the procedure. When working with percentage data, centring maintains the independence of the data (Jongman *et al.* 1987, Kovach 1990). An initial detrended correspondence analysis confirmed that a linear model best described the data; therefore, spatial assemblage composition changes were evaluated using a centered R mode principal components analysis (PCA) on the covariance matrix (Kovach 1990). Species comprising less than 0.5% of every sample were excluded from the analysis. A square root transform was applied in order to decrease dominance of the major taxa and increase the contribution from the minor taxa (a PCA on the raw data did not provide sufficient resolution to differentiate between environmental groupings on the shelf) (Kovach 1990). The PCA on the transformed data set explains 62% of the total variance with 3 components (Fig. 2); it was found to provide the most comprehensive analysis of changing floral compositions on the Ross Sea shelf. The results of this PCA (Tables I & II) are used to interpret lateral assemblage variations in this study.

Results

Biogenic silica

Biogenic silica may be used as a proxy for diatom abundances. Leventer (1992) found a correlation coefficient of 0.94 when percent biogenic silica was regressed against absolute diatom concentrations. Figure 3 shows the weight percent biogenic silica in 34 surface sediment samples. The highest percentages occur primarily in the western Ross Sea, whereas the lowest percentages are found in the central and northern Ross Sea.

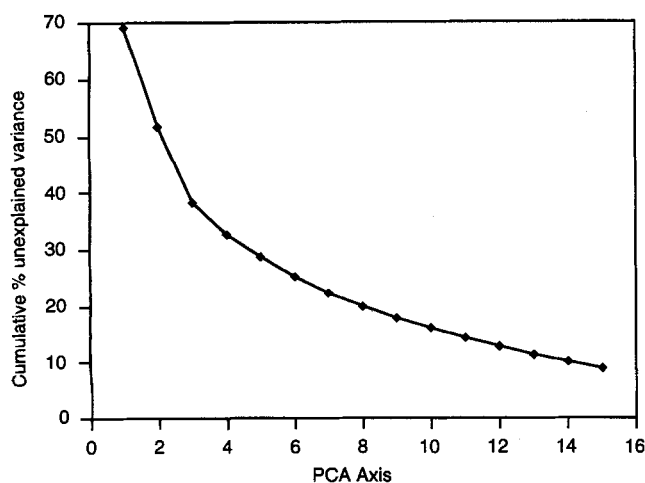


Fig. 2. Scree diagram depicting the cumulative percent unexplained variance versus the first 15 eigenvectors. The first three significant components explain 31%, 18%, and 13%, respectively, of the total variance.

Principal components analysis results

Component 1, which explains 31% of the variance, has high positive loadings on *F. curta* and resting spores (rs) of *Thalassiosira antarctica* (Table I). *F. curta* has been associated with sea ice melt-out conditions. The habitat of *T. antarctica* rs is less well understood, and will be addressed in the discussion. Component 1 has high negative loadings on *Fragilariopsis* spp. (primarily *F. kerguelensis* and *F. obliquocostata*), *Eucampia antarctica* winter growth stage (wgs), *Asteromphalus* spp., *Chaetoceros hyalochoete*, *Thalassiosira gracilis*, and *Stephanopyxis* spp. (Table I). With the exception of *Stephanopyxis* spp., these species have all been associated with open water environments, including ice marginal environments, warmer waters, and/or a wind mixed-water column. *Stephanopyxis* spp. is heavily silicified, and was abundant during the Pliocene (Schrader 1976), which suggests that this diatom was probably reworked from older deposits in these samples. The surface samples with the highest positive component scores (those samples best represented by positive component 1 loadings) occur primarily along the coast in areas A and B (see Fig. 1 for areas), whereas surface samples with the highest negative component scores occur in areas C and D (Fig. 4a, Table II).

Component 2, which explains 18% of the variance, has high positive loadings on *F. curta* and *F. cylindrus*, and high negative loadings on *T. antarctica* rs, *C. hyalochoete*, *F. separanda*, and *T. gracilis* (Table I). Surface samples with high positive component scores occur primarily in area A,

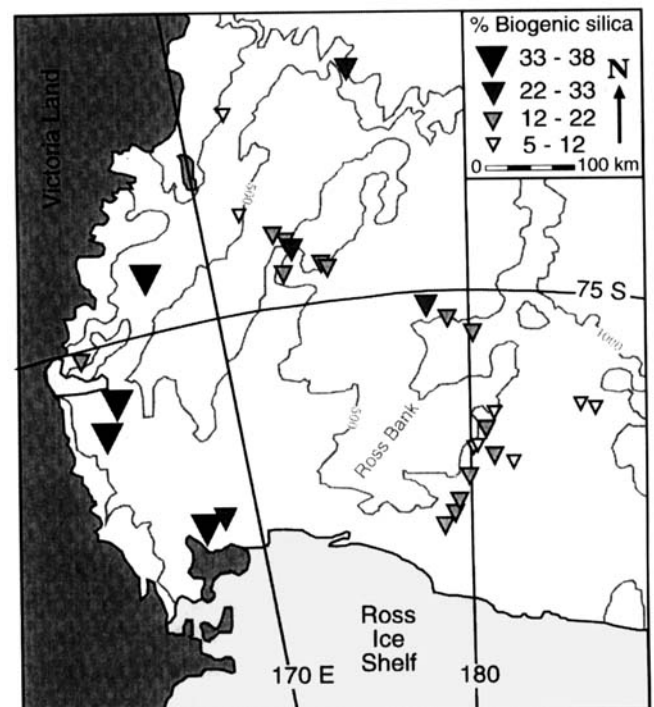


Fig. 3. Distribution of weight percent biogenic silica in the central and western Ross Sea.

