AN ABSTRACT OF THE THESIS OF

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David M. Nelson

A phytoplankton bloom dominated by the pennate diatom Nitzschia curta (Van Heurck) Hasle was observed during January-February 1983 at a receding ice-edge in the Western Ross Sea, Antarctica. The core of the bloom was found between 100-150 Km from the ice-edge. Nitzschia curta cell densities up to 22 x 10^6 cells/l were observed. The nanoplankton contributed to 18% (average) of the total biomass. The contribution of another pennate diatom, Nitzschia closterium (Ehrenberg) W. Smith, was significant in two offshore stations (22% and 90%). Other diatom species, dinoflagellates and other phytoplankton groups were very few in number. A wind-driven upwelling event occurred along the ice-edge. The presence of off-shore species (e.g. Nitzschia kerguelensis) close to the ice suggests the existence of an eddy circulation.

Results of elemental composition experiments with 10 Antarctic diatoms showed that the C:Si:N ratio for Antarctic diatoms, when compared to the Redfield-Richards ratio for diatoms of other environments, have less carbon and more silicon per unit nitrogen. Comparison of

laboratory results with the field data confirms the anomalous elemental composition of the major bloom species observed in the Ross Sea.

Blooms like the one observed in this study seem to be restricted to the Western part of the Ross Sea and appear to be produced in inshore waters late in the austral summer.

Phytoplankton of an Ice-Edge Bloom in the Ross Sea, With Special Reference to the Elemental Composition of Antarctic Diatoms

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

PREFACE

The first part of the present study details the quantitative analysis of the phytoplankton population of an ice-edge bloom in the Western Ross Sea, Antarctica, during January-February 1983. In the second part, elemental composition experiments are described in relation to the Antarctic diatoms observed in the Ross Sea.

PHYTOPLANKTON OF AN ICE-EDGE BLOOM IN THE ROSS SEA, WITH SPECIAL REFERENCE TO THE ELEMENTAL COMPOSITION OF ANTARCTIC DIATOMS

PART I

INTRODUCTION

Only 1% of the 18 x 10^6 km^2 of Antarctic continent is ice free (Laws, 1985), and significant ice cover extends seasonally over much of the surrounding ocean (Zwally et al., 1983). The maximum sea ice cover is found in September-October, covering around 20 x 10^6 km^2 while in February the minimum coverage reaches 3 x 10^6 km^2 (Gordon, 1981), i.e. 85% of the maximum total ice cover is seasonal, advancing and retreating over several months. When the ice is formed, it leaves the surrounding water more saline and when it melts, dilutes the surface waters (Knox, 1970). Sea ice cover is a very important factor in the Southern Ocean ecosystem, since it doubles the area of the Antarctic continent, increasing the reflection of solar radiation, and therefore reducing the radiant heat penetration into the sea. In addition it restricts the gas exchange between the ocean and the atmosphere, and it reduces the light available for phytoplankton (Knox, 1970). Sea ice provides a unique environment where physical and chemical processes result in a unique biological community. Ice cover may vary from year to year (Zwally et al., 1983). The findings of northern Antarctic diatoms in nearshore sediments suggest that there are times where the ice cover was very small, allowing species from the northern Antarctic Ocean to come to more southern waters (Burckle, 1984).

There are three different kinds of pack ice: congelation ice, frazil ice, and snow ice (Clark & Ackley, 1984). The congelation ice forms slowly (no more than 1 mm/h) and requires several weeks to achieve a thickness of 1 m. The frazil ice is associated with dynamic and turbulent conditions. In the water column small (ca. 1 mm) ice crystals, usually form at high growth rates (> 1 cm/h). The crystals are transported downstream by wind-induced circulation in the water column and pile up to produce a substantial thickness of ice in a short period of time. Snow ice is formed when a floe breaks, permitting seawater to flood the snow cover of the floe with subsequent freezing (Clark & Ackley, 1984). The proportion of these types of ice vary within the pack ice according to environmental conditions. For example, in a higher wind regime, more frazil ice will be found. Clark & Ackley (1984) found that the ice-edge in the Weddell Sea was composed mainly of frazil ice, and that congelation ice was the most prevalent component in the Ross Sea.

Early Antarctic algal studies (Castracane, 1886; Van Heurck, 1909; Karsten, 1905; Heiden & Kolbe, 1928; Mangin, 1915; Mangin, 1922; Hart, 1934; Hart, 1937; Hendey, 1937; Hart, 1942 among others) concentrated their attention only on phytoplankton. The sea ice flora described in those works was the result of casual observations, but there was no interest in a specific, sea ice flora. It was not until the early 1960's that sea ice epontic (algae attached to the sea ice) communities began to be intensively studied both in the Arctic and in the Antarctic Oceans (Apollonio, 1961; Meguro, 1962; Bunt, 1963; Bunt & Wood, 1963; Bunt, 1964 a,b; Apollonio, 1965; Burkholder & Mandelli, 1965; Fukushima, 1965; Bunt *et al.*, 1966;

Fukushima & Meguro, 1966; Meguro et al., 1966; Meguro et al., 1967; Andriashev, 1968; Bunt, 1968 a,b; Bunt & Lee, 1970). Significant contributions have been made recently (Bunt & Lee, 1972; Ackley et al., 1978; Ackley et al., 1979; Hsiao, 1979, 1980; Sullivan & Palmisano, 1981; Horner & Alexander, 1982; Palmisano & Sullivan, 1982; Hsiao, 1983; McGrath & Sullivan (1983); Palmisano & Sullivan, 1983; Clarke & Ackley, 1984).

Sea ice algae have been shown to be highly adapted to low light (Bunt, 1964 a,b; Bunt, 1968a). Algae in McMurdo Sound were able to photosynthetize at light intensities that were 0.01%-0.02% of those at the surface of the ice. Light intensity, and not temperature, limits sea ice algal growth (Bunt & Lee, 1970). These algae are capable of reducing their cellular metabolism by decreasing both growth and photosynthetic rate, and decreasing cellular ATP (Palmisano & Sullivan, 1982). Although heterotrophy may not be important for winter survival (Bunt & Lee, 1972; Horner & Alexander, 1972), storage of carbon and subsequent utilization has been shown to be significant (Palmisano & Sullivan, 1982). Smith & Morris (1980) found that Antarctic phytoplankton can incorporate up to 80% of the fixed carbon into lipids. Bunt et al. (1966) found that respiratory oxygen consumption in Nitzschia sublineata (O'Meara) Hasle (= Fragilaria sublinearis), a common epontic alga, was substantially depressed at $3^{o}C$ compared with $10^{o}C$ and presumably would have been lowered even further at the natural habitat temperature ($-1.8^{o}C$ to $-2.0^{o}C$).

Different microfloral habitats have been reported to occur in

the sea ice. The "snow communities" live in the snow ice, and were described by Meguro (1962) and Burkholder & Mandelli (1965). This community develops at the same time of the snow ice formation. Plankton present in the water will grow on top of the snow ice developed in the ice floe. In this case, the discoloration of the ice occurs at its surface (Ackley et al., 1978). The "ice community" described by Bunt (1963, 1968b) is found on the bottom of the ice, and may achieve a thickness of 0.50 to 1.00 m, giving the ice a typical brown-greenish color. This bottom layer consists of a loosely aggregated matrix of large, plate-like crystals and of a considerable portion of unfrozen water. This type of community is formed in a fragile layer, and thus is not expected to be found in regions of considerable drift. The ice community was observed in the present study in McMurdo Sound. Nitzschia curta has been reported from this type of community (Burkholder & Mandelli, 1965; Hargraves, 1968; Hasle, 1969; see Appendix A for a complete historical review).

The third and fourth types of ice communities are called "interior communities". They are very similar, differing in the kind of metereological conditions that are responsible for their formation (Ackley et al., 1979). The third type has been described just for the Arctic (Appolonio, 1961; Meguro et al., 1966; Meguro et al., 1967; Horner, 1976). It develops at or near the base of the sea ice sheet, when diatom colonies are frozen in the sea ice as it is formed. The diatoms are associated with brine pockets and fissures in the ice containing saline water. Diatoms are not found at distances greater than 0.30 m from the bottom of the ice, and maximum abundances are found just a few centimeters above the bottom (Meguro et al., 1967).

Surface warming causes brine to descend from upper ice layers allowing solar radiation to reach the base of the ice. As a consequence, an algal bloom develops within the lower ice level (Ackley et al., 1978). The fourth type of community corresponds to the one described from Antarctic sea ice by Ackley et al. (1978, 1979) and Hoshiai (1969, 1977). This is a community in which the maximum population is found away from either the top or the bottom of the ice. This interior community is the result of the upward transport of the summer population as the thickness of the ice increases, i.e, it is a remnant population. The algae grow as a result of a combination of optimum nutrients from brine drainage and relatively higher light levels during the summer. Nitzschia curta has also been reported from the fourth type of community in the Antarctic (Meguro et al., 1967).

The success of the epontic microflora is probably the result of: 1) Relatively stable temperature ($-3^{o}C$ to $0^{o}C$). 2) High nutrient concentrations at the start of growth and continuing supply during growth. 3) Absence of or limited grazing by zooplankton. 4) Probable abundance of organic matter (Meguro et al., 1967). In particular, high nutrient concentrations are brought by bacterial conversion of organic matter in the ice, to effect close-order nutrient recycling. Sullivan & Palmisano (1981) reported high concentration (6×10^{9} cells/l)of live bacteria in sea ice from McMurdo Sound. Nutrients also may penetrate from surrounding waters or may accompany desalination of sea ice. These conditions permit the proliferation of large numbers of cells that form a phytoplankton bloom once the ice melts.

Patchiness has been observed in diatom blooms in the Weddell Sea (El-Sayed, 1971), therefore, ice floes that are formed within several kilometers of each other may have considerable differences in biological concentrations and in species composition (Clark & Ackley, 1984). Temporal factors also affect the species composition of sea ice communities. An ice formed early in the season may have a different species composition as bloom species composition varies during the season (Hart, 1942).

The microflora within the sea ice is comprised of diatoms (mainly pennates), dinoflagellates, chrysophytes and green flagellates (Knox, 1970). The shape of the cell frustule may determine the proliferation of a certain species. Elongated species like pennate diatoms, are more likely to be caught in the pocket brines than rounded cells such as centric diatoms (Meguro et al., 1967). Pennate diatoms are attached to the ice (e.g., Pleurosigma, Nitzschia, Amphiprora, Tropidoneis) while the centric diatoms are not (e.g., Biddulphia, Asteromphalus, Eucampia (Bunt & Wood, 1963). Diatom assemblages are usually nearly monospecific, one dominant diatom accounting for up to 85% of the total population (Clark & Ackley, 1984), creating also monospecific blooms in the water column after the ice melts.

Endemism in Antarctic phytoplankters is very high. Most of the dinoflagellates (ca. 80%) are exclusively Antarctic (Balech, 1968, 1970). Many Antarctic diatoms are also endemic, although endemism is not as high as it in dinoflagellates (Hasle, 1968). Nitzschia curta, for example, is an Antarctic endemic (Appendix A).

Temperate and polar climate systems interact in ice-edge zones, resulting in strong horizontal and vertical gradients either in the atmosphere and the ocean. Theses changes will affect mesoscale processes in the ocean, which will affect the heat, salt and momentum fluxes at the ice margin (Johannessen et al., 1983). The ice-edge will cool and dilute the upper ocean, producing fronts (Josberger, 1983). The edge of the pack ice is important because it is a very productive region, due to the phytoplankton blooms that occur along the sea ice-edge, and because it is the habitat of large populations of birds and marine mammals (Laws, 1985).

Very little has been reported on the phytoplankton blooms following receding ice-edges, and even less on the mechanisms by which such blooms may develop. Several hypotheses have been postulated. The first relates ice-edge blooms to the high stability created by the meltwater from the ice (Gran, 1932; Hart, 1934; Steyaert, 1973 a,b; Steyaert, 1974; Alexander & Niebauer, 1981; Krebs (1983); Paden & Holm-Hansen, 1983; Smith & Nelson, 1983; Wilson, 1983; Smith & Nelson, 1985). Colder and more stable conditions have been reported beneath the receding ice-edge in the Ross Sea (Littlepage, 1965). According to Sverdrup's (1953) critical depth concept, the stability creates the ideal conditions for a phytoplankton bloom. In a stratified water column, if the critical depth is deeper than the base of the mixed layer, photosynthesis exceeds respiration allowing phytoplankton to grow. Also, the stratification prevents the dispersion of the bloom (Smith & Nelson, 1985), concentrating large amounts of cells of the dominant species.

A second hypothesis relating to the development of ice-edge blooms requires that sea ice algae act as an inoculum (Inova, 1964; Meguro et al., 1967; Hargraves, 1968; Ackley et al., 1978; Ackley et al., 1979; Steyaert, 1974; Schandelmeier & Alexander, 1981; Wilson, 1983; Smith & Nelson, 1985). Schandelmeier & Alexander (1981) pointed out that ice flora in the southeast Bering Sea may act as an inoculum early in the spring bloom. Ackley et al. (1979) found that the species composition within the ice was similar to that of the water column. They observed how the algae from the ice were released into the water column after the deterioration of the floes. Wilson (1983) and Wilson et al. (submitted) observed in the Ross Sea that Nitzschia curta was present in significant numbers in the only sea ice sample collected, and that the species composition in the water column was very similar to that within the ice. Third, wind-driven upwelling events have been also postulated to be trigger of ice-edge phytoplankton blooms, as a result of the enrichment of the waters. A numerical model of an ice-edge upwelling has been developed by Roed & O'Brien (1983). Upwellings have been observed in the Northern polar seas by Buckley et al. (1979), Alexander & Niebauer (1981) and Johannessen et al. (1983) and in the Antarctic in the present study. As pointed out by Smith & Nelson (1985), upwelling could be a positive factor in the Arctic Ocean where nutrient concentrations are much lower than in the Antarctic Ocean, but they seem less likely to be important in nutrient-rich Antarctic waters.

A fourth hypothesis postulates that ice-edge blooms result from accumulation (and not growth) in the water column of the epontic algae as has been suggested by Bunt (1963), Meguro et al. (1967) and

Ackley et al. (1979). However, the introduction of meltwater from the sea ice is not responsible for the strong nutrient depletion observed in the surface waters as pointed out by Jennings et al. (1984). Only 7% of the nutrient depletion reported by these authors was due to the meltwater. Thus, 93% should correspond to phytoplankton activity in the water column.

Hart (1942) proposed that the Antarctic waters were extremely rich, an idea of great persistence, but truly quantitative studies have showed that diatom concentrations in open waters were not particularly high. Quantitative studies of Antarctic phytoplankton are few. Many of these studies have referred to pigment content (Steyaert, 1973a). Data on cell numbers are scarce and, because different sampling and counting methodologies have been used and different areas have been sampled, cell density estimates are not very suitable for comparison. The main quantitative studies have covered extensive areas of the Southern Ocean, while very few are related to inshore waters (Hentschel, 1932; 1936; Hart, 1942; Hasle, 1956, 1969; Marumo, 1957; Klyashtorin, 1961; Kozlova, 1961, 1964; Fukase, 1962; Fukushima & El-Sayed, 1965; Zernova, 1970; Steyaert, 1973 a,b; 1974, and Jacques et al., 1979). Of all these studies, only Hasle (1969), Steyaert (1973 a,b; 1974) and Jacques et al. (1979), used methods similar to those in the present study (i.e., water samples and Utermöhl's sedimentation method). Most of the above studies have shown at least two distinct floras (three for Hart, 1942): one in the northern part of the Southern Ocean and one to the south, close to the continent where the highest abundances are observed. Kozlova (1970) reported 2.3×10^6 cells/l for coastal

waters in the Antarctic Indian Ocean compared to 1 x 10^3 to 3 x 10^5 cells/l in the open ocean, close to the Antarctic Convergence. Other oceanic reports can also be cited in: Fukase (1962), 10^4 cells/l; Hasle (1969), 10^6 cells/l; Steyaert (1973a, 1974), 10^4-10^6 cells/l and Jacques et al. (1979), 7 x 10^4 cells/l.

The present study describes the species composition and cell density of an ice-edge bloom observed in the Western Ross Sea, Antarctica in late January, early February 1983. No sea-ice studies were made, except for one single observation (Wilson, 1983; Wilson et al., submitted). The species composition reflects the events taking place in the ice-edge area. It is hypothesized here that ice-edge blooms occurring in inshore waters are derived from the ice flora of the melted ice.

MATERIAL AND METHODS

In January-February 1983 field studies were conducted near a receding ice-edge in the Ross Sea, Antarctica, aboard the USCGC Glacier. The study site is shown in figure 1 a-b. Twenty-six stations were sampled along three different transects normal to the ice-edge. Transect #1 includes stations 14,15, and 17 through 23; transect # 2 includes stations 36 to 43 and transect # 3 includes stations 27 to 35. Transect #1 was accomplished in 41 hours; transect # 2 in 32 hours and transect # 3 in 26 hours.

Each station consisted of a CTD (Conductivity - Temperature - Depth) cast, a hydrographic cast which collected water from nine depths in the upper 150 m. The first seven depths were selected according to percentages of light penetration (100%, 50%, 30%, 15%, 5%, 1%, 0.1%). These levels will be referred here as levels 1, 2 , 3, 4, 5, 6, and, 7 respectively. Levels 8 and 9 were chosen arbitrarily below the mixed layer as follows: level 8 at ca. half way between the surface and level 9, which was usually sampled at 150 m. Particulate carbon, particulate nitrogen, biogenic silica, chlorophyll *a*, primary productivity (including autoradiographic analysis), phytoplankton growth rates, silica and nitrogen uptake rates, and inorganic nutrients were measured in the seawater sampled. These results are reported elsewhere (Nelson & Smith, 1983; Smith & Nelson, 1983; Wilson, 1983; Wilson *et al.*, 1983; Smith & Nelson, 1985; Wilson *et al.*, submitted ; Nelson *et al.*, in prep.). Vertical sections of the salinity, temperature, sigma-t, silicate,

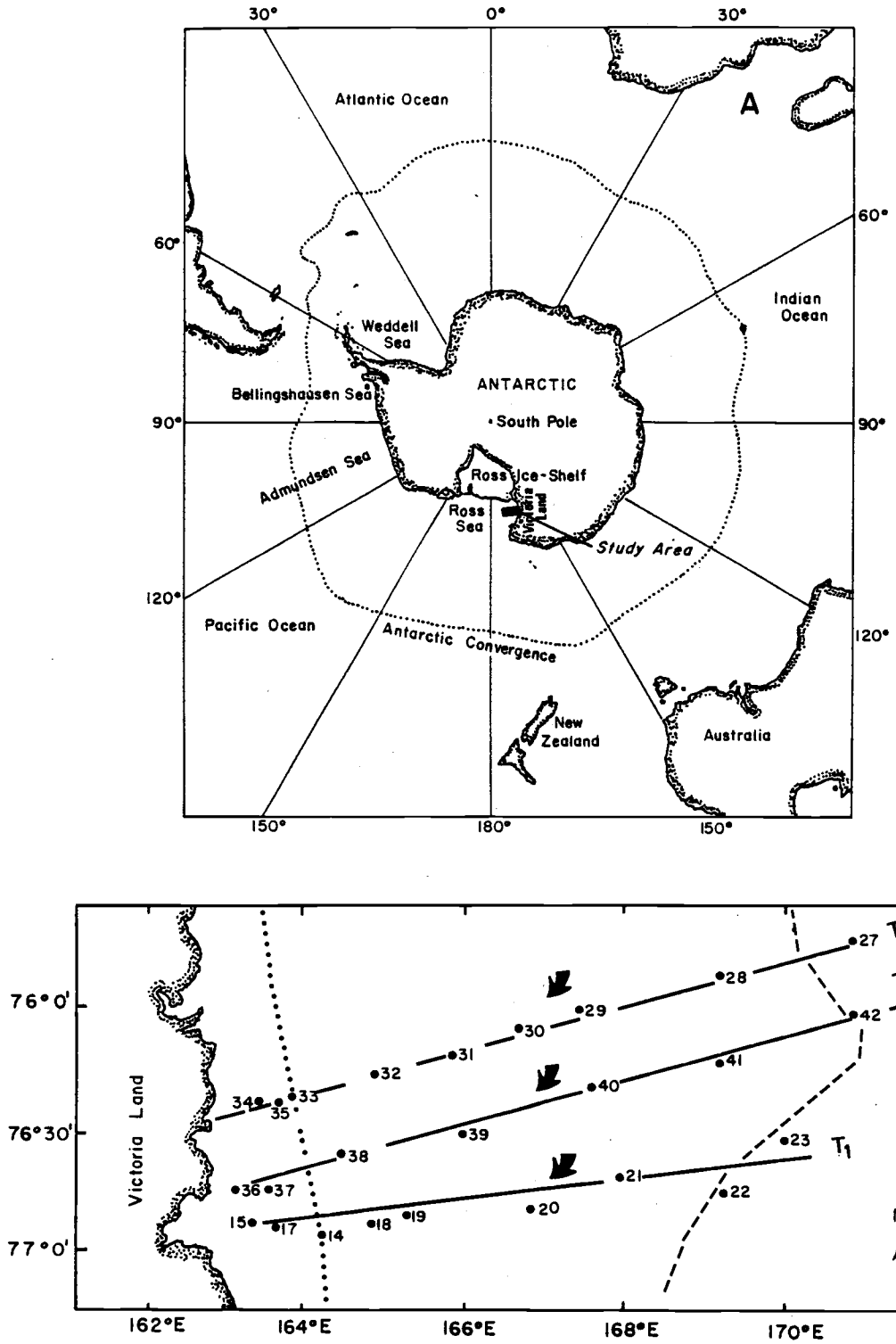

Fig. 1. a) Map of the Antarctic continent showing the study area location. b) Map of the study area and station locations. Lines labeled T_1, T_2, and T_3, denote Transect #1, Transect #2, and Transect #3.

····· ice-edge bloom core --- clear water

phosphate, the sum total of nitrate plus nitrate, and chlorophyll *a* along the three transects are shown in Appendix E.

For the cell counts 120 ml of seawater was drawn from the water sampled in the hydrocast at each station. This subsample was fixed with 5 ml of Lugol's solution (Throndsen, 1978). Fixation and preservation with Lugol's were considerably better than with glutaraldehyde. There were subsamples fixed with glutaraldehyde in which many clusters of the phytoplankton could be seen, while the sample from the same water fixed with Lugol's did not cluster the cells. Lugol's also has a big advantage over formaldehyde in preserving the Antarctic naked dinoflagellates, to the extent that in Lugol's-preserved samples some flagella were seen in *Cochlodinium* sp. On the other hand, formaldehyde completely deforms the naked dinoflagellates.

Cell counts were accomplished by the Utermöhl sedimentation method (Utermöhl, 1958; Lund *et al.*, 1958; Hasle, 1978) using a WILD-M40 inverted microscope. 10 ml sedimentation cylinders were used for levels 1 to 7 and 50 ml cylinders were used for levels 8 and 9. Bottle samples were shaken very well before settling them within the chambers. The minimum sedimentation time used was 10 hours which was sufficient to settle all the cells present. Microscopic observations were made using phase contrast. Magnification up to X 600 was used. Frames along two normal fixed sections on a Whipple disk were counted for levels 1 to 7 and the whole plate for levels 8 and 9. The actual observed volume was calculated from the measured dimensions of the cylinders, the chambers, and the frames of the

Whipple disk under X 200 magnification as follows:

Total height = height of cylinder + depth of chamber
Volume of each frame of the Whipple disk* = area of frame x total height

* the linear dimensions of the frame were calculated with an ocular micrometer

The number of frames were recorded for each sample counted, as well as the observed number of cells of each species. In this way, the total number of frames multiplied by the volume of each frame gave the actual observed volume of the sample.

The identity of Nitzschia curta as the principal bloom species, was confirmed by Dr. Lloyd H. Burckle of Lamont-Doherty Geological Observatory. For the identification of the Antarctic diatoms the following major works were used: Hendey (1937), Hustedt (1958a), and Manguin (1960). Publications by Hasle (1964, 1965a, and 1965b) were used in relation to the important Antarctic genus Nitzschia Hassall (including the genus Fragilariopsis) Hustedt. In the past Nitzschia curta (Van Heurck) Hasle has been cited in the literature as Fragilariopsis curta Hustedt, but Nitzschia curta is the actual valid name (Hasle, 1972) [See Appendix A for an overview on this subject]. For the identification of Antarctic dinoflagellates, three major works were used: Schiller (1933, 1937) and Balech (1976).

The identification of the diatoms and the dinoflagellates was made to the rank of species whenever possible. An identification to species of diatoms other than the three most abundant ones (Nitzschia curta, N. closterium and N. kerguelensis) was not within the scope of the present study, since they usually represented less than 2%

(average) of the sample, except for station 23. In this way there was no species identification for most centric diatoms, as most taxonomical characters are now based in features that can be only observed under the scanning electron microscope (not available in this study). Therefore, the majority of centric diatoms were recorded as small centric diatoms for those cells from 5 to 25 µm in diameter, and as large centric diatoms for larger diatoms, usually 70 µm in diameter.

Although vertical (150 m deep) net tows (64 µm mesh) were made at each station, these tows were of little help for quantitative data (Hasle, 1969; Steyaert, 1973b; Jacques et al., 1979). These three studies are very good examples of the advantages of water samples over net tows for quantitative studies. Net tow samples in the present study were filtered and concentrated to be used as identification material.

RESULTS

The station-by-station cell count listings appear in Appendix B. A summary list of the observed diatom species is included in Appendix C. A similar summation list of the dinoflagellates can be found in Appendix D. The vertical distribution in the upper 50 m of Nitzchia curta (intact protoplasm = living cells), N. curta (empty frustules), Nitzschia closterium, N. kerguelensis (intact protoplasm), N. kerguelensis (empty frustules), nanoplankton and dinoflagellates considered as a group are shown in figures 2 through 9.

The dominant bloom species was the pennate diatom Nitzschia curta. Nitzschia closterium was secondary in dominance but its abundance was 2-3 orders of magnitude less than that of Nitzschia curta (Appendix B). The greatest number of diatom species was observed at stations 20 and 43. The genus Nitzschia Hassall presented the greatest number of species.

