Horizontal and Vertical Distribution of Antarctic Phytoplankton at the Weddell Sea Ice Edge Zone

A Thesis

by

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Introduction

Phytoplankton is a collective term applied unicellular protists that are moved by the tides and currents of marine and fresh waters. These algae are systematically separated into several divisions--Chlorophyceae (green algae), Chrysophyceae (diatoms and silicoflagellates), Dinophyceae (dinoflagellates), Prymnesiophyceae (coccolithophorids and *Phaeocystis* sp.), and Cyanophyceae (blue-green algae). Phytoplankton inhabit the upper meters of the water column where they trap energy needed for photosynthesis from sunlight. These organisms are of paramount importance in ecosystems because they serve as primary producers of energy-rich compounds that form the basis of the food chain of all aquatic organisms. Furthermore, algae oxygenate the upper meters of the water column. Unicellular algae make up many of the plrimary producers on this earth and are responsible for the global marine carbon recycling.

The scope of this research is to quantify phytoplankton cell numbers at the Antarctic ice edge in horizontal and vertical dimensions during austral winter. Identification is to the species level where possible. Other methods of estimating phytoplankton biomass are currently used in the field. Phytoplankton biomass can be assessed by extracting chlorophyll *a*, a pigment common to all divisions of phytoplankton, and measuring its concentration spectrophotometrically. A method analyzing algal pigment fingerprints using the High Pressure Liquid Chromatography (HPLC)

has also been developed recently. These methods estimate biomass as a whole and do not, in general, delineate between the different phytoplankton divisions or assess diversity or community structure. The amount of Chlorophyll a does not always correspond to cell number since different species have different cellular volumes; chlorophyll a content is cyclical and the chlorophyll a content per cell can be bleached in surface water.

Species composition can be assessed quantitatively by several methods, such as vertical net hauls, horizontal net tows, and unconcentrated water samples. Each method has its advantages. Net hauls select for the larger phytoplankton size fractions, and small cells slip through the net. With opening and closing nets, collections are made at a certain range of depth i.e. 0-50m, 50-100m. Water samples can be taken at discrete depths from flow-through bottles closed at depth. These collect a small number of cells but a wider range of size fraction and provide a more realistic assessment of abundance.

Most commonly used is a settling chamber method known as the Utermohl method (1958) where unconcentrated water samples are settled in a chamber for one or moore days, and the preparation is observed from below with an inverted microscope. Most recently, filtration techniques that produce permanent slides such as the Filter-Transfer-Freeze (FTF) (Hewes and Holm-Hansen 1983) and 2-hydroxypropyl methacrylate (Crumpton 1987) technique, have become popular in quantitative phytoplankton studies. These filtration techniques provide many advantages over

the traditional settling techniques. The preparation time for each slide is much faster and, a permanent slide can be stored for future analysis. These slides also decrease the number of weighty water samples to be shipped back to the research lab, and the amount of preservative needed to maintain the integrity of cells is greatly decreased.

It is important to enumerate phytoplankton abundance in terms of species composition from unconcentrated water samples because the actual number of cells available to upper trophic levels can be assessed. Euphausiids, the dominant herbivores in this system, are known to graze in swarms, and seem to exhibit some size selectivity for the phytoplankton they ingest. These studies provide information on species-specific variables such as size, morphological strategies and a qualitative estimation of lipid composition and life stages can be observed. Quantitative analysis of phytoplankton in terms of species composition has ecological, evolutionary, and geological significance. Empty cells are also counted, lending evidence to the current growth conditions and the detrital pool. A qualitative assessment of detritus can also be made.

Diatoms flourish in the Antarctic waters. Diatom frustules are composed of silicon dioxide which dissolves slowly. As a result, diatoms get trapped in ocean floor sediments known as diatom oozes which have been dated as far back as 175 million years. Diatom diversity patterns may act as models for delineating climactic change in the geologic past of the Antarctic region

(Defelice and Wise 1981). It is important to quantify current phytoplankton species composition in order to aid sedimentologists by relating biological communities to the sedimentary record. Many species have been proposed as indicators for geologic time frames and even water masses (Priddle and Fryxell, 1985) Some species are associated with the ice edge (El-Sayed 1971; Fryxell and Kendrick 1988). Certain morphological characters of certain species not only reflect current growth conditions but also the history of water (Fryxell 1986) and environmental conditions (Fryxell, Hasle, and Carty 1984; Fryxell 1986; Fryxell and Prasad 1990).

It is, therefore, important to quantify Antarctic marine phytoplankton since they are the basis of the food chain. Assessment of their distribution will further the understandings of the trophodynamics of the Antarctic ecosystem as well as aid sedimentologists in future analyses of sediments. Also, they are an indication of the history of the water because some species have specific areas of growth, i.e. at the ice edge where their presence has both ecological and geological implications. Quantitative data can also be used to form realistic hypotheses for physiological experiments in the laboratory to further the knowledge of polar processes.

The Antarctic region offers many unique environmental variables that affect phytoplankton production. Light regimes are extremely variable in the Antarctic, alternating from near total darkness in the austral winter to constant daylight in austral summer. The annual variation of solar radiation is the driving force that most affects the seasonality of the phytoplankton (Clark, 1988). Extremely low water temperatures have been found to limit primary production rates at times when the light intensity is saturating the photochemical apparatus of the cells (Neori and Holm-Hansen 1982). This production limitation is at its maximum in the upper 20 meters due to the thermal stratification of the Antarctic region (El-Sayed & Tomo, 1983). Nutrient concentrations in this region are estimated to be in excess of that needed to support the high values of phytoplankton (Hayes et al., 1984).

Most unique to the Antarctic ecosystem is the seasonal sea ice that surrounds the periphery of the continent often extending up to 500-1500 km northward, covering more than 20 million km^2 of sea surface (Foster,1984) in September and October. The aerial extent is reduced by seasonal melting during the month of February and ablates to an area of 3 X 10^6 km^2 (Gordon,1981). The difference between these two extremes, 17 X 10^6 km^2, represents an area larger than the Antarctic continent, itself. The edges of the sea ice are in constant motion and can move up to 4.2 km per day. Thus, the total area of ice has the possibility of increasing up to 1 X 10^5 km^2 per day.

The presence of sea ice plays a unique role in the Antarctic ecosystem. This white blanket not only serves as a physical barrier between the atmosphere and the sea but its edges act as a dynamic frontal zone between two distinct habitats-- the open water and the pack ice. It reduces the amount of light available for photosynthesis for primary producers in the underlying water column and affects the distribution of light wavelengths. Additionally, extensive cloud cover often complicates these effects (El-Sayed, 1988). The sea ice also reduces wind driven mixing which creates a greater water column stability. (Alexander 1979). The underlying seawater is also generally more saline due to the salt rejection by the sea ice during growth (Lake and Lewis 1970).

The marginal ice edge acts as a mesoscale oceanographic front where standing stocks at all consumer levels are elevated (Smith 1987). This study is in conjunction with the phytoplankton component of a multidisciplinary program known as the AMERIEZ program (Antarctic Marine Ecosystem Research at the Ice Edge Zone) designed to investigate all consumer levels except whales at the ice edge in all four seasons of the year. The organisms studied include bacteria, phytoplankton, microzooplankton, krill, micronekton, macronekton, and marine birds and mammals. Thus far, the AMERIEZ program has sampled in the austral spring in 1983 and in late summer-early autumn conditions in 1986. Most recently, an austral winter cruise sampled in June and July 1988.

Many phytoplankton analyses have been estimated based on pigment content (Chlorophyll a) in the Weddell Sea during the

austral spring and summer (Saijo and Yawashima, 1964; El-Sayed and Mandelli, 1965; El-Sayed and Taguchi, 1981; Smith and Nelson, 1986; Smith, 1987; Weber and El-Sayed, 1987) Few phytoplankton pigment studies have been carried out during the austral winter (Marra et. al. 1982; Marra and Boardman, 1984). Studies have been also been carried out using using algal pigment fingerprints (Buma et. al. in press). Primary production data was collected from the South-Eastern Weddell Sea (Brokel, 1985)

Many studies based on species composition have been done in the Antarctic (Hart 1942; Marumo 1957; Fukase and El-Sayed, 1965; Movchan 1975; Semina 1979;) but few studies actually quantify cell numbers and species present in the water column (Kozlova 1966; Hasle 1956 and1969; Stayaert 1973a; Steyaert 1973b; Krebs 1983, Kang 1989) and even more scarce are quantitative studies within the Weddell and Scotia Seas (Fryxell and Kendrick, 1988; Garrison et. al.). The geographical distribution of phytoplankton species is seasonal (Hart 1942). Species composition is a time dependent variable and is affected by environmental factors such temperature, salinity, light, and nutrient distributions. It is, therefore, important to quantify phytoplankton biomass in the austral winter and to understand the physical processes affecting phytoplankton distribution.

Methods

Samples were collected aboard the R/V Polar Duke on the two phase AMERIEZ austral winter cruise in 1988. Observations on the cruise extended from the South Scotia Ridge at the northern boundary of the Weddell Sea. Stations were in open waters and at ice covered stations. The first phase, Leg I, was carried out in early winter from 4 June to 5 July before the ice had reached its maximum areal extent. Sea water samples were analyzed at selected stations on rapid transects normal to the ice edge along the 40 and 48°W meridions (Table 1) on the second leg of the cruise, which was carried out in mid-winter from 18 July to 13 August when pack ice was in its stages of rapid accretion (Fig. 1) . (Rapid transects are defined as a continuous sampling regime along a constant meridion. It is an attempt to achieve near synopticity within a given time.) A volume of 250ml of sea water was collected at eight depths at each station from 10-liter Niskin bottles on the conductivity-temperature-depth profiling system (CTD), and samples were immediately processed on board ship after collection using the Filter-Transfer-Freeze (FTF) technique (Hewes and Holm-Hansen 1983) by Cynthia Venn.

Table 1. The date and geographical location of stations sampled. The following depths were sampled at 2,12,20,35,55,80,120,150m at each station unless otherwise noted.

Station Number	Date (1988)	Latitude('S)	Longitude('W)
75	24 July	57°40.3	39°59.9
79	25 July	57°59.3	40°00.2
81[a]	26 July	58°15.9	40°00.1
86[b]	26 July	58°56.6	40°00.0
90[c]	27 July	58°28.9	40°00.3
92	27 July	59°46.3	40°03.3
128[a]	9 August	57°42.1	48°00.3
130	9 August	57°58.2	48°00.1
132	9 August	58°14.3	48°00.0
136	10 August	58°48.6	48°00.2
141[a]	10 August	59°28.7	47°59.0
142	11 August	59°33.8	47°59.4
144[d]	12 August	59°05.2	48°01.0

a= missing 35m sample
b= missing 2m sample
c= missing 2 &12m samples
d=10 instead of 12m

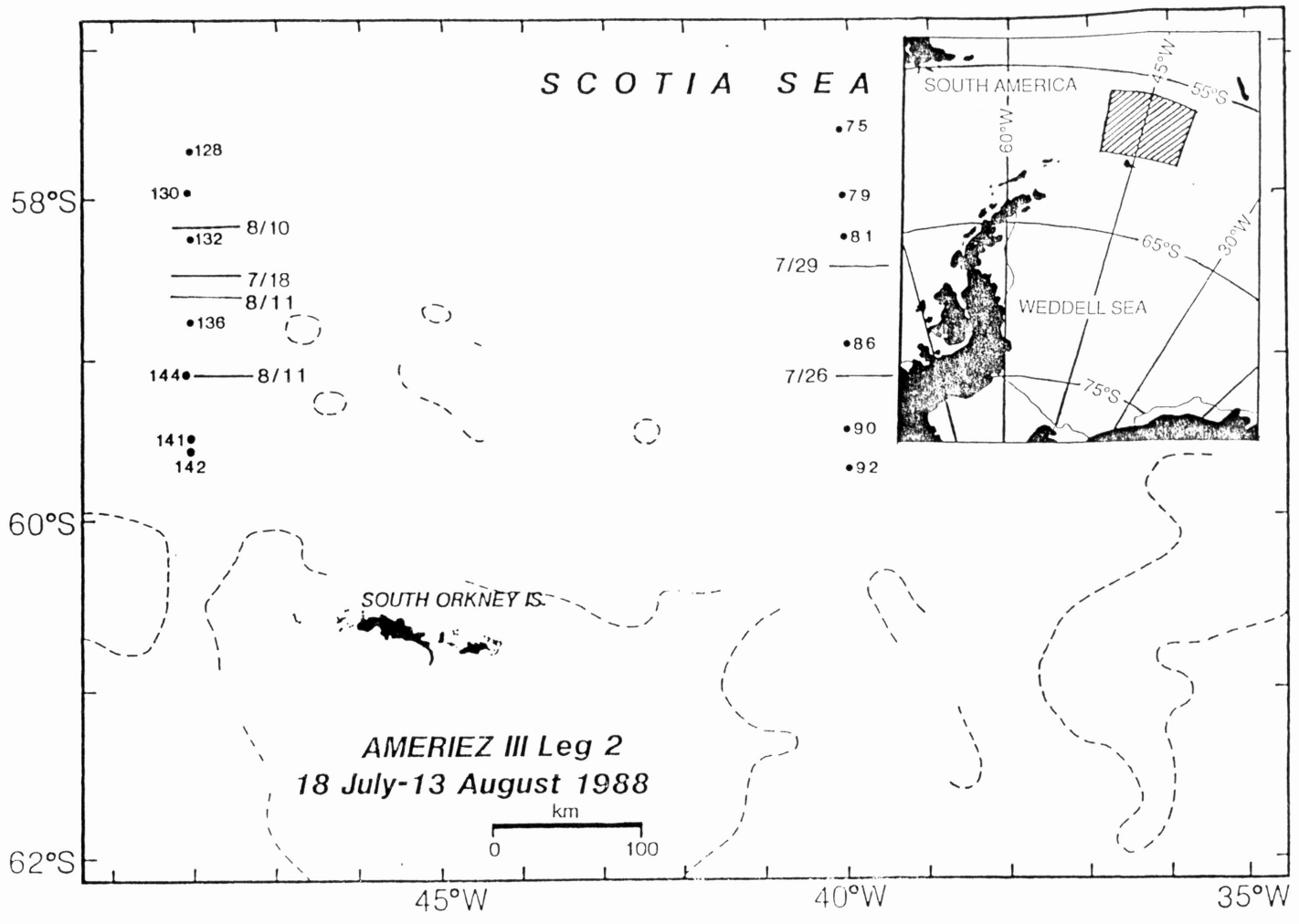


Figure 1. The geographical location of stations sampled in this study. Dates denote the approximate location of the ice edge during the course of the transect.

Filter-Transfer-Freeze Technique

Samples were shaken to insure against any settling of the sample and to release any phytoplankton that might have adhered to the sample bottle. The sample volume of 250 ml was filtered through a 0.45 micrometer polycarbonate (shiny side up) filter at <1/3 atm of pressure. During filtration, approximately 50ml of fresh water was slowly poured down the side of the filtering tower to put salts into aqueous solution. When less than 10 ml of the water sample remained to be filtered, samples were soaked in glutaraldehyde for one to two minutes; filtration resumed until the bottom of the meniscus reached the filter surface. While still wet, the filter was transferred filtered side down onto a microscope slide already on top of dry ice where it remained until the filter was firmly frozen onto the microscope slide. The filter was then rubbed free from the slide with a warm finger in a circular motion and peeled off using needle-nosed forceps. Mounting medium was applied by immersing and withdrawing a wire loop into a 30% glycerol solution, which created a thin membrane of mounting medium. The loop was centered above the frozen sample which was still frozen onto the microscope slide the area around the sample is touched to release the thin film of mounting medium. A 25 X 25 mm coverslip was immediately placed on top of the medium. One day later, after the mounting medium had completely solidified, the sample was sealed with fingernail polish

to prevent desiccation. Slides were stored at near-freezing temperatures in microscope slide boxes sealed with tape to prevent dessiccation. Storage procedures are important to follow as problems with dessiccation have been encountered in the past.

Data Analysis

FTF slides were observed with phase contrast on a standard upright Zeiss microscope at magnification 400X at the Texas A&M University. A minimum of three horizontal and three vertical swaths across the slide was counted, which is 12% of the area of the slide. If fewer than 100 cells were observed during the six swaths, additional passes across the slide were made until the minimum of 100 cells were counted. This amount was decided upon after having observed the paucity of cells in vertical net hauls taken on the cruise.

The FTF technique is useful because it preserves cells in water-soluble medium in the same state in which they were collected, and cells can be distinguished as empty or full. Full cells were considered full if organic matter was still intact; these are assumed alive when collected. An empty frustule is assumed to be dead when collected.

The number of both full and empty cells were calculated using a Fortran program with the following equation to ascertain abundance of cells in units of cells per liter:

$$\text{Abundance (cells/liter)} = \text{number of cells counted} \times \frac{\text{Total area filtered}}{\text{Total area counted}} \times \frac{1000\ \text{ml/l}}{\text{Volume filtered}}$$

Total area filtered = 268.8mm^2

Total area counted= 5.5 mm^2 X (number of passes across the slide)

Volume filtered= 250ml

Results are integrated with physical and chemical data obtained by other components of the AMERIEZ program. Temperature and salinity measurements were obtained using a Seabird SBE 9/11 conductivity-temperature-depth profiling system (CTD) coupled to a Compaq 286/20 microcomputer. The CTD was integrated into a General Oceanics rosette water sampling system equipped with ten 10-liter Niskin sample bottles. Salinity analyses were determined by a Plessey laboratory salinometer using water samples collected from rosette sample bottles of the CTD from which phytoplankton was collected.

Species Diversity Index

The following index (S) was used to measure species diversity (richness) (Margalef 1958):

$$S=\frac{\text{Number of groups-1}}{\text{Ln (total integrated cells)}}$$

Diversity it proportional to the diversity index. In other words, diversity increases as the index number increases. When the sample contains a single species, S = 0. This index does weight each individual species and assumes that each taxa contributes equally to the assemblage. Other indices are more suited for phytoplantkon work but this method was selected because it was productive and dependable if one recognizes its limitations. My main objective in using an index was to access the relative differences in the assemblages at different stations.

Classification of Phytoplankton

Cell counts from water samples using the FTF technique allow estimation of absolute numbers of phytoplankton in their natural state at the time of collection. This poses certain disadvantages in identification. The organic matter such as lipids and chloroplasts remain intact, and as a result, the ornamentation on the cell is not clearly seen for a positive identification. Diatoms were packed with lipids which may serve as storage reservoirs for food. Lipids may aid the cell in buoyancy in the austral winter turbulent water and help in keeping the cells above the critical mixing depth. Lipids apparently replaced the vacuoles in cells compared to other studies the spring. Chain formation was also preserved. Some chain formation aids in identification but some doesn't; therefore, phytoplankton was sometimes classified as follows:

Nitzschia spp. (section *Fragillariopsis*) often make long chains of up to 28 cells, connected valve to valve. When in these chains, cells are seen only in girdle view in the light microscope. Taxonomic characters used in the light microscope to identify *Nitzschia* spp. requires on seeing the cell in valve view to distinguish such characters as general shape, length, width, and the number of costa in ten micrometers. As a result of these consequences, *Nitzschia* spp. (section *Fragillariopsis*) were only

identified to genus. Individual cells that were in valve view were classisfied to species.