Table I. Component loadings for surface sediment samples. Loadings are scaled such that the sum of squares of an eigenvector equals one.

species	comp 1	comp 2	comp 3
<i>Actinocyclus actinochilus</i> (Ehr.) Sim.	-0.0629	0.0083	-0.1616
<i>A. ingins</i> Rattr.	-0.0516	-0.0201	-0.0153
<i>Actinocyclus</i> spp.	-0.0832	-0.0464	0.1167
<i>Asteromphalus</i> spp.	-0.1098	-0.0653	-0.0444
<i>Azpeitia</i> spp.	-0.0183	0.0090	0.0201
<i>Chaetoceros hyalochaete</i> (Ehr.) Gran	-0.1150	-0.3282	0.2051
<i>C. phaeoceros</i> (Ehr.) Gran	0.0169	-0.0182	-0.1084
<i>Chaetoceros</i> spp. rs	-0.0831	0.0074	0.0927
<i>Corethron</i> spp.	-0.0856	0.0028	-0.1478
<i>Coscinodiscus</i> spp.	-0.0536	0.0324	-0.0498
<i>Denticulopsis</i> spp.	-0.0758	0.0327	-0.0060
<i>Eucampia antarctica</i> (Castr.) Mang. wgs	-0.3288	-0.1215	-0.2990
<i>Fragilariopsis angulata</i> Hasle	-0.0385	-0.0026	-0.2809
<i>F. curta</i> (V. Heur.) Hasle	0.3377	0.5861	0.0213
<i>F. cylindrus</i> (Grun.) Hasle	0.0510	0.1229	-0.2531
<i>F. kerguelensis</i> (O'Mea.) Hasle	-0.1538	-0.0681	-0.1200
<i>F. obliquecostata</i> (V. Heur.) Hasle	-0.2010	-0.0591	-0.1443
<i>F. ritscheri</i> (Hust.) Hasle	-0.0734	0.0467	-0.1997
<i>F. separanda</i> (Hust.) Hasle	-0.0781	-0.1700	-0.1742
<i>F. sublinearis</i> (V. Heur.) Hasle	-0.0854	0.0430	-0.1517
<i>F. vanheurckii</i> Hasle	-0.0825	0.0070	0.0443
<i>Fragilariopsis</i> spp.	-0.0428	0.0505	0.1491
<i>Odontella</i> spp.	0.0148	-0.0184	-0.0747
<i>Paralia</i> spp.	-0.0467	0.0175	0.0312
<i>Porosira glacialis</i> (Grun.) Jørg.	0.0921	-0.0236	-0.0261
<i>P. pseudodenticulata</i> (Hust.) Jousé	-0.0782	-0.0076	0.1185
<i>Pseudonitzschia turgiduloides</i>	-0.1791	0.0698	0.2766
<i>Rhizosolenia</i> spp.	-0.0203	-0.0026	0.0368
<i>Stephanopyxis</i> spp.	-0.2516	0.0126	0.2980
<i>Stellarima microtrias</i> (Ehr.) Has. & Sims	-0.0273	-0.1044	-0.0580
<i>S. microtrias</i> (Ehr.) Has. & Sims rs	-0.0671	-0.1047	-0.0107
<i>Stellarima</i> spp.	-0.0552	-0.0066	0.1313
<i>Thalassiosira antarctica</i> Comber rs	0.6281	-0.5994	0.0573
<i>T. gracilis</i> (Karst.) Hust.	-0.1585	-0.1872	-0.1928
<i>T. gracilis</i> var. <i>expectata</i> (V. Land.) Fryx. & Has.	-0.0561	-0.0022	0.1037
<i>T. inura</i> Gers.	-0.0719	0.0091	0.1315
<i>T. lentiginosa</i> (Jan.) Fryx.	-0.0320	-0.0986	-0.1618
<i>T. ostrupii</i> (Ost.) Hasle	-0.0809	-0.0031	0.1557
<i>T. oliverana</i> (O' Mea.) Sour.	-0.0811	-0.0744	-0.0337
<i>T. torokina</i> Brady	-0.0883	0.0213	0.1605
<i>T. tumida</i> (Jan.) Hasle	-0.0059	-0.0361	-0.1946
<i>Thalassiosira</i> spp.	-0.0994	-0.0623	0.1157
Unidentified pennates	-0.0304	-0.0721	0.1791
Unidentified centrics	-0.1955	-0.1305	0.2181

whereas samples with high negative component scores occur primarily in areas B and C (Fig. 4b, Table II).

Component 3, which explains 13% of the variance, shows high positive loadings on extinct and/or heavily silicified species (*Thalassiosira torokina* – 8.2 to 1.8 Ma, *T. inura* – 4.5 to 1.8 Ma, and *Stephanopyxis* spp. (abundant during the early Pliocene)) (Schrader 1976, Harwood & Maruyama 1992) and *C. hyalochaete* (Table I). Component 3 shows high negative loadings on species common in open water environments, including: *E. antarctica* wgs, *Corethron* spp., *Actinocyclus*

Table II. Component scores for surface samples. Scores are scaled so that sum of squares equals the eigenvalue.