Three zones can be distinguished along the transects. Zone 1 corresponds to the stations either in the ice or very close to it. Zone 2 corresponds to stations within the bloom itself and zone 3 to stations away from the bloom (offshore direction). It can be observed that the intensity of the bloom increased northwards (Fig. 2a-c). The peak of the bloom is found at station 30 (transect #3) between 5 and 15 m (22×10^6 cells/l). This was the highest concentration recorded in any of the transects. It is also a much higher concentration than those recorded by Hasle (1969) or Steyaert

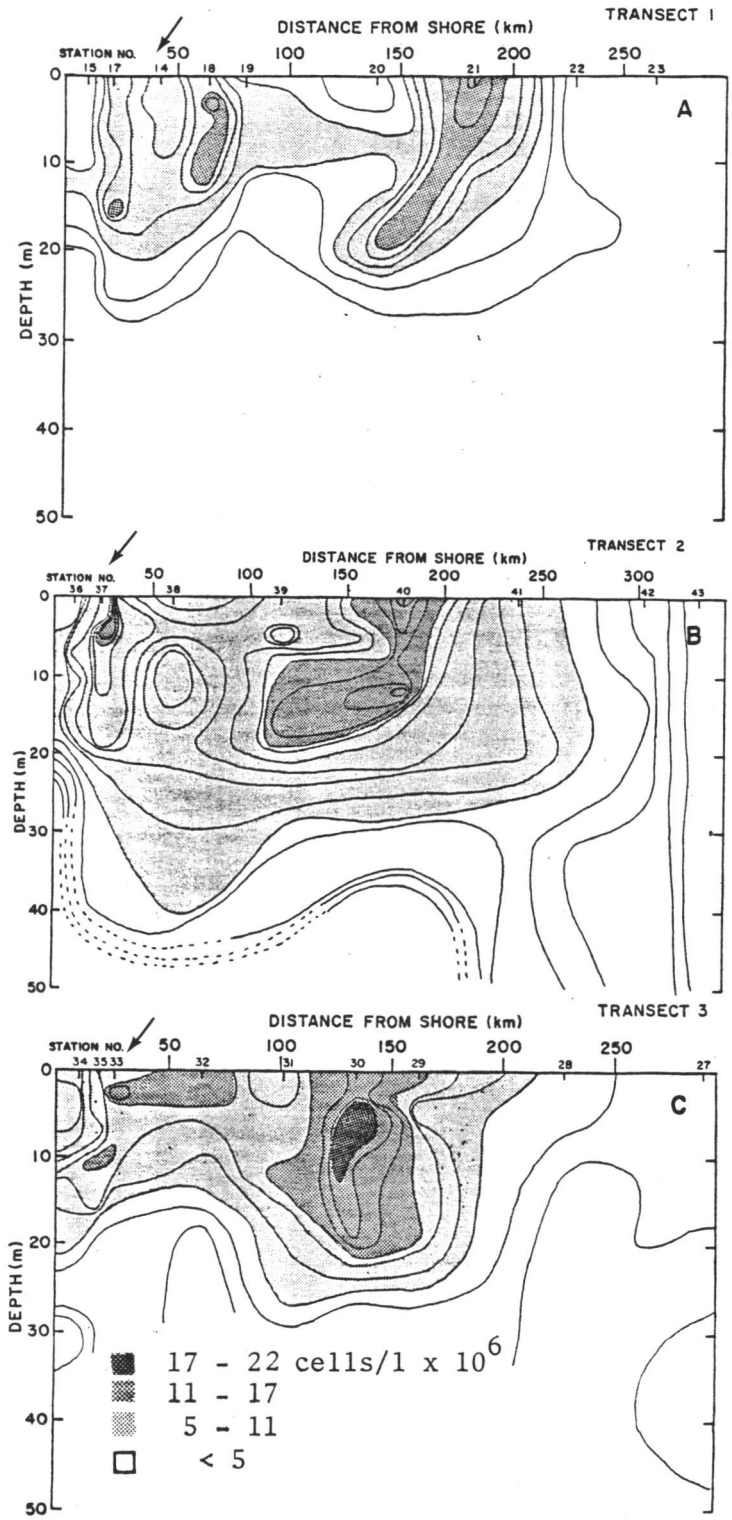

Fig. 2. Vertical distribution of Nitzschia curta (intact protoplasm). a) Transect #1. b) Transect #2. c) Transect #3.
↙ ice-edge

(1973 a,b; 1974). There was a significant decrease of Nitzschia curta cells away from the bloom, so the two most eastward stations of transects #1 and #2 presented very few cells of this species.

The empty Nitzschia curta frustules (Fig. 3a-c) have a very different distribution for each transect and did not follow those of the living N. curta cells (Fig. 2a-c). They were more abundant under the ice in transects #3 and #2 but not in #1. Empty frustules were present in significant numbers in the bloom zone in transects #1 and #3, but not in #2. In transect #2 there was an increase in the offshore stations being uniform from the surface down to 50 m at least (cf. Fig. 3b).

The ratio of living to empty cells of Nitzschia curta (Fig. 4a-c) reflects the greater abundance of empty cells in the ice stations.

The vertical sections of biogenic silica (Fig. 10a-c) agree very well with the distribution of living Nitzschia curta cells (Fig. 2a-c). Both distributions have a lower point in the center of the bloom at station 20 in the upper 10 meters, a feature found only in transect #1. The same distributional abnormality was observed in the vertical sections of the empty frustules of N. curta (Fig. 3a) and chlorophyll a (Fig. 24a).

The distribution of the nanoplankton was tightly coupled to the distribution of N. curta (Fig. 8a-c and Fig. 2a-c), although the nanoplankton seem to have a more continous distribution within the 3

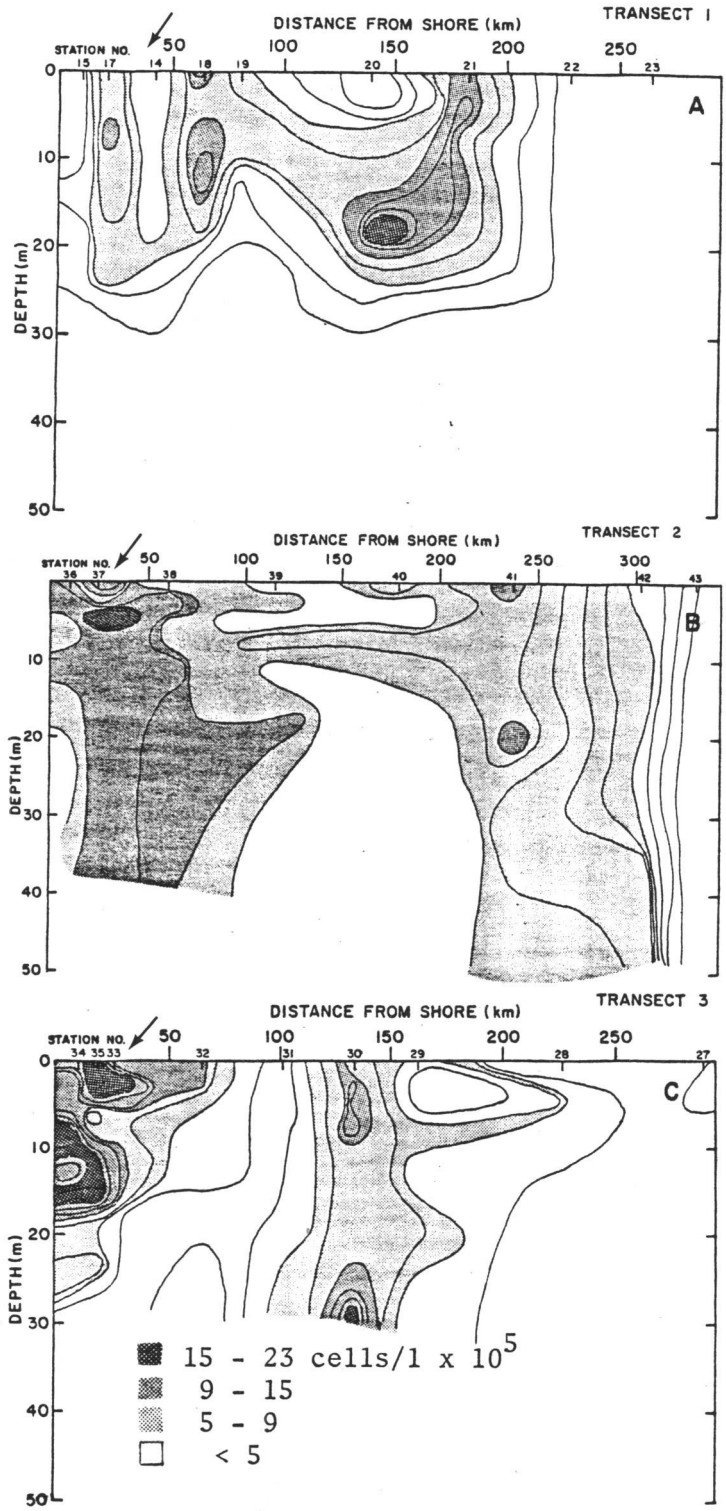

Fig. 3. Vertical distribution of Nitzschia curta (empty frustules). a) Transect #1. b) Transect #2. c) Transect #3.
↙ ice-edge

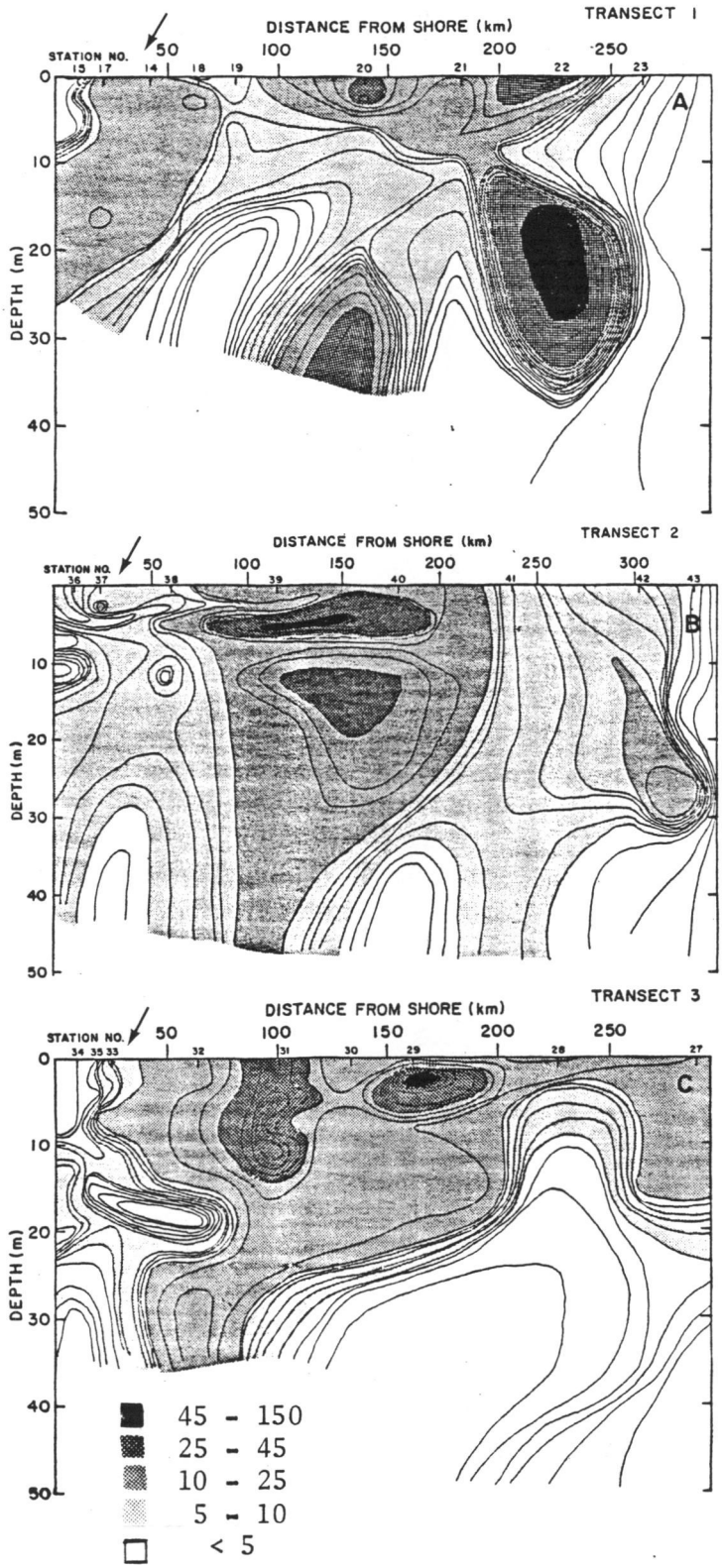

Fig. 4. Vertical distribution of the Nitzschia curta intact protoplasm cells to Nitzschia curta empty frustules ratio. a) Transect #1. b) Transect #2. c) Transect #3. ↙ ice-edge

mentioned zones than N. curta.

Nitzschia closterium was relatively abundant in the upper 10 m of station 20 where Nitzschia curta counts were anomalously low (Fig. 5c). The distribution of N. closterium is particularly discontinuous (Fig. 5a-c). It was abundant in zone 1 of transect #1, especially in the upper 15 m, and was abundant in the upper 45 m of transect #2 for the same zone. It was not present in the bloom zone in transects #1 or #2 (except for a very small section at the surface in station 40) (cf. Fig. 5b), and was very scarce in this zone in transect #3. In the offshore stations of transect #2 (stations 42, 43) there was a dramatic increase in the abundance of N. closterium. In station 43 numbers up to 8 x 10^{6} cells/l were observed. In transect #3 there was also a small increase in this species but not as dramatic as that in transect #2. Thus, N. closterium was found in high numbers either close to the ice or off-shore from the bloom, but not within the bloom proper.

Nitzschia kerguelensis (intact and empty cells) was present (especiallyin relatively high numbers) where N. curta was absent (Fig. 2a-c, Fig. 6a-c and Fig. 7a-c). With the exception of the maximum observed in the upper meters of station 32 (which coincides with a maximum of N. closterium, Fig. 5c), the distributions of N. kerguelensis and N. curta did not overlap. Maximum abundance of N. kerguelensis was found at 10m, 20m, 30m or even deeper in transect #3.

The dinoflagellate distribution was fairly patchy (Fig. 9a-c).

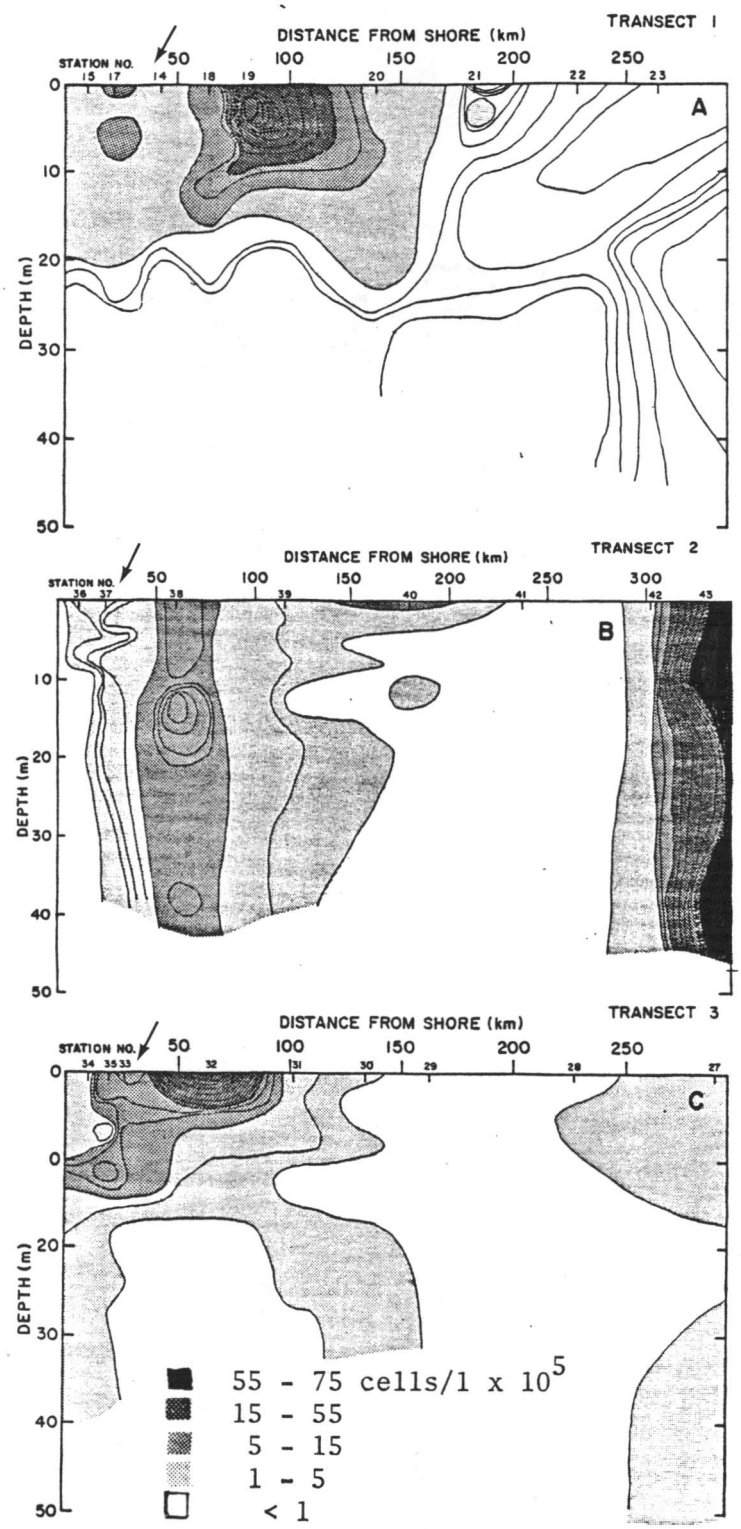

Fig. 5. Vertical distribution of Nitzschia closterium.
a) Transect #1. b) Transect #2. c) Transect #3.
↙ ice-edge

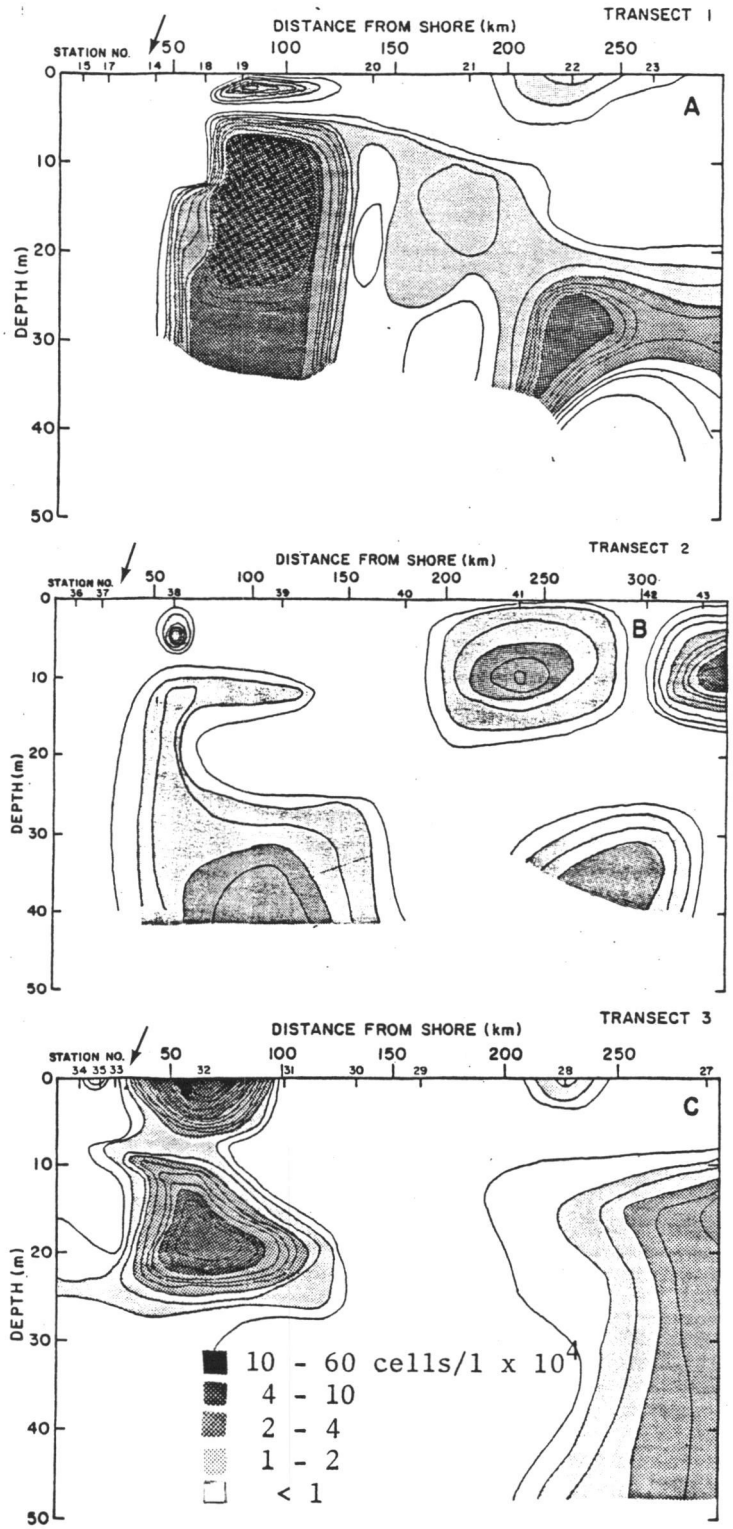

Fig. 6. Vertical distribution of Nitzschia kerguelensis (intact protoplasm). a) Transect #1. b) Transect #2. c) Transect #3. ↙ ice-edge

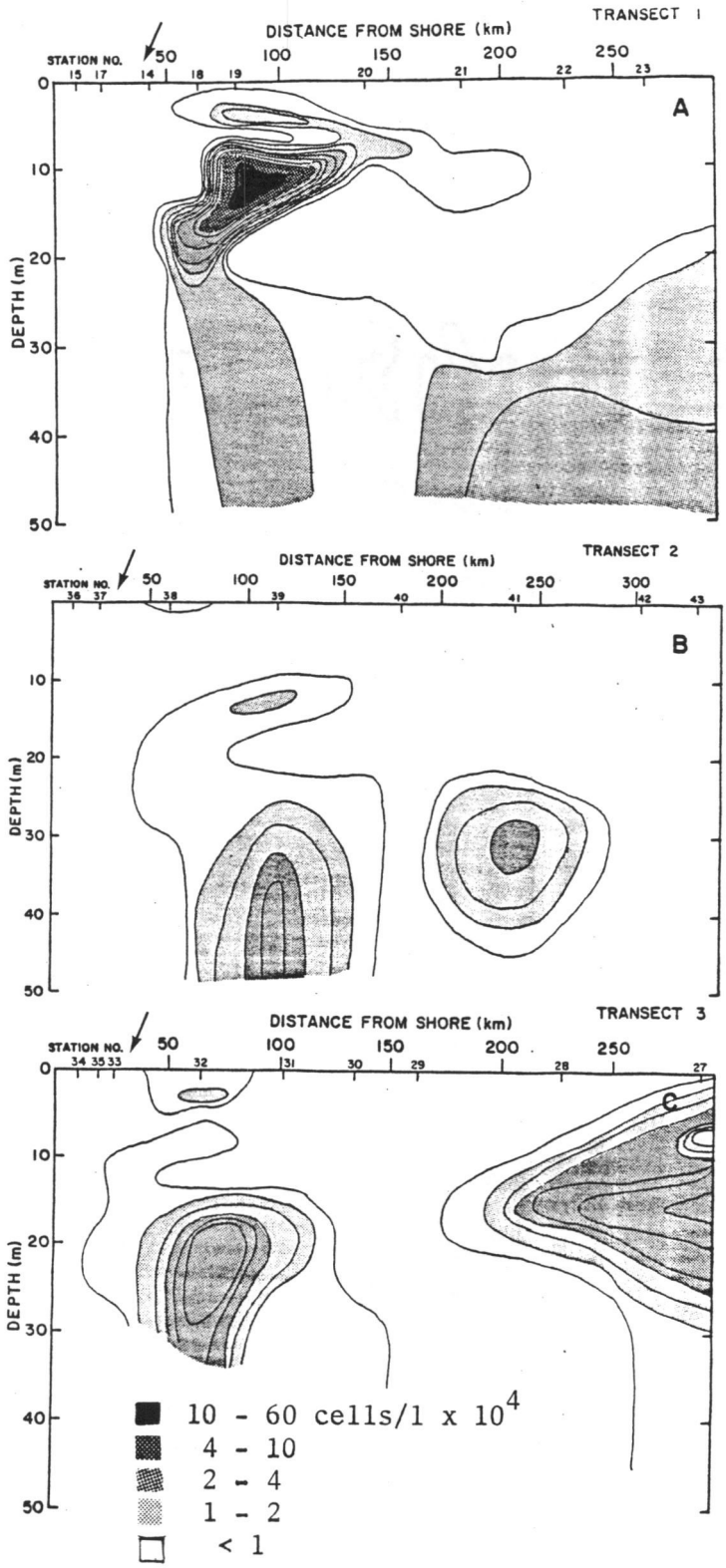

Fig. 7. Vertical distribution of Nitzschia kerguelensis (empty frustules). a) Transect #1. b) Transect #2. c) Transect #3. ↙ ice-edge

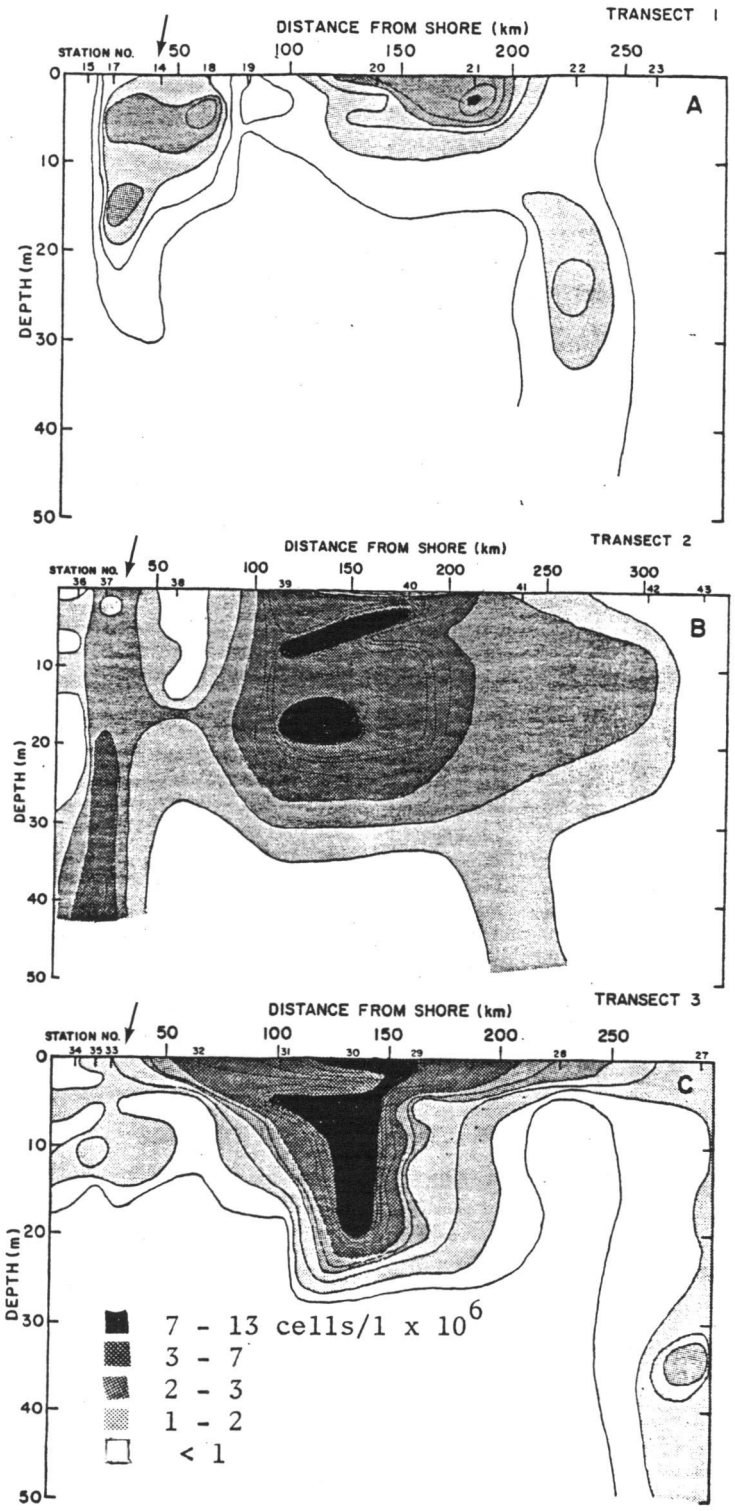

Fig. 8. Vertical distribution of nanoplankton. a) Transect #1. b) Transect #2. c) Transect #3. ↙ ice-edge