Centrics and members of Pseudonitzschia were classified as such valve ornamentation due to the large concentrations of lipids which inhabit these frustules. *Thalassiosira* spp. under 20 micrometers. were classified accordingly because processes on the face of the valve were obstructed by high concentrations of lipids and were not resolved well due to the low refractive index of the FTF medium in which they were mounted.

All dinoflagellates were identified as to genera due to the author's unfamiliarity with the species. Cysts and monads were also classified as such for this reason.

All prymnesiophytes, dinoflagellates, and silicoflagellates were assumed full when collected; therefore, total empty diatoms equals total empty phytoplankton recorded.

Physical Oceanography

The second leg of the AMERIEZ cruise took place during midwinter when the ice edge was in its stage of rapid accretion. At the onset of the cruise, the ice edge was oriented zonally approximately along 60°30.0'S latitude, and by the completion of the cruise the ice edge had advanced to 58°00.0'S in this region. During the cruise, the ice edge advanced and retreated between the cold Weddell and warmer Scotia Sea water. The behavior of the ice varied greatly in lateral movement before and during the course of the two transects. Upper layer thermal fronts coincided with the deeper Scotia front in the northern portions of both transects.

The 40°W transect took place from 26 to 28 July 1988. The ice edge was located between 58°24.2'S (Station 81) and 58°32.4'S (Station 86) on 26 July and retreated between 59°04.7 (Station 86) and 59°11.7'S (Station 90) by 29 July. (See methods for geographical representation of location of the ice edge). The ice edge had moved approximately 72 kilometers south by 29 July from its position on 26 July. Temperature (Fig. 2) as well as salinity (Fig. 3) was generally uniform throughout the top 150m of the

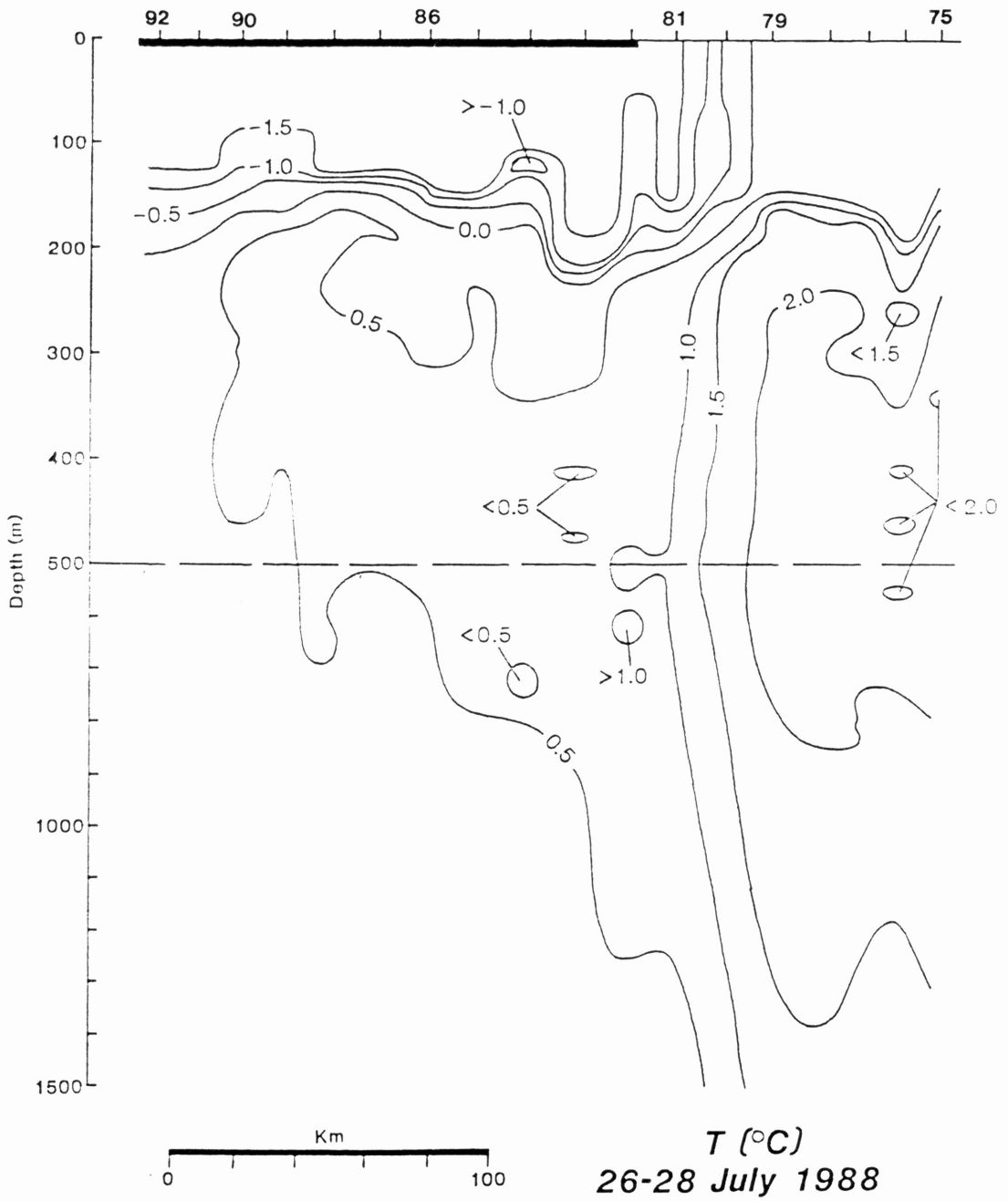


Figure 2. Vertical section of T(°C) along the 40°W Transect during Leg 2 of the AMERIEZ cruise. Depth scale change at 500m denoted by horizontal dashed line. Contour interval is 0.5°C. The heavy black line at the surface denotes the approximate extent of pack ice.

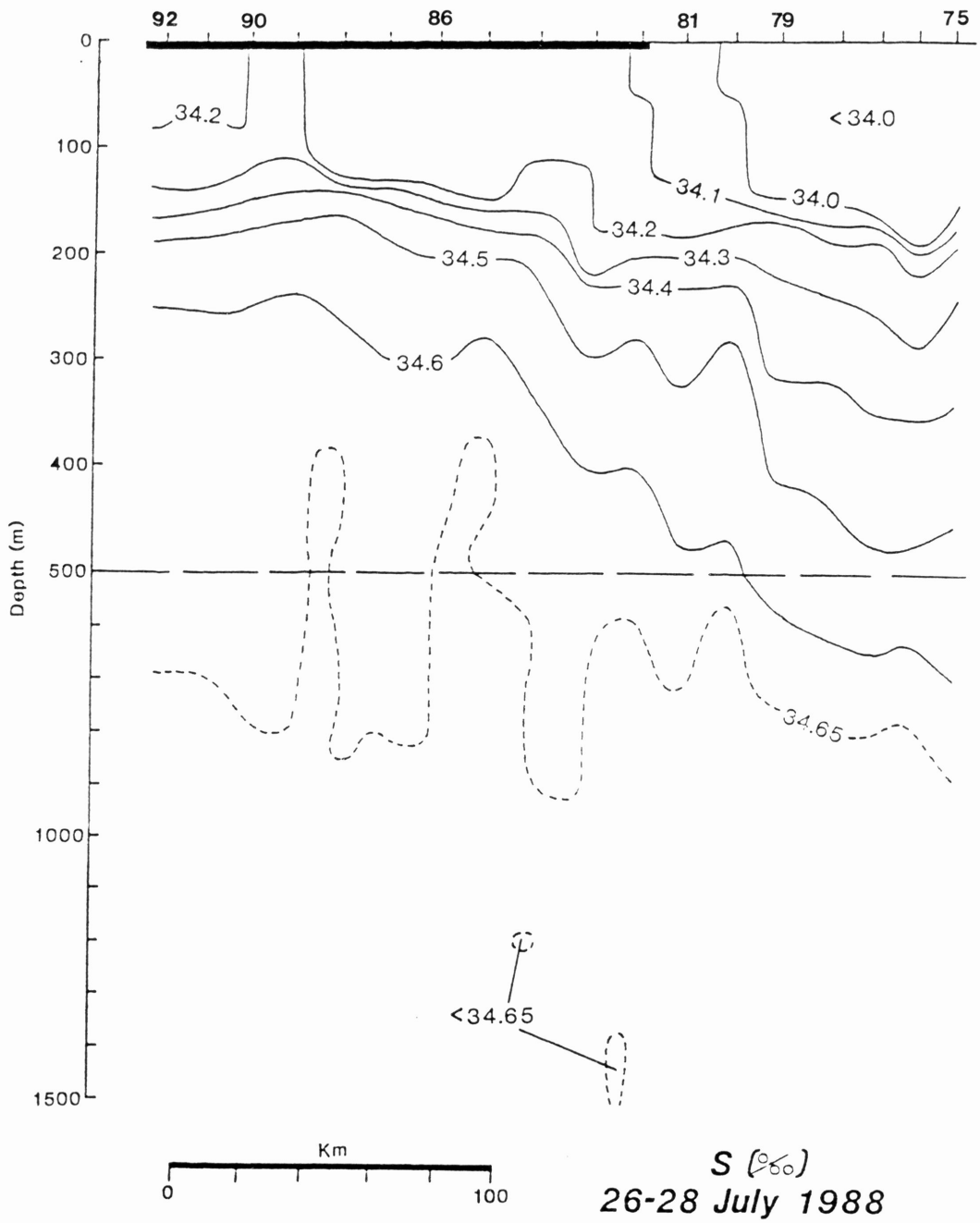


Figure 3. Vertical section of S (%) along the 40'W Transect during Leg of the AMERIEZ cruise. Depth scale change at 500m denoted by horizontal dashed line. Contour interval is 0.1 %. The heavy black line at the surface denotes the approximate extent of pack ice.

water column in the open water. Temperatures were near the freezing point of seawater in the upper 150m, and salinities were greater at ice-covered stations in the top 150m. The upper layer thermal front was centered about 25km north of the ice edge and stronger than that of the 48°'W transect.

Ice coverage was changing rapidly during the course of the 48°'W transect, 10-11 August. This transect was the farthest upstream in the Weddell-Scotia Confluence. On the 48°W transect, the pack ice moved great distances during the course of transect in a very short period of time in contrast to the distance it covered on the 40°'W transect. On 8 August, it was sighted between 58°06.8'S and 58°14.3'S and by 11 August it moved between 58°32.4'S and 58°40.5'S. Within one day, 11 August, it had moved approximately 56 kilometers. As a result of this rapid movement, the most complex temperature and salinity profiles were observed in the water column (Figs.4,5). A melt water lens along the 48°'W transect was associated with deteriorating multi-year floes and more localized ice edge-associated features were also observed. A counterclockwise eddy existed in the vicinity of this active frontal zone during 18 July-4 August, prior to the occupation of this transect, as evidenced by the results of drogued buoys employed prior to the execution of rapid transects.

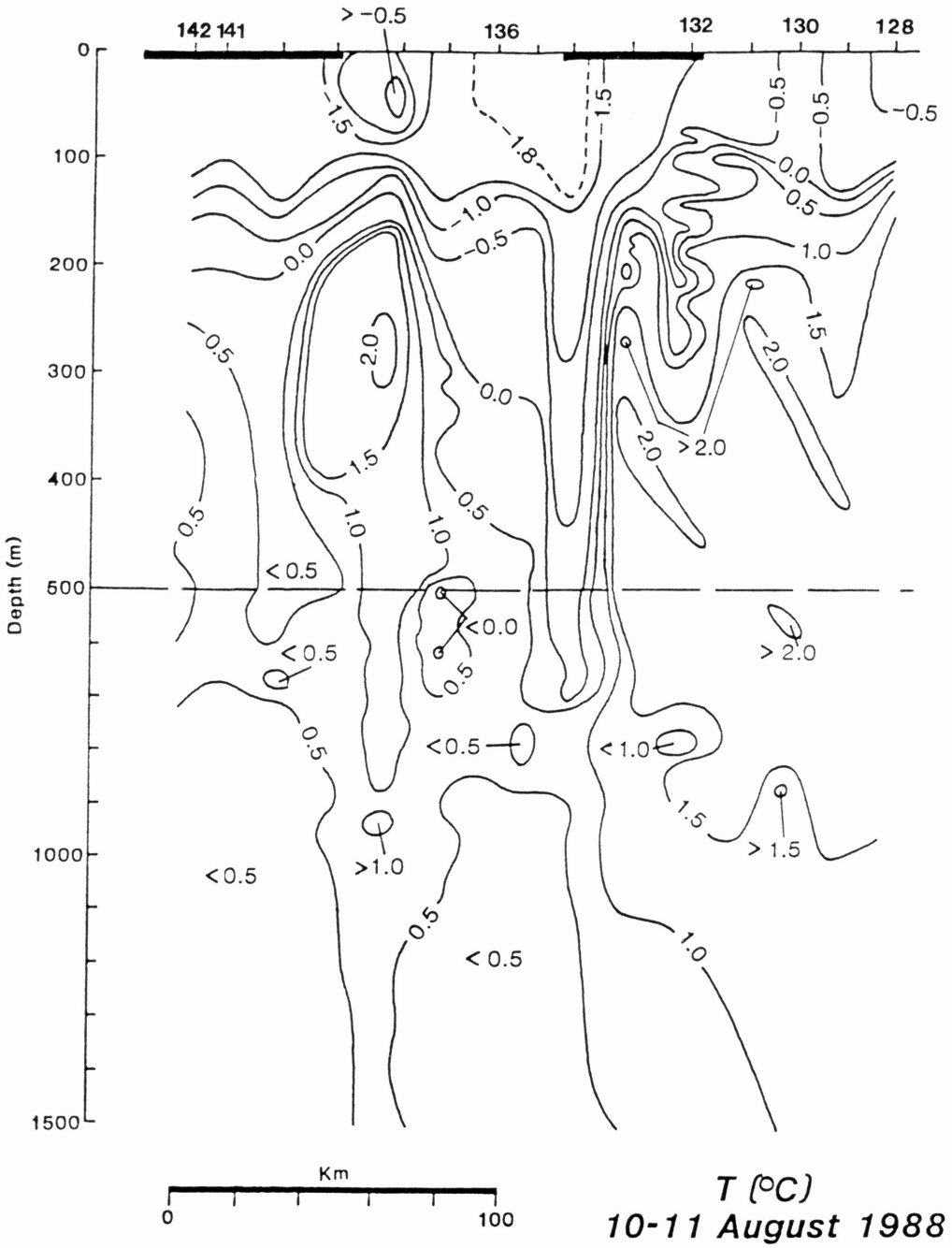


Figure 4. Vertical section of T(°C) along the 48°W Transect during Leg 2 of the AMERIEZ cruise. Depth scale change at 500m denoted by horizontal dashed line. Contour interval is 0.5°C. The heavy black line at the surface denotes the approximate extent of pack ice.

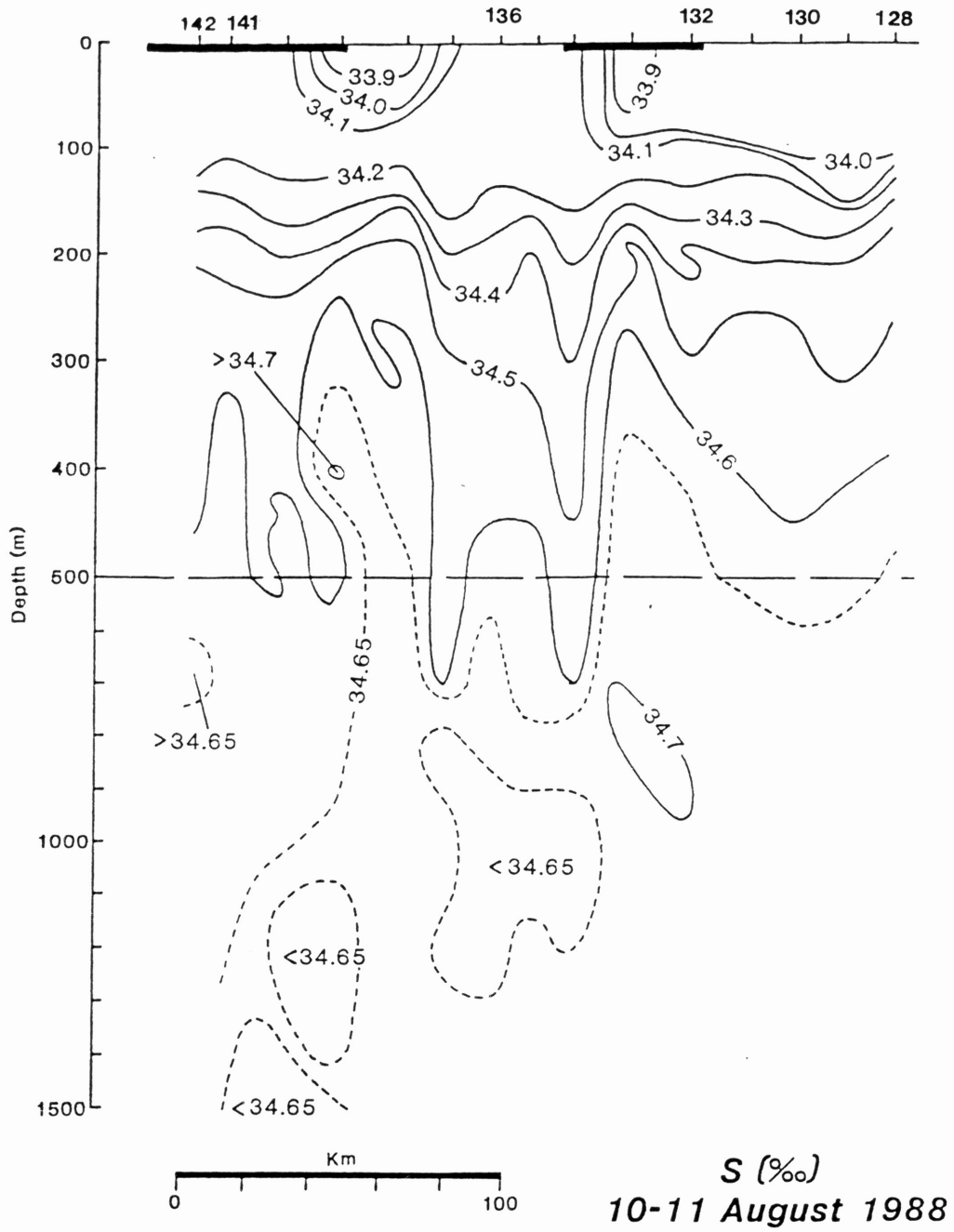


Figure 5. Vertical section of S (%) along the 48'W Transect during Leg of the AMERIEZ cruise. Depth scale change at 500m denoted by horizontal dashed line. Contour interval is 0.1%. The heavy black line at the surface denotes the approximate extent of pack ice.

RESULTS

The purpose of this study was to determine whether there was a difference in species composition and abundance between open water and ice-covered stations. I present evidence that there are indeed distinct differences between the two habitats in abundance of certain phytoplankton groups such as diatoms and sillicoflagellates. However, this was not the case for *Phaeocystis* sp., archaeomonads, and cysts. *Phaeocystis* sp. varied in abundance at the two habitats, while archaeomonads and cysts were very low in abundance throughout the study. The ice cover acted as a frontal system to other phytoplankton species as well. Differences were observed between the two transects and will be discussed in a later chapter. Despite differences the same general trends were observed on the transects that existed between open water and ice-covered stations on both transects.