sample	comp 1	comp 2	comp 3	sample	comp 1	comp 2	comp 3
92K26	-0.0403	-0.1593	-0.1606	95T21	-0.2390	0.0866	0.0735
92K50	-0.2274	-0.0151	-0.3314	95T25	0.2235	0.0265	-0.0529
92K94	0.4476	0.1060	0.0254	95K30	0.4108	-0.1993	0.0754
92K100	0.4576	0.6649	-0.0360	95K31	0.4696	-0.0587	0.0295
92K101	0.4214	0.3075	-0.0836	95K34	0.4484	-0.0660	0.1186
92K102	0.2921	0.3147	-0.0569	95K37	0.4786	0.2900	0.0941
94T01	0.1922	0.3101	-0.1614	95G38	-0.2254	-0.1395	-0.1450
94T16	-0.1530	0.1139	-0.2185	95K39	-0.1337	-0.1120	-0.2150
94T18	-0.0694	0.1671	-0.1996	95T40	-0.0376	-0.0842	-0.2382
94T20	0.0064	0.0500	-0.1886	95K46	-0.0500	-0.2057	-0.1576
94T22	0.0873	0.1016	-0.1402	95T49	0.1416	-0.0685	-0.0715
94T30	-0.1380	0.0869	0.1351	96B12	-0.0126	-0.2693	-0.1802
94T31	-0.3307	0.0070	-0.1448	96B15	0.3999	-0.0209	0.0855
94T32	-0.3674	0.0587	-0.2655	96B32	-0.1661	-0.1527	0.0617
94T33	-0.3016	0.0450	-0.3876	96B35	-0.2571	0.2534	0.2264
94T38	-0.1635	0.2595	-0.0576	96B38	-0.1700	0.0631	0.2742
95T02	0.0274	-0.1477	-0.1222	96B40	-0.2561	0.0049	0.2616
95T10	-0.3157	-0.0428	0.1810	96B42	-0.3090	-0.1359	0.5602
95T11	-0.2309	-0.0071	0.2034	96B44	-0.2354	-0.0203	0.2415
95T12	-0.3069	0.1428	0.0315	96B60	0.0673	-0.2708	-0.0172
95T13	-0.1926	-0.0530	0.1504	96B75	0.2792	-0.4381	-0.0058
95T14	-0.1437	0.1897	0.1945	96B76	0.3443	-0.2874	0.0974
95K15	-0.2135	0.1157	0.1068	96B77	0.4229	-0.2776	0.0855
95T16	-0.1799	-0.0150	0.1387	96B82	0.3478	-0.3141	0.0838
95T17	-0.1386	0.1213	0.0759	96B84	0.2075	-0.2178	0.0398
95T18	-0.1621	0.1176	0.0796	96B87	0.0048	-0.2525	-0.0417
95T19	-0.0476	0.2329	0.1120	96B91	-0.3631	-0.2066	-0.1633

actinochilus, *Thalassiosira lentiginosa*, *T. tumida*, *T. gracilis*, and *Fragilariopsis* spp. (*F. angulata*, *F. cylindrus*, *F. obliquecostata*, *F. ritscheri*, *F. separanda*, *F. sublinearis*). The surface sediment samples with the highest positive component scores occur in area D, whereas the samples with the highest negative scores occur in area C (Fig. 4c, Table II).

Figure 5 shows biplots of component 1 versus 2, and component 1 versus 3, respectively. The species loadings are scaled so that the sum of squares of an eigenvector equals 1, and the sample scores are scaled such that the sum of squares equals the eigenvalue. This scaling preserves the Euclidean distance between each sample, and allows the cosine of the angle between two species vectors to be interpreted as the correlation coefficient between the species. It is clear from Fig. 5a that *F. curta* and *T. antarctica* rs are the most important species controlling the position of components 1 and 2. Common open water species (e.g. *T. gracilis*, *Fragilariopsis* spp.) and potentially reworked species (e.g. *Stephanopyxis* spp.) are negatively correlated with *F. curta* and *T. antarctica* rs, but less important in controlling the position of the first two components. Fig. 5b shows a trilateral distribution in which *Stephanopyxis* spp. and *C. hyalochaete* are positively correlated, *E. antarctica* wgs, *T. gracilis*, and *Fragilariopsis* spp. are positively correlated, and *T. antarctica* and *F. curta* are positively correlated. The longest vectors in each group are similar in magnitude, indicating that all three groups are important in controlling the positions of components