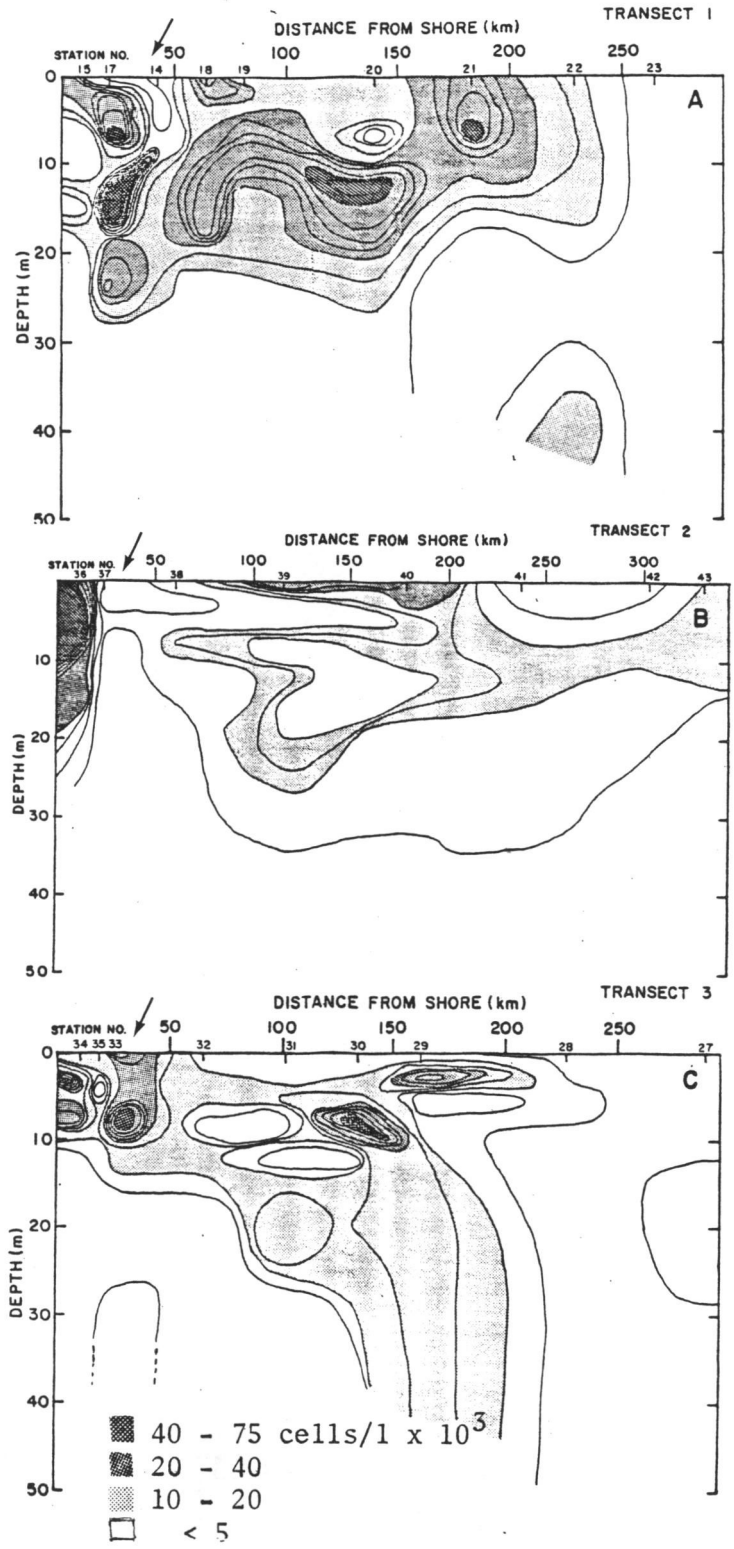

Fig. 9. Vertical distribution of dinoflagellates. a) Transect #1. b) Transect #2. c) Transect #3. ↙ ice-edge

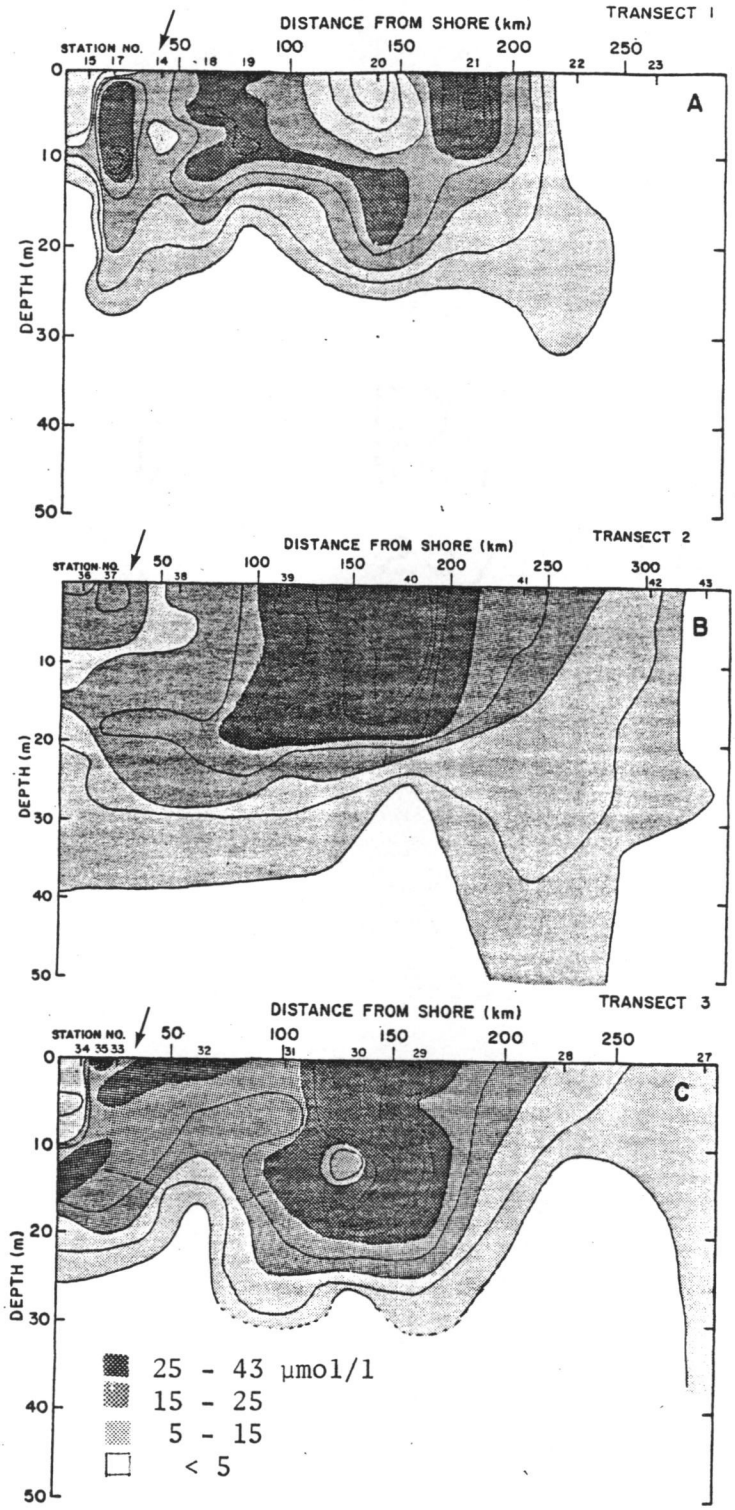

Fig. 10. Vertical distribution of biogenic silica. a) Transect #1. b) Transect #2. c) Transect #3. ↙ ice-edge

It was more continous in transect #3 with its highest abundance in station 18 and 21, becoming much less abundant in the upper 5 and 10 meters of stations 19 and 20, respectively. The distribution of the empty Nitzschia curta frustules (Fig. 3a-c) and the dinoflagellate distribution (Fig. 9a-c) in transects #1 and especially in #3 was very similar. The genus with the greatest number of species was Protoperidinium Bergh. One of the most abundant dinoflagellate species was Protoperidinium incertum (Balech) Balech (Appendix B). It was more frequent and abundant in transect #1 with the highest abundances at the stations within the ice. The same species was observed by Cassie (1963) as the most common Protoperidinium. She reported it as P. pellucidum (Bergh) Balech. According to Balech (1976) P. incertum is the P. pellucidum of the Antarctic. Hasle (1969) found P. applanatum (Balech) Balech to be the most common Protoperidinium species during the Brategg Expedition. Another common dinoflagellate species was Protoperidinium nanum (Balech) Balech (Appendix B). It was also more frequent in transect #1, especially in stations 17 and 21. It was particularly frequent in the bloom zones of all transects. Gymnodinioid type cells were common in the present study (Appendix B). These organisms have been reported to be the most frequent dinoflagellates observed in Antarctic waters (Hart, 1934; Cassie, 1963; Balech, 1968; Hasle, 1969). The largest number of dinoflagellate species was observed in stations 19 and 20. These observations, based upon the water samples, differ from observation made from net tows. When a net tow sample was observed, the dinoflagellate that appears to be the most

common was Protoperidinium antarcticum (Schimper) Balech, which is a large species (ca. 240 µm transdiameter), and, therefore, more likely to be caught by the net than a smaller cell like P. incertum (ca. 63 µm transdiameter) or P. nanum (ca. 25 µm transdiameter). 2×10^4 cells/l was the maximum abundance recorded for P. antarcticum, but its frequency was much less than that of P. incertum or P. nanum (Appendix B).

Figure 11 shows the relative abundance (frequencies expressed as percentages) of Nitzschia curta (living cells), N. curta (empty frustules), N. closterium, all the other diatoms, the nanoplankton, and the dinoflagellates (as a group) in the integrated water column. Relative abundance values of Nitzschia curta (living cells) can be as high as 78% (station 21) of the sample or as low as 4% (station 43). A high percentage of this species was not always observed within the bloom. Stations in the ice (15, 17, 36) also showed a high percentage of living cells of N. curta. The fraction of empty frustules was fairly constant in the three transects with the exception of stations 22, 23 and 43.The nanoplankton represented an important fraction of the phytoplankton population. The Prymnesiophyte (=Haptophyceae) Phaeocystis sp. was included here as part of the nanoplankton cell counts, but its actual density was not recorded except at station 13. Phaeocystis sp. was not present in high numbers and the bulk of the nanoplankton was composed of a different type of algae not identified here (not more than 5 µm in transdiameter, usually clustered in groups of 4). Diatoms were very seldom represented in the nanoplankton. The highest nanoplankton

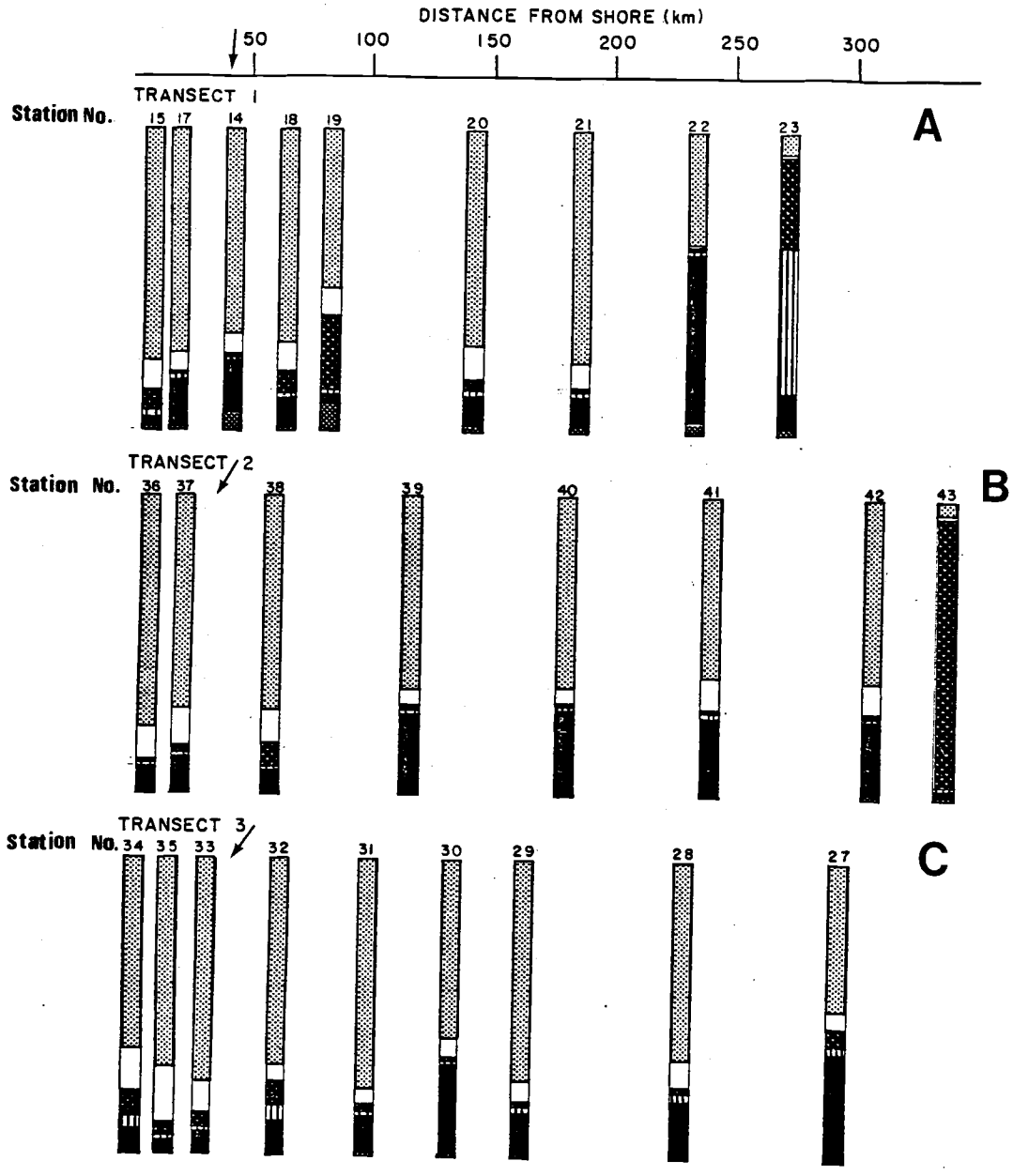

Fig. 11. Relative frequencies (as percentages) of the abundance in the integrated water column of the species observed in the bloom. a) Transect #1. b) Transect #2. c) Transect #3.

percentages were always associated with the bloom except at station 22. Nitzschia closterium did not represent a high percentage of the phytoplankton population, except for those stations off-shore the bloom (stations 23 and 43), and at station 19. Dinoflagellates usually represented less than 1 % of the sample with the exception of station 19.

Representatives of other phytoplankton groups included the silicoflagellate Distephanus speculum (Ehrenberg) Haeckel, and a very few coccolithophorids and ebridians.

DISCUSSION

The ice-edge bloom observed in the Ross Sea, dominated as it was by Nitzschia curta, appears to have been different in its species composition from other ice-edge blooms reported in the literature. Hart (1942) found that the main component of the blooms was the Prymnesiophyte (=Haptophyte) Phaeocystis brucei. El Sayed et al. (1983) reported an extensive bloom of Phaeocystis pouchetti in the Ross Sea. El-Sayed (1971) observed that Thalassiosira tumida (Janisch) Hasle was the bloom species in the Weddell Sea, while during the first AMERIEZ (Antarctic Marine Ecosystem Research at the Ice-Edge Zone) cruise, Fryxell (pers. commun.) found that both Pheocystis and Thalassiosira were the ice-edge bloom species in the Weddell Sea. Ice-edge blooms may also be dominated by other diatom species such as Rhizosolenia, Corethron, Chaetoceros or Thalassiotrix while Nitzschia curta has not been observed in high numbers during the same blooms (Ivanov, 1964). Although some authors (Hendey, 1937; Hart, 1942; Meguro et al., 1967; Hargraves, 1968) have reported Nitzschia curta as a very important species in the ice, it has not previously been reported as a principal bloom species. The sediment records suggest that Nitzschia curta blooms are restricted to the Western Ross Sea (Truesdale & Kellogg, 1979; Burckle, 1984). To what extent this is related to the anomalous elemental composition (very high Si/C and C/Chl ratios) of the Nitzschia curta bloom observed by Smith & Nelson (1985) in the Ross Sea remains to be found.

The numbers recorded here for Nitzschia curta are also much higher than the ones reported by other authors (Appendix B). Hasle (1969) reported 1.3 x 10^6 cells/l as the highest concentration of the species of the section Fragilariopsis (with the exception of F. nana). In the Ross Sea, the concentration of just one species from the section Fragilariopsis (i.e. Nitzschia curta) was as high as 22 x 10^6 cells/l. Steyaert (1973a) reported the highest cell densities of N. curta to be 1.3 x 10^4 cells/l while, Steyaert (1974) found that the highest concentration of N. curta in the water column was 0.8 x 10^6 cells/l in 1964-65 and 0.2 x 10^6 cells/l in 1966-67. However, Steyaert (1974) found that the concentration of N. curta in melted ice was 1 x 10^6 cells/l for 1966-67, i.e. almost one order of magnitude greater.

Nitzschia kerguelensis has consistently been reported as one of the most dominant oceanic species in Antarctic waters (e.g., Hart, 1942; Hendey, 1937; Manguin, 1960; Hargraves 1968; Hasle, 1969; Steyaert, 1974; Jacques et al., 1979). On the other hand, records of Nitzschia curta show that this is a neritic species, which prefers shallow waters (e.g., Manguin, 1960; Hasle, 1969; Steyaert, 1974). The sediment records corroborate this distribution. Schrader (1976) found that Nitzschia kerguelensis was very abundant in oceanic sediments while N. curta was very scarce. He found N. curta only once, northwest of the Ross Sea. Defelice & Wise (1981) and Burckle (1984) also found that N. kerguelensis was the main component in oceanic sediments. Burckle (1984) found that the diatom assemblage dominated by N. curta appeared to be restricted to the Western Ross

Sea, showing a neritic character. A similar distribution in the sediments was observed by Truesdale & Kellogg (1979).

Although the area covered by the present study is not very large, the distributions of Nitzschia curta and N. kerguelensis do not overlap. The concentrations of N. kerguelensis are much lower than those of N. curta; even so it is possible to see that N. kerguelensis was found much deeper and away from the highest concentrations of N. curta (Fig. 2a-c and Fig. 6a-c). Nitzschia kerguelensis was excluded from the low salinity waters where the bulk of the bloom was observed (see Fig. 18a-c).

The highest concentrations of Nitzschia curta were observed in the low salinity waters formed by the melting ice. This species has a wide range of salinity tolerance. Fritsch (1912) observed N. curta in melted freshwater ice. N. curta has been reported as an ice species by several authors (e.g., Van Heurck, 1909; Hendey, 1937; Hart, 1942; Burkholder & Mandelli, 1965; Fukushima & Meguro, 1966; Meguro et al., 1966, 1969; Hargraves, 1968; Hasle, 1969; Steyaert, 1974, see Appendix A). However, there are no previous reports of blooms produced by N. curta like the one observed in the present study in the western Ross Sea. Krebs (1983) found in Arthur Harbor, Antarctica, that these nearshore blooms were produced by Nitzschia glaciei Van Heurck, while N. curta was not an important component of the bloom.

A bloom like the one observed in the Ross Sea may occur in near-shore environments (Clark & Ackley, 1984), late in the summer

when the receding ice is much closer to the continent. At this time of the year, high concentrations of sea ice algae are found in the pack ice (Steyaert, 1974).

Concentrations of chlorophyll _a_ in the ice may reach very high values. Hoshiai (1977) found in Antarctic sea ice communities that chlorophyll _a_ concentrations can vary from 42 mg/m^3 in October to 829 mg/m^3 in April. Differences of two orders of magnitude may be observed between drifting sea ice and fast ice. Clark & Ackley (1984) found in drifting sea ice cores of an ice-edge in the Weddell Sea, concentrations of chlorophyll _a_ of 26.8 mg/m^3 while Sullivan & Palmisano (1981) and Palmisano & Sullivan (1983) reported values of 656 mg/m^3 in fast ice in McMurdo Sound. This last value was 2000 times greater than that of the water under the ice. In the present study, fluorescence measurements of a sea ice sample, were 20 times greater than any fluorescence value observed in the water column (S. Moore, pers. commun.).

Clark & Ackley (1984) found concentrations of algae in sea ice up to 180×10^6 cells/l, i.e. one order of magnitude higher concentrations than the reports in this study (32×10^6 cells/l of total biomass in the water column, see Appendix B). Melting ice will release these high concentrations of cells into the water column where optimal growth conditions of more light and nutrients than in the ice are encountered (Clarke & Ackley, 1984). Since sea ice algae are physiologically active in the ice, they can start to grow rapidly in the water column once released from the ice (Olson,

1980). Steyaert (1974) considered Nitzschia curta as a species released from the ice and able to grow in the water with maximum concentrations closer to the ice-edge. The growth of these algae may be restricted to the upper 20 m (Hasle, 1956; this study).

Blooms in more open waters may occur earlier in the season (spring, early summer) than the one in this study, e.g. those observed in the Weddell Sea (El-Sayed, 1971; Fryxell, pers. commun.). Hart (1942) did not find Phaeocystis blooms late in the season, but only in the spring. Zernova (1970) also reported spring blooms of ice-edge diatoms in pelagic environments, e.g., blooms of Biddulphia weissflogii Grunow, Eucampia balaustium Castracane, Chaetoceros neglectum Karsten and Nitzschia closterium (Ehrenberg W. Smith). The bloom of Thalassiosira tumida observed by El-Sayed (1971) and Fryxell (pers. commun.) indicate that this ice-edge bloom may be the result of germination of senescent cells of this species. Preliminary observations on the bloom in the Weddell Sea may correspond to big concentration of resting stages of Thalassiosira tumida (Fryxell, pers. commun.). Resting spores have neither been observed in the water column under the ice nor has it been proved that the resting spores are a survival mechanism in Antarctic waters, although some Antarctic diatoms are known to have resting spores (Fryxell, pers. commun.). Resting spores have been observed in only two marine pennate diatoms (Hargraves & French, 1983), suggesting that spores would be very unlikely to occur in sea ice flora which is comprised mainly by pennate diatoms.

The nanoplankton distribution is similar to that of Nitzschia curta. The nanoplankton contributed significantly to the total biomass (Fig. 11a-c). It has been shown to contribute up to 90% of the primary production in the pelagic Antarctic ecosystem (von Bröckel, 1981). No nanoplankton primary productivity was measured in the Ross Sea studies (Wilson, 1983), but it seems reasonable to expect that its contribution to the total primary productivity was significant.

Earlier studies on Antarctic dinoflagellates are either descriptive (Balech, 1944; 1947; 1958a; 1973; 1976) or distributional (Balech, 1958b; 1959; 1968; 1970) from open water environments. Few quantitative studies have been published, beginning with Hasle (1969). Previous works used net hauls (Peters, 1928; Hart, 1934, 1942; Ealey & Chittleborough, 1959) to give an estimate of dinoflagellate abundance. While Hart (1942) reports the maximum abundance of dinoflagellates in the stations closest to the land, Hasle (1969) found the maximum concentration in the northern stations. In the present study, although the distribution was very patchy, the highest concentration was observed in the stations in the ice or very close to it (Fig. 9a-c). Standing stocks of dinoflagellates are extremely small in Antarctic waters (Hasle, 1969). In the present study, dinoflagellates represented less than 1% of the total biomass (Fig. 11a-c). Hentschel (1932, 1936) reported an average of 15% of the total phytoplankton. Hasle (1969) found the highest concentration of dinoflagellates at the end of January (0.005×10^6 cells/l). Cell densities one order of

magnitude higher were observed in the present study (0.073 x 10^6 cells/l, see Appendix B).

Antarctic dinoflagellates are reported as very scarce in ice (Bunt, 1960, Burkholder & Mandelli, 1965; Hoshiai, 1977; Fryxell, pers. commun.). Dinoflagellates in the present study occurred more abundantly in waters with lower salinities (Fig. 9a-c and Fig. 18a-c).

The ratio of living Nitzschia curta cells to empty cell frustules (Fig. 4a-c) was much lower under the ice because old dead cells come from the bottom layer of the ice. The living ones might still be in the ice; these cells will eventually be released into the water column where they grow in better conditions and thereby produce the next bloom. Higher living/dead cell ratios at the offshore stations seem to suggest that greater concentrations of Nitzschia curta were found in deeper waters than within the core of the bloom. A similar observation was made by Steyaert (1974) and by El-Sayed (1971).

In contrast to the observation made by Smith & Nelson (1985), in the Ross Sea , the distribution of Nitzschia closterium was very different from that of N. curta (Fig. 2a-c and Fig. 5a-c). The highest concentrations of N. closterium were observed away from the core of the bloom. The remarkable increase in the concentration of this species at station 42 and especially at station 43 (up to 8 x 10^6 cells/l, Fig. 5b) did not contribute very much to the biogenic silica (Fig. 10b) suggesting that Nitzschia curta should be the

diatom species that is accounting for almost all the biogenic silica observed. Nitzschia closterium may contribute up to 34% of the total primary productivity in the area studied (Wilson, 1983).

Steyaert (1973b) found that at the offshore stations Nitzschia curta was replaced by N. closterium, as was also observed in the present study in transect #2 (Fig. 2b and Fig. 5 b). Nitzschia closterium has been associated with ice-edge blooms (Zernova, 1970; Steyaert, 1973b) and accompanying Phaeocystis blooms (Hart, 1942; Fryxell, pers. commun.). Fryxell (pers. commun.) found that Phaeocystis was more abundant in the water column than in the adjacent ice while Nitzschia closterium was more abundant in the ice than in the water. Hart (1942) observed that N. closterium was the most ubiquitous and variable of all neritic diatoms and that it was most common in the southern stations.

The high densities of Nitzschia closterium observed in the offshore stations 42 and 43, and at stations near the ice (Fig. 5b), as well as the presence of an oceanic species like Nitzschia kerguelensis close to the ice (Fig. 6a-c and Fig. 7a-c), suggest that an eddy or vertical cell circulation might be taking place. By this eddy circulation, advection of offshore species to the ice-edge may explain the presence of N. closterium close to the ice in concentrations comparable to the ones observed offshore (Fig. 5b,c).

The following evidence strongly suggest that a wind-driven upwelling event occurred in station 38: 1) High salinity water (34%) at the surface (Fig. 18b). 2) Relatively colder temperatures in the

upper water column than in the surrounding waters (Fig. 19a-c). 3) Relatively higher surface nutrient concentrations than in adjacent stations (Fig. 21b, Fig. 22 and Fig. 23b). The wind conditions (speed and direction) observed in the Ross Sea were favorable for the presence of an upwelling event.

The growth rate of Nitzschia curta as tested here in laboratory conditions (See Part II), was higher than that of the other species tested (except por Nitzschia cylindrus (Part II, Table 3). However, N. cylindrus cultures took much longer to achieve exponential growth than N. curta. In addition, cultures of N. cylindrus decayed shortly after having reached the maximum growth rate, while N. curta were still viable after several months without nutrient replenishment. Wilson (1983) pointed out that although the per cell specific activity of Nitzschia curta in the Ross Sea bloom, as shown in the autoradiographic analysis is not high, it was possible that its growth rate would have been higher than the other species released from the ice at the same time. The growth rate of Nitzschia curta in the field was much lower than was observed in the laboratory experiments (see part II).

The high cell densities (180 x 10^6 cells/l) of monospecific diatom assemblages found in the ice by Clark & Ackley (1984) are further strong evidence that the blooms likely occur by the release of these huge concentrations of sea ice algae into the stratified water column where they find optimum conditions to grow rapidly (Olson, 1980). The stratification will prevent the vertical mixing

of the algal population and will maintain it within the meltwater until meteorologic conditions change. If just a few cells were released from the ice, a long time would be required to form a bloom like the one observed in the Ross Sea because Antarctic diatoms have such slow growth rates (see part II this study). It is unfortunate that more information is not available on Nitzschia curta from the sea ice , but the indirect evidence suggests that large amounts of this species are released into the water column. This, combined with the more favorable conditions of light and nutrients found in the water column and with the fact that Nitzschia curta has been shown to present a very anomalous elemental composition (Smith & Nelson, 1985; this study) suggests that this species present unusual physiological properties that allow it to respond faster to improved growth conditions than can the other epontic algae.