The phytoplankton consisted mainly of diatoms, a single-celled prymnesiophyte, a silicoflagellate, few dinoflagellate genera, cysts, and archeomonads. A total of 71 different phytoplankton taxa were quantified. Diatoms were represented by 61 taxa. Diatom genera included: *Nitzschia, Thalassiosira, Asteromphalus, Corethron, Chaetoceros, Synedra, Actinocyclus, Dactyliosolen, Rhizosolenia, Stellarima, Eucampia, Leptocylindrus, Odontella, Navicula, Pleurosigma,* and *Porosira.* Dinoflagellates were

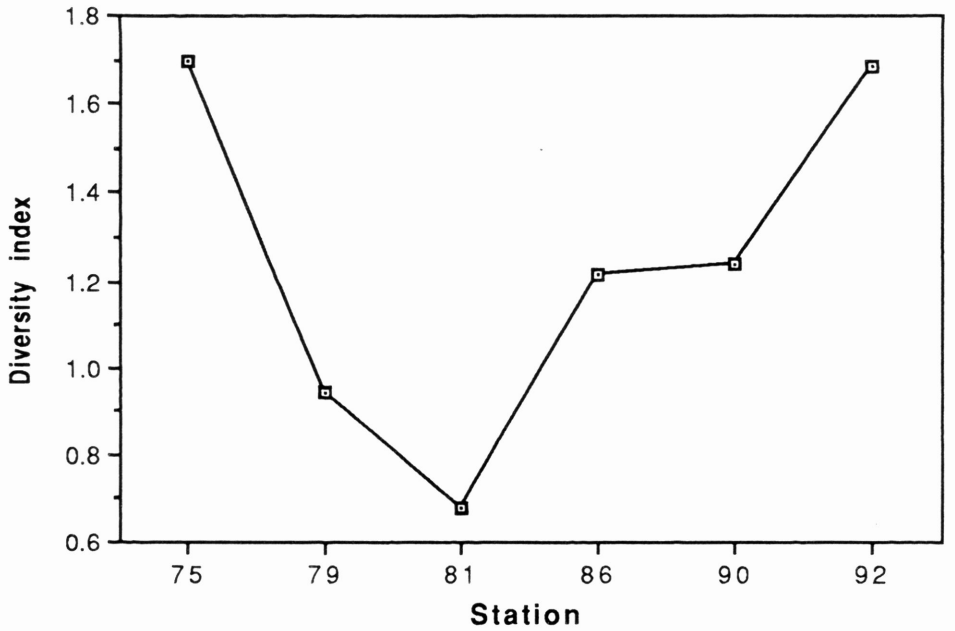
represented by the genera *Gymnodinium* and *Peridinium*. One prymnesiophyte, *Phaeocystis* sp., was noted and one silicoflagellate, *Distephanus speculum*. Archeomonads, certain dinoflagellates, and cysts were classified only to the group level.

The phytoplankton assemblage on the second leg of the cruise was characterized by low abundance, compared to past AMERIEZ collections at the ice edge during austral spring and autumn, as well as low diversity. Most taxa contributed less than one percent of total cells to the assemblage at any one station. The phytoplankton assemblage exhibited low diversity; single cells of *Phaeocystis sp.* followed by *Nitzschia spp.* (section *Fragillariopsis)* , and *Nitzschia cylindrus* consistently dominated at each station and together accounted for 73.8% of the total phytoplankton. The most abundant species at each station averaged 31.4 % of total cells on the two transects noted. Diversity measured by the species diversity index (Margalef 1958) was different at each station (Fig. 6a&b) and generally increased southward and northward from the ice edge. Diversity was relatively constant in the vertical direction (Fig. 7). The highest diversity index was often associated with the diatom maxima.

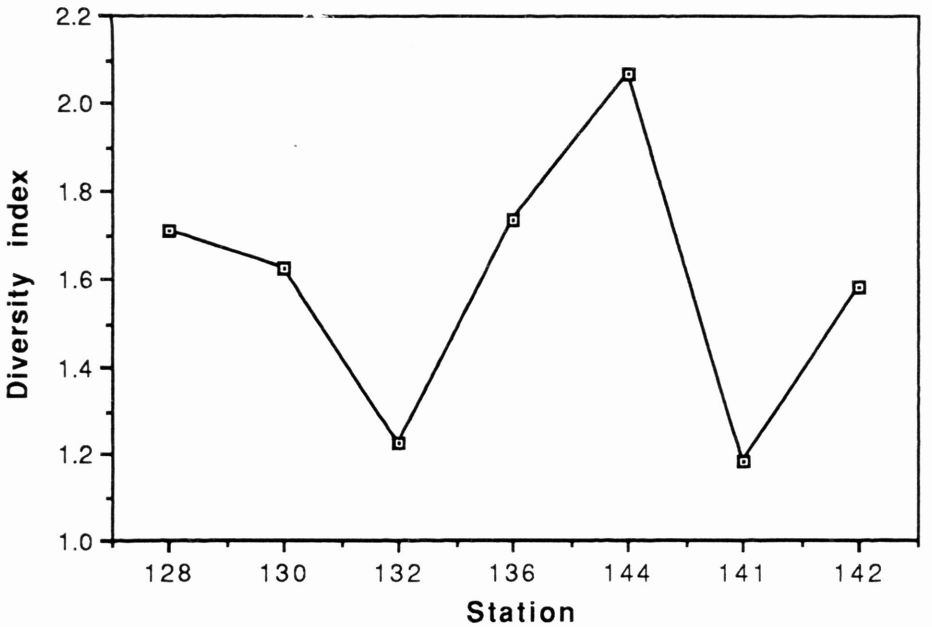
The widest range in integrated full phytoplankton counts was recorded on the 40°W transect (Fig. 8). Integrated full phytoplankton cell counts peaked at the open water Station 81, adjacent to the ice edge, with 1.58 X 10^8 cells m^{-2} dominated by *Phaeocystis* sp (96.2%). Lowest integrated full phytoplankton cell counts occurred at ice-covered Stations 90 and 92 with 1.58 and

Fig. 6 Species Diversity Index for A) 40W transect B) 48W Transect

A



B



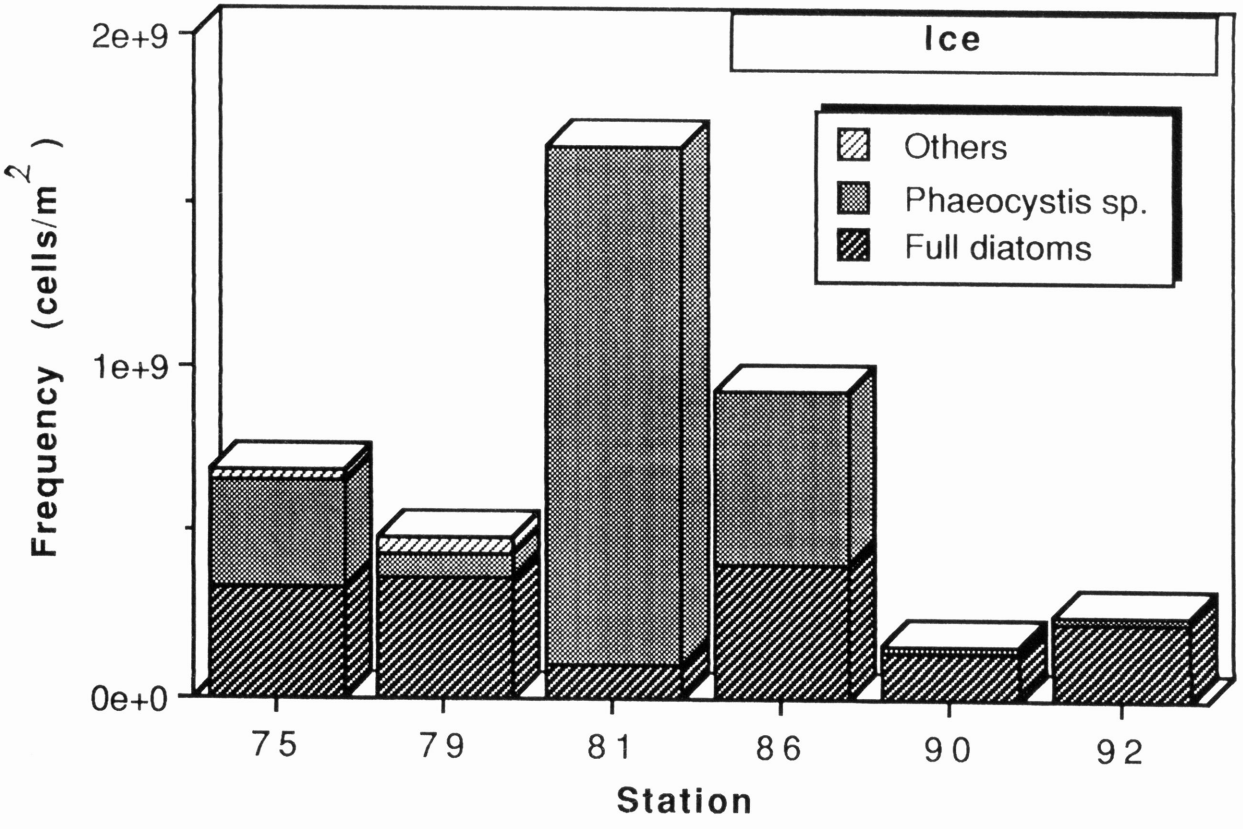


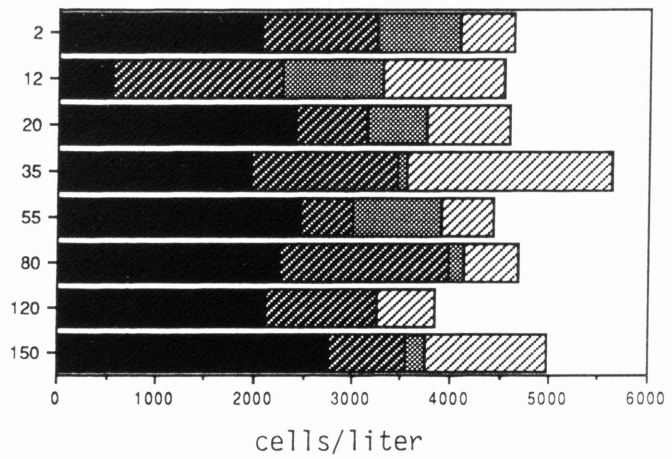
Figure 8. Integrated Cells m^2 of full phytoplankton on the 40W Transect.

2.53 X 10^7 cells m^{-2} respectively. The abundance of cells was generally low at the surface depth and phytoplankton cells decreased with depth down to 150m. The maxima were usually below the surface with the exception of Stations 79 and 144. The upper mixed layer along the 40°'W transect ranged in depth from 90 to 140m (Muench and Husby 1989) and was generally deepest at open water stations. Open water stations were sampled in two different bodies of water, the warmer Scotia Sea (Stations 75 and 79) and the Weddell-Scotia Confluence (Station 81). Cellular maxima occurred in the upper meters of the water column at 20m at Stations 75 and 81 and at 2m at Station 79 (Fig. 9). Station 79 was at the southern end of the warm Scotia Sea, nearest to the Weddell-Scotia Confluence and was the only station on this transect that had a surface cellular maximum at 2m dominated by Phaeocystis unlike Station 81, where it dominated throughout the water column. Station 81 was in a body of water that was intensely mixed according to Husby and Muench (1988). Total full diatoms were especially low at this station. Parts of the Weddell-Scotia Confluence were also covered with pack ice (Sta. 86 and 90) as was the Weddell Sea (Station 92). Cellular maxima at all stations occurred at subsurface depths -- 20, 55, 12m at Stations 86, 90, and 92 respectively (Fig. 10).

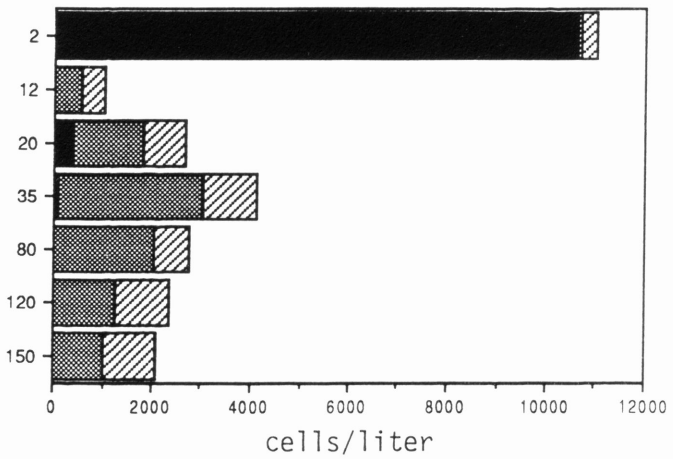
Like the 40°W transect, integrated full phytoplankton cell totals on the 48°W were generally higher in the open water and lower at ice-covered stations. Station 144 was sampled after the rapid transect and ranges do not include this station. The range of

Figure 9. Vertical Distribution of Phytoplankton at Open Water Stations on the 40W Transect.

A. Station 75



B. Station 79



C. Station 81

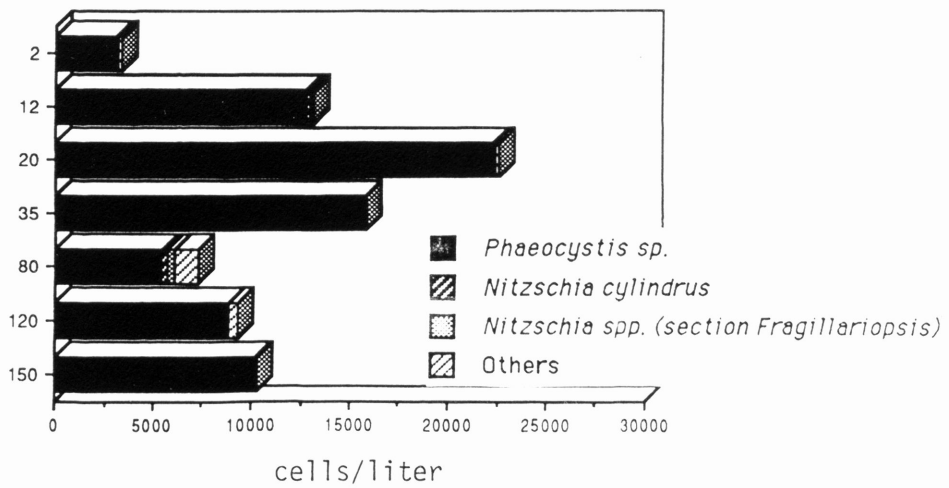
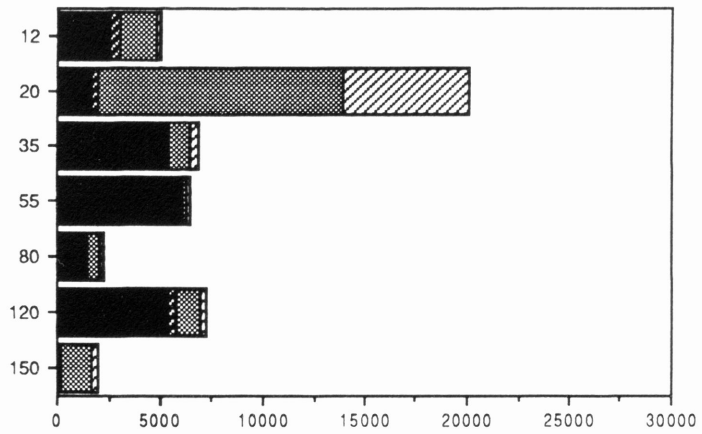
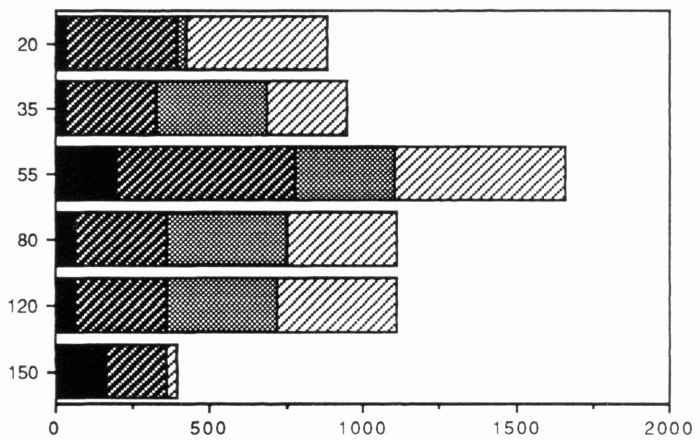


Figure 10. Vertical Distribution of Phytoplankton at ice-covered stations on the 40W Transect.

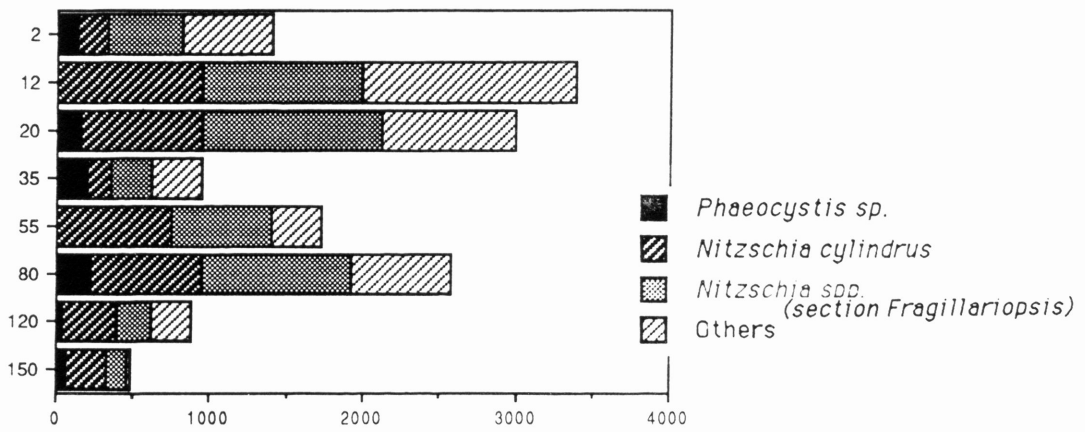
D. Station 86



E. Station 90



F. Station 92



integrated phytoplankton was narrower than that of the 40°W transect. Integrated totals on the 48°W transect ranged from 2.91 X 10^8 at Station 141 to 7.92 X 10^8 cells m^{-2} at Station 128 (Fig. 11).

The mixed layers were generally deeper at stations on the 48°W transect. The upper layer at the southern end of the transect was vertically well-mixed in both temperature and salinity to depths of 100-130m (Husby, Muench, and Gunn 1988). Open water Stations 128 and 130 were sampled in the warmer and less saline Scotia Sea, and Station 132 was sampled in the more saline and colder Weddell Sea. Station 136 had the coldest water in the upper surface layer. All had deep cellular maxima: 80m at the northernmost Sta. 128 and 55m at Stations 130 and 136 (Fig. 12). Stations 141, and 142 were ice-covered and sampled in the colder and more saline Weddell Sea. Cellular maxima were at 80 and 35m at Stations 141 and 142 respectively (Fig. 13).