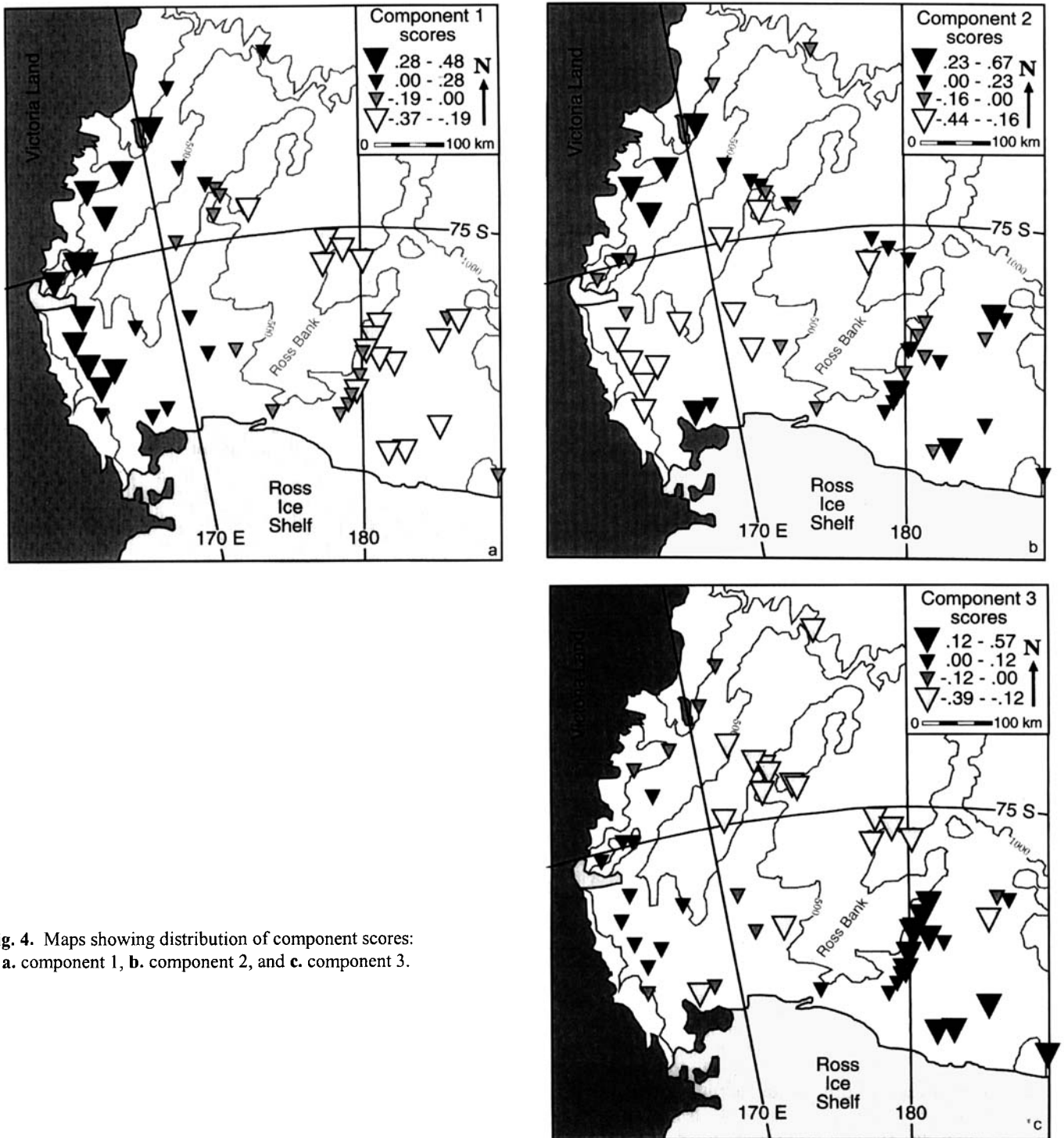


Fig. 4. Maps showing distribution of component scores: a. component 1, b. component 2, and c. component 3.

1 and 3.

Figure 6 shows graphical representations of Fig. 5, where each sample is represented by the diatom (*T. gracilis*, *Stephanopyxis* spp., *F. curta* or *T. antarctica* rs) that is closest (in Euclidean distance) to that sample. Although the heavily silicified *E. antarctica* wgs has high loadings on the first and third component, is positively correlated with other open

water species in Fig. 5b, and has been documented in ice marginal open water, it is unclear whether its distribution in sediments reflects an environmental signal or a preservational signal. Our study does not clarify the issue (*E. antarctica* wgs is as highly correlated with *T. gracilis* as it is with *Stephanopyxis* spp. in Fig. 5a); therefore, *T. gracilis* was selected to represent open water conditions despite its

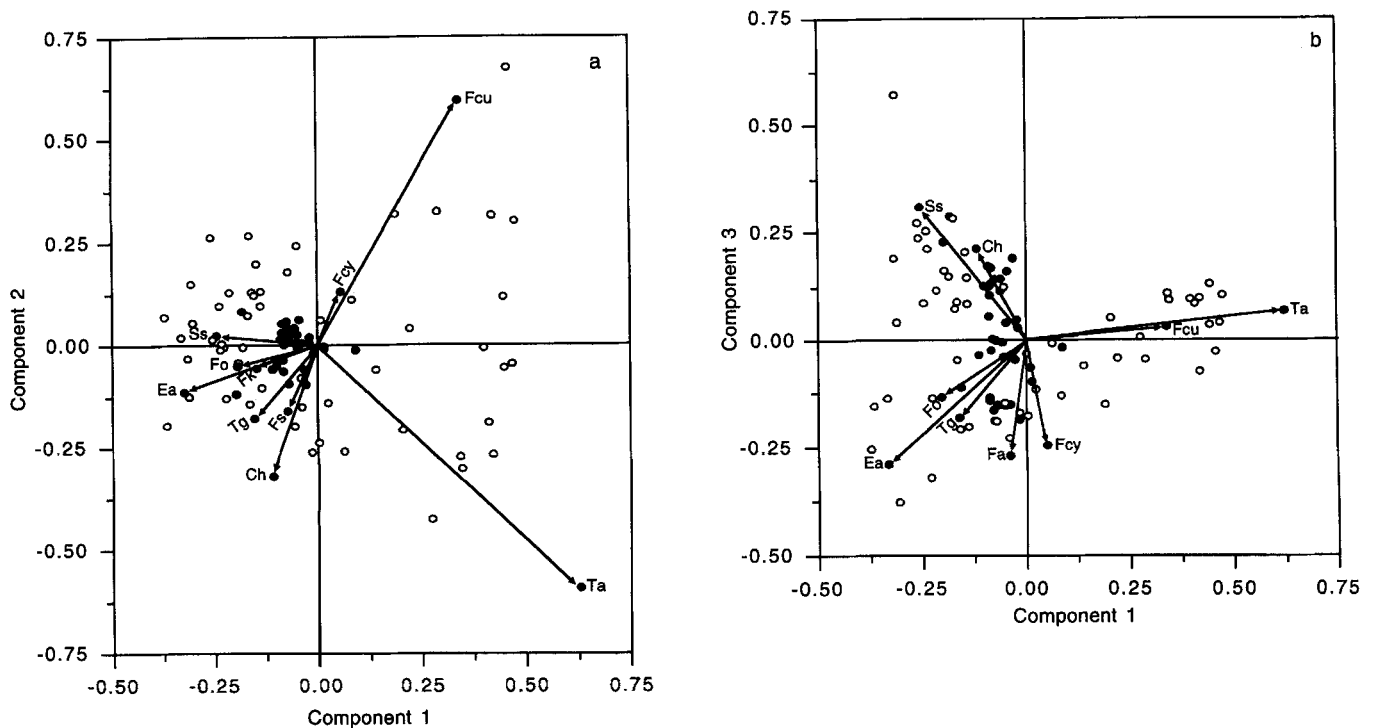


Fig. 5. Biplots based on principal components analysis: a. component 1 versus component 2, and b. component 1 versus component 3.