We can find the time that it took the observed bloom in the Ross Sea to develop, by assuming that the melting of sea ice provided the inoculum for the bloom of Nitzschia curta. Assuming an initial concentration of N. curta in the ice of 1×10^6 cells/l [cell density in the ice observed by Steyart (1974) in Breid Bay], and that the layer of algae in the ice was 0.30 m thick, there would be 3×10^8 cells in 1 m^2 of ice to be spread over a 19 m mixed layer when the ice melts. Using the average growth rate of 0.15 div/day in the Ross Sea bloom measured by Wilson et al. (submitted), it would take ca. 66 days for the cells to grow to the integrated cell number of 3×10^{11} cells/m^2 observed in transect #3 (Station 30).

PART II

INTRODUCTION

Studies on elemental composition or growth rates of Antarctic diatoms, either in the field or in culture, are very few. The commonly held belief is that Antarctic diatoms have a very different physiological response from diatoms in other environments (Bunt et al., 1966; Bunt, 1968 a,b; Copin-Montegut & Copin-Montegut, 1978; Palmisano & Sullivan (1982, 1983); Jacques, 1983; Le Jehan & Treguer, 1983; Smith & Nelson, 1985).

The hypothesis that Antarctic diatoms are characteristically different in their elemental composition from diatoms of the rest of the world is tested here. This has become an important issue after the findings of Smith & Nelson (1985) of extremely high Si/C and C/Chl ratios of the diatom bloom observed in the Ross Sea in January-February 1983.

MATERIAL AND METHODS

Nitzschia curta AA-9 clone was received from Dr. Anna C. Palmisano of the University of Southern California. All other algal cultures were supplied by Dr. Greta A. Fryxell of Texas A & M University. Table 1 indicates the locations from which these cultures were first isolated.

Batch cultures were grown under constant illumination. They were initially grown in three growth chambers. Temperature and light intensity in these chambers are shown in table 2. Chamber A consisted of a plexiglas aquarium (1.07 m x 41 cm x 64 cm) filled with freshwater up to one third of its height. It had three cool-white light bulbs under the lid and one screen above the cultures to reduce light intensity. Temperature was kept constant by means of a circulating cooling system. The entire chamber was insulated thermally with styrofoam (2.55 cm in thickness). Chamber B was a simple refrigerator illuminated by one cool-white flourescent bulb. Chamber C was a big room kept at 2°C by a refrigeration system. Batch cultures were illuminated there by a desk lamp with two cool white fluorescent light bulbs (15 watts each) at 70 cm above cultures and by 2 incandescent light bulbs (100 W)) on the ceiling, 4 m above cultures.

Guillard's F/2 medium (Mc Lachlan,1973) made with North Pacific Central Gyre water was used. Silicate content was doubled to prevent a premature depletion of this nutrient. Analysis of dissolved silicate in preliminary growth experiments suggested that

Table 1. Clone designations and locations of the 10 Antarctic diatoms used in the elemental composition experiments.

CLONE	SPECIES	LONG.	LAT.	LOCALITY	DATE
AA-9	*Nitzschia curta* (van Heurck) Hasle	31° 52' W	57° 46' S	Orcades Islands	1978
AA-176	*N. cylindrus* (Grunow) Krieger	36° 35' W	62° 10' S	Weddell Sea	1983
AA-184	*N.* cf. *ritscheri* (Hustedt) Hasle	36° 35' W	62° 10' S	Weddell Sea	1984
AA-41	*Chaetoceros flexuosum* Mangin	39° 30' W	51° 47' S	Orcades Islands	1978
AA-178	*C.* cf. *gracile* Schütt	36° 27' W	61° 6' S	Weddell Sea	1983
AA-167	*Coscinodiscus furcatus* Karsten	38° 9' W	61° 51' S	Weddell Sea	1983
AA-189	*C. furcatus* Karsten	38° 9' W	61° 51' S	Weddell Sea	1983
AA-163	*Actinocyclus actinochilus* (H. Péragallo) Simonsen	166° 38' E	77° 50' S	Mc Murdo Sound	1981
AA-21	*Porosira glacialis* (Grunow) Jörgensen	39° 30' W	51° 47' S	Orcades Islands	1978
AA-198	*Eucampia balaustium* Castracane	41° 57' W	60° 14' S	Weddell Sea	1983

Table 2. Temperature and light intensities of the three culture chambers.

CHAMBER	TEMPERATURE (^{o}C)	LIGHT INTENSITY ($\mu E\ m^{-2}\ sec^{-1}$)
A	3	51
B	3	33
C	2	14

Table 3. Apparent growth rates obtained from *in vivo* fluorescence measurements. (Growth rates in div/day).

CLONE	CHAMBER A	CHAMBER B	CHAMBER C	
AA-9	0.22	0.27	0.17	0.60
AA-176	0.36	0.38	0.21	0.70
AA-184	0.10	0.44	0.10	0.28
AA-41	0.22	0.21	0.17	0.33
AA-178	0.34	0.45	0.14	0.36
AA-167	0.44	0.44	0.13	0.21
AA-189	0.28	0.23	0.06	0.29
AA-163	0.32	0.45	0.11	0.31
AA-21	0.20	0.35	0.09	0.27
AA-198	0.01	0.64	0.05	0.35

silicic acid was close to depletion after harvesting the cultures at the end of exponential growth in unmodified f/2 medium.

Growth (interpreted as the increase in the amount of in vivo fluorescence, assuming that the amount of flourescence is a function of cell number) was monitored by measuring fluorescence with a Turner Designs Fluorometer. Fluorescence units were used to estimate the growth rates in divisions per day using the formula given by Guillard (1973):

$$k \text{ (div/day)} = \frac{\ln [N_1/N_o]}{[t_1 - t_2] [0.6931]}$$

where N_o = cell number at time zero (t_o) and N_1 = cell number at time (t_1). Fl (fluorescence units at day t_1) and F_o (fluorescence at day zero t_o) were used instead of cell numbers (N_1 and N_o). The estimate of the growth rates and the determination of the fluorescence level at which exponential growth ceased gave the approximate fluorescence value at which each culture should be sampled to obtain exponentially growing cells unaffected by nutrient limitation.

Comparisons among the growth of batch cultures in the three different chambers determined which was the best in which to carry out the final experiment. Preliminary experiments were run using 100 ml culture test tubes with polypropylene screw caps and F/2 medium. As cultures grew most rapidly and reliably in chamber C, that chamber was chosen to run the main elemental composition experiment. 300 ml of F/2 medium were put in 500 ml erlenmeyer

flasks and capped with cotton-cheese cloth stoppers and with 150 ml beakers. Media and all glassware were at 2°C for transfers after autoclaving. Low inoculations of cultures were done to begin the experiment and growth was monitored by fluorescence measurements every three days. Batch cultures were sampled during log phase for particulate carbon, particulate nitrogen, biogenic silica, chlorophyll *a* and cell counts. The volume that should be sampled was determined after the preliminary experiments.

Between 25 and 83 ml of culture was filtered for particulate carbon and nitrogen, depending on the thickness of cultures, using microfibre Whatman QM-A filters. Filters were dried at 60°C for 2-3 days and analyzed on a Perkin-Elmer 240 C elemental analyzer.

For biogenic silica, 20-29 ml was filtered through a 0.6 µm polycarbonate Nuclepore filter. Filters were folded in quarters set in disposable petri-dishes and dried at 60°C for one day. Analysis of these filters was done manually using the sodium hydroxide digestion method described by Paasche (1973 a,b).

Glass microfibre Whatman GF/C filters were used for extracted chlorophyll *a* fluorometric analysis. Between 25 and 30 ml of each culture was filtered and chlorophyll *a* was measured according to the method described by Holm-Hansen *et al.* (1965).

A Wild compound microscope was used for cell counts under X 600 and X 1000 magnification. A combination of a Whipple disc and a Palmer-Maloney chamber was used to assess cell numbers. Between 6

and 9 chambers were counted for each culture and the mean was used to compute the cell numbers. For thin cultures the entire chamber was counted, while for dense cultures only 24 Whipple fields were counted. These 24 fields had fixed positions and were evenly distributed on the chamber. Cell density (d) was found using the following formula:

$$d\ (\text{cells/ml}) = \frac{M \times \text{Area of Palmer-Maloney Cell}}{\text{Area of Whipple Field} \times \text{P-M cell vol.}}$$

where M = the average number of cells per Whipple field (Guillard, 1973).

Cell surface area and cell volume were computed from averaged linear dimensions, assuming the cells to be ellipsoidal (Chaetoceros flexuosum; C. cf. gracile; Eucampia balaustium), cylindrical (Porosira glacialis; Actinocylus actinochylus, and Coscinodiscus furcatus), and rectangular (Nitzschia curta; N. cylindrus; N.cf.ritscheri). This procedure was preferred over the one suggested by Hitchcock (1983) who gives two sets of formulae for cell surface and cell volume of centric and pennate diatoms based in laboratory studies, natural populations and model solids of diatoms in relation to plasma volume. By applying Hitchcock's formulae instead of the simple geometric formulae for the Nitzschia spp., an overestimate for both area and volume of more than 3 times is obtained in the present study. As the valvae of these Nitzschia spp. are not rectangular, an overestimate of cell surface and cell volume is already being found when these values are calculated using the

geometric formulae, resulting then in a much larger overestimate if Hitchcock's formulae are used in this case as well as in the case of ellipsoidal valvae like those found in Eucampia. However, for cylindrical frustules the results obtained with Hitchcock's formulae for centric diatoms were exactly the same as the ones estimated here using simple formulae for cylinders.

RESULTS

Table 4 summarizes the results for the elemental composition analyses of the 10 algae studied. All ratios are by atoms except C/Chl, which is expressed as a mass ratio.

Higher growth rates and higher final fluorescence yields were observed using lower light intensities and large flasks as in the case of chamber C (Table 2). Apparent doubling rates for the three chambers are listed in Table 3. The mean growth rate of the 10 algae was 0.37 div/day, with the growth rates of individual clones ranging from to 0.21 to 0.70 div/day during the main experiment (chamber C).

Cell surface-to-volume ratios presented differences of one order of magnitude as a consequence of the range of sizes and cell frustule shapes within the species studied (Table 4).

C/N ratios were very close together ranging from 4.8 to 6.7 with a mean of 5.7 (standard deviation [s.d.] = 0.60) (Table 4). Although having almost identical S/V ratios, Nitzschia curta and N. cylindrus had very different C/N ratios. The same was true for Actinocyclus actinochilus and Porosira glacialis. C/N ratios were higher in N. curta and A. actinochilus.

The highest C/N ratios were shown by Actinocyclus actinochilus, Chaetoceros cf. gracile, Nitzschia curta and Coscinodiscus furcatus (AA-167 clone), while the lowest values were found in Chaetoceros flexuosum, Coscinodiscus furcatus (AA-189 clone) and Porosira glacialis.

Table 4. Cell size, cell density, elemental composition and elemental ratios of the 10 Antarctic diatoms studied.

Clone	Species	Cell Volume $(\mu m)^3$	Cell Surf.Area $(\mu m)^2$	Cell Density cells/ml	S:V (μm^{-1})	Elemental Composition								Elemental Ratio			
						pmol C/cell	pmol N/cell	pmol Si/cell	pg Chl/cell	fmol C/μm^3	fmol N/μm^3	fmol Si/μm^2	fg Chl/μm^2	C:N	Si:C	Si:N	C:Chl
														(by atoms)			(by weight)
AA-9	*Nitzschia curta*	151	182	243,055	1.21	0.62	0.10	0.13	0.26	4.11	0.66	0.71	1.43	6.19	0.21	1.29	28.65
AA-176	*N. cylindrus*	160	189	123,148	1.19	2.99	0.57	0.26	0.47	18.7	3.59	1.39	2.49	5.21	0.09	0.46	75.82
AA-184	*N. cf. ritscheri*	1,877	1,034	19,878	0.55	17.9	3.17	4.09	3.67	9.54	1.69	3.96	3.55	5.66	0.23	1.29	58.56
AA-41	*Chaetoceros flexuosum*	5,398	1,740	11,979	0.32	10.0	19.7	1.66	4.10	1.87	3.65	0.95	2.37	5.10	0.16	0.82	29.37
AA-178	*C. cf. gracile*	280	322	72,724	1.15	6.79	1.09	0.18	0.90	24.3	3.89	0.56	2.80	6.22	0.03	0.17	90.20
AA-167	*Coscinodiscus furcatus*	222,484	25,610	1,932	0.12	221	37.2	62.4	86.4	0.99	0.17	2.44	3.37	5.95	0.28	1.68	30.76
AA-189	*C. furcatus*	218,491	24,179	2,520	0.11	128	24.6	46.0	53.7	0.58	0.11	1.90	2.22	5.18	0.36	1.86	28.54
AA-163	*Actinocyclus actinochilus*	16,426	3,950	10,677	0.24	44.3	6.60	10.8	10.7	2.70	0.40	2.73	2.71	6.70	0.24	1.64	49.51
AA-21	*Porosira glacialis*	16,219	3,975	18,455	0.24	16.9	3.57	1.65	7.09	1.04	0.22	0.42	1.78	4.81	0.10	0.46	28.68
AA-198	*Eucampia balaustium*	62,820	9,569	3,117	0.15	66.1	11.2	7.62	45.4	1.05	0.18	0.80	4.74	5.93	0.12	0.68	17.51

The range for Si/C ratios was very broad, from 0.03 to 0.36 with a mean of 0.18 [s.d.= 0.10] (Table 4). Differences of one order of magnitude were observed between congeneric species that were morphologically very similar (e.g. Nitzschia curta and N. cylindrus). There was not a correlation between the Si/C and S/V ratios ($r = -0.26887$). For species with almost exactly the same cell surface to cell volume ratio, the Si/C ratio differed by one order of magnitude (e.g. Actinocyclus actinochilus and Porosira glacialis, or Nitzschia curta and N. cylindrus).

Contrary to what might have been expected, the highest cell surface to cell volume ratios corresponded to the lowest values of Si/C ratios with the exception of N. curta. Nitzschia curta and N. cylindrus had almost the same cell volume but the carbon content per cell was one order of magnitude less in N. curta than in N. cylindrus. Cell silica content was very similar in these two species, as was the surface area per cell. Cell carbon per unit volume was one order of magnitude less in N. curta than in N. cylindrus while silica per unit area was nearly the same, resulting in a much higher Si/C ratio in the former species. The opposite case was found in Actinocyclus actinochilus and Porosira glacialis. Although they had nearly identical S/V ratios, the silica content was also one order of magnitude higher in the former species, whereas the carbon content was more similar, resulting again in different Si/C ratios.

The Si/N ratio range was almost as wide as the Si/C ratio

range, from 0.17 to 1.86 with a mean of 1.04 [s.d.=0.60] (Table 4). As before, differences of one order of magnitude were observed for species within the same genus, morphologically very similar (e.g. Nitzschia curta and N. cylindrus) although the silica and nitrogen per cell values were within the same order of magnitude (Table 4). So, for very similar surface to volume ratio, the Si/N ratio was 2.8 times higher in N. curta as nitrogen content per cell was much higher (as in the case of carbon), in N. cylindrus. In the case of Actinocyclus actinochilus and Porosira glacialis which have almost identical S/V ratio, the Si/N ratio was also very different due to a much higher silica content per cell (one order of magnitude) in the former species, whereas the nitrogen per cell was not. The lowest values for Si/N ratios were those of Chaetoceros cf.gracile, Nitzschia cylindrus and Porosira glacialis. The last two species have quite similar Si/N ratios despite the huge difference in the S/V ratio. Both have similar silica content per unit area, but not nitrogen per unit volume.

C/Chl ratios were all within the same order of magnitude, ranging from 17.5 to 90.2 (mean = 43.8 [s.d.= 24.0], Table 4). Once again, species very closely related morphologically, showed a large difference in the C/Chl ratio (e.g. Nitzschia curta and N. cylindrus). The highest C/Chl ratios were those of Chaetoceros cf. gracile and Nitzschia cylindrus, while the lowest value was that of Eucampia balaustium. Microscopic observations of E. balaustium cultures transferred after the main experiment (to the same media and sea water used earlier) showed more pigmented cells than those

used for the main elemental composition experiment, due to a reduction of the light intensity in chamber C.

The lowest values of all elemental constituents per cell corresponded to cells with the highest S/V ratios, i.e. Nitzschia curta. A difference of one order of magnitude can be seen in species within the same genus, e.g. Chaetoceros flexuosum and C. cf. gracile. The amount of carbon per cell varied by four orders of magnitude for the 10 species studied. Silica, nitrogen and clorophyll a content per cell, varied up to 3 orders of magnitude. The carbon per cell values of the three species of Nitzschia studied differed by two orders of magnitude .

DISCUSSION

There were several factors influencing the growth of the algae examined. The growth of the batch cultures studied here depended very much on the type of water used for the media as well as the kind of flasks. This was clear in cultures incubated in chamber C. The use of culture test tubes in the preliminary experiments yielded much lower growth rates than were obtained using erlenmeyer flasks (Table 3). Light intensity also affected the growth response of the cultures. For the same type of culture tubes and media, it was evident that the algae grew faster at lower light intensity (33μE m^2 sec^{-1}, than in chamber A with higher light intensity (51μE m^{-2} sec^{-1}). After the main experiment, light intensity in chamber C dropped to (7μE m^{-2} sec^{-1}) due to the burnout of several overhead lights. Healthier and bigger cells of Eucampia balaustium resulted at this lower light intensity, as seen under the light microscope. Bunt (1968a) working with sea-ice flora from McMurdo Sound, showed the extreme capacity for shade adaptation of these algae. The light intensity in the Ross Sea decreased very rapidly with depth as a consequence of the bloom itself. There, cells at light intensities comparable to the one in chamber C appeared very healthy.

The difference in temperature (1°C) between chambers A or B and C should not have accounted for any significant difference in growth. According to Eppley (1972), the absolute change of growth rate of phytoplankton with a decrease in temperature is relatively small below 10°C.

Although the growth rates calculated here are apparent values, these can be compared with those in the literature. The mean value obtained in chamber C in the main experiment was 0.37 div/day. Doucette & Fryxell (1983) found a doubling rate of 0.5 div/day for Thalassiosira antarctica var. antarctica while Bunt (1968a) found that this rate was 0.17 div/day with very dim light.

Eppley (1972) working with algae at 0°C found a doubling rate of 0.64 div/day comparable to the one found by Jacques (1983) of 0.6 div/day, who worked with Antarctic diatoms at 5°C. Holm-Hansen et al. (1977) reported 0.33 div/day as the specific growth rates of phytoplankton for the Ross Sea. El-Sayed & Taguchi (1981) reported higher growth rates along the ice-edge of the Weddell Sea (0.46 - 0.88 div/day). Paden et al. (1981) found that the generation time of phytoplankton in the Scotia Sea was 0.23 div/day at ambient surface water temperature (0 - 1°C). Palmisano & Sullivan (1982) showed an averaged division rate of 0.26 div/day for three sea ice diatom clones (Nitzschia cylindrus among them). Fiala & Oriol (1984) found that the doubling rate for the Antarctic diatom Nitzschia turgiduloides was 0.45 div/day and for one Antarctic species of Chaetoceros it was 0.6 div/day. The integrated mean value of growth rate in the water column in the Ross sea during the bloom observed in this study was 0.15 div/day, but values up to 0.41 div/day were found (Wilson et al., submitted).

Figure 12 shows the logarithm of cell carbon and cell nitrogen as function of the logarithm of cell volume. The slopes of the two

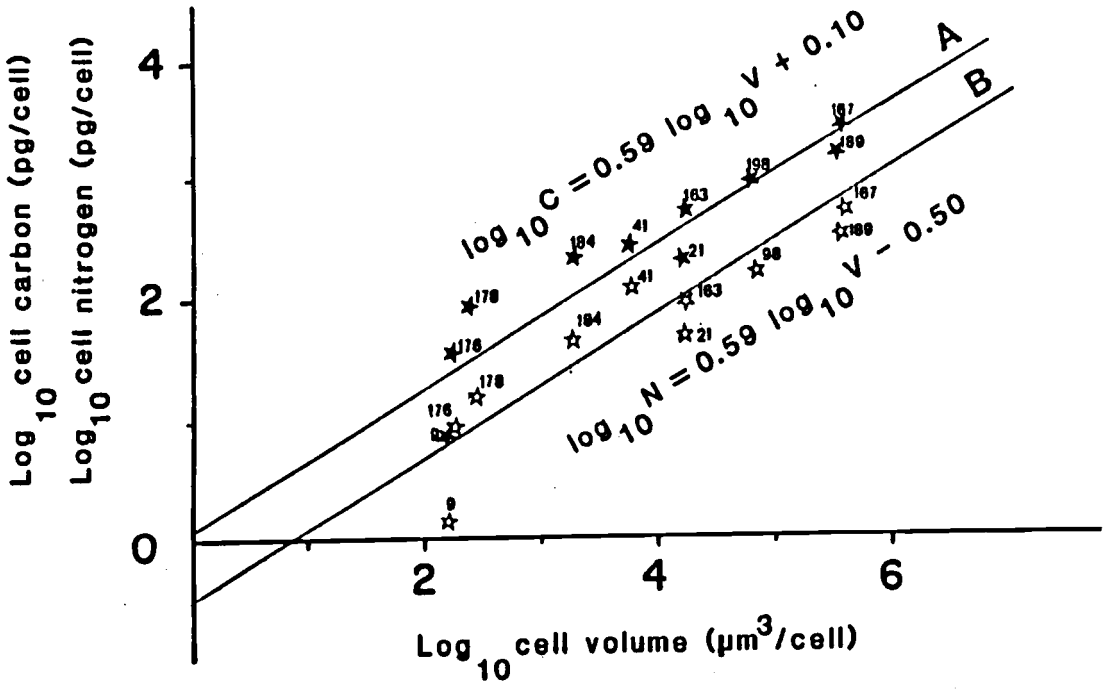

Fig. 12. a) Logarithm of cell carbon content as a function of the logarithm of cell volume. b) Logarithm of cell nitrogen content as a function of the logarithm of cell volume. Antarctic clone designation number is indicated beside each symbol.

★ Carbon

☆ Nitrogen

regression lines obtained for these two functions were identical to the second decimal figure but the Y-intercepts were not. This means that the difference in the carbon and nitrogen values of the species studied remained constant with increasing the cell volume, this value being given by the difference of the Y-intercepts of the two equations (i.e. + 0.60). The same parallelism between C and N values was also observed by Durbin (1977) for cultures of different sizes of Thalassiosira nordenskioeldii grown both at $0^{o}C$ and $10^{o}C$. A similar log-log plot (Fig. 13) of the data of Brzezinski (1985) of 18 diatom species from different localities including temperate and tropical species and grown under continuous illumination, resulted in the same parallelism between C and N values but with slopes different from the ones found in the present study.

Although a multilinear regression analysis (Neter et al., 1983) indicated that the two sets of regression equations were not significantly different ($p < 0.05$) it is interesting to look at the general trends of these two somewhat similar studies which include such a wide range of diatom species. The regression equations of Antarctic diatoms have a lesser slope than those for algae from temperate and tropical environments (Fig. 13), i.e. cell carbon (or nitrogen) seems to increase more rapidly with cell volume in diatoms from lower latitudes than in Antarctic ones. Also, for large cells, the Antarctic diatoms will have less carbon or nitrogen than the diatoms from other environments. Durbin (1977) also found a slightly higher content of carbon for the cells grown at $0^{o}C$ than the ones grown at $10^{o}C$ in opposition to what Yoder (1979) found.

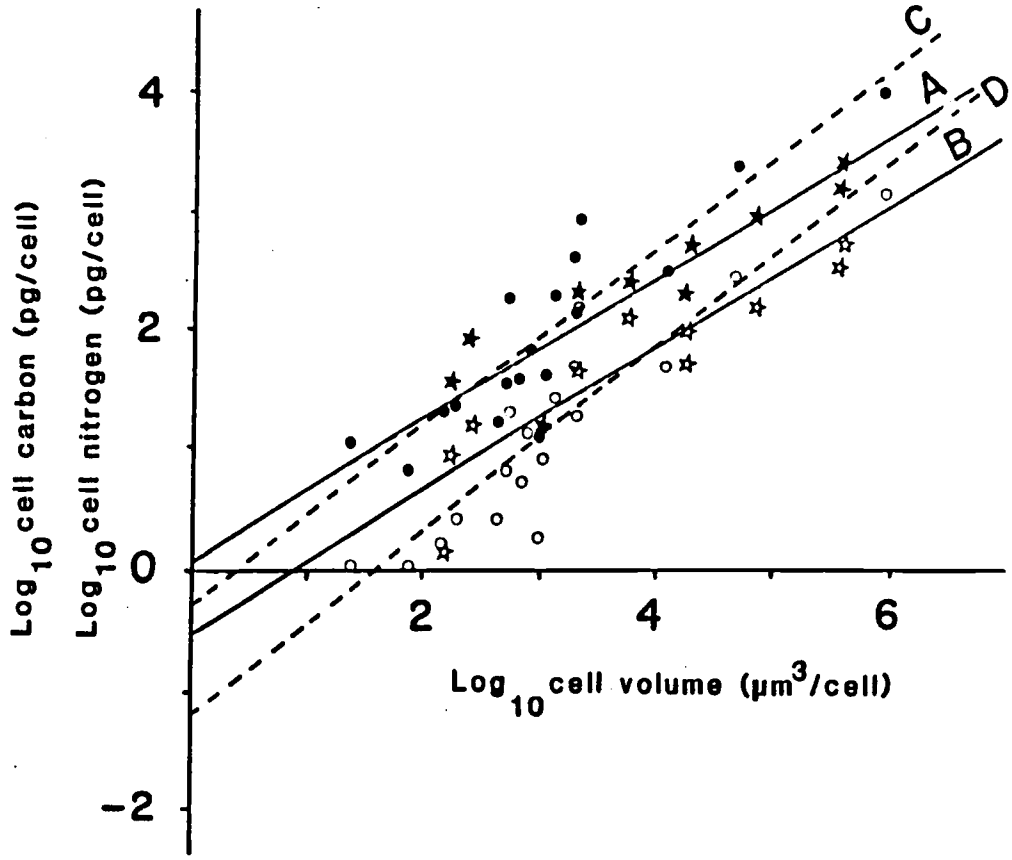

Fig. 13. a) Logarithm of cell carbon content of Antarctic diatoms as a function of the logarithm of cell volume. b) Logarithm of cell nitrogen of Antarctic diatoms as a function of the logarithm of cell volume. c) Logarithm of cell carbon content of other diatoms as a function of cell volume. d) Logarithm of cell nitrogen content of other diatoms as a function of cell volume. (c and d data from Brzezinski, 1985).

★ Carbon - Antarctic diatoms
☆ Nitrogen - Antarctic diatoms
● Carbon - Other diatoms
○ Nitrogen - Other diatoms

Yoder obtained a lower cell carbon content for cultures of Skeletonema costatum at low temperatures. Strathmann's (1967) equation for converting cell volume (V) of diatoms to cell carbon (C) is: log C = 0.758 log V - 0.422 which is very close to the one obtained from Brzezinski's (1985) data: log C = 0.750 log V - 0.303. Durbin (1977) found a good agreement of Strathmann's equation with the cell carbon measured at 10°C and a slight underestimate at 0°C (less carbon at lower temperatures). Mullin et al.(1966) had found that the regression equation for the cell carbon content as a function of cell volume of different groups of phytoplankters (mainly diatoms) grown at temperatures between 10°C and 21°C was: log C = 0.760 log V - 0.29 which is also very close to the above equations. Not so the one found in the present study: log C = 0.59 log V + 0.10. It is remarkable that three different authors working with algae from areas other than the Antartic found such similar results, while the only ones that differ are the results found here for Antarctic diatoms.

