To the Graduate Council:

I am submitting herewith a thesis written by David Lee Wilson entitled "Species-Specific Productivity of Phytoplankton in an Ice-Edge Bloom in the Ross Sea." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Botany.

Walker O. Smith, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the Council:

The Graduate School

SPECIES-SPECIFIC PRODUCTIVITY OF PHYTOPLANKTON IN AN ICE-EDGE BLOOM IN THE ROSS SEA

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

David Lee Wilson

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ABSTRACT

During January and February, 1983 studies were conducted in a phytoplankton bloom associated with a receding ice-edge in the Ross Sea. Physical and biological data indicated that the bloom was characterized by elevated biomass and primary productivity; which were tightly coupled with a surface lens of reduced salinity and density. Taxanomic and autoradiographic analysis of the phytoplankton population revealed that the bloom was dominated by a single diatom species of Nitzschia curta (section Fragilariopsis). N. curta accounted for greater than 80% of the total primary productivity and greater than 65% of the total standing stock (cells m^{-3}) at stations tested. Statistical analysis of the regression of relative productivity versus station (as distance from shore) indicated that the importance of N. curta decreased seaward. Further, taxanomic analysis of the epontic community revealed a considerable overlap of taxa with the bloom community. These data suggest that N. curta was released from the ice and that this process may have been important in providing a viable seed stock for the bloom.

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CHAPTER I

INTRODUCTION

High latitude marine ecosystems are characterized by extremes in environmental conditions. For example, these regions exhibit pronounced seasonal cycles in solar radiation, low water temperatures, and are often covered by sea ice. These environmental factors serve to greatly limit productivity and growth rate, and result in generally lower species diversity, few trophic transfers within the food webs, and a greater population density for a given species (Nemoto and Harrison, 1981).

The variations in the light environment of high latitudes are the result of the large change in angle of the sun's rays relative to the earth's surface. This produces extreme seasonal variations in intensity and angles of incident radiation. These factors become more pronounced with increasing latitude and extended periods of total darkness or light occur. For example, at 65° latitude, 24 hours of daylight occur in December but only 4 hours occur in June (Nemoto and Harrison, 1981). Similarly, at 80 to 85° latitudes, total darkness occurs for 5 months of the year (Tranter, 1982). The extreme seasonal variations in daylength can result in an integrated daily light flux in austral summer equal to or greater than that of the tropics (Nemoto and Harrison, 1981).

The angle of incidence of light also varies with latitude. As latitude increases the angle of incidence decreases resulting in greater surface reflection and a corresponding reduction in the amount of light which penetrates the water column. El-Sayed (1966) reported 50% of

incident radiation being lost due to reflection in Marqueite Bay (68° S latitude). In addition to seasonal variations, considerable short term variability in incident radiation has been reported, both temporally and spatially (El-Sayed and Mandelli, 1965; Raymont, 1980).

The southern ocean is also characterized by the presence of sea ice which covers much of the region throughout most of the year. Ice can be formed either from direct freezing of sea water or from precipitation on the continent which forms glaciers and ice shelves. The former, as a result of the freezing process, contains a significant concentration of sea salts, while the latter two contain very low salt concentrations (Everson, 1977).

The extensive ice cover and its seasonal variations are the result of high latitude solar radiation and temperature conditions. In the Antarctic the spatial extent of sea ice may vary tenfold. At its maximum in September it covers approximately 25.5×10^7 km^2 of the southern ocean while at the minimum in February it covers about 13×10^6 km^2 (Lewis and Weeks, 1971; Deacon, 1982). This large seasonal difference in sea ice cover clearly illustrates that most of the winter ice formation melts in situ each summer.

The presence of sea ice affects many of the physical processes which govern primary productivity. By forming an effective barrier between the sea and the atmosphere, it restricts gas exchange and greatly reduces the amount of light penetration into the sea. In addition, sea ice serves to reduce wind induced turbulence in ice-edge waters and

imparts vertical stability to the water column by the input of relatively less saline (hence less dense) water (Knox, 1970).