Closed circles represent species loadings; open circles represent sample scores. Significant taxa are abbreviated as follows:

Ss, *Stephanopyxis* spp.; Ea, *E. antarctica* wgs; Tg, *T. gracilis*; Ta, *T. antarctica*; Fcu, *F. curta*; Fcy, *F. cylindrus*; Fo, *F. obliquecostata*; Fk, *F. kerguelensis*; Fa, *F. angulata*; Ch, *C. hyalochaete*.

consistently shorter vector length. Fig. 6a shows that samples in area B are most highly associated with *T. antarctica* rs, whereas samples in area A are most highly associated with *F. curta*. The distribution of percent *T. antarctica* rs and *F. curta* in surface sediments of the Ross Sea (including 13 samples collected in 1996, which were added to the data set after statistics were performed) reflect this statistical distinction (Fig. 7). The highest percentages of *T. antarctica* rs occur in area B, and the highest percentages of *F. curta* occur in area A. Figure 6b differentiates samples most highly associated with *T. gracilis* (primarily area C) from samples most highly associated with *Stephanopyxis* spp. (primarily area D).

Discussion

Our present biogenic silica results agree with those of previous workers (Dunbar *et al.* 1985, Ledford-Hoffman *et al.* 1986, Jaeger *et al.* 1996, Nelson *et al.* 1996). Ledford-Hoffman *et al.* (1986) and Nelson *et al.* (1996) attributed the high percentages of biogenic silica in the south-western Ross Sea to a higher level of primary productivity, dominance of siliceous over non-siliceous algal production, and advection of frustules into this area from the eastern Ross Sea. By contrast, all authors noted low biogenic silica concentrations in the central, eastern and north-western Ross Sea. Dunbar *et al.* (1985) and Ledford-Hoffman *et al.* (1986) attributed

low silica in the central and eastern Ross Sea to lower siliceous primary productivity, and advection of frustules out of this area.

Area D: extinct and/or heavily silicified assemblage

The majority of the samples most closely associated with *Stephanopyxis* spp. are located in area D, along a north-east transect located slightly east of the 500 m contour outlining Ross Bank (Fig. 6b). The sediment on Ross Bank is comprised of winnowed glacial marine sediments (Dunbar *et al.* 1985). This suggests that the surface assemblage in area D results partially from resuspension events which would transport the older, heavily silicified diatoms remaining in the winnowed bank sediments into the deeper troughs.

The mode of primary production in area D may also affect the assemblage recorded in the sedimentary record. Area D shows low percentages of biogenic silica compared with areas A and B (Fig. 3). This may in part result from a higher fraction of non-siliceous primary production in the upper water-column of this area (Leventer & Dunbar 1996, DiTullio & Smith 1996, Smith & Gordon 1997); an algal assemblage with a low relative abundance of diatoms will reduce the amount of siliceous material available for preservation. Therefore, input of diatoms from a winnowed glacial marine source combined with deposition of an algal assemblage dominated by non-siliceous algae may produce the silica

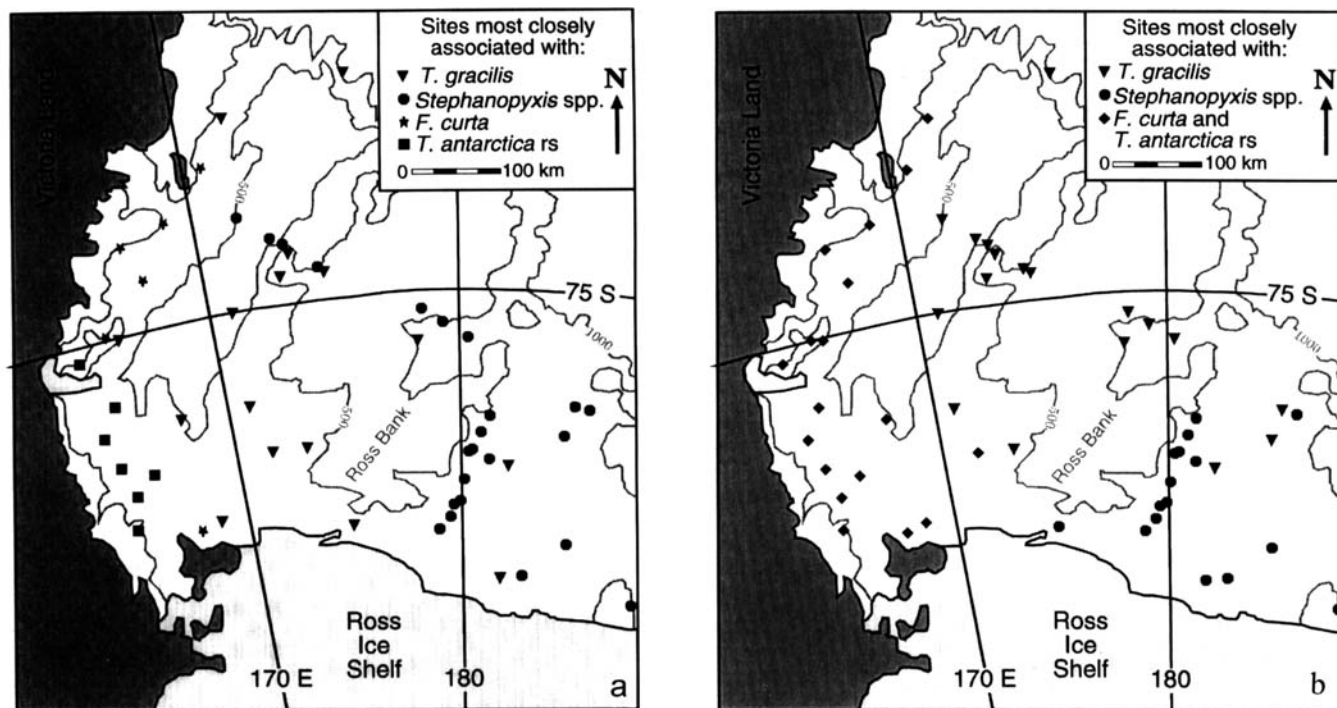


Fig. 6. Graphical representations of biplots: a. component 1 versus component 2, and b. component 1 versus component 3. Each sample is represented by the diatom that is closest (in Euclidean distance) to that sample (see Fig. 5).

poor, extinct and/or heavily silicified diatom assemblage observed in area D.