An expected value of cell carbon, nitrogen, silica and chlorophyll a content for Nitzschia curta in the Ross Sea can be computed using the respective linear regression equations of the logarithm of these constituents as function of the logarithm of the cell volume or cell surface obtained from the 10 clones studied in laboratory. These equations are listed in the Table 5.

The cell volume and cell surface area of N. curta in the Ross Sea was found using the average linear dimensions of 100 cells from

Table 5. Regression equations of the logarithm cell carbon, cell nitrogen, biosilica and chlorophyll *a* as a function of the logarithm of the cell volume or the cell surface area of the 10 Antarctic clones.

$$\log_{10} C = 0.59 \log_{10} V + 0.10$$

$$\log_{10} N = 0.59 \log_{10} V - 0.50$$

$$\log_{10} Si = 1.12 \log_{10} A - 1.84$$

$$\log_{10} \text{Chl } a = 1.07 \log_{10} A - 2.82$$

Table 6. Expected values of cell carbon, cell nitrogen, biogenic silica and chlorophyll *a* per cell for a *Nitzschia curta* species with the dimensions of that in the Ross Sea, based on the values obtained for the same species in laboratory cultures.

$$C = 5.172 \times 10^{-6} \ \mu\text{mol/cell}$$

$$N = 1.114 \times 10^{-6} \ \mu\text{mol/cell}$$

$$Si = 6.895 \times 10^{-7} \ \mu\text{mol/cell}$$

$$\text{Chl a} = 1.478 \times 10^{-6} \ \mu\text{g/cell}$$

the bloom. The calculation of the volume and the surface area was done as described previously for the culture experiments. The mean cell volume was found to be 741 μm^3 and the mean cell surface area 619 μm^2. This gave a S/V ratio of 0.84. Nitzschia curta cells in the field were thus much larger than those in culture (Table 4). Hendey (1964) pointed out that a prolonged culture of some diatoms (e.g. Nitzschia palea (Kützing.) W.Smith) results in a decrease in size and often in an increase of color intensity of the chromatophores. Both of these effects were observed in the cultures of N.curta, as compared to cells of this species growing naturally.

The expected values of the four constituents in the Ross Sea bloom were computed for transect #2, at stations where N. curta was dominant (i.e., stations 36-42). The counts of live (intact protoplasm) cells times the expected values of carbon, nitrogen and chlorophyll a per cell gives the expected values in the Ross Sea (Table 6). In the case of silica, the counts of empty frustules plus the counts of intact protoplasm cells were used.

The observed values of particulate carbon, particulate nitrogen, biogenic silica and chlorophyll a vs. the expected values in the Ross Sea bloom are plotted in figure 14. The slopes of the regression equations of all constituents forced through origin were compared with the slope of the equation $x = y$. A t-test ($p<0.05$) [Neter et al., 1983] showed significant difference between the slopes in each case. The slope of the equation for carbon was much less different than that of biogenic silica or chlorophyll a.

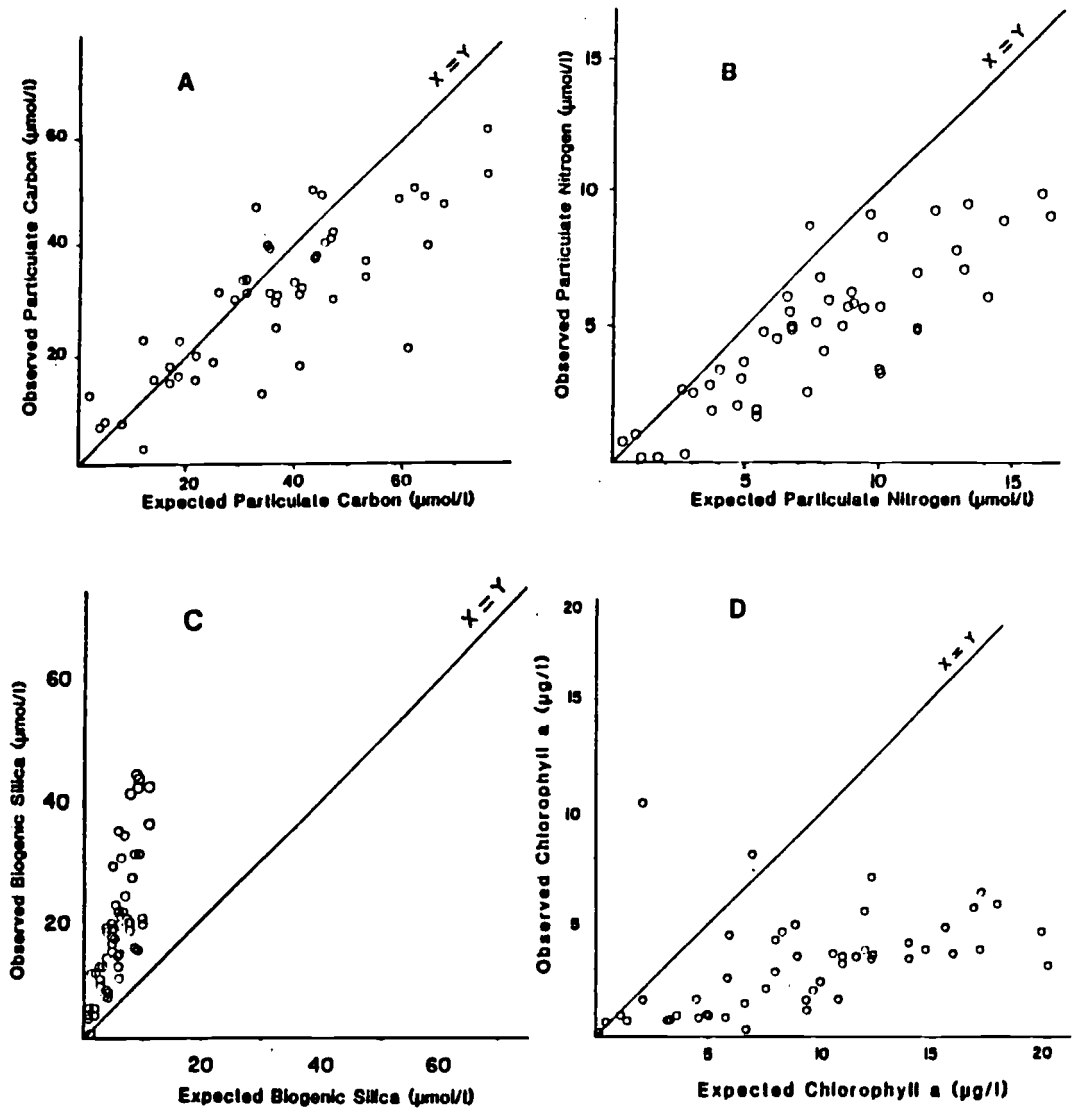

Fig. 14. Expected vs. observed values of elemental composition of the Nitzschia curta bloom in the Ross Sea (Transect #2). a) Particulate carbon. b) Particulate nitrogen. c) Biogenic Silica. d) Chlorophyll a.

Therefore, the expected Si/C and C/Chl ratios are much lower than the ratios observed by Smith & Nelson (1985). It is possible that these physiological differences are due to the fact that the clone of the Nitzschia curta examined in the laboratory might be a different genetic strain, as it comes from the Weddell Sea. It might have also been possible that the sea-ice algae have a different physiological response once they are in the water after the ice melts. Bunt (1968b) points out that field data from various sources for the same species indicates that assimilation numbers may differ widely from place to place in the Antarctic. Palmisano & Sullivan (1982) found remarkable physiological differences between two different clones of the Antarctic diatom Nitzschia cylindrus. In the present study, different clones of Coscinodiscus furcatus did show distinctly different elemental composition (Table 4).

In order to get the high biogenic silica concentrations observed in the Ross Sea, the concentration of silica per cell of Nitzschia curta would have have to be 2.6 x 10-6 umol, which is almost one order of magnitude more than the expected value used from the culture data.

Although the nanoplankton fraction in the bloom can reach very high numbers, a cleaning treatment for diatoms (Hasle & Fryxell, 1970) of one of the bloom samples destroyed all the nanoplankton except for very few nanodiatoms. This procedure confirmed the non-silicious nature of the nanoplankton. Also, the proportion of empty frustules within the bloom was less than 10% (see Part I).

Thus the very high biogenic silica levels within the bloom must reflect a very high silica content of living, identified diatom cells.

Data from the culture of Nitzchia curta in the laboratory are in agreement with the observation made by Smith & Nelson (1985) that the bloom in the Ross Sea produced by this species had a very anomalous composition. Since the cell counts of the Ross Sea bloom material (see Part I) showed that this bloom consisted mainly in N. curta living cells, the elemental ratios values found by Smith & Nelson (1985) can be compared with the ones found here for the 10 Antarctic clones. Although the difference in the elemental ratios between the N. curta and the other clones cultured was not as great as the difference observed in the Ross Sea, this difference is reflected in higher Si/C and lower C/Chl ratios in N. curta than in the other clones cultured. The difference in this direction (higher Si/C and lower C/Chl ratios) may happen with time as a pennate diatom is maintained in culture. It was mentioned before that prolonged cultures of some diatoms results in a decrease in size and in an increase of the color intensity of the chromatophores (Hendey, 1964). This might imply that the chlorophyll per cell (and presumably the Chl/C ratio) increase and the cell size decrease were observed in Nitzschia curta in culture.

The linear regression equations of the logarithm of cell silica content as a function of the logarithm of cell surface area of this study and Brzezinski's (1985) turned out to be very similar [Fig.

15]. This would suggest that for Antarctic diatoms the Si/C ratio would be higher than for other diatoms of the same size as the cell carbon content is much less in Antarctic diatoms. This might reflect the fact that large Antarctic diatoms generally present heavily silicified frustules.

A plot of the logarithm of the cell silica content per unit surface as a function of the cell surface (Fig. 16) shows that Si/surface area is independent of size, in opposition to what Durbin (1977) found. In his study a linear relationship between cell silica per unit surface and the cell surface area is shown. This relationship was also dependent on temperature. In the clones grown at $0^{o}C$ the amount of Si/unit cell surface area was signifcantly higher than for clones of similar size grown at $10^{o}C$. On the other hand, Paasche (1973), found the Si/unit surface area to be nearly constant for different-sized clones of Thalassiosira dicipiens.

The plots of the logarithm of the silica content per unit surface area as a function of the logarithm of the cell surface (Fig. 16) and the logarithm of the carbon cell content as function of the logarithm of the cell volume of both sets of data (Fig. 17) (this study and Brzezinski's) shows several interesting relationships as follows: 1) In both studies, silica per unit area showed to be independent of size and cell surface area (correlation coefficients = - 0.26887 and 0.51602 respectively). 2) Carbon per unit volume correlates reasonably well with cell volume in both cases (correlation coefficients = 0.87576 and 0.64119)

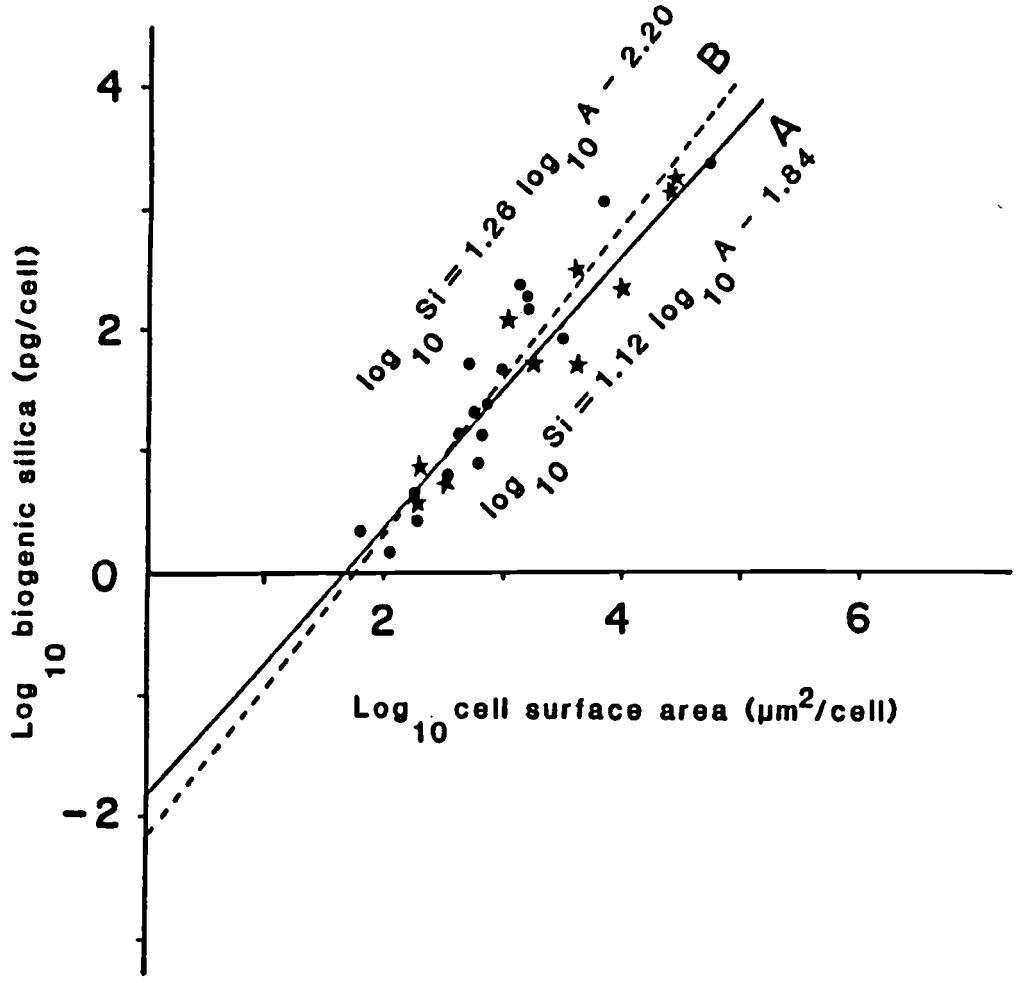

Fig. 15. Logarithm of biogenic silica as a function of the logarithm of cell surface area. a) Antarctic diatoms. b) Other diatoms (data from Brzezinski, 1985).

★ Antarctic diatoms

● Other diatoms

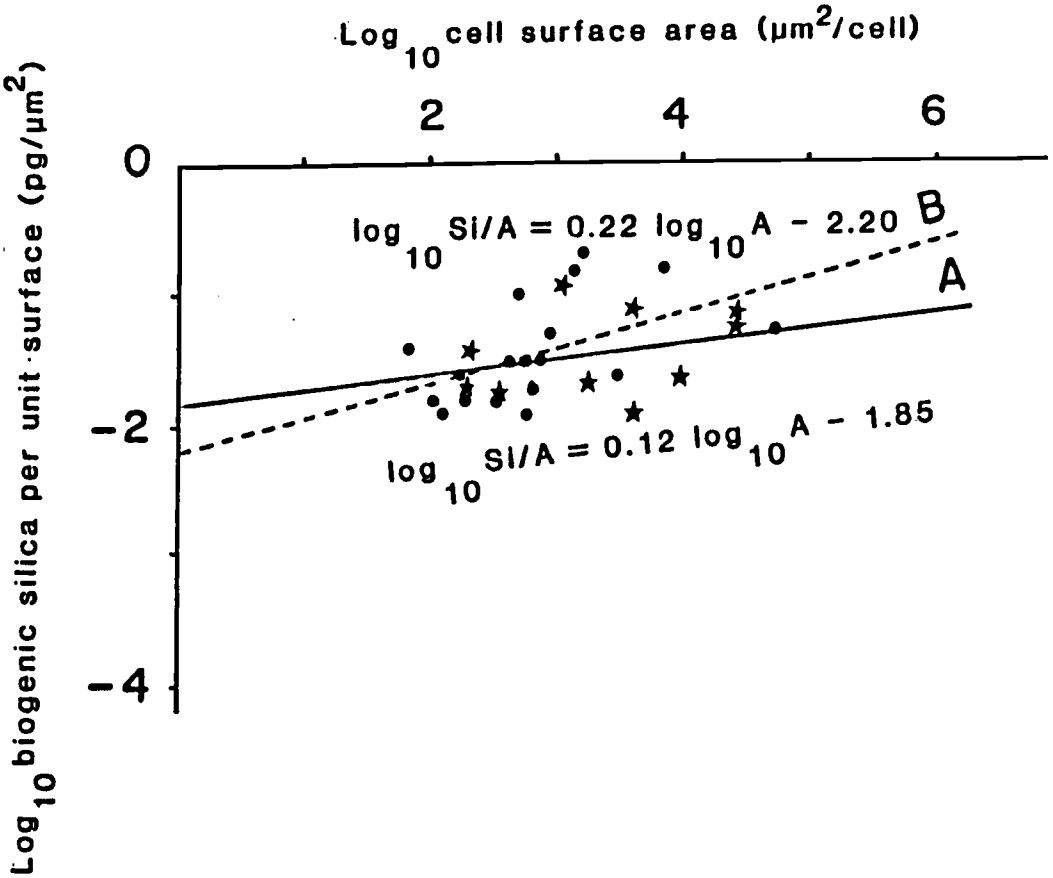

Fig. 16. Logarithm of biogenic silica per unit surface as a function of the logarithm of cell surface area. a) Antarctic diatoms. b) Other diatoms (data from Brzezinski, 1985).

★ Antarctic diatoms

● Other diatoms

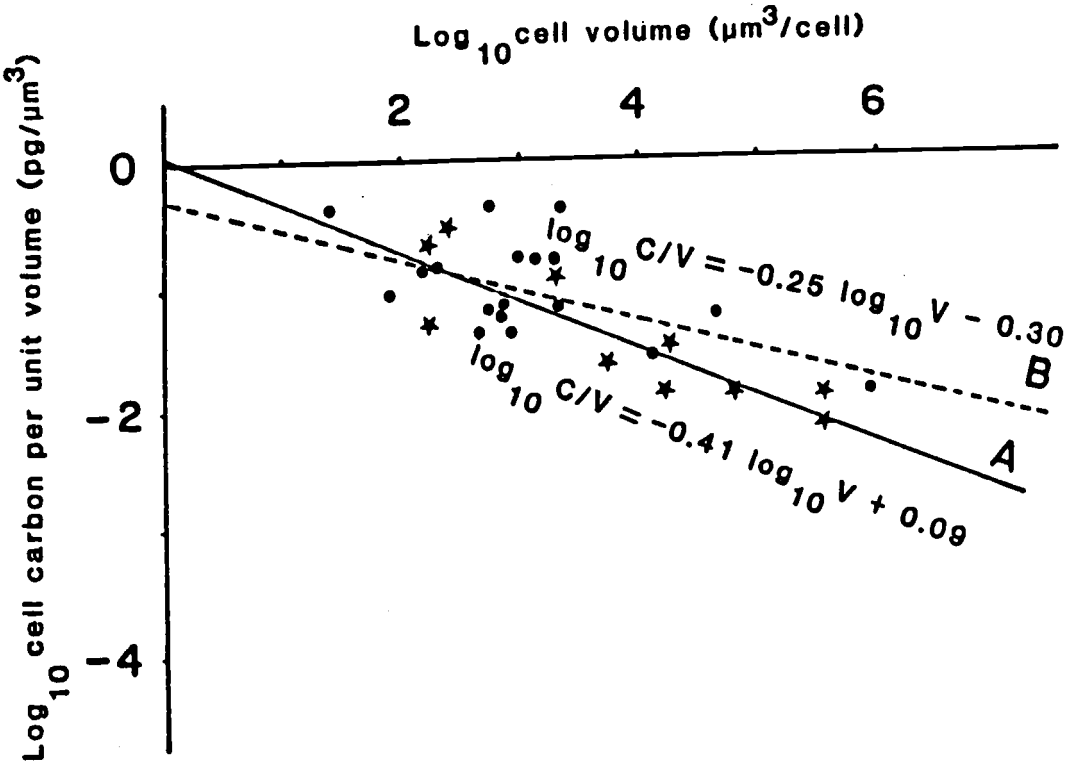

Fig. 17. Logarithm of cell carbon per unit volume as a function of the logarithm of cell volume. a) Antarctic diatoms. b) Other diatoms (data from Brzezinski, 1985).

★ Antarctic diatoms

● Other diatoms

respectively. 3) The negative slope of the regression equation of the logarithm of cell carbon per unit volume as a function of the logarithm of cell volume is steeper in this study than in Brzezinski's, i.e. there is a greater decrease in carbon per unit volume with increasing size in the present study. 4) If silica per unit area is relatively constant, for large diatoms the Si/C ratio will be relatively greater in Antarctic diatoms than in other diatoms (i.e. the decrease in carbon per unit volume by increasing cell size in other diatoms is less than in Antarctic diatoms, resulting in a higher carbon content for the same cell size in diatoms other than Antarctic). Therefore, the Si/C ratio will be higher in Antarctic diatoms which would be, once again, a confirmation of the heavily silicified appearance of the frustules of large Antarctic diatoms.

Nevertheless, not all large diatoms in this study presented a high Si/C ratio (Table 4). The exception, Porosira glacialis, showed a very low Si/C ratio (i.e. 0.10), less than the half of the Si/C ratio of diatoms with comparable S/V ratio, although species with very dissimilar S/V ratio like Nitzschia curta and N. cf. ritscherii showed very similar Si/C ratio as well as Si/N ratio. Durbin (1977) found a 10% increase in the Si/C ratio for the clones of Thalassiosira antarctica grown at $0^{o}C$ compared wih clones grown at $10^{o}C$.

The idea that temperature affects the silica content of diatoms comes from the beginning of the century when Gran (1912) illustrated

two types of Chaetoceros decipiens collected from cold and warm waters as strongly and weakly silicified cells respectively. Paasche (1980) suggested that low ambient silica concentrations would account better for the weakly silicified frustules rather than temperature. In his work, the Si/C ratio in 4 of 5 species of diatoms increased with the increase of temperature while the fifth diatom species showed a decrease in the Si/C ratio. In both Brzezinski's study and the one reported here the nutrient conditons of the growth media were adjusted to prevent silicon limitation. Therefore the observed difference in Si/C do not result from differences in the availability of silicic acid during the experiments. It is possible, though, that the elemental composition of Antarctic and low latitude diatoms reflect genetic adaptation to persistently high and low nutrient environments, respectively as suggested by Smith and Nelson (1985).

Although light intensity was not tested in the present study in relation with the elemental ratios, data from the literature suggest that low light intensity generally increases the Si/C and Si/N ratios. Brzezinski (1985) found that for clones under low light these ratios increased by a factor of two from those under high light intensity. A reanalysis of the data of Furnas (1978) made by Brzezinski (1985) suggests that light limitation might have increased both ratios from the ones this last author reports. Davis (1976) working with Skeletonema costatum also found an increase in the Si/N ratio under limiting light, in opposition to what was found by Paasche (1980) for the same species.

By comparing the Redfield-Richards ratio C:Si:N (Richards, 1958; Redfield et al., 1963) for the elemental composition of phytoplankton (Phosphorus not considered here) with the mean ratio found in this study,i.e. 6.63:0.94:1 with 5.7:1.03:1.0, it can be observed that Antarctic diatoms have less carbon and slightly more silica per unit nitrogen, resulting in higher Si/C ratios.

Si/N, C/N and C/Chl ratios show no correlation to either cell volume or cell surface ($p<0.05$, $r = 0.3443$, -0.0867 and -0.0022 respectively), while the Si/C ratio showed a weak correlation to cell surface area ($p<0.05$, $r = 0.6629$). Durbin (1977) did not find a change in the C/N ratio with cell size. He found a C/N ratio of 4.57 for cells grown at $0^{o}C$ and of 4.45 for cells grown at $10^{o}C$.

There are very few data in the literature on elemental composition of diatoms grown at very low temperatures. Doucette & Fryxell (1983) showed for Thalassiosira antarctica var. antarctica grown at $4^{o}C$ a C/N ratio (by atoms) of 3.03 for rapidly growing vegetative cells and 4.03-7.10 for resting spores. Yoder (1979) observed a range of 5-8 for C/N ratios, with a slight tendency to lower values at low irradiance.

In the present study, the highest and lowest values of C/N ratios were shown by 2 species with almost identical S/V ratio (i.e. Actinocyclus actinochilus and Porosira glacialis) [Table 4]. Other data from the literature deal with species grown at higher temperatures and light intensities, and show C/N ratios that are

somewhat different. French & Hargraves (1980) culturing 5 different species of diatoms at 15°C and 120 μE m^{-2} sec^{-1} obtained a range of C/N ratios (by atoms) between 1.4 and 5.48 for vegetative cells and 8.51 to 12.71 for resting spores. Harrison et al. (1977) cultured 3 species of diatoms at 18 C under continous illumination and found C/N ratios (by atoms) between 2.7 and 5.1. One of the species they studied, Thalassiosira gravida Cleve, is present in Antarctica (Balech & El-Sayed, 1965), and it showed the 2.7 value. The C/N ratios found by Brzezinski (1985) were much higher than the ones found in the present study. El-Sayed & Taguchi (1981) found C/N ratios for the phytoplankton population of the ice-edge in the Weddell Sea to be within the range of 6 and 7.3. Copin-Montegut & Copin-Montegut (1978) found a C/N ratio (by atoms) range of 5.39 to 5.77 for natural assemblages of phytoplankton along the Antarctic convergence in the Indian Ocean sector. These ratios are very close to the ones found in this study and to the ones found in the Ross Sea (Nelson et al., in preparation).

It is very difficult to compare Si/C ratios values in culture with those in the field, since populations having different floristic compositon must have different degrees of silicification as well (Spencer, 1983). The Si/C ratio (by atoms) range found by Copin-Montegut & Copin-Montegut (1978) in the Antarctic zone was 0.27 tp 0.41 (this latter value south of the Kerguelen Islands) which is generally higher than the ones found here: 0.03-0.36 for just 10 Antarctic clones. Durbin (1977) found a range of 0.37 to 0.41 for Thalassiosira nordenskioeldii grown either at 0°C or 10°C.

Nelson & Gordon (1982) suggest an empirical ratio of 0.12 for Si/C ratios as a reasonable estimate for natural diatom assemblages, but did not consider the possibility that this ratio may be higher in the Antarctic. Brzezinski (1985) showed a value of 0.13 for this ratio in continuous illumination experiments on temperate and tropical diatoms. Other data from the literature suggest values of 0.12 to 0.25 (Eppley et al., 1967) and 0.10 to 0.11 (Paasche, 1980). With the considerations made here, one might expect to find very high values in Antarctica. Smith & Nelson (1985) found a mean value of 0.62 for the euphotic zone in the Ross Sea which is the highest ratio ever reported.

There is not much information on Si/N ratios. Harrison et al. (1977) found a range of 0.43 to 0.54 while the mean value reported by Brzezinski (1985) was 1.12 which is very close to the mean value reported here of 1.04 for the Antarctic diatoms. Despite the parallelism showed by carbon and nitrogen values, the Si/N ratio did not behave as the C/N ratio did. The Si/N ratio was apparently not much higher in Antarctic diatoms than in other diatoms, as the nitrogen values for both data sets (this study and Brzezinski's) are not as far apart as the carbon values are. Le Jehan & Treguer (1983) found a much higher value for the Si/N ratio of natural phytoplankton along a transect between the Kerguelen Islands and the Antarctic continent. The ratio range was 8-13 which is much higher than the one given by Richards (1958) suggesting that these algae had an anomalous composition as well. In the Ross Sea, for the transect #2, the mean value of Si/N ratio was 3.89 with a high value

of 6.52 and a low of 1.88. Jacques (1983) mentions very high values for Si/N as well. He did some preliminary silicate uptake experiments with two Antarctic diatoms, Nitzschia (=Fragilariopsis) kerguelensis and N. turgiduloides finding a high Vmax despite the low temperatures. The half-saturation constants were also high, 2-4 times higher than the ones found in other species. These data support the idea of a low efficiency of Si-uptake, and thus a need for high ambient silicic acid concentration to approach the Vmax and probably the optimal growth rate (Jacques, 1983). Consequently, silica may be at times a limiting factor even with the high values found in the Antarctic. Although no uptake experiments were made in the present study, the preliminary silica analysis suggested that silica was close to depletion after harvesting the cultures at the end of exponential growth.