Differences in the dominant phytoplankton group(s) were noted for the two habitats. These differences are demonstrated by the most abundant species at each station (Table 2). Many diatom species were associated with ice cover (Table 3). Open water stations included diatoms, dinoflagellates, sillicoflagellates, cysts, and archaeomonads. At ice-covered stations, diatoms and the prymnesiophyte, *Phaeocystis* sp., were the predominating phytoplankton groups. No differences between the two habitats for archaeomonad abundance were not noted (Fig. 14).

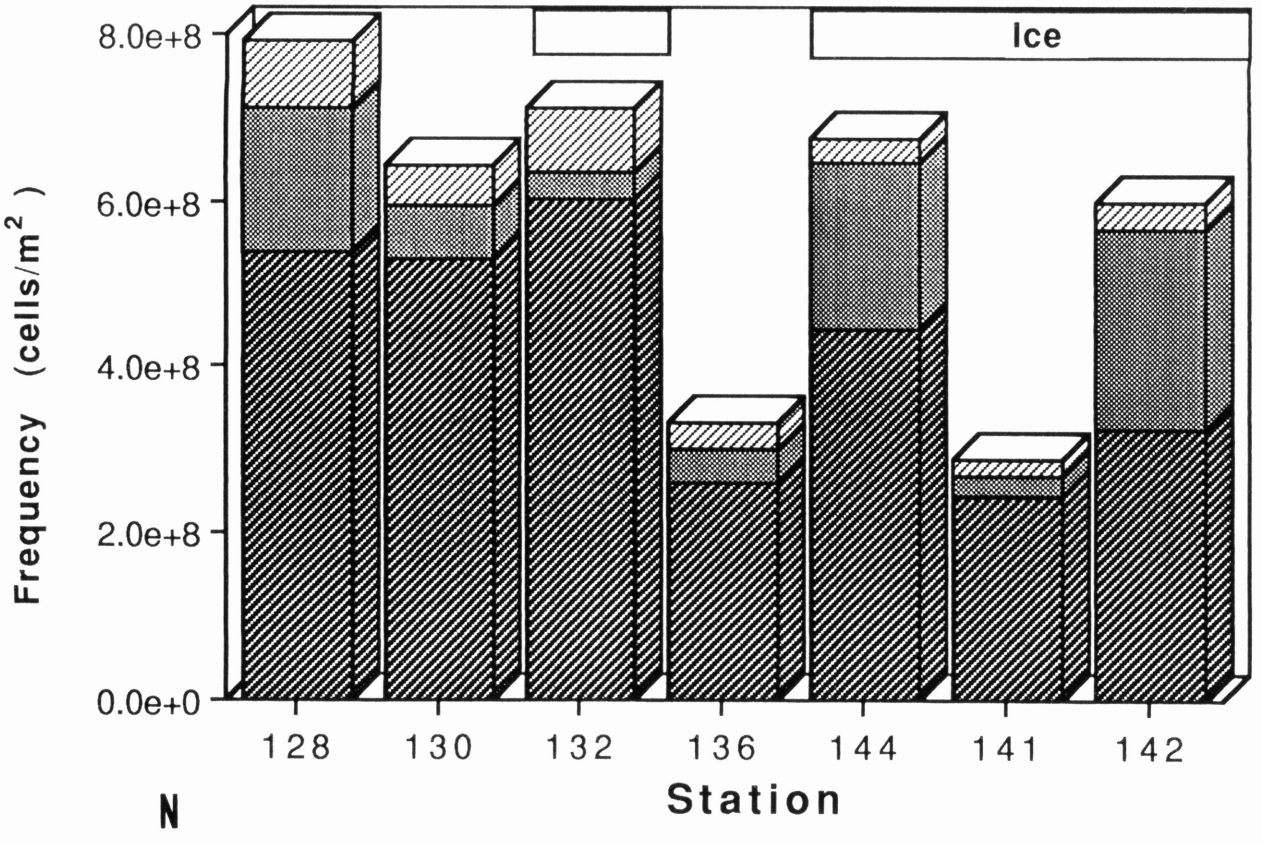


Figure 11. Integrated full phytoplankton counts under $1m^2$, on the 48W Transect.

Figure 12. Vertical Distribution of Phytoplankton on the 48W Transect.

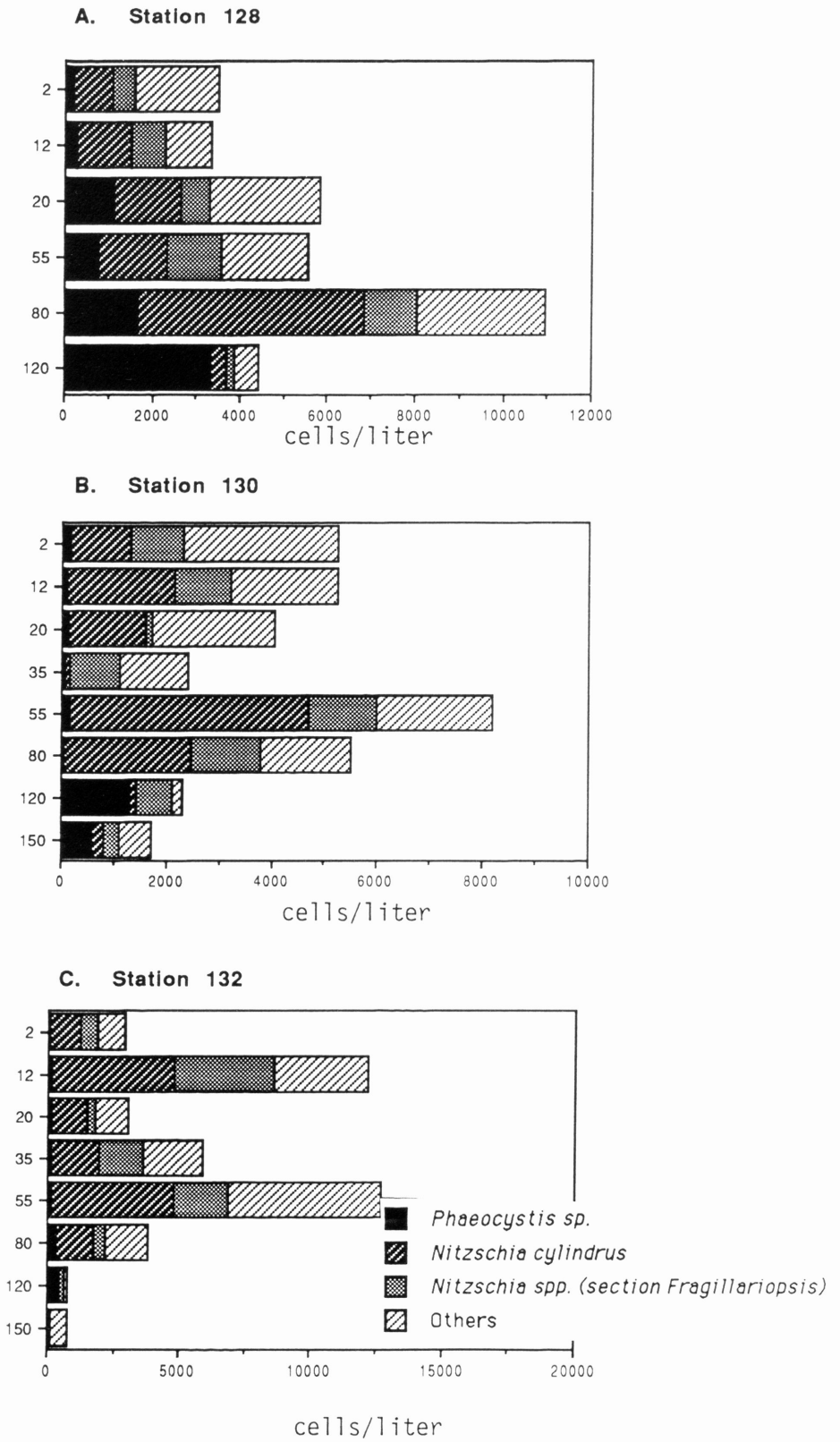
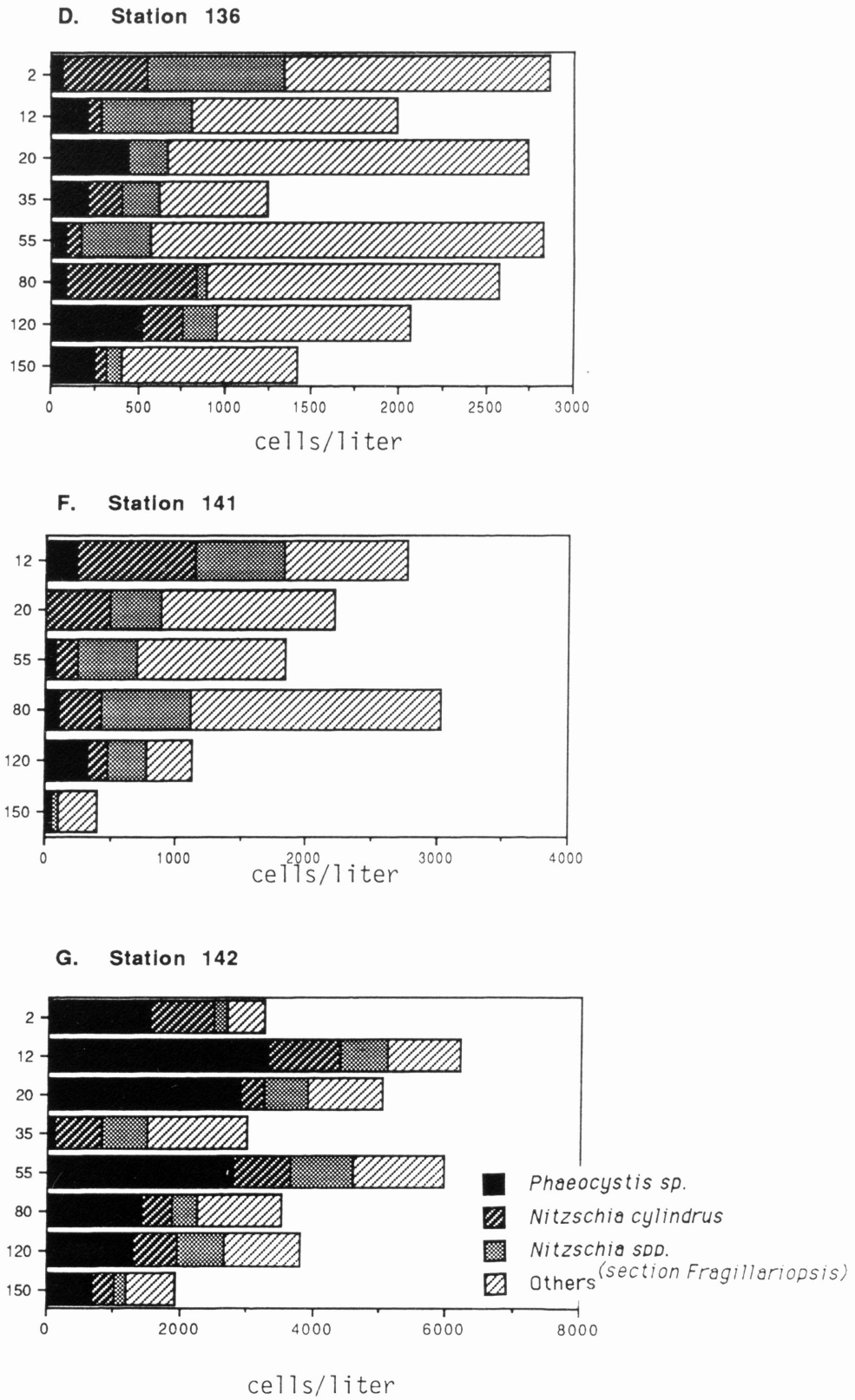


Figure 13. Vertical Distributin of Phytoplankton on the 48W Transect.



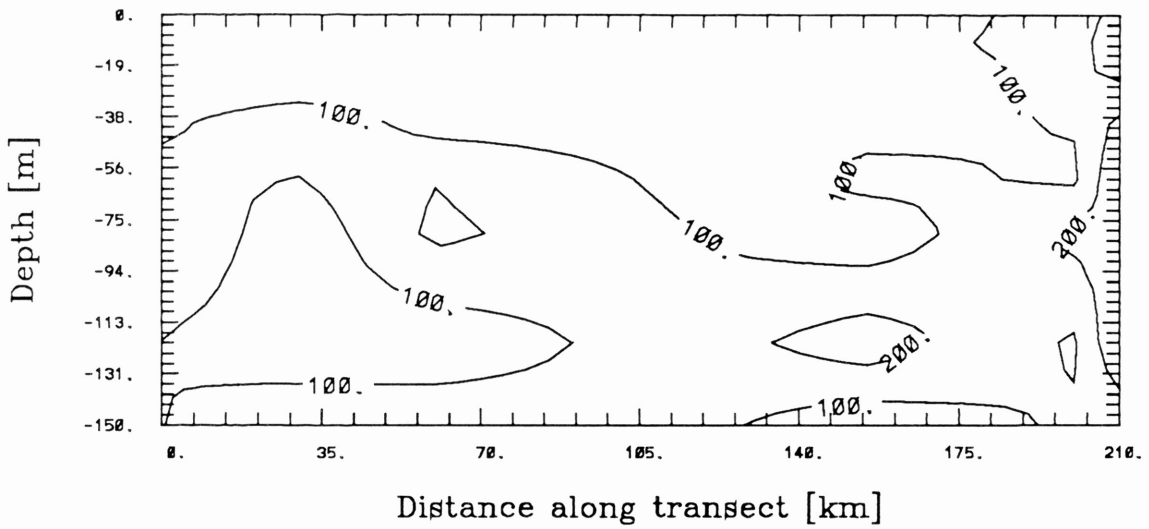


Figure 14. Contour plot of archaeomonad abundance (cells/liter) in the upper 150m of the water column on the 48W Transect.

Table 3. Presence of full taxa at each station on the 40 and 48W Transects.

128	130	132	136	144	141	142	**Taxa Present (full)**	75	79	81	86	90	92
	X	X	X	X	X	X	*Actinocyclus actinochilus*		X		X		X
X				X		X	*Actinocyclus spp.*	X		X	X	X	
X				X			*Actinocyclus cf. cholnokyi*	X			X		
				X			*Amphora spp.*						
X	X	X	X	X		X	*Asteromphalus hookeri*	X	X		X	X	X
							Asteromphalus hyalinus						
							Asteromphalus parvulus						X
	X		X	X	X		unidentifiable diatom						
	X	X		X			Chaetoceros bulbosum complex						
X	X	X	X	X	X	X	unidentifiable centric diatom	X	X	X	X	X	X
X	X	X	X	X	X	X	*Chaetoceros atlanticus*	X	X		X	X	
							Chaetoceros bulbosus	X	X				
X			X			X	*Chaetoceros convolutus*						
	X	X	X	X	X	X	*Chaetoceros criophilus*	X	X	X	X	X	X
X	X		X	X			*Chaetoceros curvisetus*			X		X	
			X				*Chaetoceros dichaeta*			X	X	X	X
X	X	X	X	X	X		*Chaetoceros flexuosus*	X					
				X			*Chaetoceros neglectus*						
X	X	X		X			*Chaetoceros neogracile*	X	X	X	X	X	X
			X				*Chaetoceros pendulus*						X
X	X	X	X	X			*Chaetoceros spp.*	X					
X	X	X	X	X	X	X	*Corethron criophilum*	X	X	X	X	X	X
	X		X				*Coscinodiscus oculoides*				X		X
X	X		X	X			*Dactyliosolen antarcticus*	X	X		X		X
X		X	X	X			*Eucampia antarctica*				X	X	
				X		X	*Leptocylindrus mediterraneus*				X		
							Navicula spp.						
							Nitzschia angulata						
X	X	X	X	X	X	X	*Nitzschia closterium*	X	X		X	X	X
X	X		X	X	X	X	*Nitzschia curta*	X					X
X	X	X	X	X	X	X	*Nitzschia cylindrus*	X	X	X	X	X	X
X	X	X	X	X	X	X	*Nitzschia spp. (section Fragillariopsis*	X	X	X	X	X	X
X	X	X		X	X	X	*Nitzschia kerguelensis*	X				X	X
X				X	X		*Nitzschia linearis*				X	X	X
X	X	X	X	X	X	X	*Nitzschia pseudonana*	X					
				X			*Nitzschia rhombica*						
X				X		X	*Nitzschia ritscheri*					X	X
X	X	X	X	X		X	*Nitzschia spp.*	X	X	X	X	X	X
X	X	X		X			*Nitzschia spp. (pseudonitzschia)*		X		X	X	X
						X	*Nitzschia sublinearis*						
X						X	*Nitzschia sublineata*						X
	X		X		X		*Odontella weissflogii*						X
						X	*Odontella weissflogii resting spore*						
							Pleurosigma spp.						X
							Porosira pseudodenticulata		X				
				X		X	*Porosira spp.*				X		
			X				*Rhizosolenia alata f. inerme*	X	X	X	X	X	X
	X						*Rhizosolenia chunii*	X				X	

				X			*Rhizosolenia hebetata forma semispina*							
X	X	X	X	X		X	*Stellarima microtrias*	X					X	X
				X	X		*Synedra spp.*	X	X	X	X	X	X	X
X	X			X	X	X	*Thalassiosira antarctica*							
							Thalassiosira gracilis var. gracilis							
	X		X	X	X	X	*Thalassiosira gravida*							X
X	X	X	X	X		X	*Thalassiosira lentiginosa*							
							Thalassiosira spp.	X	X	X	X	X	X	X
X				X	X	X	*Thalassiosira trifulata*							X
			X	X	X	X	*Thalassiosira tumida*	X			X			
X	X	X	X	X	X	X	*Thalassiosira spp. <20 um*							
X	X	X	X			X	*Tropidoneis belgica*							X
X			X				*Tropidoneis spp.*						X	X
X	X	X	X	X	X	X	*dinoflagellate (unidentified)*	X	X					
X	X	X	X	X		X	*Pennate (unidentified)*	X						X
X							*Gymnodiniaceae*	X	X					
							Peridinium sp.							
X	X	X	X	X	X	X	*Phaeocystis pouchetti (single cells)*	X	X	X	X	X	X	X
			X				cysts							
X	X	X	X	X	X	X	*Distephanus speculum*	X	X	X	X			X
X	X	X	X	X	X	X	monad	X						

Table 2.