Area C: open water assemblage

Surface assemblages in area C are most closely associated with *T. gracilis* (Fig. 6b). *T. gracilis* is part of the genus *Thalassiosira*, members of which are commonly reported in open water environments (Buck *et al.* 1985, Burckle *et al.* 1987, Fryxell & Kendrick 1988, Pichon *et al.* 1992, Leventer & Dunbar 1987, 1988, 1996, Zielinski & Gersonde 1997). Leventer & Dunbar (1996) found *T. gracilis* to be more common in the upper water column and surface sediments of the southern central Ross Sea than in the western Ross Sea, and invoke the Ross Sea polynya to explain the development of an open water assemblage in this area. Leventer & Dunbar (1996) suggest that the late spring onset of wind stress from the Ross Sea polynya may:

- induce ice break up before significant melting sets in, which would result in a decrease in the importance of spring water column seeding by ice species to the seasonally early algal bloom, and
- produce an unstable, deeply mixed upper water column.

A study of surface salinity in the central Ross Sea in mid November 1994 confirms that salinity dilution from melting ice was insignificant (Smith & Gordon 1997). Further, this study confirms the presence of a deep mixed layer in mid

November (average depth: 29 m) and early December (average depth: 33 m) (Smith & Gordon 1997). The results of our surface sediment study concur with those of Leventer & Dunbar (1996). We therefore support their suggestion that development of an open water diatom assemblage in area C may result from early seasonal sea ice reduction (Fig. 1), a decrease in the importance of seeding by ice species, and the development of a deeply mixed upper water column due to wind stress from the Ross Sea polynya.

Area B: *T. antarctica rs* coastal assemblage

Figure 6a shows that the samples most closely associated with *T. antarctica rs* and *F. curta* are located nearshore, along the western coast (areas A & B). The statistics reflect percentage data (Fig. 7), which show an increase in percentages of *F. curta* and *T. antarctica rs* toward the coast. However, although both *T. antarctica rs* and *F. curta* clearly dominate the surface sediment algal assemblage along the west coast of the Ross Sea, their distributions are distinct. Fig. 6b shows that the samples most closely associated with *F. curta* occur primarily in area A, whereas the samples most closely associated with *T. antarctica rs* occur primarily in area B.

The environmental significance of *F. curta* has been well established; *F. curta* is common in fast and pack ice, as well as in the meltwater-stratified surface layer associated with a retreating ice edge (Smith & Nelson 1985, Garrison *et al.* 1987, Leventer & Dunbar 1987, 1988, 1996, Gleitz *et al.* in

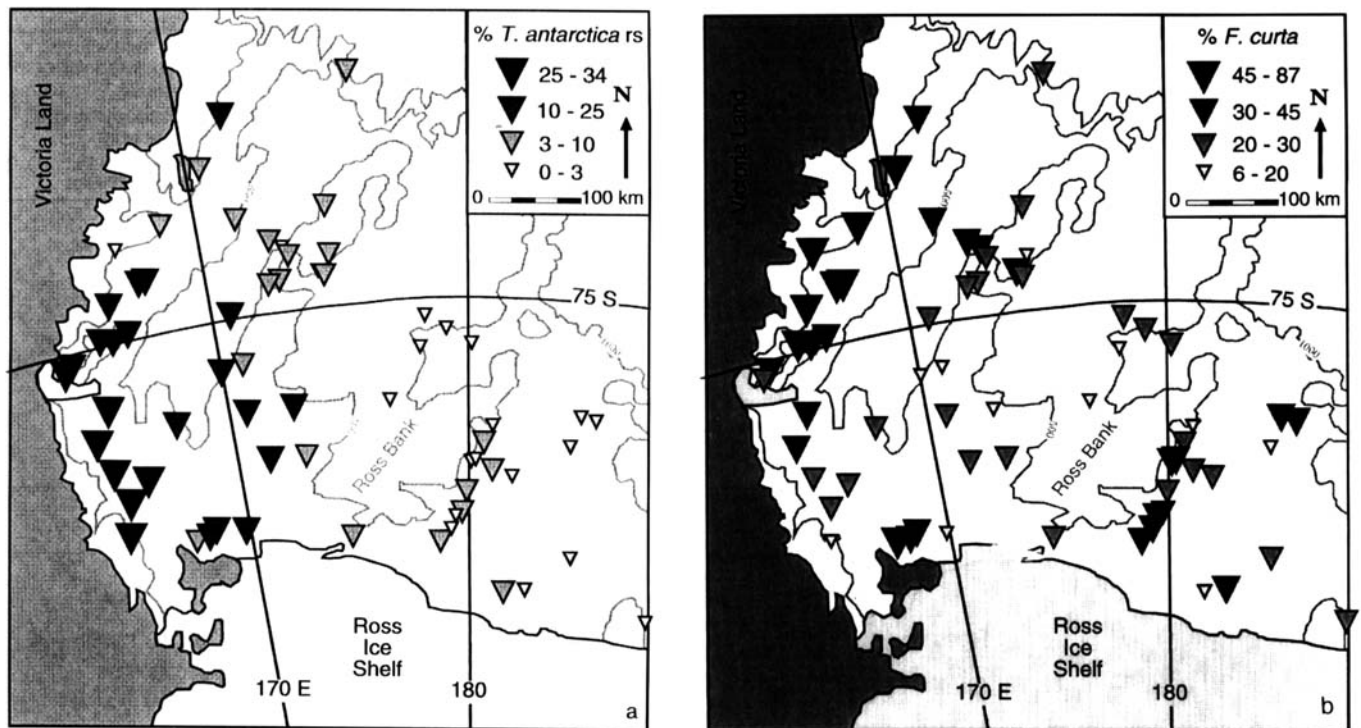


Fig. 7. Percentage of each species in 67 surface samples of the Ross Sea: a. *T. antarctica* rs, and b. *F. curta*. Thirteen samples collected in 1996 by Leventer are reported in addition to the 54 on which statistics were performed.