In spite of the strong seasonal changes in solar radiation, the water temperatures south of the Antarctic Convergence remain relatively constant. Seawater temperatures south of the Antarctic convergence range by no more than 3 to 5°C (Sverdrup et al., 1943), while waters close to the continent range from ca. -1.7 to +1.9°C (Bunt, 1964; Knox, 1970; Nemoto and Harrison, 1981). Few austral winter temperature data are available. Neori and Holm-Hansen (1982) found that these relatively low water temperatures limit phytoplankton growth in the Southern Ocean. Specifically, they demonstrated that the photosynthetic rates (as measured by half-day radiocarbon incubations) of phytoplankton increased by as much as 2X at temperatures of 7°C. Above 7°C, photosynthetic rates were found to drop rapidly and at 28°C they were only approximately 3% of that at ambient water temperature. This demonstrates that Antarctic phytoplankton are truly psychrophilic.

The occurrence of high concentrations of inorganic nutrients in the Antarctic surface water is well documented. Holm-Hansen et al. (1977) reported nitrates, silicates, and phosphates in the range of 15 to 30, 40 to 90, and 1 to 2 μg atoms l^{-3}, respectively, in the euphotic zone. The concentrations of these nutrients appear to remain high throughout the year and presumably impose no significant limitation on primary production (Holdgate, 1967; El-Sayed, 1970; Olson, 1980; Nemoto and Harrison, 1981).

CHAPTER 2

LITERATURE REVIEW

The Southern Ocean has long been generally considered a region of high biological production. Captain James Cook drew attention to the apparent productivity of this region as far back as 1772. Data collected over the next century confirmed the richness of the Antarctic Seas. The general relationships between the productivity and the circulation and nutrient regimes associated with the Antarctic Divergence became apparent with the Discovery expeditions of the 1930's (Hart, 1934; Deacon, 1937; Clowes, 1938). These studies revealed that circumpolar bands of divergence and upwelling transport massive amounts of nutrients into the surface waters where there is sufficient light to support photosynthesis. More recent investigations have substantiated and quantified both the high nutrient concentrations of the surface waters and the high, although extremely variable, rates of primary production associated with Antarctic upwelling (e.g. Saijo and Kawashima, 1964; Burkholder and Mandelli, 1965; El-Sayed, 1967, 1970, 1978; Holm-Hansen et al., 1977). These and other recent investigations have provided data covering a wide geographic range, and have shown that although upwelling and high nutrient concentrations are generalized phenomena in the Southern Ocean, high rates of productivity are discontinuous both spatially and temporally. A few investigations demonstrated that the waters adjacent to the receding ice edge in late spring and summer can support massive phytoplankton blooms (El-Sayed, 1971; El-Sayed and Taguchi, 1981). Coastal waters and waters adjacent to islands were

also found to support elevated production. For example, El-Sayed (1967) measured productivity to be 3.2 $gCm^{-2}d^{-1}$ in the Gerlache Strait, while Mandeli and Burkholder (1966) reported 3.62 $gCm^{-2}d^{-1}$ near Deception Island. These values are comparable to those found in the highly productive upwelling regions off Peru and Africa (Smith, et al., 1977). El-Sayed and Taguchi (1981) reported chlorophyll values of 31.6 ± 9.5 mg m^{-2} and productivity values of 410 ± 230 mg C m^{-2} d^{-1} for stations associated with the ice-edge in the Weddell Sea. Corresponding values for the northern-central Weddell Sea were 4.36 ± 1.75 mg m^{-2} and 104 ± 92 mg C m^{-2} d^{-1} respectively. Most recently, Smith and Nelson (1983) have quantified and described the distribution of chlorophyll associated with an ice-edge region in the Ross Sea. They reported chlorophyll values of 128.2 ± 91.7 mg m^{-2} with the highest values being associated with a stable surface layer. Control stations outside of the ice-edge bloom exhibited markedly lower chlorophyll concentrations and reduced vertical stability.