An actively growing phytoplankton population in recently upwelled water may have a C/Chl ratio (by weight) of 30 (Parsons & Takahashi, 1977). The data reported in the literature are not very far from this value. Bunt & Lee (1972) found that the C/Chl ratio for the common sea ice algae Nitzschia sublineata (Van Heurck) Hasle was within the range of 26 to 61. Palmisano & Sullivan (1983) found a mean ratio of 31 for ice microalgae in Mc Murdo Sound and Doucette & Fryxell (1983) for Thalassiosira antarctica showed a value of 35.6 for vegetative cells. Durbin (1977) found a ratio of 48 for the clones grown at $0^{o}C$ and 32.6 for the ones grown at $10^{o}C$. The Antarctic algae examined showed a mean value of 43.8, with a maximum value of 90.2 and a minimum of 18. The maximum value exhibited by

Chaetoceros cf. gracile is confirmed by the slight pigmentation of these cells as seen under the microscope. Yoder (1979) found that C/Chl ratios were much higher in cultures of Skeletonema costatum at $0^{o}C$ than at higher temperatures at the same light intensity.

As mentioned before, when the expected values of chlorophyll a for Nitzschia curta in the Ross Sea are calculated, these values are much higher than the ones observed in the field while the carbon values are very close, causing the observed C/Chl ratio to be overwhelmingly higher than the expected value. The mean value found by Smith & Nelson (1985) was 118.2 for the euphotic zone.

The culture of the Antarctic diatoms was made to find an explanation for the anomalous composition of the bloom observed in the Ross Sea. The hypothesis tested was that Antarctic diatoms are characteristically different in their composition from diatoms growing elsewhere in the ocean. The results support this hypothesis qualitatively by showing a different relationship between silica content, chlorophyll a content and cell size for Antarctic diatoms than for other diatoms. Nevertheless, the differences apparent in field data (Jacques, 1983; Le Jehan & Treguer, 1983; Smith & Nelson, 1985) are even greater than those observed in the culture study of the 10 Antartic diatom clones. Comparison of laboratory and field data allows the following conclusions to be drawn: 1) The anomalous composition of Nitzschia curta in the Ross Sea derives from very high silica concentrations and very low concentrations of chlorophyll a, compared to what was observed in the laboratory

experiments. 2) The Si/C ratios in large diatoms of the Antarctic are expected to be much higher than those observed in other diatoms. 3) The C:Si:N ratio for Antarctic diatoms, when compared to the Redfield-Richards ratio for diatoms of other environments, results in lower carbon and higher silica numbers per unit nitrogen for Antarctic diatoms. 4) Similar S/V ratios do not lead to similar elemental ratios. These depend almost exclusively upon the physiology of a particular strain, rather than on its morphology. This emphasizes the importance of good and precise taxonomy. In ecological studies, the misidentification of species will lead to misinterpretation of their ecological role. In the case of Nitzschia curta and N. cylindrus the morphological differences between the two are very small (mainly number of costae, differences in length and polarity of the valves), but the distinction of two species in this case is more than justified when their elemental ratios are compared, as these ratios are markedly different (Table 4).

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APPENDICES

APPENDIX A

Since the diatom species which dominated the bloom in the Ross Sea plays such an important role in this study, a brief historical review is given in this section. Nitzschia curta (Van Heurck) Hasle was first described by H. Van Heurck (Director of the Botanical Gardens of Anvers, Belgium) in 1909 as Fragilaria curta in his report of the diatoms collected by the Antarctic Belgian Expedition of the "Belgica" between 1897-1899. The sample in which Nitzschia curta was found was melted sea ice and was green-brownish in color. It was collected the 13 of February of 1898 at 65°15' S and 64°30' W (close to the Antarctic Peninsula). Dimensions: apical axis: 20 µm. Transapical axis: 6 µm.

The second report of Nitzschia curta (also as Fragilaria curta is by Fritsch (1912) in his report of the Freshwater-Algae collected by the "Discovery" National Antarctic Expedition (1901-1904). It was also found in the ice in a pond in Cape Adare (71°S). Fritsch says in his report that the sample came from freshwater ice under a boulder, and if this is so, it makes this species exceptionally euryhaline. Fritsch points out for the first time the heteropolarity of the valvae, which had not been mentioned by Van Heurck. Dimensions: apical axis: 19 µm. Transapical axis: 6 µm.

Nitzschia curta might have been reported by Heiden & Kolbe (1928, p.551) during the German South Polar Expedition of 1901-1903 as Fragilaria linearis Castracane 1886. These authors made the hypothesis that Castracane's original species might have had the

curved costae that are one of the characteristics of Nitzschia curta (= Fragilaria curta) and that these might have been overlooked by Castracane in the original description. Heiden & Kolbe point out that if after an examination of the original specimens of Castracane their hypothesis proved not to be true, then they would have to include some of their specimens under Fragilaria curta Van Heurck. Some of the records given by Heiden & Kolbe of Fragilaria linearis Castr. derived from samples from the ice, which strongly suggests that some of the specimens included by them under F. linearis were, in fact, Nitzschia curta.

Another record of Nitzschia curta is given by Hendey (1937) in the "Discovery" reports. He recorded this species (as Fragilaria curta Van Heurck) in great numbers in a melted ice sample (ca. 66°S, 69°W). According to Hendey (1937) Nitzschia curta must be characteristic of the coastal diatom flora of the land-masses within the Antarctic Convergence. Dimensions: apical axis: 24-30 µm. Transapical axis: 8 µm.

The genus Fragilariopsis was established by F. Hustedt in 1913 in A. Schmidt's Atlas (Pl.299) based upon a species previously described as Fragilaria antarctica Castracane (=Nitzschia kerguelensis (O'Meara) Hasle 1972). The reason for the creation of the genus Fragilariopsis was the absence of a pseudoraphe which is a diagnostic feature of the genus Fragilaria.

Hart (1942) found that Nitzschia curta (cited as Fragilariopsis curta (Van. Heurck)) was one of the most abundant species among ice

forms, together with Nitzschia lineata and N. sublineata.

Frenguelli (1943) reported Nitzschia curta from the South Orkney Islands. He recorded this species as Fragilariopsis linearis (Castracane.) Hustedt in part., (i.e. not all cells recorded were Nitzschia curta). Frenguelli (1960) cited Nitzschia curta in his report on diatoms and silicoflagellates from Adelie Land during the French polar expeditions of the "Paul-Emile Victor" between 1949 and 1952. He regarded the species Nitzschia curta as a variety of Fragilariopsis linearis, reporting it as F. linearis var. curta. He found that the variety frequently accompanied F. linearis, but that it was never abundant. Samples were taken in net tows through holes or larger openings in the ice. Frenguelli & Orlando (1958, 1959) also reported Nitzschia curta as Fragilariopsis linearis var. curta (cf. Hasle, 1965).

The northernmost records of Nitzschia curta can be found in Balech (1959) and Frenguelli & Orlando (1959). Balech (1959) points out in his report of the dinoflagellates of the Operación Merluza-V cruise that samples collected between 39°30'S 53°40'W and 41°30'S 59°20'W contained many Antarctic dinoflagellates. In his samples he found also Antarctic diatoms like Fragilariopsis linearis var. curta, as a rare species (the identification was done by J. Frenguelli). The temperature of the water was less than 6°C.

Hustedt (1958a) found N. curta (reported as Fragilariopsis curta for the first time) in the stomach contents of Euphasia, Salpa fusiformis and S. confoederata in samples from 69°41'S to 39°14'S,

$0^{o}03'W$. Hustedt (1958b) recorded Nitzschia curta as Fragilariopsis curta both from the Antarctic ice edge and as a subtropical species from the South Atlantic (cf. Hasle, 1965).

Manguin (1960) in his report on diatoms of Adelie Land ($66^{o}50'S$ $141^{o}25'E$ also recorded Nitzschia curta as Fragilaria curta Van Heurck. He reported this species from stations the Antarctic Ocean. It was more abundant towards the continent and became rare close to the subantarctic zone where temperature was between 4 to $8^{o}C$. He did not find the species where the temperature was above 8^{o}. Manguin reported N. curta as an endemic Antarctic species inhabiting both neritic and oceanic environments. He found it more abundant close to the ice in the neritic zone. The collections were made during February of 1950 (end of austral summer). Dimensions: Apical axis, 15-45 µm. Transapical axis, 5-6 µm.

The species has been reported also for the Antarctic as Fragilariopsis curta by Kozlova (1962, 1964) (cf. Hasle, 1965 and Burckle, 1984). Ivanov (1964) reported it from the Soviet Antarctic Expedition (1957-1958). Cassie (1963) recorded Fragilaria curta from samples collected between $74^{o}40'S$ and $77^{o}37'W$. She reported an increase of the species towards the Antarctic continent. Burkholder & Mandelli (1965) found Nitzschia curta (reported as Fragilariopsis curta) in moderate amounts in the ice along the west coast of the Antarctic Peninsula. Fukushima & Meguro (1966) reported Nitzschia curta (as Fragilariopsis curta in sea ice as a subdominant species. Meguro et al. (1967) also reported N. curta (as Fragilariopsis

curta as a species abundant in ice in Lutzow-Holm Bay, Antarctica. Hargraves (1968) reported Nitzschia curta (as Fragilariopsis curta) from the Pacific sector of the Antarctic Ocean as a very abundant species in pack ice ($65^{o}54'S$ $115^{o}08'$ W and $62^{o}51'S$ $159^{o}W$). He also found it in net tow samples ($56^{o}59'S$ $150^{o}10'W$). Dimensions: 12-13 µm apical axis. 4-7 µm transapical axis.

In the "Brategg Expedition" (1947-1948) the records of Nitzschia curta (reported as Fragilariopsis curta (Van Heurck) Hustedt) indicate that this species was endemic to the Antarctic zone and that its abundance increased southward towards the Antarctic continent. Close to the ice edge, its abundance was equal to that of Nitzschia kerguelensis, these two species being the two most numerous of the genus. In the samples from the under-surface of pack-ice, N. curta and N. cylindrus were the predominant species of the genus (Hasle, 1969).

El-Sayed (1971) found Nitzschia curta (reported as Fragilariopsis curta in water samples in the Southwestern Weddell Sea. Steyaert (1973a,b; 1974) also reported Nitzschia curta (as Fragilariopsis curta) during the Belgian-Dutch Antarctic Expeditions of 1964-1965 and 1966-1967. She found that the abundance of this species increased towards the Antarctic continent and that its maximum abundance was in inshore waters.

Hasle (1972) in a short communication transferred the genus Fragilariopsis Hustedt to a section of the genus Nitzschia Hassall. She did not consider that there was sufficient difference to justify

the existance of two separate genera. In this way, all the previous Fragilariopsis species were transferred to Nitzschia. Kalinsky (1973) in his PhD dessertion made a complete nomenclatural revision of the genus Nitzschia Hassall, and, although he refers to the Hasle's 1969 paper, he does not include the old Fragilariopsis species within the Nitzschia Hassall genus.

Recently, Krebs (1983) reported Nitzschia curta as part of the sea ice flora associated with the fall and spring blooms that occurred in Arthur Harbor, Antarctica between Janurary 1972 and January 1973.

Records of Nitzschia curta in Antarctic sediments can also be found in the literature. Josue et al., 1962, cited Fragilariopsis curta from the sediments of the Indian sector of the Antarctic Ocean. Truesdale & Kellogg (1979) reported this species as a very important component of modern sediments in the Western Ross Sea. Burckle (1984) also found that the sediments in the Ross Sea were dominated by Nitzschia curta. However, Schrader (1976) found Nitzschia curta only in one site in the northwestern Ross Sea.

Nitzschia curta has always been reported as an Antarctic species mainly from the South Antarctic zone (Guillard & Kilham, 1976). The record of Nitzschia curta for the Canadian Arctic by Hsiao (1979, 1980, 1983) is questionable. It is based upon a single observation made during the analysis of sea ice microalgae of Eclipse Sound, not having been observed during routine cell counts. A misidentification seems very likely in this case.

APPENDIX B

Table 7. Phytoplankton cell count data. Station 14. (Concentrations in cells/1 x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	6.160	5.910	6.590	6.610	7.690	6.700	0.757	0.001	
N. curta (empty frustules)	0.529	0.417	0.599	0.456	0.576	0.603	0.178	0.003	
N. closterium	0.232	0.243	0.309	0.247	0.127	0.031			
N. kerguelensis (intact cells)					0.004		0.015		
N. kerguelensis (empty frustules)					0.004			0.001	
N. sicula		0.008	0.004			0.004			
N. barkleyi			0.004	0.004	0.004		0.004	0.009	
N. pacifica							0.004		
Nitzschia sp.							0.004		
Chaetoceros sp.		0.004	0.012		0.012	0.019	0.004		
C. dichaeta					0.004		0.015		
Asteromphalus hyalinus				0.004					
Tropidoneis aff. antarctica				0.004					
Thalassiosira sp.							0.004		
Big Central Diatoms	0.008				0.004	0.015	0.008		
Small Central Diatoms	0.019	0.015	0.046	0.015	0.015	0.012		0.003	
Nanoplankton	1.720	1.810	2.100	2.020	1.440	0.514	0.541		
Amphidinium cf. hadai						0.008			
Amphidinium sp.			0.004			0.004			
Gyrodinium cf. lachryma	0.004								
Prorocentrum antarcticum		0.004							
Diplopeltopsis minor					0.004	0.008			
Protoperidinium incertum	0.004			0.008					
P. nanum					0.004	0.004	0.008		
Distephanus speculum			0.004		0.004	0.008	0.004		
TOTAL BIOMASS	8.680	8.410	9.660	9.370	9.900	7.920	1.060	0.017	

Table 8. Phytoplankton cell count data. Station 15. (Concentrations in cells/l x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	0.792	1.210	0.734	1.020	3.440	4.890	0.591	0.002	
N. curta (empty frustules)	0.286	0.135	0.155	0.251	0.263	0.340	0.127		
N. closterium	0.263	0.274	0.212	0.259	0.456	0.336	0.031		
N. barkleyi					0.004				
N. sicula						0.004	0.0008		
N. kerguelensis (empty frustules)								0.004	
N. pacifica								0.0008	
N. aff. marina						0.004			
Nitzschia sp. A		0.012							
Big centric diatoms							0.012	0.002	
Small centric diatoms	0.004	0.008	0.019		0.019	0.008	0.008		
N. cf. barkleyi							0.004		
Nanoplankton	0.131	0.379	0.081	0.089	0.108	0.135	0.023		
Diplopeltopsis minor			0.004			0.004			
Gyrodinium cf. lachryma	0.004								
Amphidinium sp.				0.004					
Protoperidinium antarcticum			0.012						
P. incertum	0.004	0.015	0.004		0.008				
P. cf. mediocre						0.008			
P. nanum				0.004	0.008	0.004			
Unidentified naked dinoflagellates		0.008							
TOTAL BIOMASS	1.490	2.040	1.220	1.630	4.300	5.730	0.796	0.008	

Table 9. Phytoplankton cell count data. Station 17. (Concentrations in cells/l x 10^6)

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	10.380	9.590	9.50	9.360	8.270	11.360	4.770	0.004	
N. curta (empty frustules)	0.722	0.742	0.869	0.966	0.788	0.738	0.545	0.007	
N. closterium	0.661	0.294	0.587	0.549	0.494	0.444	0.695		
N. kerguelensis (empty frustules)	0.004							0.001	
N. sicula		0.012	0.004	0.004					
N. cf. barkleyi		0.004							
N. barkleyi					0.004	0.004		0.007	
Nitzschia sp. B							0.004		
Asteromphalus hookeri					0.004	0.004	0.004		
Chaetoceros sp.	0.004	0.004				0.012	0.004		
C. dichaeta						0.004			
Melosira sp.			0.004						
Eucampia balaustium							0.004		
Big Central Diatoms	0.004	0.004	0.004	0.008	0.004		0.004		
Small Central Diatoms	0.008	0.008	0.004	0.023	0.004	0.008			
Unidentified empty naviculoid			0.004						
Nanoplankton	1.090	1.630	2.310	2.240	1.720	2.330	0.927		
Amphidinium cf. hadai				0.004		0.004	0.008		
Gymnodinium minor			0.004						
Gymnodinium sp.			0.004						
Gyrodinium rhabdomonte				0.004					
G. fusiforme		0.008	0.008						
G. cf. lachryma				0.004					
Diplopeltopsis minor			0.004	0.004	0.004	0.031	0.004		
Protoperidinium nanum		0.012	0.004	0.008	0.004	0.019	0.004		
P. incertum	0.004	0.019	0.012	0.015	0.004	0.008			
P. cf. mediocre			0.004						
P. glyptopterum							0.008		
P. defectum							0.008		
Amphidinium sp.				0.004					
Unidentified naked dinoflagellate						0.008			
Distephanus speculum		0.004		0.008		0.004			
TOTAL BIOMASS	12.880	12.330	13.210	11.310	14.970	6.37	0.020		

Table 10. Phytoplankton cell count data. Station 18. (Concentrations in cells/1 x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	9.870	13.530	10.38	11.47	11.70	3.16	0.027	0.001	
N. curta (empty frustules)	1.290	0.807	0.877	0.912	1.260	0.711	0.073	0.005	
N. closterium	0.657	0.726	0.525	0.552	1.260	0.475	0.004	0.001	
N. kerguelensis (intact cells)						0.031	0.066	0.001	
N. kerguelensis (empty frustules)		0.008				0.031	0.012	0.010	
N. sicula	0.004					0.004			
N. barkleyi		0.008	0.004	0.012		0.031	0.004		
N. aff. obliquecostata						0.012			
Chaetoceros sp.	0.004	0.008							
C. dichaeta						0.046			
Eucampia balaustium						0.012	0.008		
Asteromphalus parvulus	0.004			0.004	0.004				
A. hookeri	0.004	0.004		0.004					
Rhizosolenia aff. styliformis			0.004						
Big Central Diatoms	0.004		0.12					0.001	
Small Central Diatoms	0.008	0.008	0.004	0.008	0.008	0.035			
Nanoplankton	1.430	2.720	2.540	1.960	1.030	1.700			
Amphidinium cf. hadai					0.008	0.004			
Gymnodinium minor	0.004								
G. flavum					0.004				
Gyrodinium rhabdomonte		0.008	0.008						
Diplopeltopsis minor						0.015			
Protoperidinium applanatum						0.008			
P. antarcticum	0.004		0.004						
P. nanum	0.015	0.012		0.015	0.008				
P. incertum	0.012	0.019	0.008	0.004	0.019	0.004			
P. mediocre						0.008			
P. cf. mediocre				0.004					
Distephanus speculum		0.004	0.004		0.004	0.008			
TOTAL BIOMASS	13.310	17.860	14.370	14.950	15.300	4.770	0.193	0.022	

Table 11. Phytoplankton cell count data. Station 19. (Concentrations in cells/1 x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	4.720	6.140	6.910	6.230	6.36	2.17	0.050		
N. curta (empty frustules)	0.579	0.510	0.769	0.838	0.807	0.294	0.066		
N. closterium	3.370	5.210	5.580	2.390	1.780	0.155	0.008		
N. kerguelensis (intact cells)		0.031		0.031	0.606	0.305	0.209		
N. kerguelensis (empty frustules)		0.008	0.019		0.120	0.081	0.004	0.012	
N. sicula		0.004	0.004		0.012	0.004			
N. aff. obliquecostata		0.004							
N. barkleyi				0.008	0.004	0.004			
N. pacifica					0.004				
Nitzschia sp. A		0.008							
Chaetoceros sp.	0.004								
C. dichaeta	0.004	0.008	0.004	0.015	0.039	0.043			
Thalassiosira sp.		0.004							
Eucampia balaustium						0.019	0.023		
Big Central Diatoms		0.004			0.004				
Small Central Diatoms	0.012		0.012	0.008	0.019	0.035	0.015		
Unidentified pennate					0.004				
Nanoplankton	0.506	0.193	0.193	0.552	0.251	0.116	0.035		
Gyrodinium rhabdomonte	0.004		0.004	0.008					
Amphidinium cf. hadai			0.004		0.008	0.004	0.004		
Cochlodinium sp.				0.008					
Diplopeltopsis minor			0.004	0.004	0.004	0.004			
Dinophysis contracta							0.008		
Protoperidinium adeliense						0.004			
P. incertum	0.012		0.004	0.004	0.012				
P. raphanum	0.004	0.012							
P. glyptopterum		0.004					0.004		
P. applanatum		0.004							
P. antarcticum		0.004		0.004					
P. nanum					0.012				
P. cf. raphanum				0.004					
P. elegantissimum					0.004				
Distephanus speculum	0.004	0.004		0.008	0.012	0.008	0.004		
TOTAL BIOMASS	9.210	12.160	13.500	10.650	10.050	3.26	0.464	0.012	

Table 12. Phytoplankton cell count data. Station 20. (Concentrations in cells/l x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	2.780	2.260	3.150	5.590	4.920	11.10	0.498	0.001	
N. curta (empty frustules)	0.093	0.062	0.224	0.742	0.800	1.52	0.162	0.001	
N. closterium	0.359	0.406	0.479	0.715	0.448	0.309	0.015		
N. barkleyi					0.004	0.012	0.008		
N. kerguelensis (intact cells)				0.012	0.008		0.008		
N. kerguelensis (empty frustules)				0.012			0.008	0.002	
N. sicula	0.008		0.004	0.004	0.012		0.001		
Nitzschia sp. B	0.004	0.004		0.004					
N. pacifica	0.008								
Chaetoceros sp.						0.004			
C. dichaeta					0.004	0.008	0.008		
Eucampia balaustium						0.008	0.008		
Actinocyclus divisus	0.004								
Tropidoneis sp.					0.004				
Nitzschia medioconstricta				0.012					
Asteromphalus parvulus				0.004					
A. hookeri						0.004			
Small Central Diatoms	0.031	0.008	0.031	0.023	0.008	0.023	0.019		
Big Central Diatoms	0.004	0.015		0.008	0.004				
Unidentified empty naviculoid	0.004								
Nanoplankton	2.720	1.440	1.860	1.360	0.742	0.344	0.054		
Amphidinium sp.								0.001	
Amphidinium cf. hadai					0.004	0.015			
Gyrodinium rhabdomonte		0.004		0.004					
G. cf. lachryma	0.004								
Cochlodinium sp.			0.004						
Diplopeltopsis minor					0.012	0.004	0.004	0.004	
Unidentified naked dinoflagellate	0.004							0.004	
Prorocentrum antarcticum							0.004		
D. perlata				0.004					
Protoperidinium nanum			0.008			0.008			
P. incertum	0.004	0.012			0.027				
P. applanatum	0.004								
P. raphanum	0.004							0.001	
P. defectum			0.004			0.004			
P. cf. applanatum								0.001	

Table 12. Phytoplankton cell count data. Station 20 (cont.) (Concentrations in cells/l x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Distephanus speculum				0.008	0.004	0.015			
Ebridians					0.004				
TOTAL BIOMASS	6.030	4.210	5.760	8.510	7.000	13.390	0.796	0.011	

Table 13. Phytoplankton cell count data. Station 21. (Concentrations in cells/l x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	15.040	13.980	13.020	11.030	6.790	3.87	0.008	0.002	
Nitzschia curta (empty frustules)	1.004	1.110	1.120	0.715	0.993	0.738	0.008		
N. closterium	0.062	0.127	0.100	0.073	0.023	0.024		0.001	
N. kerguelensis (intact cells)					0.015	0.015			
N. kerguelensis (empty frustules)					0.008		0.004		
N. barkleyi					0.004		0.004		
N. sicula			0.008	0.004					
Chaetoceros sp.	0.004		0.004						
Asteromphalus hyalinus				0.004					
A. parvulus			0.015						
A. cf. hepactis		0.008							
Surirella aff. fastuosa					0.019				
Big Central Diatoms			0.004		0.008				
Small Central Diatoms	0.008	0.012	0.004	0.012	0.008	0.104			
Nanoplankton	2.810	3.590	2.710	1.130	0.734	0.189			
Amphidinium cf. hadai		0.012							
Amphidinium sp.			0.004		0.004				
Gymnodinium minor		0.004						0.001	
Gyrodinium cf. lachryma					0.004				
G. rhabdomonte			0.004						
Unidentified naked dinoflagellate				0.004				0.006	
Diplopeltopsis minor	0.012		0.012	0.004	0.004				
D. perlata	0.008								
Protoperidinium nanum	0.012	0.008	0.012	0.023	0.004				
P. incertum		0.012	0.008	0.027					
P. defectum					0.004				
P. cf. raphanum		0.004							
P. thulesense								0.001	
Gyrodinium cf. fusiforme								0.001	
Distephanus speculum	0.004		0.008		0.012	0.004			
Phaeocystis sp.								2.470	
TOTAL BIOMASS	18.970	18.870	17.030	13.030	8.630	4.95	0.023	2.480	

Table 14. Phytoplankton cell count data. Station 22. (Concentrations in cell/1 x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	0.664	0.552	1.580	0.776	0.135	0.124	0.127		
N. curta (empty frustules)	0.015		0.012	0.008	0.062		0.004		
N. closterium	0.043	0.004	0.027	0.008	0.004	0.012			
N. kerguelensis (intact cells)	0.015		0.004	0.058		0.008			
N. kerguelensis (empty frustules)					0.019				
N. sicula	0.004			0.015	0.008				
N. barkleyi	0.035				0.015				
N. vanheurckii			0.046		0.004				
Nitzschia sp. B.	0.008								
Chaetoceros sp.	0.023	0.046	0.046	0.012	0.008				
Eucampia balaustium			0.004						
Navicula sp.					0.004				
Unidentified pennate		0.004	0.008			0.004			
Small Central Diatoms		0.015	0.004						
Nanoplankton	0.888	0.618	1.150	1.690	0.888	0.089	0.093		
Gyrodinium rhabdomonte	0.004	0.004							
Unidentified naked dinoflagellates	0.004	0.008	0.008	0.004		0.004			
Dinoflagellate cyst ?	0.004								
Protoperidinium nanum					0.004				
P. defectum					0.008				
P. raphanum		0.004	0.004						
P. cf. unipes								0.001	
Distephanus speculum	0.008			0.004	0.004				
TOTAL BIOMASS	1.720	1.260	2.850	2.580	1.160	0.232	0.224	0.001	

Table 15. Phytoplankton cell count data. Station 23. (Concentrations in cells/l x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	0.006	0.020		0.044	0.004				
N. curta (empty frustules)			0.004	0.018	0.004	0.015	0.008		
N. closterium	0.005	0.019	0.124	0.086	0.070				
N. kerguelensis (intact frustules)	0.006			0.030					
N. kerguelensis (empty frustules)		0.004	0.004	0.012	0.015	0.012	0.004	0.001	
N. barkleyi		0.008		0.002	0.008	0.019		0.003	
N. sicula		0.012	0.004	0.011		0.004			
Chaetoceros sp.	0.001	0.008	0.015	0.008	0.004	0.008			
C. dichaeta				0.002	0.015				
Coretron criophilum					0.019				
Eucampia balaustium	0.002								
Asteromphalus hookeri			0.004			0.004			
Rhizosolenia sp.	0.001								
Thalassiosira sp.						0.004			
Amphora sp.							0.004		
Big Central Diatoms		0.004		0.001				0.002	
Small Central Diatoms	0.001	0.004		0.004	0.004		0.004	0.002	
Unidentified pennates	0.001								
Nanoplankton				0.071	0.031				
Amphidinium sp.				0.001					
Diplopeltopsis minor						0.004			
Prorocentrum antarcticum					0.004				
Protoperidinium nanum			0.004						
Protoperidinium sp.							0.004		
Distephanus speculum			0.004						
TOTAL BIOMASS	0.022	0.081	0.162	0.291	0.178	0.070	0.023	0.008	