press). *Fragilariopsis curta* may therefore be used as a proxy for meltwater stratification resulting from fast and pack ice melt-out. The environmental significance of *T. antarctica* rs is less well understood. Although the genus *Thalassiosira* has traditionally been associated with open water (Fryxell & Kendrick 1988, Pichon *et al.* 1992, Leventer *et al.* 1993, Leventer & Dunbar 1987, 1988, 1996, Zielinski & Gersonde 1997), recent work shows that different species may have different distributions in the upper water-column (Leventer & Dunbar 1996). With more work, individual species in this genus may be used as distinct environmental proxies. Early studies on *T. antarctica* have documented this diatom in association with low temperature, ice marginal, coastal regions (Hasle & Heimdal 1968, Villareal & Fryxell 1983). Later studies have documented *T. antarctica* in zones of loose platelet ice underlying coastal ice cover (Horner 1985, Smetacek *et al.* 1992, Gleitz *et al.* in press). Surface sediment and sediment traps studies in the Ross Sea have reported significant percentages of *T. antarctica* rs in area B (Leventer *et al.* 1993, Leventer & Dunbar 1987, 1988, 1996). Leventer & Dunbar (1996) noted a gradual increase in percent *T. antarctica* rs from May 1991 to January 1992 in a trap situated 50 m above the sea floor in area B; Leventer & Dunbar (1988) found that *T. antarctica* rs comprised 20% to >30% of the surface sediment algal assemblage in eastern McMurdo Sound. It is worthy of note that although *T. antarctica* rs has been extensively documented in sediments of the Ross Sea, no blooms of this diatom in the upper water

column have yet been reported. Until we gain more information concerning the environmental significance of *T. antarctica*, it is not possible to interpret the distribution of this diatom in the sediments with certainty. However, the information currently available raises several questions, to which we suggest tentative hypotheses in the hope that these ideas will foster avenues for continued research.

Question 1: why is *T. antarctica* rs found in such high abundances in surface sediments of area B, but has not been documented in the upper water column? The majority of upper water column phytoplankton studies in the Ross Sea have occurred during sea ice break out in the austral spring and summer. These studies document high percentages of *F. curta* (indicative of extensive melt water stratification) in the water column of the south-western Ross Sea (Smith & Nelson 1985, DeMaster *et al.* 1992, Leventer & Dunbar 1996), which explains the relatively high abundances of this diatom in surface samples from area B (Fig. 7b). The few studies of autumnal diatom assemblages come from the Weddell Sea. These studies identify a second type of bloom which is associated with sea ice formation instead of spring melt water stratification (El-Sayed 1971, Smetacek *et al.* 1992). El-Sayed (1971) documented an extensive bloom of *Thalassiosira tumida* in the forming "slush-ice" (perhaps platelet ice?) and pancake ice near the Ronne Ice Shelf during mid February of 1968. Smetacek *et al.* (1992) reported a bloom dominated by *T. antarctica*, *Porosira pseudodenticulata*, and *Stellarima microtrias* in a zone of

loose platelet ice underlying pack ice bordering the Weddell Sea Ice Shelf in October/November of 1986. An equivalent study of upper water column phytoplankton composition during sea ice formation in the Ross Sea has never been done, although preliminary sediment trap data from 1996 suggests the existence of a flux peak in area B during the autumn (R.B. Dunbar, personal communication 1997). The growing evidence that:

- a) *T. antarctica* has some type of relationship with sea ice, particularly coastal sea ice and zones of loose (possibly platelet) ice crystals (Hasle & Heimdal 1968, Villareal & Fryxell 1983, Horner 1985, Smetacek *et al.* 1992, Gleitz *et al.* in press), and
- b) autumn algal blooms may make a significant contribution to the yearly algal flux (Krebs 1983, Fritsen *et al.* 1994)

suggests that the high abundance of *T. antarctica* rs in surface samples of area B (Fig. 7a) may be related to an autumnal bloom event which has never been documented in the Ross Sea. Resting spore formation (possibly triggered by nutrient depletion) (Hargraves & French 1983, Smetacek *et al.* 1992) followed by seasonal disintegration of the platelet ice layer may then explain the timing of the *T. antarctica* rs flux increase from May to January in the sediment trap from area B (Leventer & Dunbar 1996). However, due to lack of sampling, we still cannot rule out the possibility that *T. antarctica* blooms in the early spring. Future year-round sampling of the upper water column in area B should help answer this question.