In contrast, the oceanic regions have been shown to have much lower levels of production and biomass (El-Sayed, 1978). Holm-Hansen et. al. (1977) showed that integrated values for productivity ranged from a mean of 84 $mgCm^{-2}d^{-1}$ (range = 50-114) in the subantarctic region of the Ross Sea to a mean of 172 $mgCm^{-2}d^{-1}$ (range = 40-294) near the continent. Based on <u>in situ</u> primary productivity measurements conducted during the Eltanin Cruise, El-Sayed (1978) calculated a mean productivity of 134 $mgCm^{-2}d^{-1}$. Earlier higher estimates (El-Sayed,

1967) resulted from the fact that previous studies focused on the more productive coastal waters. For example, Ryther (1963) gave an estimated potential yield for the Southern Ocean of 100 $gCm^{-2}yr^{-1}$. Currie (1964) presented a somewhat reduced estimate of 43 $gCm^{-2}yr^{-1}$ while Bunt (1968) estimated that the annual production for the region could exceed 70 $gCm^{-2}yr^{-1}$. Most recently, Holm-Hansen et al. (1977) calculated a value of 16 g $Cm^{2}yr$. These reduced estimates have forced a reevaluation of the potential yield of the Southern Ocean marine ecosystem and have serious implications with regard to resource management in the region.

Several processes have been hypothesized as being important in initiating and sustaining ice-edge blooms. These can be grouped into physical (wind dampening by ice), chemical (meltwater induced vertical stability), and biological (seeding of surface waters by ice-algae). Marshall (1957) proposed an explanation of ice-edge blooms in the Artic based on light penetration and vertical mixing. He hypothesized that low salinity, low density meltwater from the receding ice-edge imparts vertical stability to an otherwise homogeneous water column. This surface layer of "relatively" fresh water limits phytoplankton circulation to depths where their total, vertically integrated light experience is sufficient to allow photosynthesis to keep pace with respiration. Under these vertical light and mixing conditions, phytoplankton biomass should increase with time, resulting in a phytoplankton bloom in accordance with the "critical depth" concept presented by Sverdrup (1953). Foster (1976) presented evidence that this mechanism is also important in the

initiation of ice-edge blooms in the Antarctic. He demonstrated that the surface waters were more stable due to freshwater input by adjacent melting ice. Similar differences in density can be seen in data recorded at the ice-edge stations from the numerous Eltanin Cruises (e.g. Jacobs, 1965; Jacobs et al., 1974). Some of these stations had massive phytoplankton blooms associated with them (e.g. El-Sayed, 1971). Alexander (1980) also showed a strong correlation between elevated chlorophyll and reduced salinity in the ice-edge region of the Bering Sea.

Additional data which supports this hypothesis were collected in the Southern Ocean by Nelson and Gordon (1983). Their data illustrated that the ice-edge region had increased levels of biogenic particulate matter which occurred in a surface layer of reduced salinity, low density water. This stable layer became less pronounced as the distance from the ice-edge increased (i.e. the depth of vertical mixing increased), and phytoplankton biomass was correspondingly reduced. At stations removed from ice influence, only very small increases in biogenic particulate matter were observed. Thus, it appears that the reduction in turbulent mixing by the low density meltwater may have resulted in the observed increases.

Decreased, near-surface turbulence, due to wind dampening by ice, has also been hypothesized as a mechanism by which ice-edge blooms are initiated. This physical mechanism is similar to the meltwater/stability hypothesis in that the cause of increased primary productivity is a reduction in vertical mixing between the euphotic and hypophotic depths. However, unlike the meltwater/stability hypothesis,

reduced vertical mixing and increased vertical stability are not the result of internal stability within the water column (i.e. a vertical density gradient). Decreased mixing has been shown to enhance primary productivity in non-polar nutrient rich waters (Huntsman and Barber, 1977).