Table 16. Phytoplankton cell count data. Station 27. (Concentrations in cells/1 x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	1.760	1.430	1.660	2.050	0.958	1.970	.803		
N. curta (empty frustules)	0.116	0.073	0.120	0.158	0.182	0.236	0.108		
N. closterium	0.336	0.270	0.270	0.174	0.060	0.394	0.012		
N. kerguelensis (intact frustules)				0.031	0.027	0.004			
N. kerguelensis (empty frustules)		0.023	0.008	0.035	0.008				
N. sicula	0.004	0.008		0.004			0.004		
N. barkleyi		0.012	0.004	0.008	0.012	0.012	0.004		
Corethron criophilum			0.008						
Eucampia balaustium	0.008								
Asteromphalus hyalinus						0.004			
Chaetoceros sp.	0.012	0.008		0.019	0.004		0.012		
C. dichaeta		0.004					0.004		
Cocconeis sp.	0.004	0.004							
Small Central Diatoms	0.004		0.004	0.008	0.031	0.004	0.004		
Nanoplankton	1.390	1.220	0.792	1.030	0.923	2.030	0.537		
Prorocentrum antarcticum					0.004				
Protoperidinium nanum				0.004		0.004		0.001	
P. incertum				0.004	0.004				
Distephanus speculum				0.012					
TOTAL BIOMASS	3.630	3.060	2.860	3.540	2.210	4.650	1.490	0.001	

Table 17. Phytoplankton cell count data. Station 28. (Concentrations in cells/l x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	4.580	3.730	0.112	0.023	0.077	0.077			
N. curta (empty frustules)	0.282	0.502	0.035	0.012	0.039	0.012	0.004		
N. closterium	0.062	0.131	0.039	0.004					
N. kerguelensis (intact cells)	0.015		0.012	0.004		0.015			
N. kerguelensis (empty frustules)			0.027						
Nitzschia sp. A		0.004		0.004					
Nitzschia sp. B		0.015		0.004					
Nitzschia sp. C							0.004		
Chaetoceros sp.	0.004	0.015	0.004	0.004	0.004				
Tropidoneis sp.		0.004							
Corethron criophilum				0.008					
Asteromphalus hookeri		0.008		0.004					
Cocconeis sp.		0.008	0.004						
Amphiprora sp.		0.004							
Thalassiosira sp.			0.008	0.008					
Chaetoceros dichaeta						0.004			
Unidentified pennate		0.004	0.031	0.012	0.004	0.004			
Big Central Diatoms				0.004					
Small Central Diatoms	0.004	0.012	0.019	0.004		0.004			
Nanoplankton	2.390	0.438	0.031	0.043	0.100	0.043	0.023		
Dinophysis contracta		0.004							
Protoperidinium nanum		0.004							
P. archiovatum				0.004					
Distephanus speculum					0.004				
TOTAL BIOMASS	7.340	4.930	0.286	0.147	0.232	0.162	0.031		

Table 18. Phytoplankton cell count data. Station 29. (Concentrations in cells/1 x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	11.670	9.850	6.920	9.310	10.340	11.020	2.850	0.015	
N. curta (empty frustules)	0.595	0.147	0.212	0.614	0.438	0.711	0.417	0.348	
N. closterium	0.077	0.62	0.012	0.085	0.035	0.081	0.066	0.008	
N. kerguelensis (intact cells)								0.003	
N. kerguelensis (empty frustules)							0.004	0.014	
N. cylindrus	0.012	0.004	0.008	0.027			0.031		
N. heimii								0.010	
N. barkleyi								0.001	
Nitzschia sp. C		0.004					0.004		
Chaetoceros sp.	0.008	0.004			0.004				
Asteromphalus parvulus			0.004		0.004				
Small Central Diatoms	0.019	0.043	0.012	0.019	0.031	0.015	0.015		
Big Central Diatoms		0.004	0.004						
Unidentified naviculoid	0.004								
Nanoplankton	6.650	6.690	1.830	2.300	1.940	2.440	0.259		
Gymnodinium flavum					0.004				
G. guttula		0.004	0.004						
Gyrodinium fusiforme							0.004		
Cochlodinium sp.		0.012							
Unidentified naked dinoflagellates						0.004			
Diplopeltopsis minor		0.004							
Protoperidinium nanum	0.004			0.004	0.004	0.012			
P. incertum	0.004	0.012		0.004	0.008				
P. applanatum							0.012		
Distephanus speculum						0.004			
TOTAL BIOMASS	19.040	16.840	9.000	12.360	12.850	14.280	3.670	0.058	

Table 19. Phytoplankton cell count data. Station 30. (Concentrations in cells/1 x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	14.260	13.260	22.200	17.680	14.550	15.200	1.230	0.008	
N. curta (empty frustules)	0.819	1.140	0.970	1.110	0.838	0.835	0.506		
N. closterium	0.116	0.062	0.050	0.114	0.043	0.143	0.023		
N. kerguelensis (intact cells)							0.004		
N. kerguelensis (empty frustules)							0.008		
Nitzschia sp. B							0.019		
Chaetoceros sp.	0.004								
Asteromphalus hookeri		0.015	0.008						
Small Central Diatoms	0.008		0.012		0.019	0.008	0.015		
Big Central Diatoms		0.004			0.008	0.004			
Nitzschia sp. C				0.010		0.004			
Nanoplankton	10.120	3.04	9.16	13.200	12.160	8.830	0.054		
Amphidinium cf. hadai			0.004						
Gyrodinium rhabdomonte		0.004		0.010					
G. fusiforme								0.004	
Gymnodinium guttula			0.004						
Diplopeltopsis minor								0.004	
Protoperidinium archiovatum	0.004					0.004	0.008		
P. nanum	0.004	0.008	0.004	0.010		0.008			
P. incertum			0.004		0.004		0.004		
P. raphanum				0.010		0.004			
Distephanus speculum		0.004	0.004		0.012				
Coccolithophorids				0.010					
TOTAL BIOMASS	25.340	17.540	32.450	32.140	27.630	25.040	1.880	0.016	

Table 20. Phytoplankton cell count data. Station 31. (Concentrations in cells/l x 10^6).

Special	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	8.350	7.430	9.480	9.290	11.630	7.340	4.450	0.012	
N. curta (empty frustules)	0.259	0.228	0.247	0.332	0.290	0.406	0.665		
N.closterium	0.379	0.305	0.332	0.340	0.062	0.255	0.104		
N. kerguelensis (intact cells)						0.035			
N. kerguelensis (empty frustules)						0.019			
N. heimii							0.008		
Nitzschia sp. B	0.023		0.012	0.015	0.015	0.012	0.008		
Nitzschia sp. C	0.008	0.012	0.012						
Chaetoceros dichaeta	0.004	0.004							
Melosira sp.		0.004							
Amphiprora kufferathii			0.004						
Chaetoceros sp.			0.004			0.004			
Nitzschia sp. A				0.004	0.004				
Navicula sp.	0.004	0.008			0.004				
Small Central Diatoms	0.031	0.039	0.027	0.035	0.012	0.023	0.015	0.012	
Big Central Diatoms			0.004						
Nanoplankton	5.440	3.130	9.120	3.340	2.000	0.290	0.043	0.023	
Gymnodinium cf. lachryma	0.004	0.004							
Protoperidinium incertum	0.004	0.004							
P. archiovatum			0.015			0.004	0.004		
P. applanatum						0.004			
P. penitum						0.004			
P. nanum						0.008			
Distephanus speculum						0.027	0.004		
TOTAL BIOMASS	14.510	11.160	19.260	13.350	14.010	8.44	5.30	0.047	

Table 21. Phytoplankton cell count data. Station 32. (Concentrations in cells/1 x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	12.500	12.200	9.390	7.360	6.190	0.089	0.089	0.004	
N. curta (empty frustules)	0.939	0.904	0.502	0.375	0.344	0.139	0.004		
N. closterium	5.400	2.530	0.579	0.424	0.131	0.031	0.004		
N. kerguelensis (intact cells)	0.158	0.097	0.035	0.012	0.035	0.097	0.066		
N. kerguelensis (empty frustules)	0.008	0.012	0.004	0.008		0.035	0.039		
N. cylindrus		0.012			0.004		0.004		
Nitzschia sp. B	0.012	0.012	0.031	0.050	0.031	0.023	0.015		
Nitzschia sp. C	0.004	0.008	0.008	0.012					
Eucampia balaustium			0.008				0.015		
Chaetoceros sp.			0.004						
C. dichaeta	0.027	0.004			0.004		0.004		
Actinocyclus actinochilus	0.004								
Cocconeis sp.		0.004			0.004				
Asteromphalus hookeri					0.004				
Big Central Diatoms		0.004	0.008						
Small Central Diatoms	0.039	0.031	0.023	0.019	0.031	0.008	0.019		
Unidentified pennates		0.012				0.004	0.015		
Nanoplankton	4.56	3.16	0.676	0.834	0.649	0.425			
Gymnodinium minor	0.004								
Gyrodinium rhabdomonte		0.004							
Prorocentrum antarcticum					0.004				
Protoperidinium incertum			0.004	0.004					
P. nanum		0.004							
P. archiovatum			0.008						
P. antarcticum					0.004				
P. applanatum					0.004				
Protoperidinium sp. A		0.004							
Protoperidinium sp. B	0.004								
Distephanus speculum	0.012	0.004	0.004	0.004	0.004		0.004		
TOTAL BIOMASS	23.690	19.050	11.280	9.100	7.44	0.467	0.270	0.004	

Table 22. Phytoplankton cell count data. Station 33. (Concentrations in cells/1 x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	9.180	13.740	9.750	10.100	0.090	1.700	1.160	0.019	
N. curta (empty frustules)	0.985	2.010	1.260	0.779	1.280	0.301	0.228	0.015	
N. closterium	0.711	0.900	0.750	0.629	0.803	0.015	0.056		
N. kerguelensis (intact cells)				0.015					
N. kerguelensis (empty frustules)					0.008	0.007			
Nitzschia sp. B		0.004	0.012		0.004				
Asteromphalus parvulus				0.004					
Chaetoceros dichaeta		0.008							
Small Central Diatoms	0.015	0.019	0.035	0.008	0.271	0.015	0.012		
Big Central Diatoms			0.004				0.004		
Unidentified naviculoids		0.004	0.008						
Nanoplankton	1.370	1.270	1.080	1.370	1.430	0.155	0.005		
Gyrodinium cf. lachryma	0.004								
Gymnodinium minor			0.004						
G. cf. soyai			0.004						
Amphidinium cf. hadai				0.004				0.004	
Protoperidinium incertum	0.023	0.015	0.008	0.015	0.008				
P. antarcticum	0.004	0.004	0.004						
P. nanum				0.023	0.004				
P. defectum							0.008	0.008	
Distephanus speculum		0.004							
TOTAL BIOMASS	12.290	17.970	12.920	12.970	12.680	2.190	1.50	0.046	

Table 23. Phytoplankton cell count data. Station 34. (Concentrations in cells/1 x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	4.310	2.580	2.830	3.840	9.050	5.410	0.093		
N. curta (empty frustules)	1.340	0.857	0.947	1.690	1.130	0.629	0.155		0.016
N. closterium	0.267	0.336	0.398	0.355	0.510	0.236	0.313		0.008
N. kerguelensis (intact cells)						0.008			
N. sublineata							0.004		
Nitzschia sp. A	0.008								
Nitzschia sp. B				0.004	0.004				
Chaetoceros sp.		0.004	0.004		0.004				
C. dichaeta							0.004		
Surirella ovata							0.015		
Small Central Diatoms	0.008	0.015		0.27	0.004	0.023		0.004	
Big Central Diatoms					0.008	0.004	0.004		
Unidentified naviculoid						0.004			
Nanoplankton	0.807	0.931	0.147	0.776	1.190	0.309	0.025		
Gyrodinium cf. lachryma		0.012	0.008	0.004					
Protoperidinium cf. applanatum						0.004			
P. incertum	0.015	0.031	0.012	0.023					
Distephanus speculum							0.004		
TOTAL BIOMASS	6.760	4.770	5.670	6.720	11.900	6.630	0.722	0.035	0.027

Table 24. Phytoplankton cell count data. Station 35. (Concentrations in cells/1 x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	9.450	7.920	7.490	5.850	11.10	10.20	1.550	0.015	
N. curta (empty frustules)	2.130	1.550	2.110	0.556	1.550	2.230	0.792	0.004	
N. closterium	1.110	1.010	0.649	0.170	1.360	0.267	0.123		
N. kerguelensis (intact cells)	0.012						0.012		
N. kerguelensis (empty frustules)	0.004						0.008		
Amphiprora kufferathii			0.004						
Pseudoamphiprora manginii			0.004						
Asteromphalus hookeri				0.004					
Nitzschia sp. B							0.004		
Small Central Diatoms	0.015	0.015		0.030		0.004	0.015		
Big Central Diatoms							0.004		
Unidentified pennates					0.004	0.012			
Nanoplankton	1.160	0.827	1.260	0.726	1.570	0.328	0.012		
Gymnodinium guttula		0.004							
Diplopeltopsis minor			0.004	0.004					
Protoperidinium nanum	0.004			0.008	0.004				
P. archiovatum							0.004		
P. incertum	0.012	0.004			0.004				
Distephanus speculum				0.004		0.004			
TOTAL BIOMASS	13.900	11.340	11.530	7.730	15.620	13.030	2.58	0.019	

Table 25. Phytoplankton cell count data. Station 36. (Concentrations in cells/l x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	4.430	5.840		8.040	6.580	7.900	2.390		
N. curta (empty frustules)	0.765	1.230		0.684	1.380	0.869	0.313		
N. closterium	0.286	0.108		0.127	0.309	0.012	0.043		
N. sicula					0.004	0.004			
N. pacifica							0.004		
Asteromphalus parvulus					0.004				
S. aff. smithii		0.004							
Pleurosigma sp.	0.004								
Navicula aff. crucigera	0.004								
Small Central Diatoms	0.023	0.015		0.008	0.004	0.004			
Nanoplankton	0.904	1.140		0.726	1.460	0.834	0.267		
Gyrodinium rhabdomonte	0.004	0.019		0.012		0.004			
Gymnodinium guttula						0.004			
Amphidinium sp.		0.004							
Unidentified naked dinoflagellates		0.004							
Diplopeltopsis minor	0.004	0.004			0.004				
Protoperidinium incertum	0.027	0.019		0.035	0.019				
P. antarcticum		0.004							
P. raphanum				0.004					
Distephanus speculum					0.004				
TOTAL BIOMASS	6.440	8.390		9.640	9.760	9.740	3.020		

Table 26. Phytoplankton cell count data. Station 37. (Concentrations in cells/ 1 x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	8.470	8.990	12.510	10.190	10.210	9.050	4.860	0.205	
N. curta (empty frustules)	1.120	0.896	2.260	1.180	1.140	1.170	1.180	0.046	
N. closterium	0.298	0.464	0.201	0.475	0.370	0.320	0.104		
N. kerguelensis (intact cells)			0.001						
N. kerguelensis (empty frustules)			0.002						
N. aff. obliquecostata						0.001			
Nitzschia sp. A	0.004				0.004		0.004		
Nitzschia sp. B		0.004		0.012					
Chaetoceros sp.				0.004		0.004			
C. dichaeta	0.019								
Biddulphia striata			0.013						
Thalassiotrix sp.			0.005						
Asteromphalus parvulus							0.004		
Thalassiosira sp.			0.005						
Big Central Diatoms			0.002						
Small Central Diatoms	0.015	0.027	0.032		0.027	0.012	0.008	0.004	
Unidentified naviculoids		0.008							
Nanoplankton	2.810	1.670	2.300	2.680	2.480	3.060	0.475	0.017	
Amphidinium cf. hadai								0.002	
Unidentified naked dinoflagellates								0.002	
Diplopeltopsis minor								0.002	
Protoperidinium defectum			0.002						
P. applanatum			0.002						
P. nanum					0.004				
P. aff. rosaceum								0.001	
Protoperidinium sp. A	0.004		0.002		0.004				
Protoperidinium sp. B		0.004							
Distephanus speculum			0.002						
TOTAL BIOMASS	12.75	12.06	17.33	14.55	14.23	13.62	6.640	0.280	

Table 27. Phytoplankton cell count data. Station 38. (Concentrations in cells/1 x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	6.860	7.250	8.020	5.930	5.100	7.720	5.510	0.046	
N. curta (empty frustules)	0.734	1.090	0.746	0.746	1.080	0.985	0.939	0.008	
N. closterium	0.633	0.664	0.622	0.618	0.962	0.772	0.606	0.002	
N. kerguelensis (intact cells)		0.012	0.031		0.015	0.015	0.019		
N. kerguelensis (empty frustules)	0.008	0.004	0.004			0.008	0.004	0.001	
N. sicula	0.004	0.012	0.004			0.012	0.012		
Nitzschia sp. B						0.004			
N. barkleyi	0.004	0.012			0.004		0.008		
Chaetoceros dichaeta	0.093	0.734	0.019	0.050	0.174	0.100	0.081		
Eucampia balaustium	0.008			0.008		0.012			
Small Central Diatoms	0.035	0.050	0.012		0.023	0.015	0.027		
Big Central Diatoms			0.008	0.008					
Unidentified pennate		0.012							
Thalassiosira tumida								0.001	
Nanoplankton	0.355	0.954	0.560	1.320	0.927	1.580	0.537	0.003	
Dinophysis contracta	0.004								
Gyrodinium rhabdomonte					0.004				
Nanodinoflagellates								0.004	
Diplopeltopsis minor			0.004		0.004			0.002	
Prorocentrum antarcticum				0.004					
Protoperidinium nanum					0.004	0.004	0.004	0.001	
P. aff. macrapicatum								0.001	
P. incertum		0.004	0.004	0.004	0.004	0.004			
P. raphanum	0.004								
P. aff. mediocre								0.002	
Distephanus speculum	0.004	0.019			0.008	0.019	0.004		
TOTAL BIOMASS	8.750	10.160	10.030	8.690	8.310	11.240	7.520	0.070	

Table 28. Phytoplankton cell count data. Station 39. (Concentrations in cells/l x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	8.740	8.740	6.510	10.800	11.450	11.750	3.270	0.016	
N. curta (empty frustules)	0.371	0.811	0.100	0.803	0.464	0.939	0.305	0.011	
N. closterium	0.170	0.201	0.012	0.228	0.100	0.236	0.112	0.005	
N. kerguelensis (intact cells)					0.012		0.027		
N. kerguelensis (empty frustules)		0.004					0.008		
N. barkleyi	0.019	0.008		0.004	0.004	0.023	0.027		
N. sicula		0.012	0.004		0.019	0.008			
N. heimii								0.002	
Asteromphalus hookeri						0.004			
Synedra sp.						0.004			
Cocconeis sp.				0.004			0.004		
S. aff. striatula			0.004						
Small Central Diatoms	0.004	0.012		0.008	0.004		0.023		
Big Central Diatoms	0.004	0.004			0.004			0.001	
Chaetoceros sp.						0.004			
Unidentified pennates				0.015		0.012			
Nanoplankton	3.920	4.940	4.890	7.720	6.540	7.460	0.166	0.004	
Amphidinium cf. hadai					0.008				
Gyrodinium rhabdomonte	0.004								
G. fusiforme							0.004		
Diplopeltopsis minor	0.019	0.004	0.004	0.004	0.008	0.004			
Protoperidinium defectum							0.004		
P. nanum	0.004			0.004	0.004	0.004	0.004		
P. incertum	0.008	0.004			0.012	0.004			
P. applanatum							0.004		
P. aff. concavum							0.004		
Distephanus speculum	0.004					0.004	0.012		
TOTAL BIOMASS	13.260	14.730	11.630	19.590	18.620	20.460	3.970	0.039	

Table 29. Phytoplankton cell count data. Station 40. (Concentrations in cells/l x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	14.720	13.070	12.350	11.870	14.760	8.990	0.765	0.008	
N. curta (emtpy frustules)	0.776	0.317	0.324	0.865	0.587	0.398	0.297		
N. closterium	0.888	0.131	0.062	0.077	0.116	0.097	0.004		
N. kerguelensis (empty frustules)				0.004					
N. cylindrus						0.015			
Nitzschia sp. B					0.004		0.023		
Nitzschia sp. C		0.004	0.008			0.004			
Asteromphalus hookeri				0.004					
Small Central Diatoms	0.004				0.004	0.008	0.023		
Big Central Diatoms	0.004		0.004	0.004		0.004			
Unidentified pennates					0.004		0.023		
Nanoplankton	0.460	7.650	3.410	6.470	6.610	6.740	0.116		
Gymnodinium flavum					0.004				
Gymnodinium sp.		0.004							
Diplopeltopsis minor	0.012			0.004	0.008	0.004			
Protoperidinium nanum	0.004	0.004			0.004	0.004			
P. applanatum				0.004	0.004				
P. defectum	0.004			0.004					
P. incertum	0.004	0.008	0.004		0.004				
P. aff. rosaceum				0.004					
P. elegantissimum		0.008							
Distephanus speculum			0.008						
TOTAL BIOMASS	16.070	21.190	16.170	19.300	22.110	16.270	1.250	0.008	

Table 30. Phytoplankton cell count data. Station 41. (Concentrations in cells/l x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	6.810	6.050	7.060	4.280	4.840	1.550	1.000	0.193	
N. curta (empty frustules)	0.981	0.834	0.985	0.630	0.842	0.328	0.382	0.464	
N. closterium	0.027	0.043	0.054	0.031	0.012	0.004		0.008	
N. kerguelensis (intact cells)	0.008	0.031							
N. kerguelensis (empty frustules)		0.012	0.004	0.023	0.004	0.031			
N. heimii						0.004			
N. cylindrus	0.004	0.004		0.004	0.023	0.004	0.015	0.004	
Nitzschia sp. B	0.004		0.008		0.004	0.004			
Nitzschia sp. C			0.004		0.004				
Asteromphalus hookeri			0.004						
Chaetoceros sp.	0.004			0.012					
Cocconeis sp.				0.004					
Small Central Diatoms	0.008		0.008	0.004		0.015	0.004		
Big Central Diatoms			0.008	0.008		0.004			
Unidentified pennates	0.008	0.027	0.043	0.085	0.050				
Nanoplankton	1.830	2.740	2.640	1.350	1.190	1.240	1.360	0.363	
Gyrodinium cf. lachryma					0.004	0.004			
Gymnodinium sphaericum				0.004					
Protoperidinium nanum		0.004		0.004		0.004			
P. applanatum				0.004					
P. aff. raphanum		0.004							
P. incertum	0.004								
Distephanus speculum	0.008		0.015	0.004					
TOTAL BIOMASS	9.700	9.750	10.830	6.440	6.980	3.200	2.760	0.614	

Table 31. Phytoplankton cell count data. Station 42. (Concentrations in cells/1 x 10^6)

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	2.650	3.650	4.220	3.340	2.320	0.340	0.043	0.379	
N. curta (empty frustules)	0.363	0.425	0.413	0.321	0.664	0.093	0.015	0.089	
N. closterium	0.139	0.147	0.135	0.155	0.154	0.004		0.004	
N. kerguelensis (intact cells)					0.023		0.027		
N. kerguelensis (empty frustules)			0.004			0.012		0.004	
N. cylindrus	0.046	0.023	0.015	0.019	0.008				
N. angulata					0.004				
Nitzschia sp. A							0.015		
Nitzschia sp. B	0.004		0.004		0.012	0.012	0.004		
Nitzschia sp. C	0.004	0.004	0.004						
Melosira sp.							0.046		
Chaetoceros sp.	0.015	0.012	0.008						
Chaetoceros dichaeta			0.004	0.035	0.015				
Cocconeis sp.			0.004		0.004				
Asteromphalus parvulus	0.004								
A. hookeri			0.004						
Small Central Diatoms	0.004	0.015	0.004	0.008	0.008	0.015		0.008	
Big Central Diatoms		0.004		0.008					
Unidentified Pennates	0.046	0.066	0.008						
Nanoplankton	0.850	2.130	2.140	1.450	0.626	0.085		0.015	
Gyrodinium rhabdomonte		0.008							
Amphidinium sp.			0.004						
Unidentified naked dinoflagellates								0.004	
Protoperidinium cf. adeliense					0.004				
P. nanum				0.004					
P. antarcticum		0.004							
P. incertum			0.004						
Coccolithophorids								0.004	
TOTAL BIOMASS	4.130	6.490	6.970	5.330	3.790	0.560	0.151	0.506	

Table 32. Phytoplankton cell count data. Station 43. (Concentrations in cells/1 x 10^6).

Species	Level								
	1	2	3	4	5	6	7	8	9
Nitzschia curta (intact cells)	0.357	0.214	0.108	0.215	0.125	0.019	0.008	0.020	
Nitzschia curta (empty frustules)	0.091	0.052	0.057	0.011	0.067		0.020		
N. closterium	4.220	7.640	3.460	3.310	6.350	0.019	0.0001	0.001	
N. kerguelensis (intact cells)		0.045				0.005	0.001		
N. kerguelensis (empty frustules)	0.002	0.004				0.003	0.003		
N. aff. obliquecostata						0.001	0.0001		
N. aff. closterium							0.0001		
N. sicula				0.001		0.001			
Nitzschia sp. A					0.004	0.003			
Nitzschia sp. B						0.003			
Corethron criophilum						0.001			
Thalassiosira sp.						0.0001	0.010		
Chaetoceros sp.		0.002			0.055				
Asteromphalus parvulus			0.003	0.002		0.0001			
Thalassiotrix sp.	0.008	0.002			0.004	0.0001			
Cocconeis sp.	0.004		0.003						
Big Central Diatoms	0.002		0.002			0.008	0.001		
Small Central Diatoms	0.002	0.011	0.002		0.004	0.001		0.002	
Unidentified pennates	0.004	0.002				0.002	0.001		
Nanoplankton		0.089	0.773	0.038	0.103	0.104	0.019		
Gyrodinium sp.								0.010	
Protoperidinium nanum	0.010	0.016		0.007					
P. concavum						0.0001			
Protoperidinium sp.						0.0001			
Unidentified naked dinoflagellates						0.001			
Distephanus speculum	0.004		0.002						
TOTAL BIOMASS	4.720	8.070	3.660	3.580	6.720	0.169	0.019	0.033	

APPENDIX C

Table 33. List of diatoms.

Actinocyclus actinochilus (H. Péragallo) Simonsen
A. divisus (Grunow) Hustedt
Amphiprora sp.
Amphora sp.
Asteromphalus cf. *hepactis* (de Brébisson) Ralfs
A. hookeri Ehrenberg
A. hyalinus Karsten
A. parvulus Karsten
Biddulphia striata Karsten
Chaetoceros dichaeta Ehrenberg
Chaetoceros sp.
Cocconeis sp.
Coretheon criophilum Castracane
Eucampia balaustium Castracane
Melosira sp.
Navicula aff. *crucigera*
Navicula sp.
Nitzschia angulata (O'Meara) Hasle
N. barkleyi Hustedt
N. cf. *barkleyi* Hustedt
N. closterium (Ehrenberg) W. Smith
N. aff. *closterium* (Ehrenberg) W. Smith
N. cylindrus (Grunow) Hasle
N. heimii Manguin
N. kerguelensis (O'Meara) Hasle
N. aff. *marina* Grunow
N. medioconstricta Hustedt
N. pacifica Cupp (sensu Hustedt 1958a)
N. aff. *obliquecostata* (Van Heurck) Hasle
N. sicula (Castracane) Hustedt
N. sublineata (Van Heurck) Hasle
N. vanheurckii (M. Péragallo) Hasle
Nitzschia sp. *A*
Nitzschia sp. *B*
Nitzschia sp. *C*
Odontella sp.
Pleurosigma sp.
Pseudoamphiphrora manginii Manguin
Rhizosolenia aff. *styliformis* Brightwell
Rhizosolenia sp.