Question 2: what accounts for the difference in abundance of *T. antarctica* rs between areas A and B, both of which are coastal? Compared to the entire Ross Sea, percentages of *T. antarctica* rs along the coast are considerably greater than percentages in areas C and D. This agrees with other studies, most of which document high percentages of *T. antarctica* in near coastal areas (Hasle & Heimdal 1968, Smetacek *et al.* 1992, Zielinski & Gersonde 1997, Gleitz *et al.* in press). However, within coastal areas A and B, the distribution of *T. antarctica* rs is distinct, which leads us to suspect that a process local to certain parts of the coast may account for the distribution of *T. antarctica* in the Ross Sea. Because *T. antarctica* has been documented in zones of loosely suspended ice crystals (Horner 1985, Smetacek *et al.* 1992, Gleitz *et al.* in press), we speculate that differences in genesis of these crystalline suspensions may account for the differences in *T. antarctica* rs percentages between areas A and B. Frazil ice, which forms at or near the surface during the autumn (Maykut 1985), would only scavenge plankton living near the surface of the water column (primarily the summer bloom). However, loose platelet ice originating by supercooling beneath ice masses (Jeffries & Weeks 1992) must rise long distances through the water column, and might scavenge microorganisms from lower levels of the water column during its ascent (Dieckmann *et al.* 1986, Spindler & Dieckmann

1986). Although frazil ice would be found throughout the Ross Sea prior to sea ice formation, platelet ice may be native to area B due to the proximity of the Ross Ice Shelf. We therefore speculate that the autumn bloom in area B may contain different algal species than the bloom in area A due to the addition of plankton scavenged from lower levels in the water column by platelets rising from depth. Platelet ice has previously been documented in McMurdo Sound (Barry 1988, Jeffries *et al.* 1993) and south of Drygalski Ice Tongue (Jeffries & Weeks 1992); however, more extensive research is required before sea ice distributions between McMurdo Sound and Drygalski Ice Tongue can be confidently assessed. While the difference in algal assemblage between areas A and B is intriguing, efforts to explain the difference are at present speculative. Future research on detailed sea ice distributions and seasonal algal assemblages in the western Ross Sea are crucial to the interpretation of modern and historic variations in the distribution of *T. antarctica*.

Area A: melt water stratification assemblage

Samples in area A are most closely associated with *F. curta* (Fig. 6a), a diatom which comprises up to 87% of the assemblage in this area (Fig. 7b). High percentages of *F. curta* in area A may result from the type of sea ice present and the mode of ice break out. Because the surface sample assemblages in area A are similar to assemblages observed in the upper water column by Leventer & Dunbar (1996), we accept their hypothesis that spring ice melt-out of land fast ice (which persists into summer; Fig. 1) and subsequent water column stratification and seeding by *F. curta* may be important in determining the composition of the algal assemblage in the upper water column (and consequently, in the sediments) north of Terra Nova Bay.

We also observe high percentages of *F. curta* in and slightly north of Terra Nova Bay (Fig. 7b). This area is dominated by the Terra Nova Bay polynya, which forms north of Drygalski Ice Tongue during the winter (Kurtz & Bromwich 1985). Due to polynya formation, the types of sea ice and the timing of open water are quite different from those observed to the north of this area (Kurtz & Bromwich 1985). Although one might expect the development of an open water bloom similar to area C in this polynya-dominated area, we argue that the sedimentary diatom assemblage associated with melt water stratification in Terra Nova Bay can be explained by the interaction between polynya wind cessation and timing of the summer algal bloom. The Terra Nova Bay polynya remains free of ice throughout most of the winter due to:

- a) the persistent katabatic winds which continuously blow pack ice formed in Terra Nova Bay to the north, and
- b) the blockage of northward ice movement by Drygalski Ice Tongue.

Since the area affected by the polynya is rarely insulated from

the atmosphere by winter sea ice, surface temperatures remain below the freezing point. During the late winter/early spring, the winds die down, and the supercooled surface layers freeze rapidly (Kurtz & Bromwich 1985). We suggest that this newly formed sea ice melts as spring progresses to summer, creating a stratified water column which coincides with the observed summer algal bloom (Arrigo & McClain 1994). Recent algal data from December 1996 in Terra Nova Bay support this hypothesis. These data show that the summer bloom is diatom-dominated and associated with the receding ice edge; *F. curta* made a significant contribution to this bloom. Thus, the presence of *F. curta* in the summer water-column combined with high percentages of *F. curta* in the surface sediment samples suggests that seeding from pack ice melt-out as well as polynya dynamics are important in establishing the algal population in Terra Nova Bay, while seeding from melt-out of land fast ice is important in establishing the summer bloom north of Terra Nova Bay.

Comparison of the Ross Sea polynya and the Terra Nova Bay polynya

The difference in algal assemblages between the Ross Sea polynya and the Terra Nova Bay polynya is intriguing. Although both polynyas are maintained by high winds, the timing of wind revival and cessation is distinctly different for each. We suggest that the interaction between the timing of polynya development and the annual algal bloom creates the significant differences in algal assemblages observed in the water-column and surface sediments. The Ross Sea polynya develops in late spring, prior to melting of the pack ice-dominated sea ice (Smith & Gordon 1997). The decrease in melt water may decrease the contribution of sea ice diatoms which may otherwise seed the spring/summer bloom, and promote the development of a well mixed water-column dominated by a diverse, open water algal assemblage. In contrast, the Terra Nova Bay polynya is active into the late winter, at which point the winds die down and sea ice cover forms. Melt-out of this newly formed sea ice during late spring and early summer may explain the observed diatom-dominated ice edge bloom seeded by *F. curta*.

The results of this study confirm the results of the pilot surface sediment study by Leventer & Dunbar (1996), and suggest that spatial changes in surface sediment diatom assemblages accurately reflect spatial changes in the structure of the upper water-column. The proposed environmental controls will be tested as more seasonal information on currents, sea ice distributions, upper water-column structure, species-specific habitats, and interactions between algal blooms and polynyas becomes available. Refining the link between modern processes and surface sediment diatom assemblages is crucial to the future development of high resolution paleoceanographic records.

Acknowledgements

This research was funded through the National Science Foundation (DPP 91-17958, OPP 94-20682, and OPP 96-14287). We wish to thank John Andrews and Anne Jennings for providing the opportunity to do this research; Jessica McNair for her work in the laboratory; and Nelson Caine, David Harwood, Martin Jeffries, Kathy Licht, Eric Steig, and Alexander Wolfe for helpful discussions. We are grateful to Greta Fryxell and Victor Smetacek for constructive comments on the original manuscript.

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