Upwelling has been proposed as a potentially important process in initiating and sustaining ice-edge blooms (Neshyba, 1977). By this mechanism, primary production would be enhanced by nutrient input from deep nutrient-rich waters which are transported to the surface via wind action (Roed and O'Brien, 1983) and/or rising meltwater originating below the pycnocline (Greisman, 1979). Ice-edge upwelling has been observed in the Arctic (Alexander and Niebauer, 1981; Johannessen et al., 1983) but has never been documented in the Antarctic. Furthermore, it is difficult to imagine how an influx of nutrients into an already nutrient-rich environment could be responsible for the observed enhanced productivity associated with Antarctic ice-edge regions. Gordon and Huber (in press) have demonstrated that surface nutrient concentrations remain relatively high even with the reductions caused by meltwater dilution and phytoplankton uptake.

Another hypothesis for the formation of ice-edge blooms suggests that blooms could be formed via release of large amounts of epontic algae from melting sea-ice. It has been demonstrated that algae (mainly diatoms) can attain high biomass by growth within sea ice (Bunt, 1968; Bunt and Lee, 1970; Ackley et al., 1979). Clasby et al. (1976) reported a chlorophyll maximum in the ice of the Chuckhi Sea of 30 mg chlorophyll m^{-3}. Smith and Nelson (1983) reported a chlorophyll value of 179 mg

m^{-3} for epontic algae in the Ross Sea. Similar studies have reported chlorophyll concentrations within the epontic community as being two orders of magnitude greater than in the associated phytoplankton community (e.g. Meguro et al., 1967). In addition it has been demonstrated that this epontic community often contributes significantly to the overall production of marginal ice zones (Bunt and Lee, 1970; Clasby et al., 1976). However, no data are available to indicate the activity of epontic algae after their release via melting. Data are also lacking concerning the fate of newly released epontic algae. Schrader (1982) has indicated that ice-algae sink rapidly when released from melting ice. Further, there is little agreement as to whether the bloom regions contain primarily epontic or open ocean forms (Hart, 1934; McRoy and Goering, 1974; Ackley et al., 1979; Schandelmeier and Alexander, 1981).

A second related mechanism by which ice algae may initiate ice-edge blooms is that ice algae may serve as an inoculum for a phytoplankton bloom. By this mechanism the sea-ice provides a winter refuge for some species, preventing them from being lost from the euphotic zone or being deeply mixed during periods of extreme turbulence, low solar radiation and slow growth (Bunt, 1963; Bunt and Lee, 1970). Ackley et al. (1979) observed that taxa abundant in the ice-edge phytoplankton were also represented within the ice-algal community. If this relationship proves to have general application, it would provide strong indirect evidence for this "seeding" mechanism. Presently no direct evidence is available to indicate the importance of

ice algae in initiating ice-edge blooms. However, it is important to note that any hypothesis concerning the initiation and sustaining of ice-edge blooms must incorporate both physical and biological mechanisms.

CHAPTER 3

OBJECTIVES

In this study the distribution of phytoplankton biomass and productivity within an ice-edge bloom in the Ross Sea, Antarctica, are described. However, the primary objective of this study is to describe the ice-edge bloom with regard to species-specific productivity and to test for spatial trends of productivity for various species. Specifically, the objectives are as follows:

1. To assess the relative contribution of individual species to the overall production within the bloom.

2. To examine spatial trends in production of individual species.

3. To describe the spatial distribution of production within the bloom.

4. To describe the spatial distribution of biomass within the bloom.

5. To describe the relationship between production and the physical characteristics of the water column within the bloom.

CHAPTER 4

MATERIALS AND METHODS

Field studies were conducted in the Ross Sea, off Victorialand, Antarctica between January 26-February 2, 1983 on board the U.S. Coast Guard Icebreaker GLACIER (Figure 1). The study area, located between 75° 30' and 77° 00' South Latitude and 163° 00' and 172° 20' East Longitude had a total of 36 stations which were occupied along three transects extending normal to the ice edge. Two transects can be defined by stations at which "species-specific" productivity was measured:

Transect 1: Stations 2, 3, 4, 5, 11

Transect 2: Stations 34, 35, 32, 29, 27

Each transect was sampled within 30-36 hours.