Table 33. List of diatoms (cont.).

Surirella aff. *fastuosa* (Ehrenberg) Kützing

S. ovata de Brébisson

S. aff. *smithii* Ralfs

S. aff. *striatula* Turpin

Synedra sp.

Thalassiosira tumida (Janisch) Hasle

Thalassiosira sp.

Thalassiotrix sp.

Tropidoneis aff. *antarctica* (Grunow) Cleve

Tropidoneis sp.

APPENDIX D

Table 34. List of dinoflagellates.

Amphidinium cf. *hadai* Balech
Amphidinium sp.
Cochlodinium sp. *
Gymnodinium flavum Kofoid & Swezy
G. guttula Balech
G. minor Lebour
G. cf. *soyai* Hada
G. aff. *sphaericum* Calkins
G. aff. *sphaericum* Calkins
Gymnodinium sp.
Gyrodinium fusiforme Kofoid & Swezy *
G. cf. *lachryma* (Meunier) Kofoid & Swezy
G. rhabdomonte Balech
Gyrodinium cf. *fusiforme* Kofoid & Swezy
Gyrodinium sp.
Prorocentrum antarcticum (Hada) Balech
Diplopeltopsis minor (Paulsen) Pavillard
D. perlata Balech
Dinophysis contracta (Kofoid & Sokgsberg) Balech
Protoperidinium adeliense (Balech) Balech
P. antarcticum (Schimper) Balech
P. applanatum (Mangin) Balech
P. cf. *applanatum* (Mangin) Balech
P. cf. *adeliense* (Balech) Balech
P. archiovatum (Balech) Balech
P. concavum (Mangin) Balech
P. aff. *concavum* (Mangin) Balech
P. defectum (Balech) Balech
P. elegantissimum (Balech) Balech
P. glyptopterum Balech
P. incertum (Balech) Balech
P. aff. *macrapicatum* (Balech) Balech
P. mediocre (Balech) Balech
P. aff. *mediocre* (Balech)
P. nanum (Balech) Balech
P. penitum (Balech) Balech
P. raphanum (Balech) Balech
P. aff. *raphanum* (Balech) Balech
P. aff. *rosaceum* (Balech) Balech
P. thulesense (Balech) Balech
P. cf. *unipes* (Balech) Balech
Oxytosum sp.

* First record for Antarctic waters

APPENDIX E

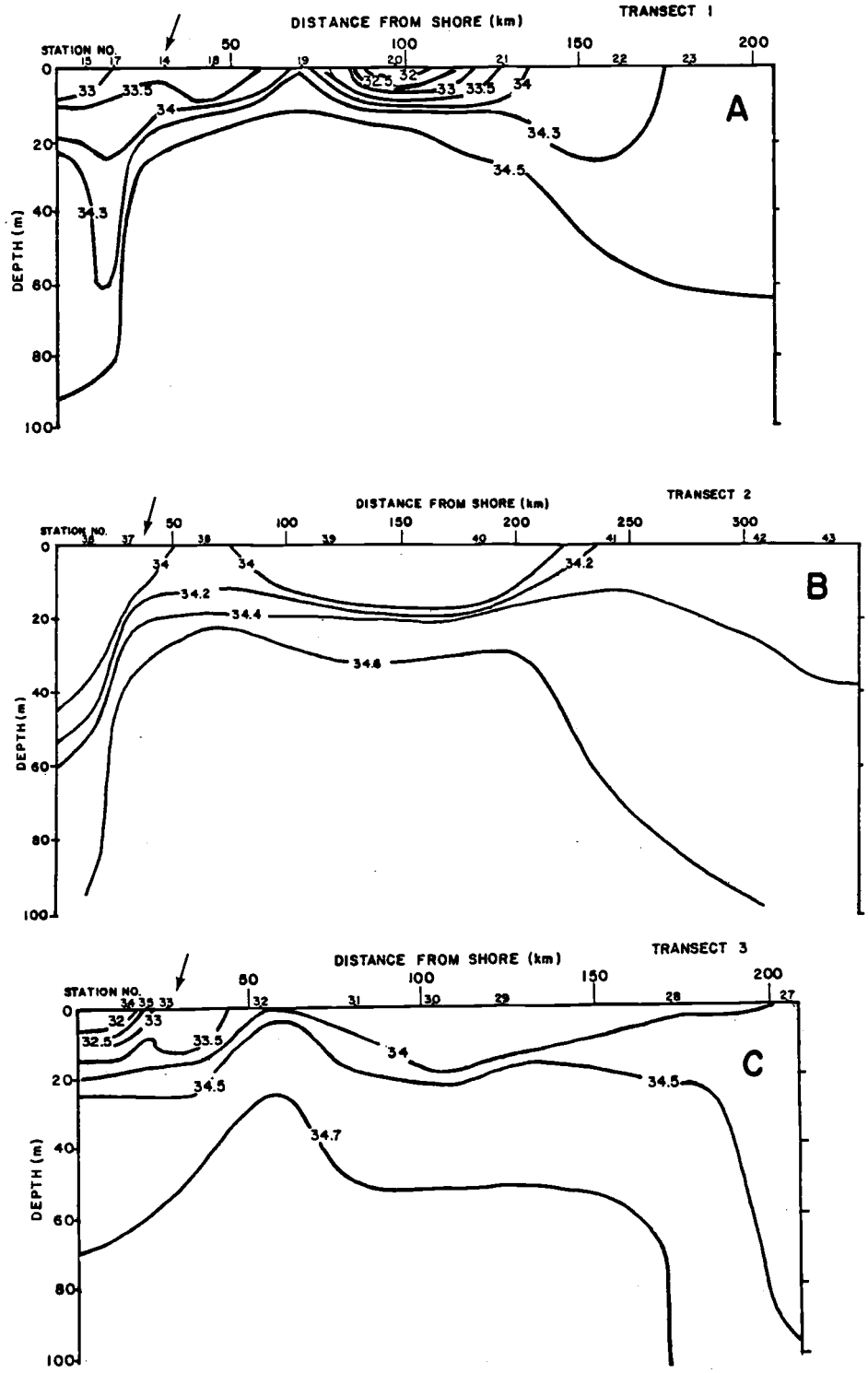

Fig. 18. Vertical section of salinity (in parts per thousand). a) Transect #1. b) Transect #2. c) Transect #3. a) and c) after Wilson (1983); b) after Smith & Nelson (1985). ↙ ice-edge

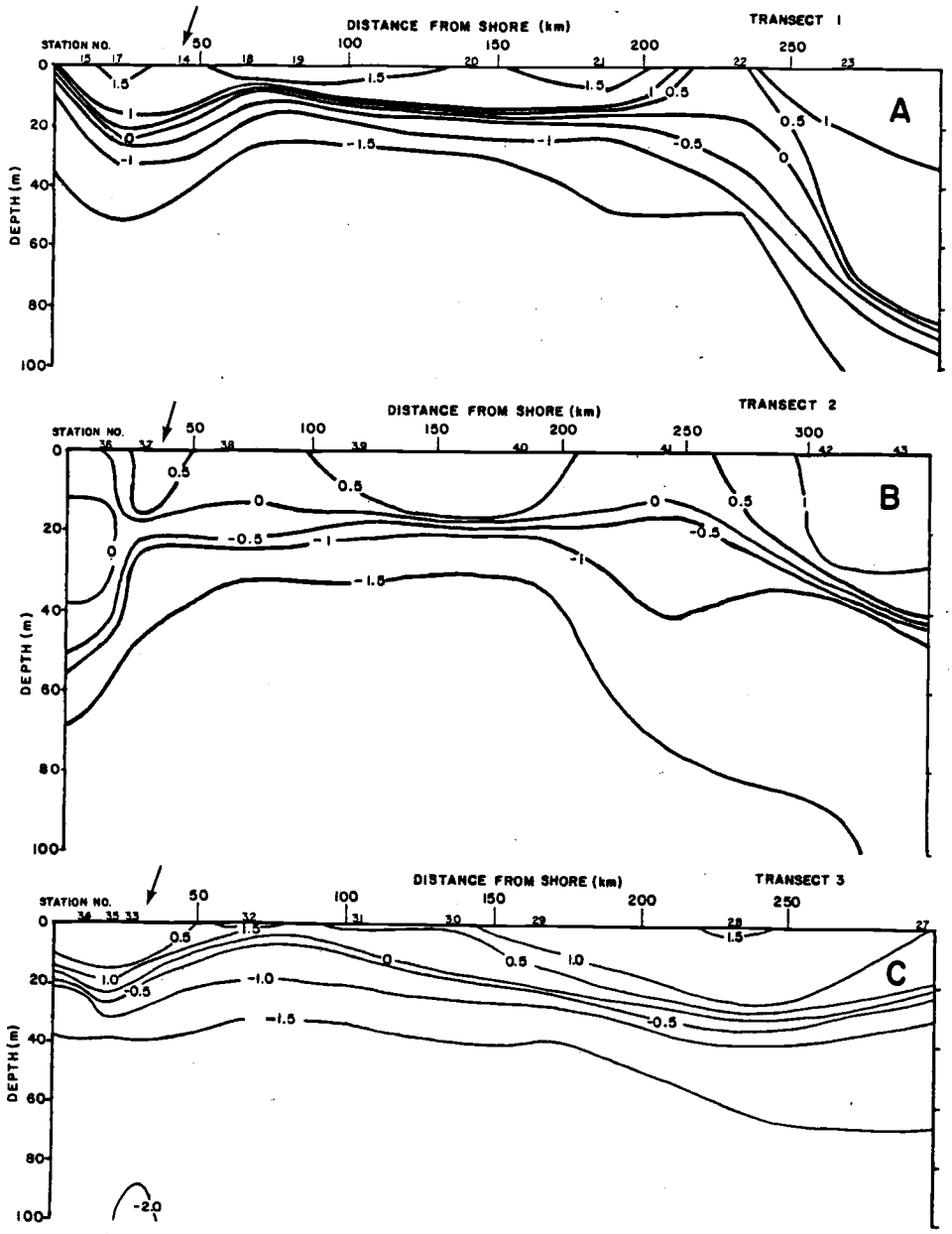

Fig. 19. Vertical section of temperature (°C) a) Transect #1. b) Transect #2. c) Transect #3. b) after Smith & Nelson (1985). ↙ ice-edge

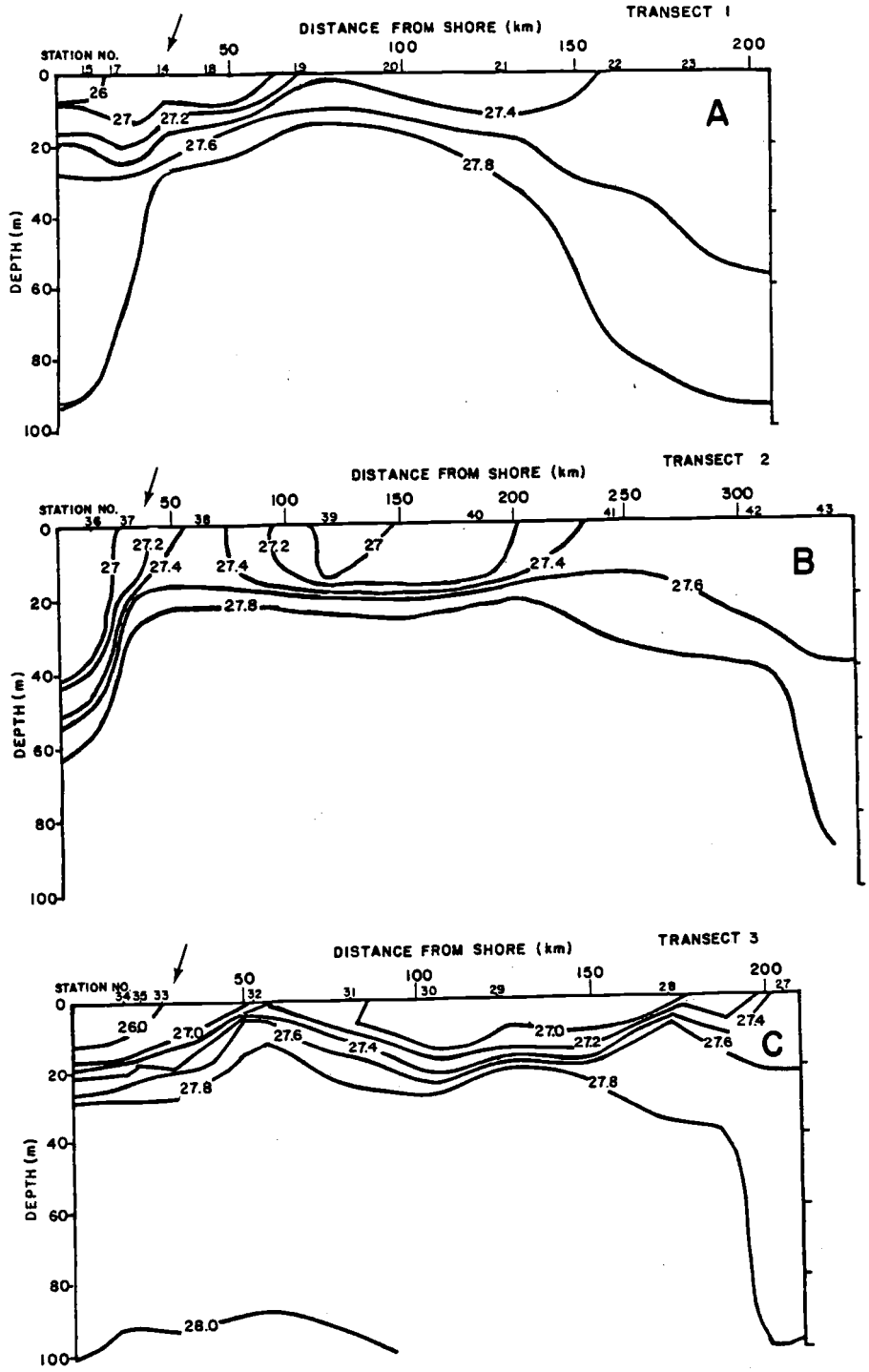

Fig. 20. Vertical section of Sigma-t a) Transect #1. b) Transect #2. c) Transect #3. a) and c) after Wilson (1983); b) after Smith & Nelson (1985). ↙ ice-edge

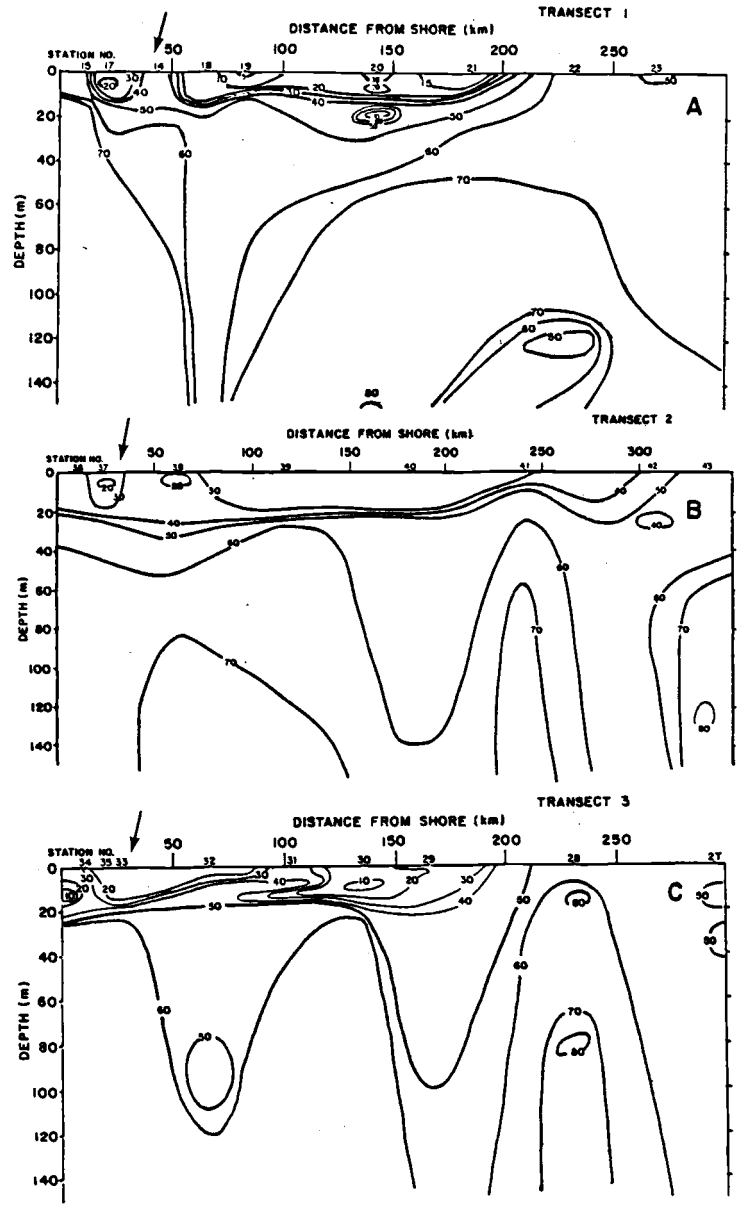

Fig. 21. Vertical section of Silicate (μmol/l). a) Transect #1. Transect #2. b) Transect #3. ↙ ice-edge

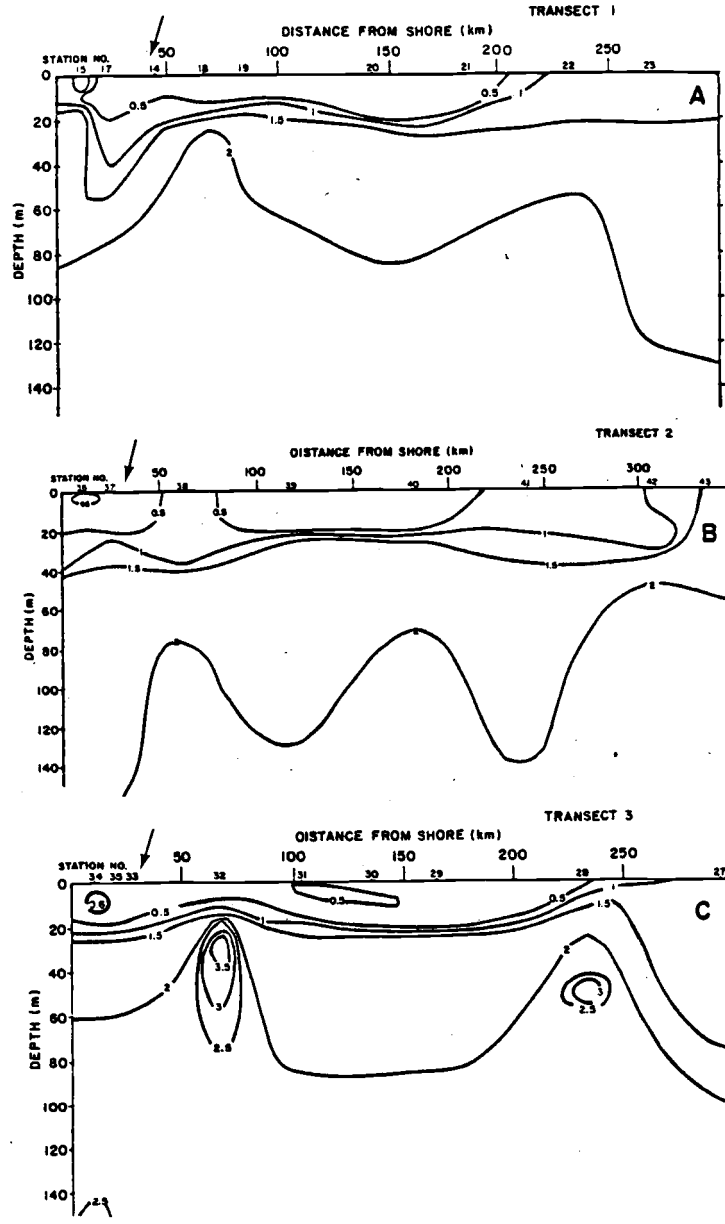

Fig. 22. Vertical section of phosphate (µmol/l) a) Transect #1. b) Transect #2. c) Transect #3. ↙ ice-edge

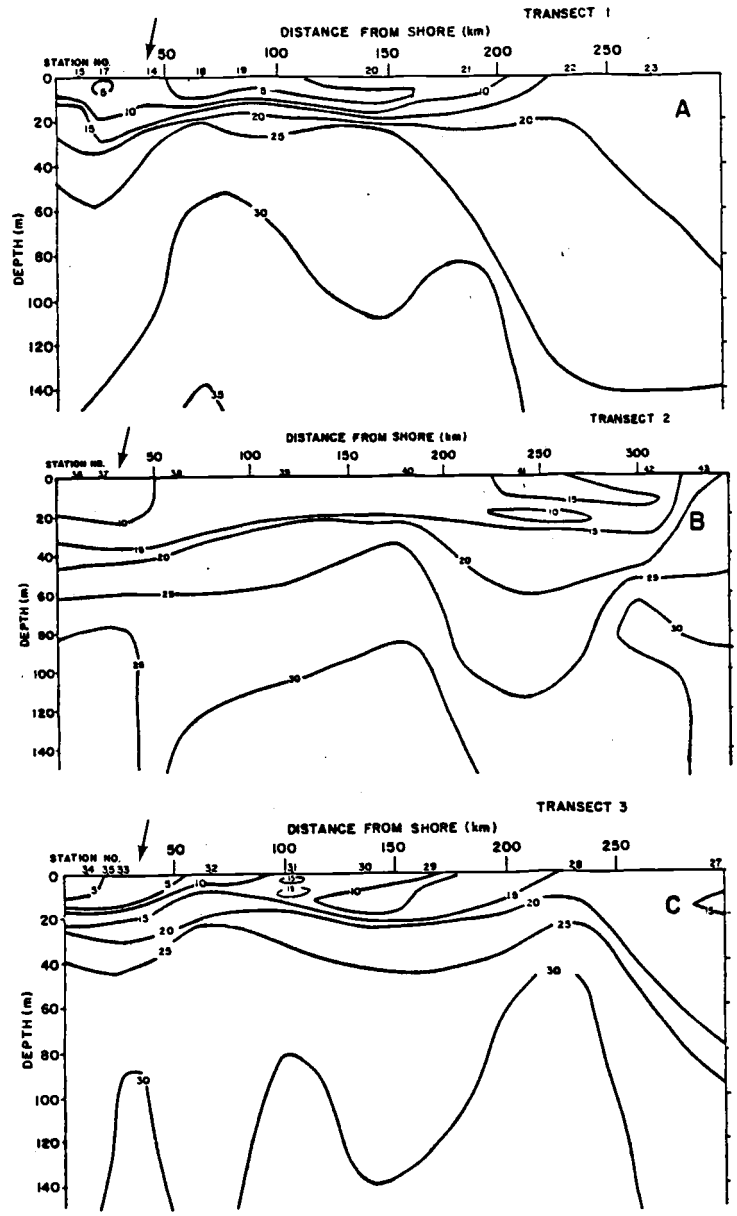

Fig. 23. Vertical section of the sum total of nitrate + nitrite (μmol/l). a) Transect #1. b) Transect #2. c) Transect #3. ↙ ice-edge

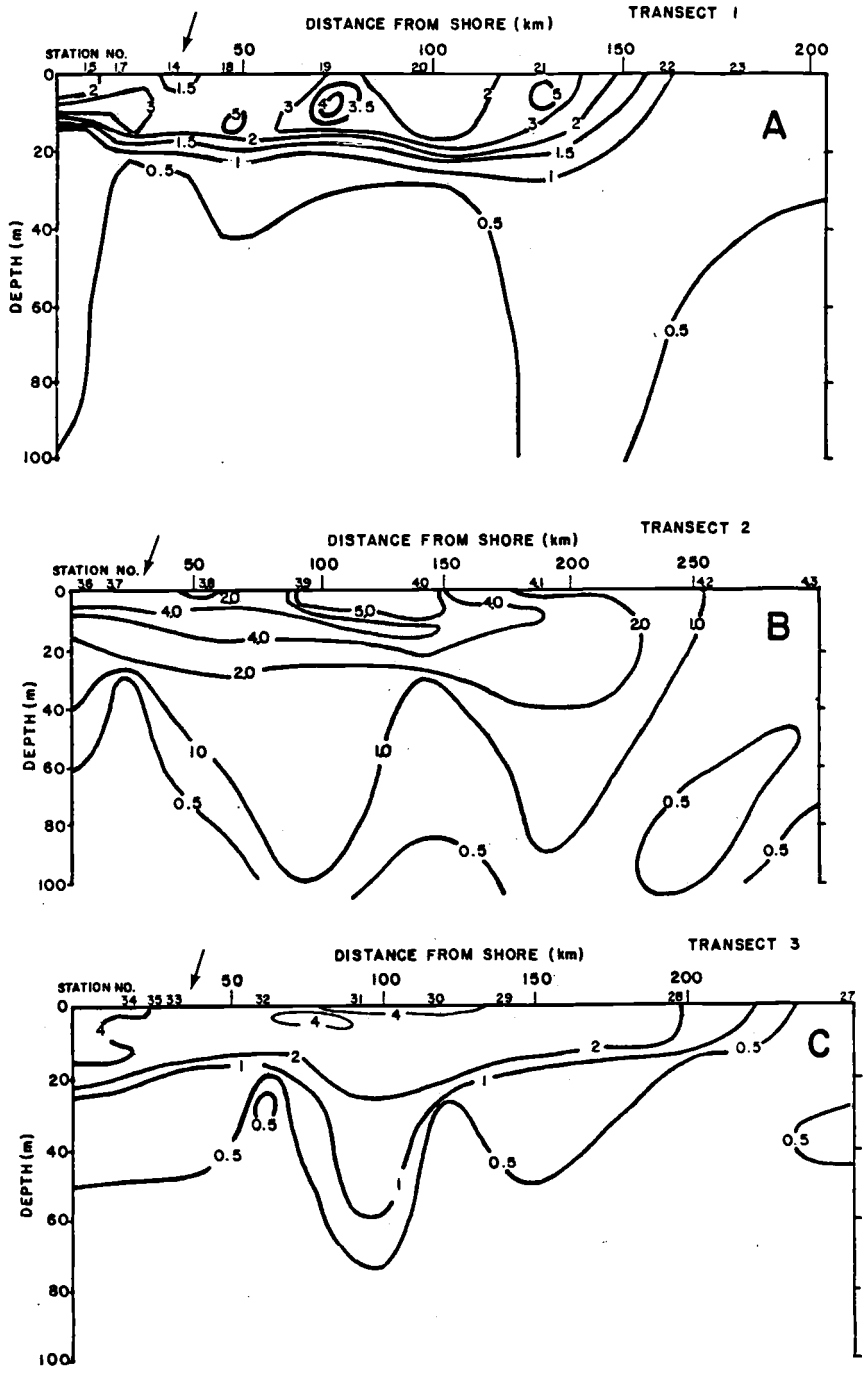

Fig. 24. Vertical section of Chlorophyll a (mg/m^3) a) Transect #1. b) Transect #2. c) Transect #3. (After Wilson, 1983).
/ ice-edge