Transect	Most Abundant Taxa of Each Station**	
	Open Water	Ice-covered
40°'W	*Chaetoceros criophilus*	*Corethron criophilum*
	Distephanus speculum	*Nitzschia curta*
	Nitzschia closterium	*Nitzschia linearis*
	Nitzschia kerguelensis	*Nitzschia kerguensis*
		Stellarima microtrias
48°'W	*`Chaetoceros convolutus*	*Chaetoceros flexuosus*
	Distephanus speculum	archaeomonads
	Nitzschia kerguelensis	*Thalassiosira* spp.
	Nitzschia pseudonana	(diameter under 20um)

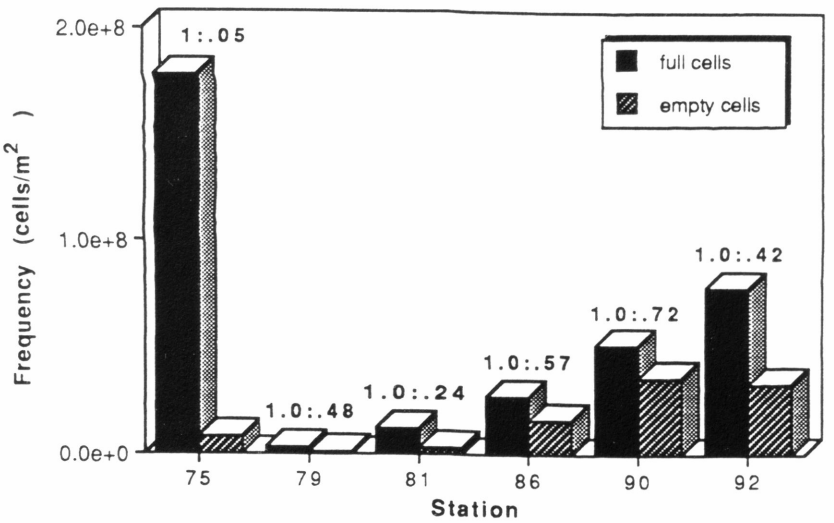
** All Categories include *Phaeocystis sp., Nitzschia spp.* (section *Fragillariopsis*), and *Nitzschia cylindrus*.. Other species are in the top five of at least on station.

Phaeocystis sp., *Nitzschia cylindrus, Nitzschia* spp. (section *Fragillariopsis*) were found at all stations on both transects and at all sampled depths. The dominant taxa at each habitat did not consistently dominated in the same habitat. Strict areas were observed as to where the most abundant taxa dominated (Table. 4).

Table 4. Dominants at each station

Station	Dominant	Percentage
40°'W Transect		
75	*Phaeocystis sp.*	44.4
79	*Phaeocystis sp.*	54.0
81	*Phaeocystis sp.*	95.7
86	*Phaeocystis sp.*	36.6
90	*N. cylindrus*	33.1
92	*N. cylindrus*	28.8
48° W Transect		
128	*N. cylindrus*	32.0
130	*N. cylindrus*	34.7
132	*N. cylindrus*	36.4
136	*N. spp. frag. colonies*	13.9
141	*N. spp. frag. colonies*	22.5
142	*Phaeocystis* sp.	43.0
144	*Phaeocystis* sp.	17.4

The distribution of the dominants was variable not only between the two habitats on the 40°W transect but on the two transects. Integrated cell numbers of *Nitzschia cylindrus* were highest at the open water station 75 and generally increased from Station 79 southward into the pack ice. It often peaked at 12m and was distributed throughout the water column (Fig. 15). Integrated numbers of *Nitzschia* spp. (section *Fragillariopsis*) were highly variable at the two habitats (Fig.16). Highest integrated totals peaked at Stations 86, where *Nitzschia* spp. (section *Fragillariopsis*) dominated. In general, cell numbers were low at the surface and peaked at 20m in the open water, 35m at Station 86, and at 120m



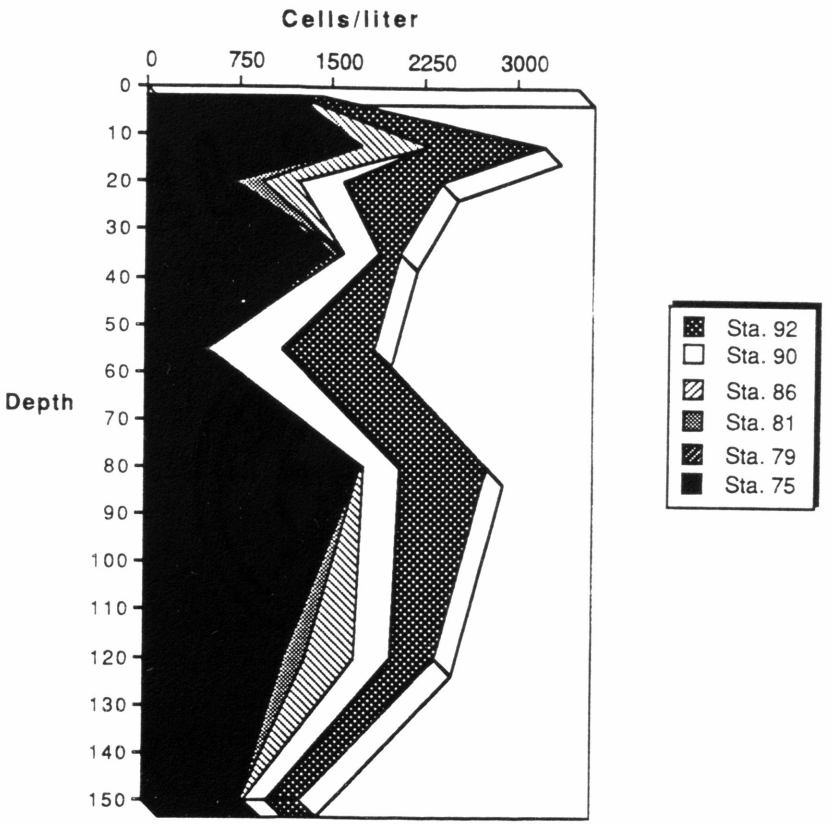
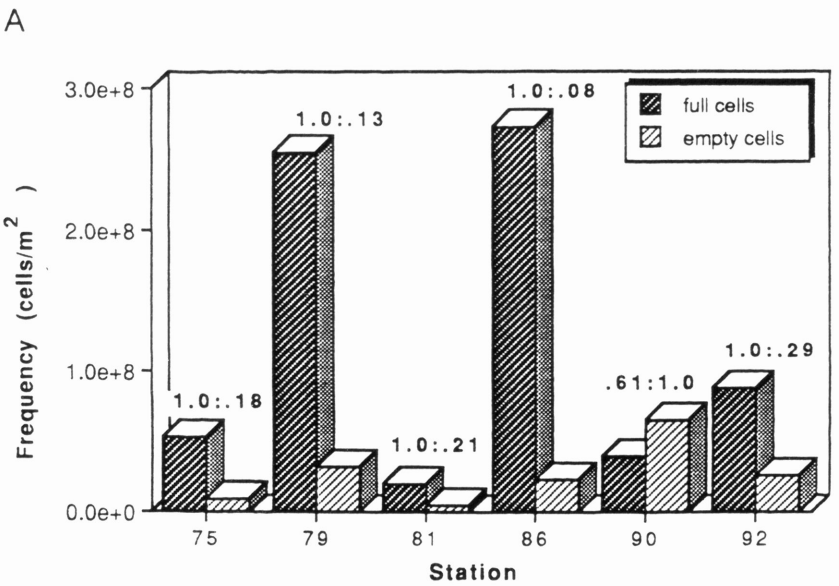


Figure 15. The horizontal and vertical distribution of Nitzschia cylindrus on the 40W Transect. The ratio of full to empty cells is denoted for each station on the above plot.



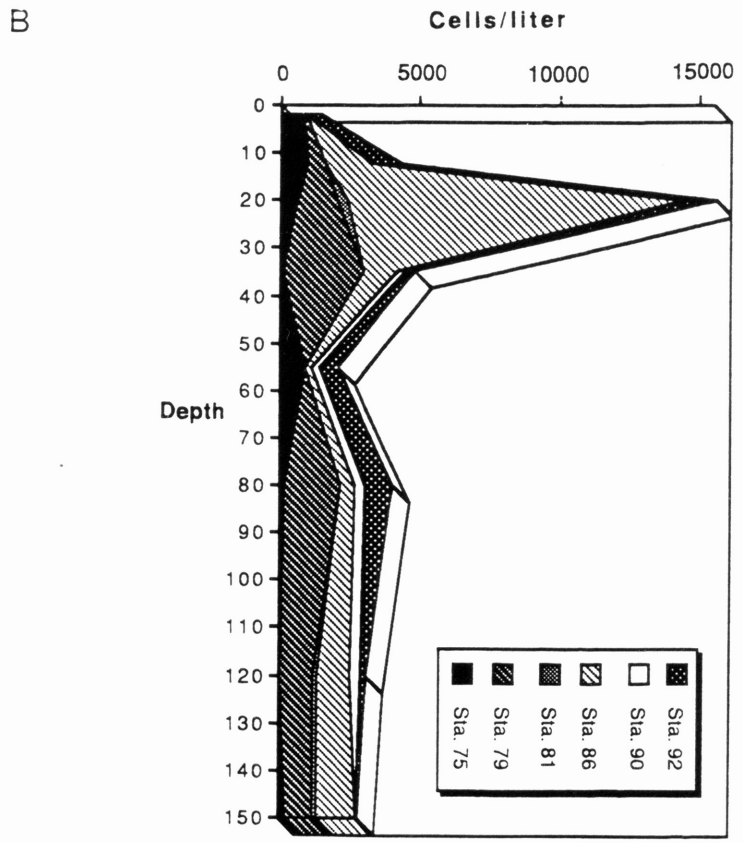


Figure 16. The horizontal and vertical distribution of Nitzschia spp. (section Fragillariopsis) on the 48 W Transect.

at Stations 90 and 92 deep within the pack ice. *Phaeocystis* sp. peaked at Stations 81 and 86 and was mainly distributed in the upper 55m of the water column at all Stations (Fig. 17).

On the 48°W transect, distinct differences were seen between the open water and ice-covered stations even though the sea ice was laterally northward and southward. The diatoms (Figs.18&19) *Nitzschia cylindrus* and *Nitzschia* spp. (section *Fragillariopsis*) showed similar horizontal distribution patterns. Both had lowest integrated cells numbers at the open water Station 136 and the stations under the sea ice. *Nitzschia* spp. (section *Fragillariopsis*) had higher ratios of full to empty cells than *Nitzschia cylindrus*. This may indicate that there are more empty cells in the ice floes or that *Nitzschia* spp. (section *Fragillariopsis*) was not able to withstand the change in physical conditions such as temperature and salinity due to melting. Both had similar vertical distributions. Both peaked at 12m and 55m and these peaks were most pronounced at Stations 132 and 136.

Phaeocystis sp. appeared random in its horizontal distribution. But it often peaked at 12m and 55m like that of the two dominant diatoms but its maximum peak was often at 120m, deeper into the water column (Fig.20).

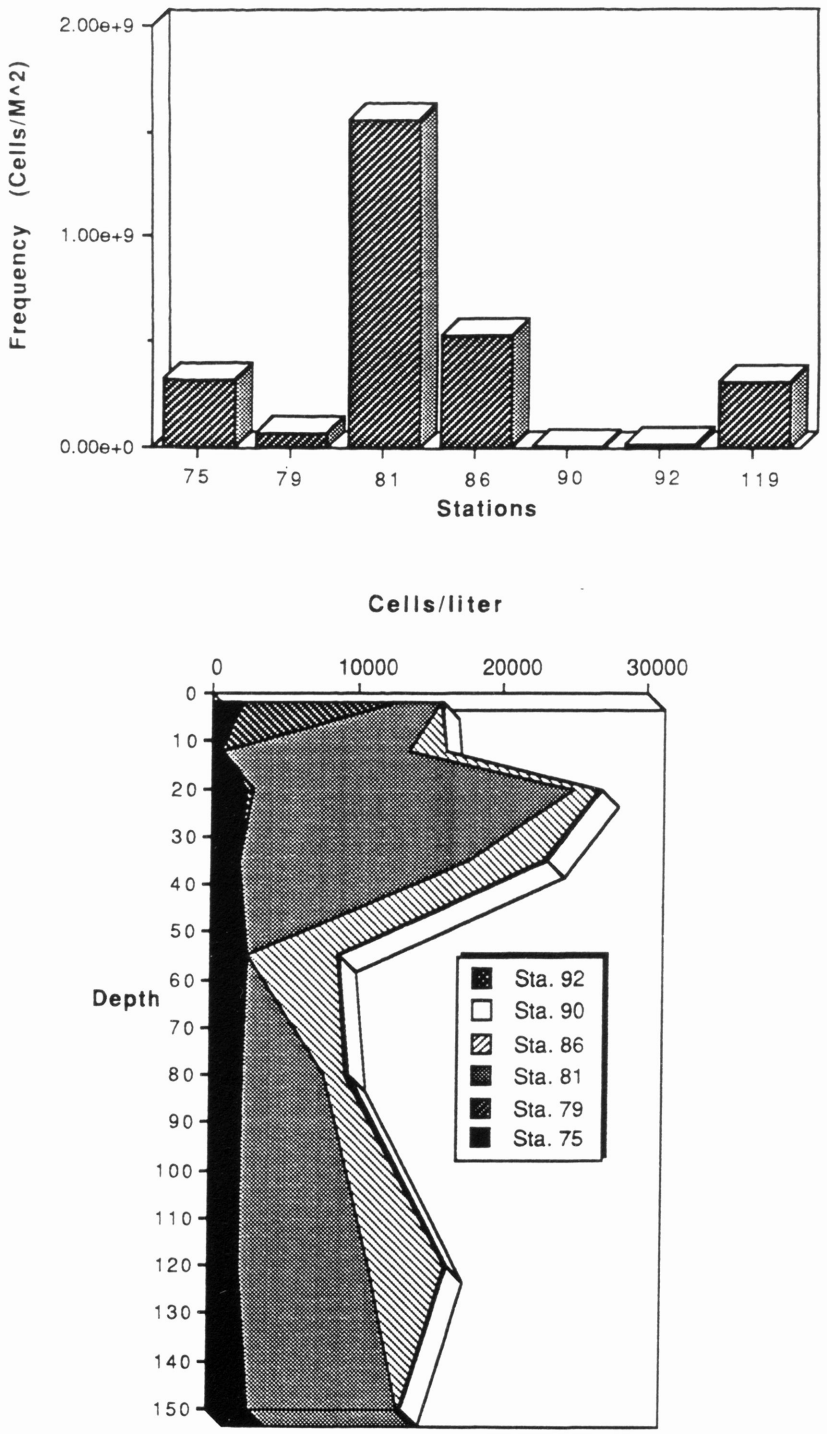


Figure 17. The horizontal and vertical distribution of Phaeocystis sp. on the 40W Transect.

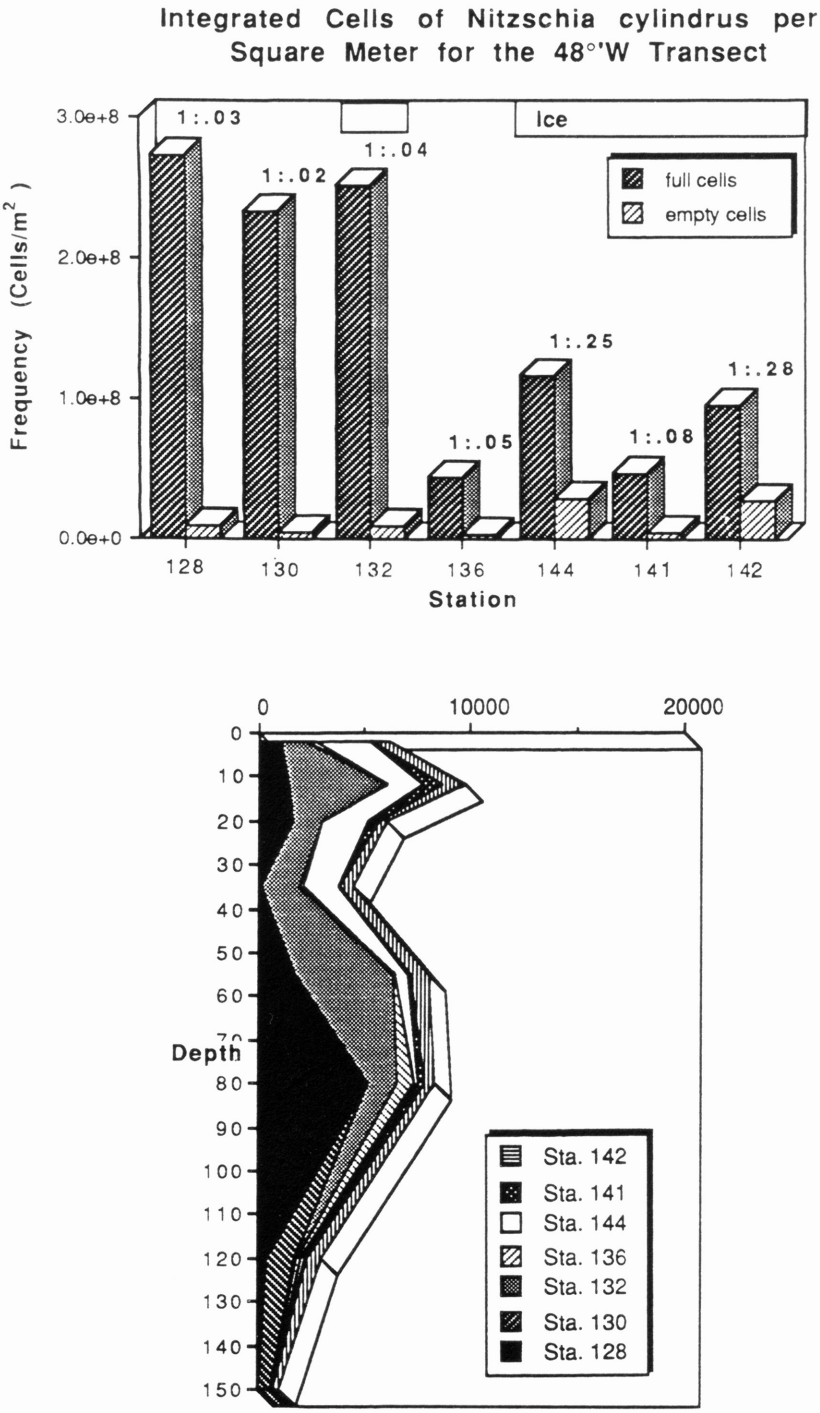


Figure 18. The horizontal and vertical distribution of Nitzschia cylindrus on the 48W Transect. Ratios of full to empty cells of N. cylindrus is denoted for each station on the above plot.