At each station water samples were collected in 10-liter Niskin bottles from depths corresponding to 100, 50, 30, 15, 5, 1, and 0.1% of incident light penetration. Two additional depths were sampled to a maximum depth of 150 m. Primary production, chlorophyll *a*, salinity, temperature, and particulate matter concentrations were measured for each depth from subsamples of this water. Autoradiographs were prepared from subsamples corresponding to 100, 30, 15, and 5% light penetration.

Primary productivity was measured by the ^{14}C-method (Steemann Nielsen, 1952). Subsamples from each depth were placed in clear 1.1 l PVC bottles covered with neutral density screens (Perforated Products, Inc.; Brookline, MA) corresponding to the light intensity of the depth

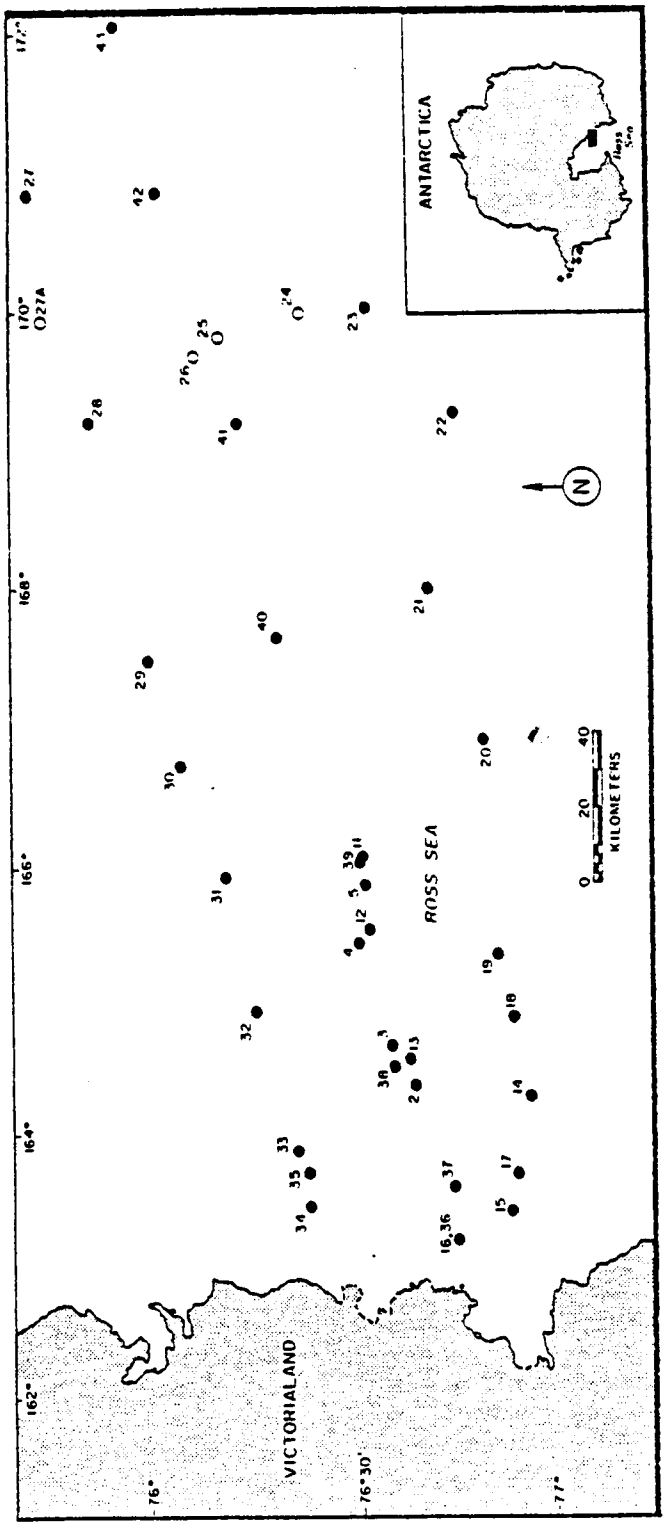

Figure 1. Study Area

sampled. Each subsample was inoculated with ca. 50 μCi $NaH^{14}CO_3$ (Amersham) and placed in on-deck incubators equipped with circulating surface water to maintain surface temperatures.

After an incubation period of 6-7 hours, 100-200 ml from each depth were filtered onto 25 mm 0.8 μm Millipore (Millipore Corporation, Bedford, Mass.) filters. All filters were rinsed with ca. 5 ml of 0.01 N HCl in filtered sea water and dried at 60° C. Time zero controls were made by filtering 100 ml of subsample immediately after inoculation (Huntsman and Barber, 1977). Each filter was then carefully folded, placed in glassine envelopes, and returned to The University of Tennessee, Knoxville. To assess the total amount of $NaH^{14}CO_3$ added, a 0.5 ml unfiltered aliquot from selected samples was placed in a scintillation vial. To avoid volitilization of tracer, 0.1 ml of Protoso (New England Nuclear) was added to each vial (Iverson et al., 1976). Each filter was carefully transferred from the glassine envelope into a scintillation vial to which 10 ml of Omnifluor (NEN) were added. To each seawater-Protosol vial, 10 ml Scintiverse I (Fisher Scientific; Atlanta, GA) was added. The activity of all samples was measured using a Tracor Analytic model 6892 scintillation counter. The efficiency of counting was determined by the external standard ratio method.

Primary productivity was calculated as follows:

$$\text{Productivity (mg C m}^{-3}\text{ h}^{-1}) = \frac{(CPM_n - CPM_o)\,\frac{Vi}{Vf}\;A \cdot 1.05}{DPM \cdot E_2 \cdot t}$$

where:

CPM_o = the counts per minute of the time zero blank;

Vi = the volume incubated (ml);

V_f = the volume filtered (l);

A = the amount of available inorganic carbon (24,000 mg m^{-3}; Strickland and Parsons, 1968);

DPM = the total activity (disintegrations per minute);

E_2 = the counting efficiency of the filtered samples; and

t = the incubation length in hours.

The factor 1.05 is included to correct for the discrimination between the uptake of ^{12}C and ^{14}C (Strickland and Parsons, 1968).

Total activity (DPM) was calculated as follows:

$$DPM = CPM_t * 2 * Vi / E_1$$

where:

CPM_t = the counts per minute from the ½ ml sample;

E_1 = the counting efficiency of the ½ ml sample.

The value of 24,000 mg m^{-3} for available inorganic carbon is one commonly used in productivity studies (Parsons et al., 1977). The absolute value of available inorganic carbon in water is primarily a function of temperature, salinity, and pH. In sea water this value is nearly constant since variations in pH and salinity are slight.

Chlorophyll a concentrations were determined by the fluorometric method of Holm-Hansen et al. (1965). Filtered samples were ground by hand and extracted with 90% acetone. Chlorophyll a was quantified, after centrifugation, by measuring the fluorescence before and after acidification with a few drops of 5% HCl. The fluorometer (Turner

Model III) was calibrated with a known amount of pure chlorophyll a (Sigma Chemical Company; St. Louis, MO) dissolved in 90% acetone.

Phytoplankton samples were collected for taxanomic analysis and enumeration. Whole water samples were collected from each depth and transferred to 150 ml bottles. Each sample was preserved with gluteraldehyde at a final concentration of approximately 2.0% (V/V).