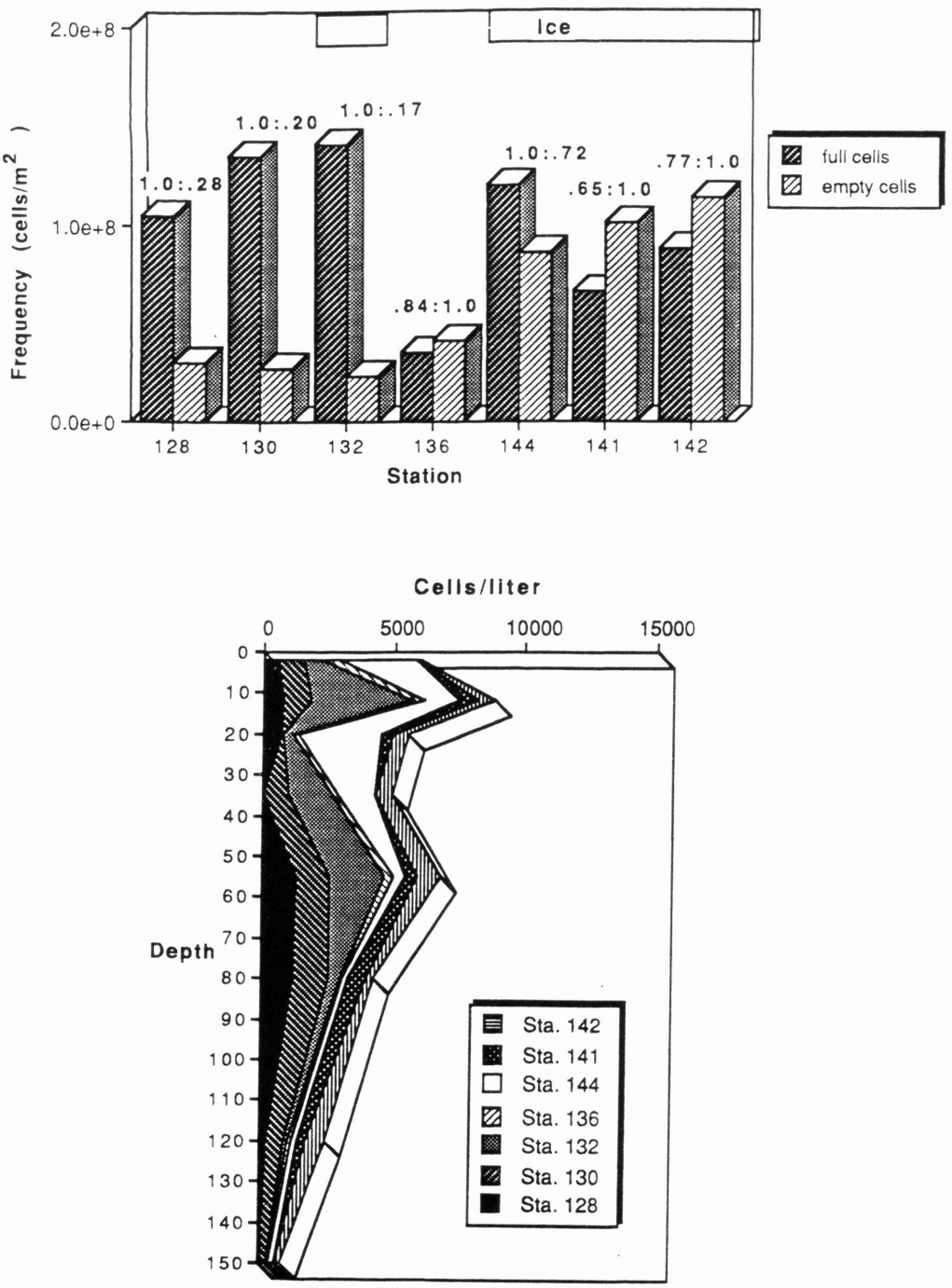
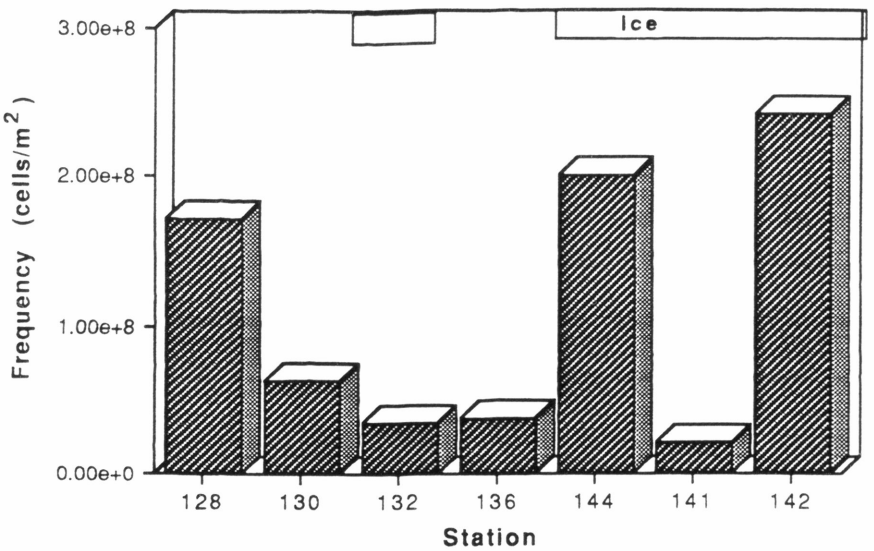


Figure 19. The horizontal and vertical distribution of Nitzschia spp. (section Fragillariopsis) on the 48W Transect. The ratio of full to empty cells of N. spp. (section Fragillariopsis) is denoted for each station.



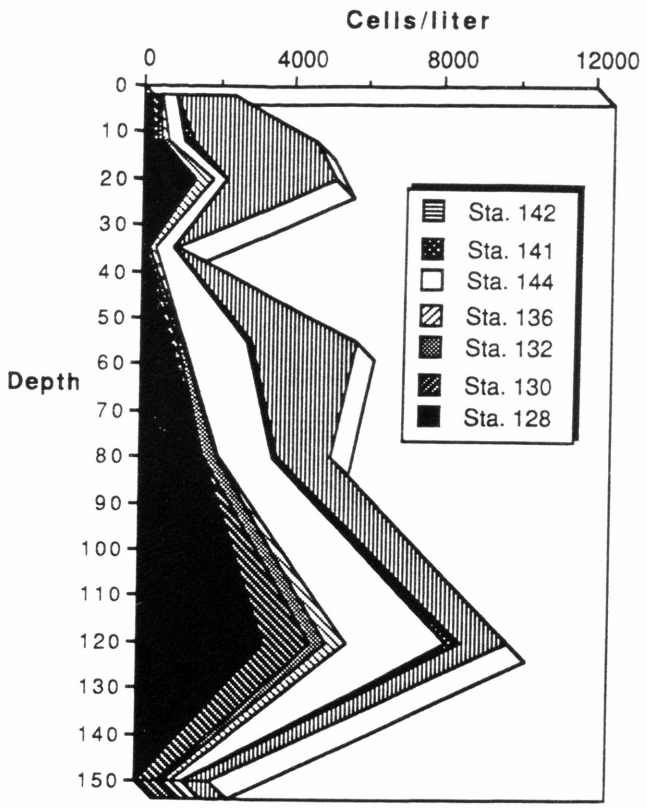


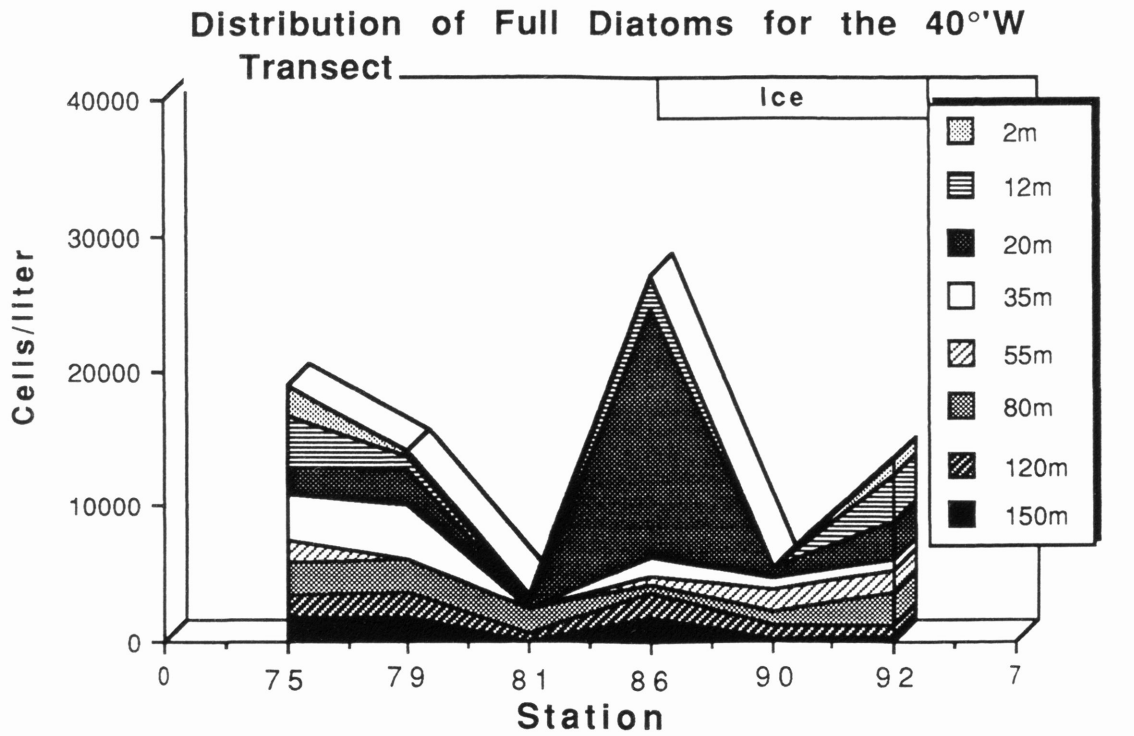
Figure 20. The horizontal and vertical distribution of Phaeocystis sp on the 48W Transect.

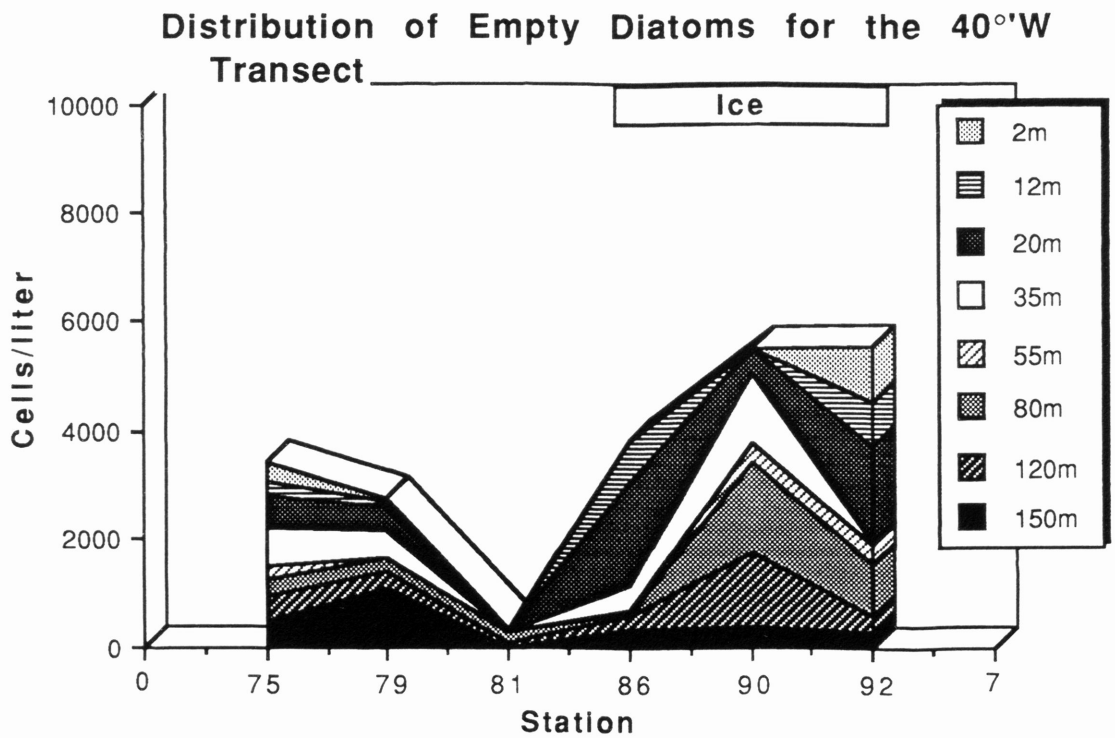
Diatoms

40°'W Transect

There were distinct differences in diatom abundance under ice cover and open water with respect to both full and empty cells (Fig. 21 &22). Full diatoms were distributed more uniformly at depths at the open water stations while the abundance of full cells decreased at the 120 and 150m depths at ice-covered stations Full diatoms peaked at ice-covered Station 86, 4.01 X 10^8 cells m^{-2}, dominated by *Nitzschia* spp. (section *Fragilariopsis*), a diatom with a large cellular volume (Fig. 23). *Phaeocystis* sp. dominated (96.2%) the phytoplankton at Station 81, where integrated full diatom counts were lowest with 1.06 X 10^8 cells m^{-2}. Integrated empty diatoms increased in number with increasing ice cover ranging from 1.34 X 10^7 cells m^{-2} at Station 81 to 1.50 X 10^8 cells m^{-2} at the ice-covered Station 90 (Fig. 24). Highest percentages of full diatoms out of total integrated diatoms (empty + full) occurred at open water stations. The percentage of full diatoms out of total integrated diatoms (full + empty) was $\geq$84 %at open water stations and below 74 % at pack ice stations.

Diatoms were generally low at the surface (2m) sample and increased at subsurface depths and thereafter generally decreased with depth. Diatom cells maxima occurred at 12, 35, and 80m at Stations 75, 79, 81, respectively (Fig. 25) and diatom maxima under the ice were 20, 55, and 12m at Stations 86, 90, 92. Because temperature and salinity appeared to be somewhat uniform in the top 150m, it appeared that distribution was mostly affected by





Figures 21 and 22. Comparison of cell numbers (cells/liter) of full and empty diatoms.

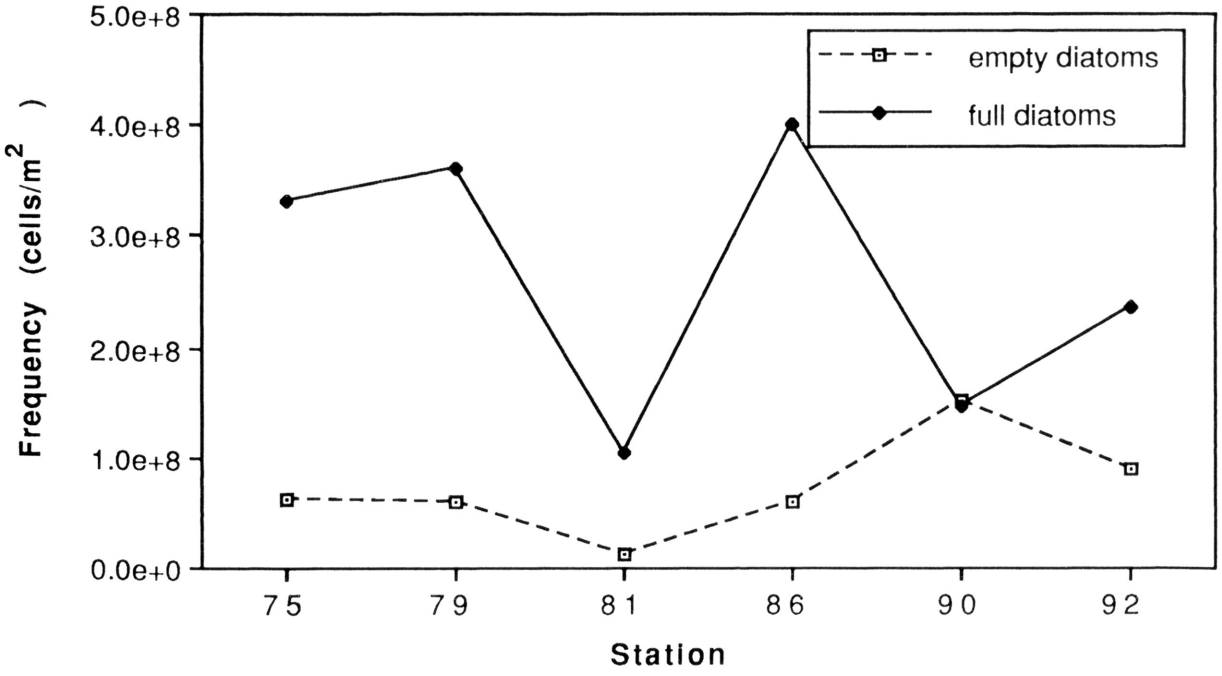


Figure 23. Integrated full diatoms on the 40W Transect.

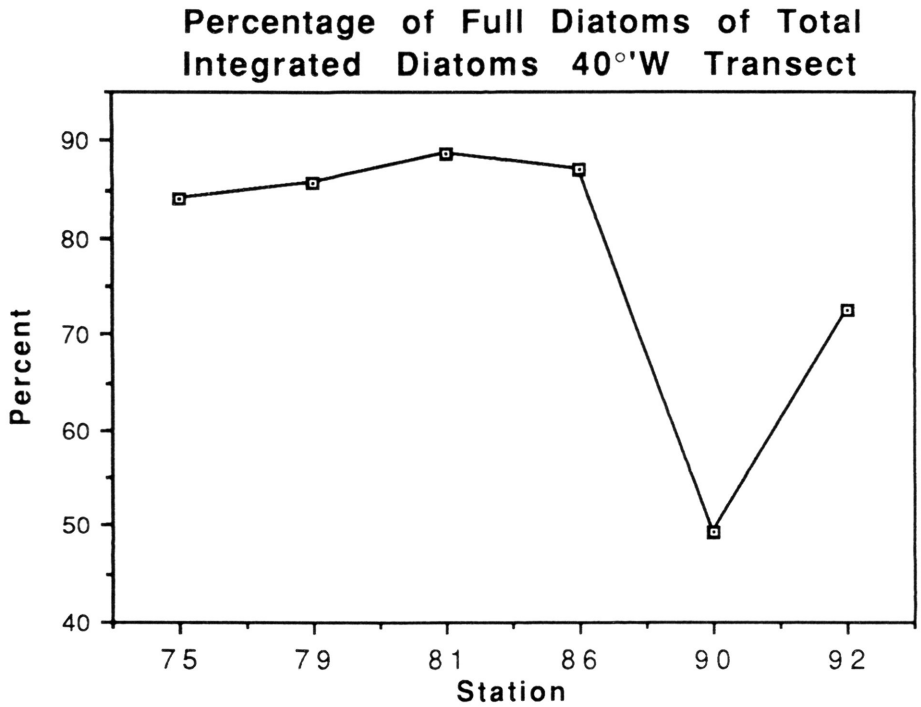


Figure 24. The percentage of full diatoms out of total integrated diatoms (full + empty) diatoms on the 40W Transect.

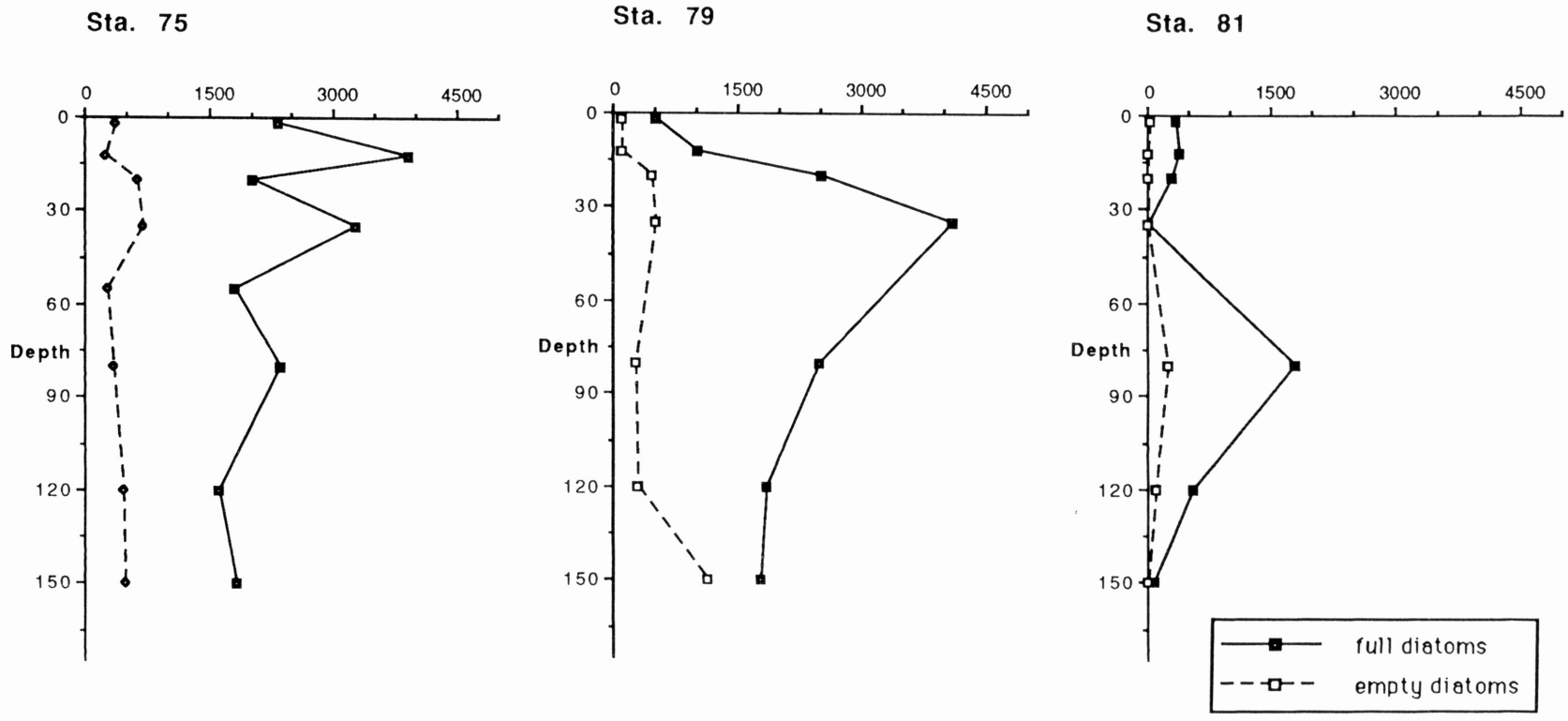
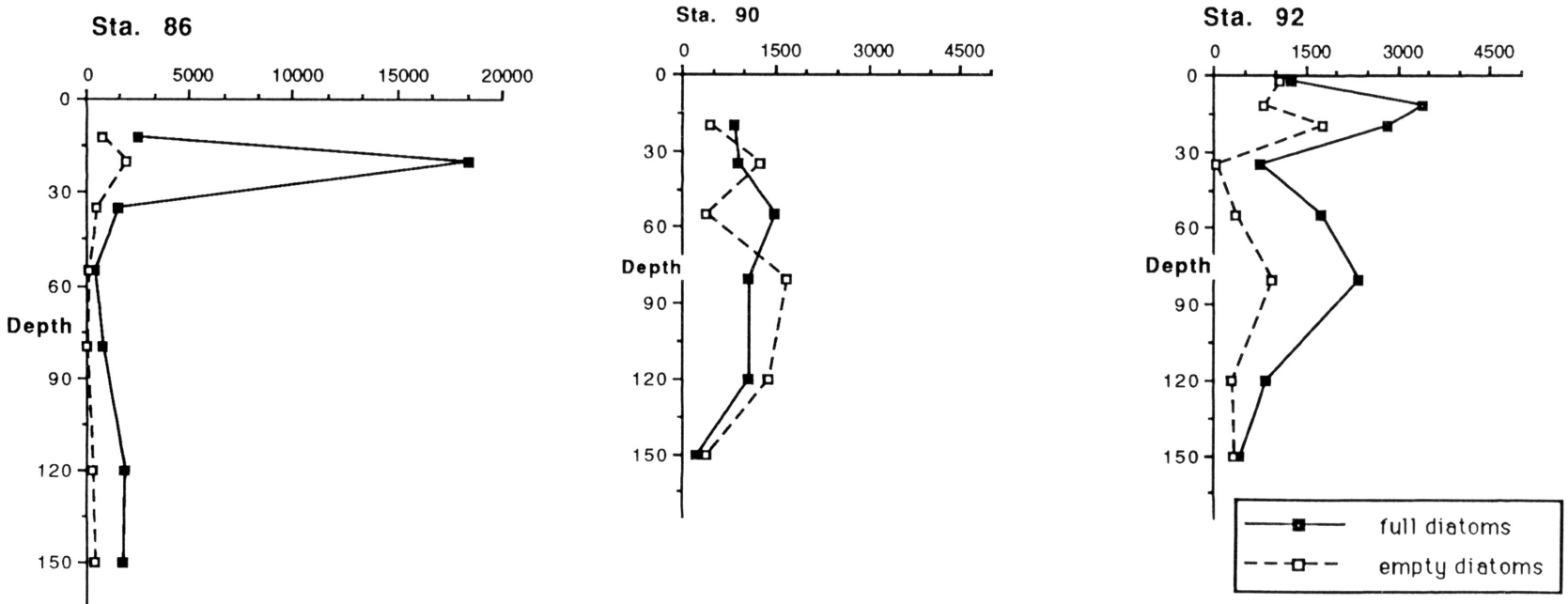


Figure 25. Vertical Distribution of full and empty diatoms. Full diatoms are denoted by the solid line and empty diatoms by the dotted line.


Sta. 86
0
5000
10000
15000
20000
0
30
60
90
120
150
Depth
Sta. 90
0
1500
3000
4500
0
30
60
90
120
150
Depth
Sta. 92
0
1500
3000
4500
0
30
60
90
120
150
Depth
full diatoms
empty diatoms

light. Diatoms were concentrated in the euphotic zone. The vertical distribution of empty diatoms closely followed that of full diatoms. Empty diatoms never exceeded the number of full diatoms at any one depth at open water stations and Station 86, the station shallowest into the pack ice. At Station 90, the number of empty diatoms exceeded the number of full diatoms at depths 80, 120, and 150m. However, this was not seen at Station 92.

48°W Transect

The abundance of full and empty diatoms was again higher at open water stations and lowest at ice-covered stations (Fig. 26). Empty diatoms were highest at ice-covered stations and lower at open water stations. Integrated full diatoms ranged 2.46- 6.03 X 10^8 cells m^{-2} at Stations 141 and 132 respectively and empty diatoms ranged 1.05 X 10^8 cells per square meter at the northernmost Station 128 to 3.08 X 10^8 cells m^{-2} at the southernmost Station 142 (Fig. 27). Stations 128 and 130 were sampled in the warmer Scotia Sea. Vertical distribution was similar at the two habitats; all had two peaks, one at the 12m depth and the other varied at either 55 or 80m (Fig. 28). Cellular maxima occurred either at 80m and 120m.

The percentage of full diatoms out of total integrated diatoms (full + empty diatoms) decreased from the northernmost (Station 128) to southernmost station (Station 142). The percentage of full diatoms at open water stations were close in number to the percentages on the 40°'W transect for open water stations.

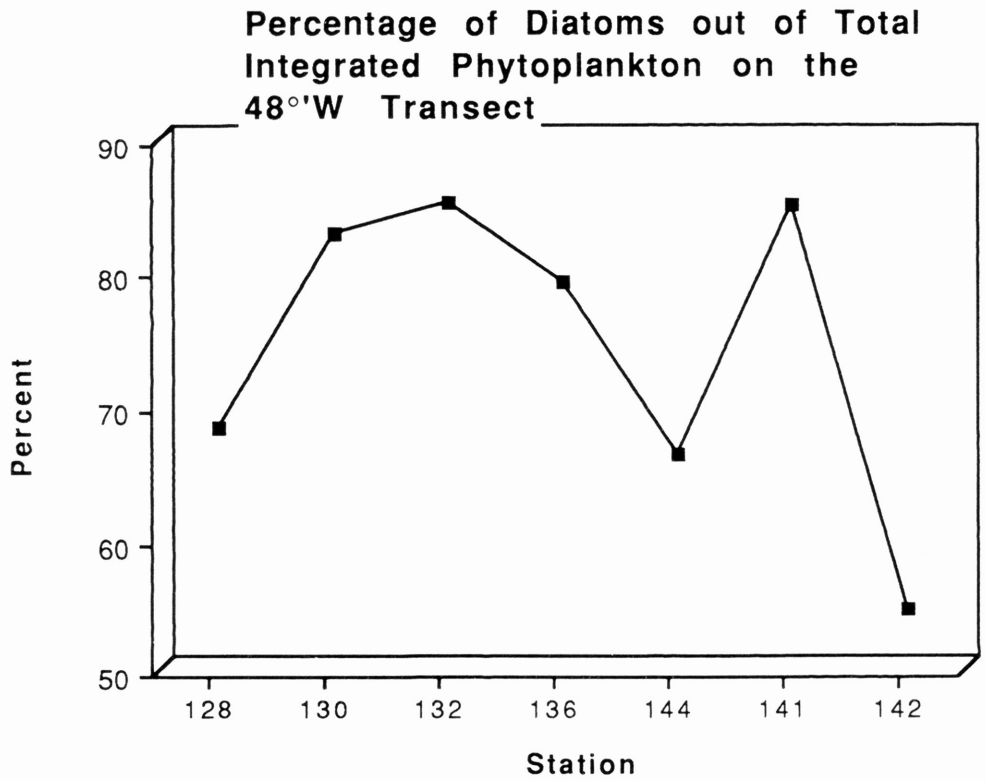


Figure 28a. The percentage of full diatoms out of total integrated diatoms (empty + full) for the 48W Transect.

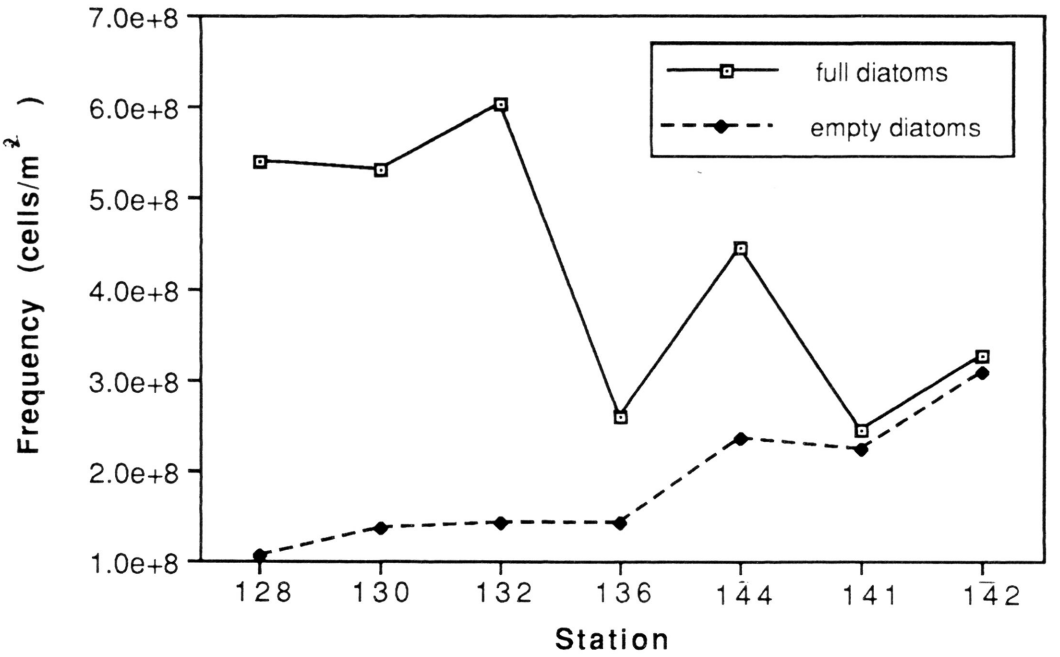


Figure 27. Integrated full and empty diatom counts for the 48W Transect.

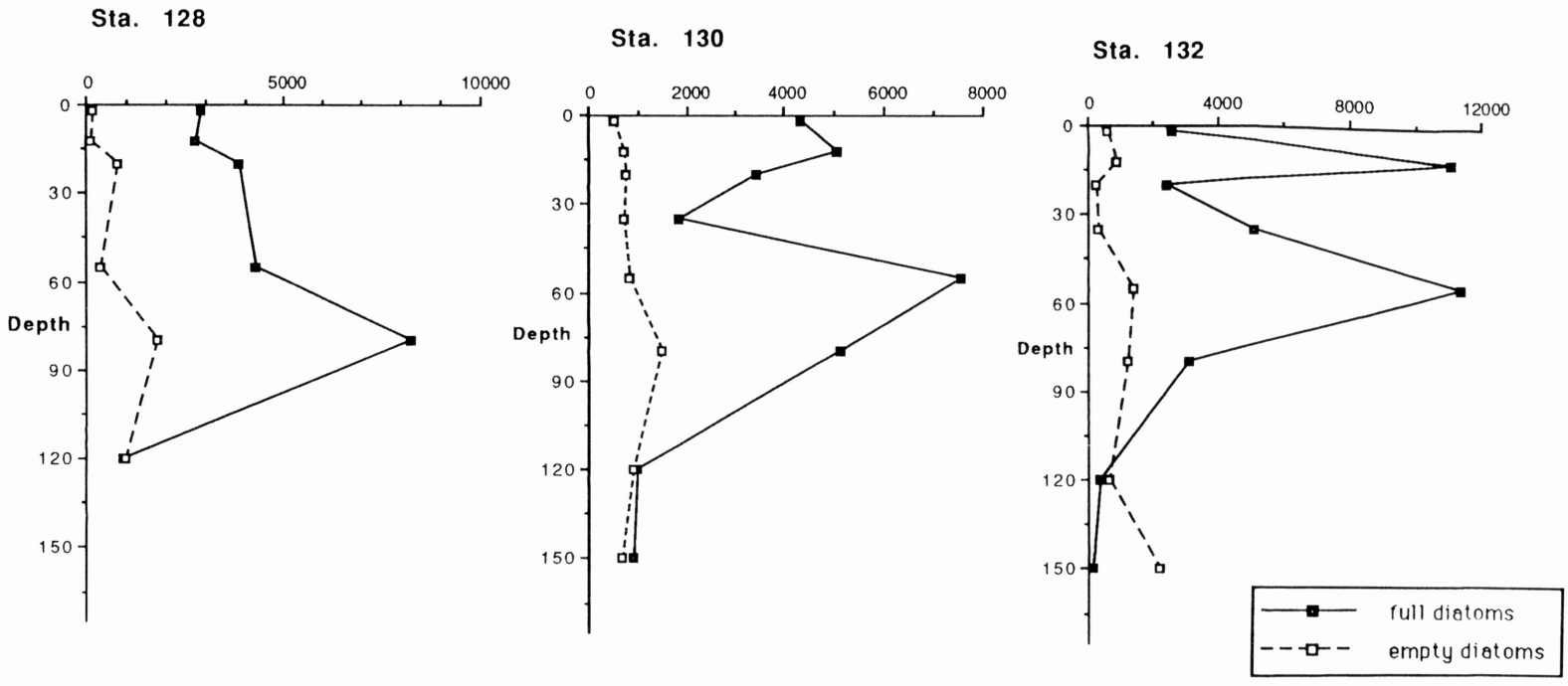
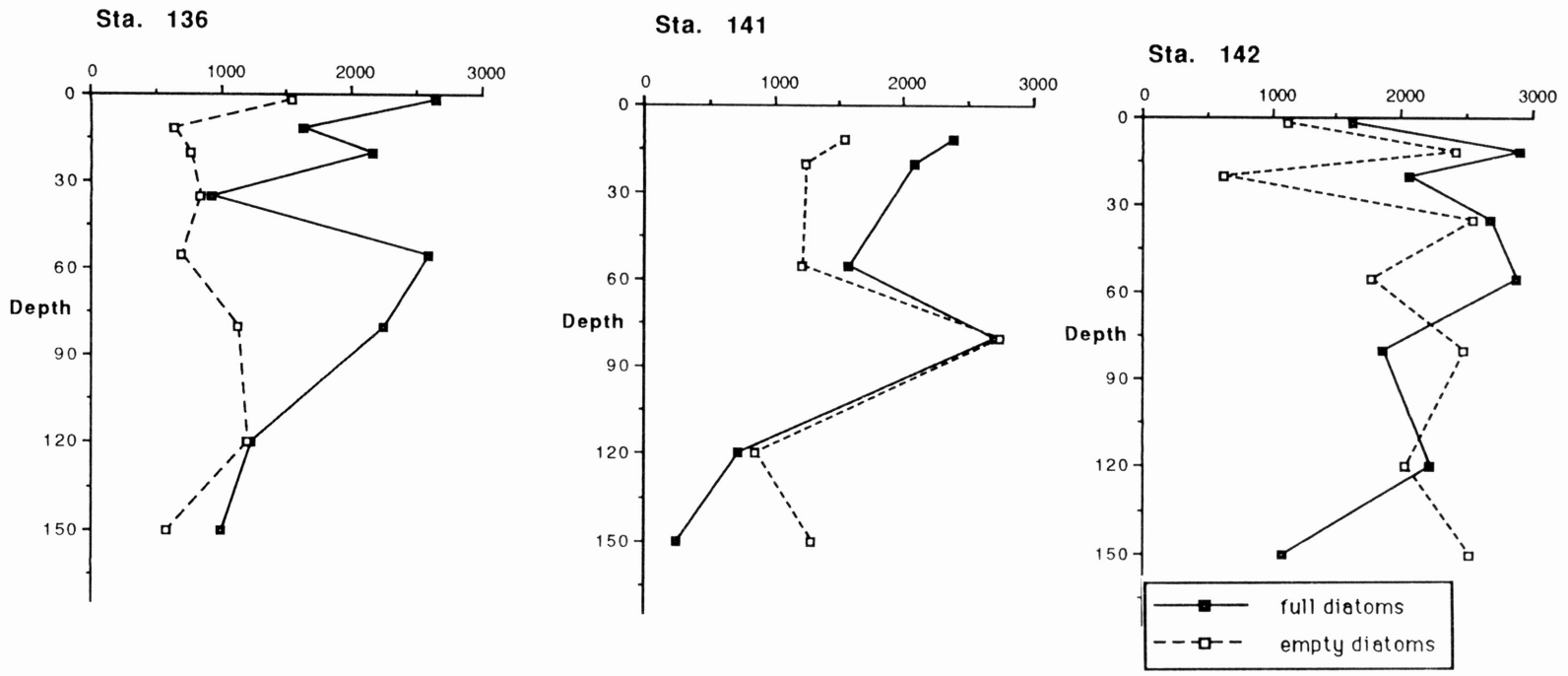


Figure 28. Full and Empty Diatom Distribution on the 48W Transect.


Sta. 136
Sta. 141
Sta. 142
0
1000
2000
3000
Depth
0
30
60
90
120
150
full diatoms
empty diatoms

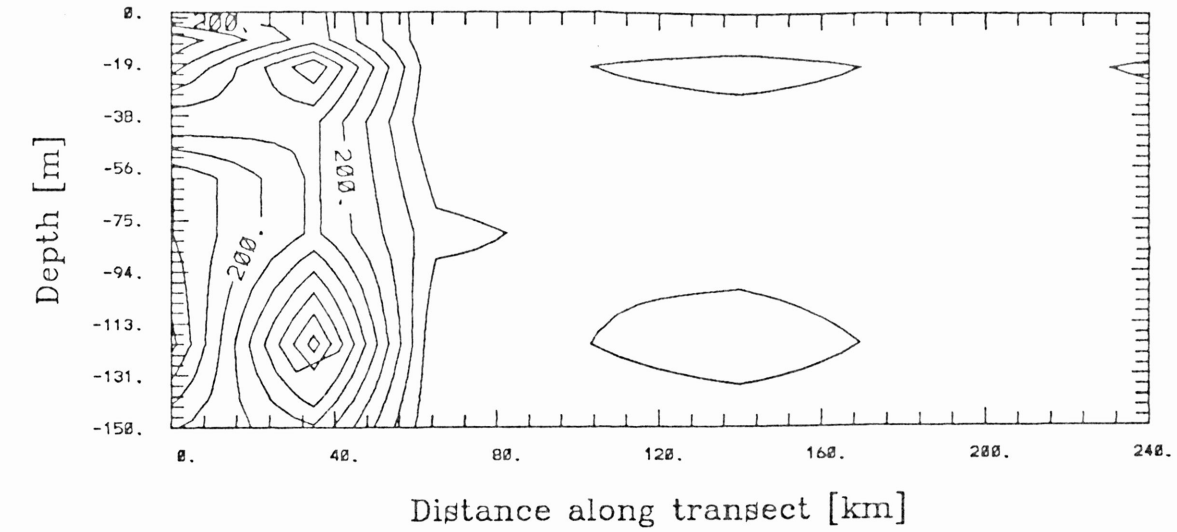
The ice cover appeared to have a negative influence on sillicoflagellates and dinoflagellates. Archaeomonads were present at both ice-covered and open water stations on the 48°'W transect.

Silicoflagellates

Distephanus speculum was the only representative of the silicoflagellate group. It ranged from 0 to 4.96 X 10^6 cells m^{-2} on the 40°'W transect and from 3.36 X 10^6 to 5.71 X 10^7 cells m^{-2} on the 48°'W transect. It was present on both transects but was lower in abundance on the 40°'W transect. It was often in the ten most abundant taxa at each station on the 48°'W transect. On both transects, *Distephanus speculum* favored the open water. The relative abundance of this species generally decreased with increasing ice cover. It was distributed at the open water stations on the 40°'W transect peaking at 120m with 521 cells/liter (Fig. 29). Again on the 48°'W transect, it was distributed at stations that were not covered with pack ice peaking at the open water Station 132 at 55m with 1043 cells/liter (Fig. 30).

Dinoflagellates

Dinoflagellates were not at all abundant in this study. The number of cells/liter ranged from 22-65 at the depths at which they were present. *Gymnodinium* was the most abundant genus followed by a group of unidentifiable dinoflagellates and *Peridinium* sp. Dinoflagellates were present at Stations 75 and 79 on the 40°'W transect. Dinoflagellates were present at both open



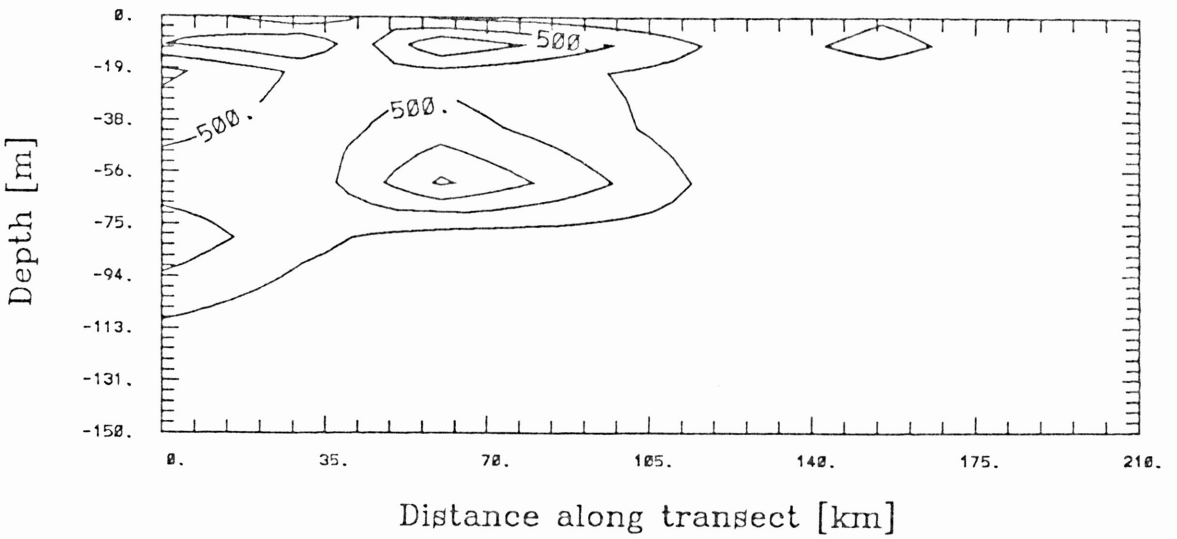


Figure 29 and 30. Contour plots of Distephanus speculum on the 40W Transect (upper) and 48W Transect (lower).

water and ice-covered on the 48°'W transect but species-specific regions were delineated.

Individual Species Distributions

The sea ice acted as a front to certain species. However, most species were not horizontally distributed like *Distephanus speculum* in that species were always associated with one habitat. A species often had a particular distributional pattern on one transect but not the other probably caused by different physical conditions on the two transects and the behavior of the sea ice. These distributional patterns emphasize how dynamic this frontal system and how immediate phytoplankton response is. Most species were associated with the open water; very few species were associated with the ice cover. The differences in these distributional patterns demonstrate how different these dynamical ice boundaries are between the two habitats.

Chaetoceros neogracile (Fig. 31a) was most abundant at open water stations on the 40°'W transect. It peaked at Station 79 with 261 cell/liter. Empty *Thalassiosira* spp. (under 20um) were present at Stations 136, 141, 142, and 144 (Fig. 31b). These species peaked at Station 141 at 80m with 674 cells/liter. Full cells peaked at Station 144 with 1206 cells/liter. This species was not present at all on the 40°'W transect. *Pseudonitzschia* spp. peaked at 80m at Station 132 with 447 cells/liter(Fig. 32a). *Nitzschia kerguelensis* was most abundant at open water stations and peaked at Station 132 with 847 cells/liter at 80m (Fig. 33b).

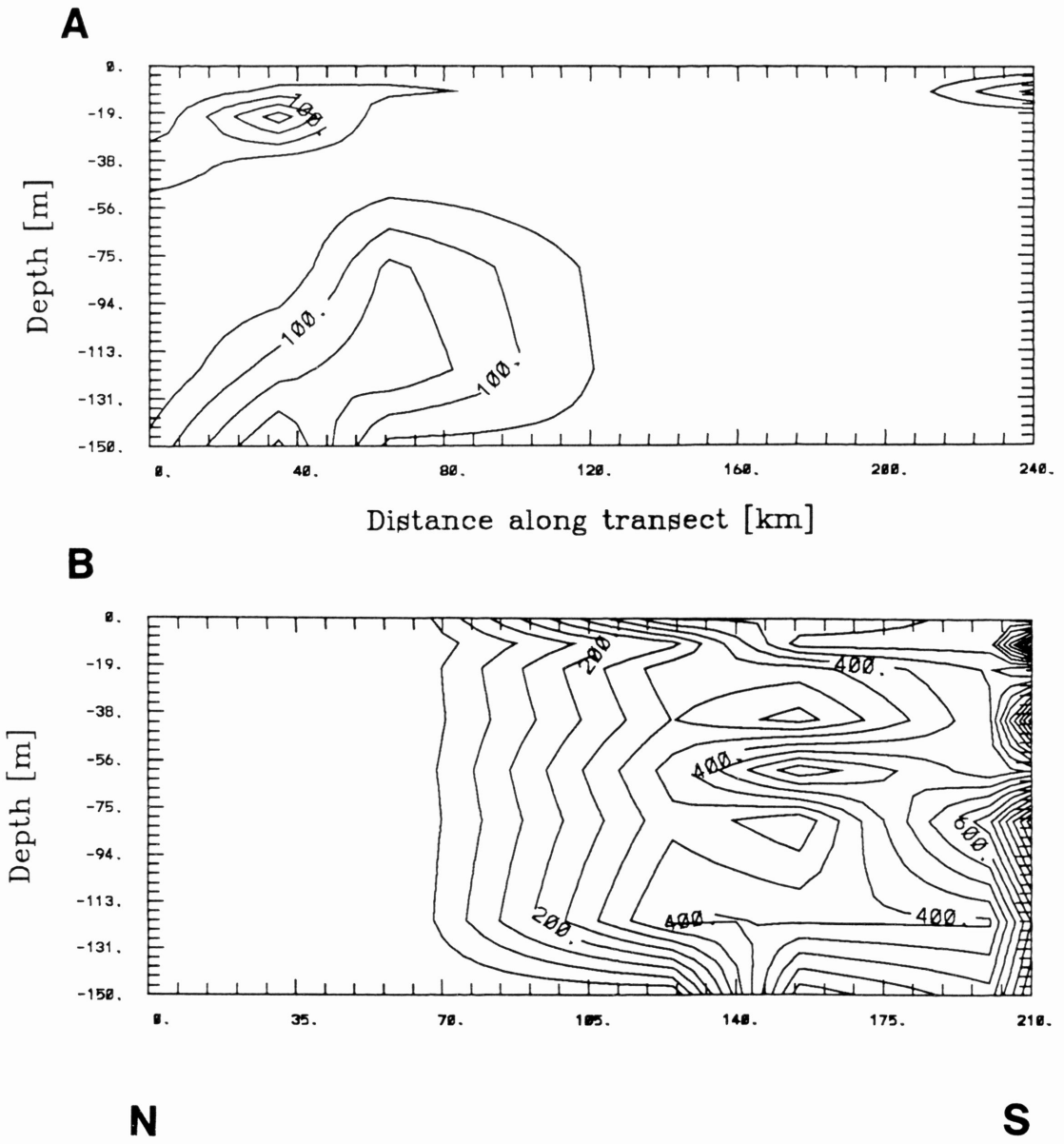


Figure 31. A) Contour plot of Chaetoceros neogracile on the 40W Transect B) Contour plot of Empty Thalassiosira spp.(diameter under 20 um) on the 48W Transect. (cells/liter)

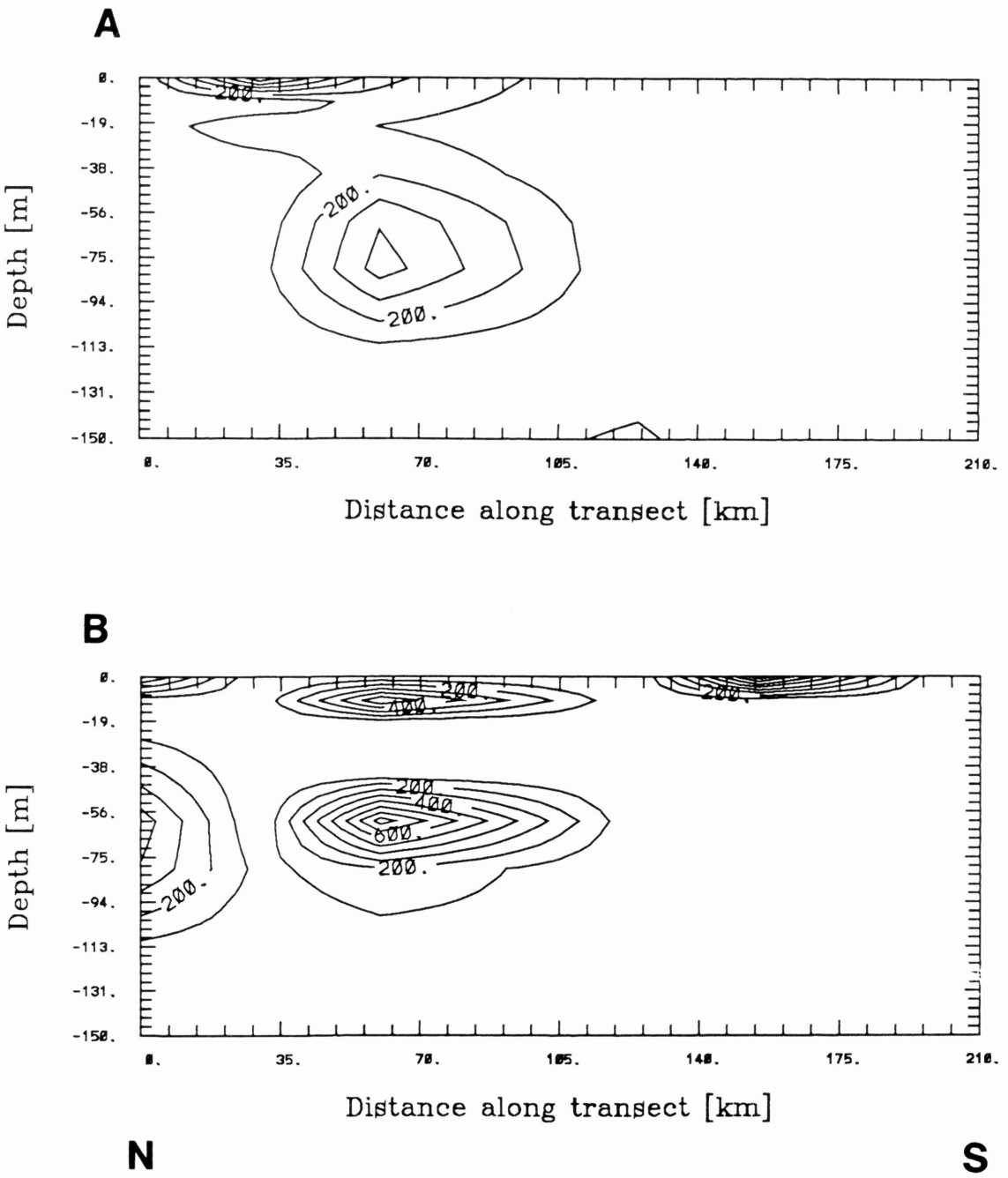


Figure 32. A) Contour plot of full Pseudonitzschia spp. (cells/liter) on the 40W transect. B) Contour plot of full Nitzschia kerguelensis on the 48W Transect. (cells/liter)

Discussion

It is the general concensus that light is the limiting factor of phytoplankton productivity on the seasonal time scale. The austral winter season must be the season of low primary productivity (Smith and Nelson1986). This study certainly confirms this statement. Phytoplankton abundance ranging from 4.28 X 10^7 to 1.58 X 10^8 cells m^{-2} was very low compared to past studies at the ice edge. Integrated counts ranged from (15.3 to 68.7) X 10^9 cells m^{-2} in the austral spring in spring extending northward into spring bloom conditions Fryxell and Kendrick (1988).

Despite the low light regimes of the austral winter, phytoplankton appeared healthy. Brightman and Smith (1989) showed that the low standing stocks in the Bransfield Strait were adapted to the low irradiances of this season. Phytoplankton cells were packed full of lipids, in general. However, phytoplankton did not appear to be reproducing. The species that were capable of making long chains were often found in short chains of 2-6 cells long and few cells were observed in mitotic division. Certain diatom groups create resting spores in unfavorable growth conditions, especially in coastal temperate climates. However, no resting spores were noted except a few cells of *Odontella weisflogii*. Few Antarctic species produce resting spores, although evidence is increasing that heavily silicified winter growth stages are common.

Although, species composition was generally similar over space and time on the winter transects reported here, differences in relative abundance of species were noted between the ice-

covered habitat and open ocean. Phytoplankton mainly consisted of diatoms with small pennate diatoms of the genus *Nitzschia* and*Phacocystis* sp. dominating the assemblage. This dominance is in concurrence with other studies that have reported that nanoplankton (<20um) constitutes the majority of the biomass (Weber and Sayed 1987) and productivity (Brokel 1985).

High latitude ecosystems are generally considered to be low in diversity, and these findings certainly are in agreement. Much phytoplankton research (Staeyart 1973; Kang 1988) has documented low diversity at the phytoplankton level. Krebs (1983) found that species diversity showed little change with season. Fryxell and Kendrick (1988) also found low phytoplankton diversity in the austral spring; phytoplankton was dominated by gelatinouss colonies of *Thalassiosira Cleve* (1873), *Nitzschia Hassall* (1845) as well as *Phaeocystis pouchetti* in colonial form. Single-celled *Phaeocystis* sp. follwed by *Nitzschia cylindrus*, and *Nitzschia* spp. (section *Fragillariopsis*) dominated. Most taxa contributed less than 1% of the cell numbers to the assemblage at any one station and only 5-7 taxa contributed high cell numbers. For the autumn cruise in 1986, results from net haul indicate that different life stages of *Phaeocystis* sp. represented a large percentage of the net hauls.

Total numbers of empty frustules were generally low in the open water and generally increased deep into the pack ice. Total empty cells appeared uniformly distributed at all sampled depths in the open water and were highest in number at deepest depths

under ice cover. Empty cells never exceeded the number of full cells, even at ice-covered stations. The higher concentrations of empty cells were could have been a result of intense grazing at the ice edge; as the ice edge moved, it left the history of grazing in terms of empty cells. It is also possible that empty cells were a result of grazing at the bottom of ice floes where phytoplankton concentrations are high (Grossi and Sullivan 1985). Also many empty cells were observed within the sea ice (personal communication, CW Sullivan) and empty cells may have fallen from the melting sea ice.

Much detritus in addition to numerous empty diatom cells was observed under ice cover. Slides for ice-covered stations were often yellow to brownish in color which resulted primarily from high concentrations of detritus. The number of empty frustules never exceeded the number of full diatoms on the general level. This was observed at the species leve as shown by *Nitzschia* spp. (section *Fragillariopsis*) and *Nitzschia cylindrus* and most profound for *Thalassiosira* spp. (under 20um) *Phaeocystis* sp. was assumed full.

Differences were noted between open water and ice-covered stations in terms of phytoplankton abundance and species relative abundance. The higher abundance was associated with the open water and the lower was associated with the ice cover. On the 40°W transect, the lowest integrated full phytoplankton cell counts at the ice-covered station was an order of magnitude lower than the highest. Fryxell and Kendrick (1988) also showed differences

in phytoplankton abundance between open water and ice-covered stations during the austral spring on a transect normal to the ice edge. However, their results showed a gradual decrease in phytoplankton integrated abundance from the northermost station to the southernmost station within the pack ice. This may be anomalous to the geography location of my sampling since there were great distances between the stations. Smith (1987) has also found that integrated chlorophyll a peaked at at the ice edge and differences in chl a concentrations were noted between the two habitats and chl a peaked at the ice edge.

It is the general concensus that light is the factor that controls phytoplankton on the seasonal level. Light intensity encompasses a large time and space scale. The factors that control the phytoplankton at the ice edge must be redefined, since the ice edge acts as a dynamic frontal system and ice movement varies on the order of days. These physical changes are dynamic and the responses of the phytoplankton can be assessed. A time series study would prove useful in understanding the physical factors that control spatial distribution.

Conclusions:

1. The ice edge zone acts as a dynamic front to the phytoplankton.

2. Abundance and diversity changes with increasing ice cover.

3. There are limits to interpretations in this kind of study since rates of processes cannot be assessed.

4. New techniques must be used to record the behavior of ice movement in view of rapid changes encountered.

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