Autoradiographs were prepared by the method of Paerl and Goldman (1972). After a 6 hour incubation between 5 and 10 ml aliquots were taken from primary productivity incubations, corresponding to the depths analyzed, and gently filtered onto 0.8 um Millipore filters. Those incubations used for autoradiography received an initial inoculation of ca. 150 μCiNaH$^{14}CO_3$ (as opposed to 50 μCi used in productivity measurements). The filters were gently rinsed with ca. 5 ml of 0.01 N HCl in filtered sea water. To remove salts the filters were placed on gauze pads in contact with decreasing concentrations of sea water (75, 50, 25, and 0%) for ca. 15 minutes each (Paerl, 1974). The filters were attached to acetone cleaned microscope slides with a small drop of white glue, placed in a slide box with dessicant, and allowed to thoroughly air dry. The filters were optically cleared and permanently attached to the slides by passing the slide over boiling acetone. The slides were then packed by station in individual dessicated slide boxes, sealed, and returned to UTK.

In a darkroom equipped with a Wratten Series-2 safe light (or equivalent), each slide was coated with a nuclear track emulsion (Kodak NTB; Rochester, New York) by dipping three times in 5 seconds in

emulsion which was diluted 1:1 with distilled water. During coating the emulsion was maintained at 45°C. The slides were placed vertically in slide racks and allowed to air dry for 2 hours. They were then repacked in slide boxes with dessicant and placed in an additional light-tight box. Autoradiographs were exposed for 7.5 days at 4° C. The optimal exposure time was determined by developing a series of autoradiographs which had been exposed for 2, 4, 6, 8, and 10 days. Exposed autoradiographs were developed in complete darkness for 2 minutes in full strength Kodak D-19 developer. They were then quickly rinsed by dipping in distilled water followed by a 5 minute fixation in Kodak fixer and a 20 minute distilled water rinse. The temperature was maintained at 20° C ± 2° throughout the process. Finally, the autoradiographs were slowly air dried in a dust free environment.

Exposed silver grains were enumerated using a Nikon DIAPHOT - TMD inverted microscope with phase contrast optics at X 1500 magnification. Grains were counted directly over and within 5 µm of the organisms. To ensure accurate counting, fields were focused on the plane of the organism and then focused up (in this case down) counting all grains as they came into view (Paerl and Merkel, 1981). All cells which showed a superimposed count above background were considered as viable cells (Paerl, 1978). Background exposure was determined from autoradiographs prepared immediately after inoculation with $NaH^{14}CO_3$.

Phytoplankton standing crop (cells m^{-3}) was assayed by the Utermohl method (Hasle, 1978). Between 10 and 25 ml of preserved samples were settled for ca. 12 hours. Thirty random fields were

counted for each sample with phase contrast optics at X 600 magnification. Standing crop was calculated as follows:

$$\text{Phytoplankton (Cells } m^{-3}) = \frac{\#\text{ cells: All fields counted}}{(\#\text{ fields})\ (\text{Area/Field})\ (\text{Total Area})} \Big/ \text{Volume settled } (m^{-3})$$

The data were sorted into four groups for statistical analysis. These were:

1. Productivity index (as % total productivity)
2. Station (as distance from shore)
3. Depth (as % light penetration)
4. Transect

Seperate linear regressions of productivity index vs. station were determined for each prominent species. Analysis of covariance (ANCOVA), without the assumption of parallel regressions; (Sokal and Rohlf, 1981) was performed to determine the significance of this relationship with depth and transect. Further, the data was tested separately with transects considered as both "fixed" and "random" effects. The significance level at which the null hypothesis was tested was set a priori at 5%, but significance levels are reported as found.

Density, as sigma-t, was calculated from salinity and temperature data using tables presented in special publication number SP-11 of the U.S. Navy Hydrographic Office (1956). Salinity was determined from whole water samples using a Bisset-Berman Salinometer. Vertical water

temperature profiles were determined with expendable bathyometric thermographs (XBT) at each station. Density and sigma-t are related in the following way:

$$\sigma = 10^3 (\rho - 1.0)$$

where:

ρ = the relative density of the seawater.

The symbol σ_t represents the value of σ at atmospheric pressure and in situ temperature (Phillips, 1966).

CHAPTER 5

RESULTS

Distribution of Chlorophyll

The bloom region could be defined by elevated chlorophyll concentrations in the surface layers relative to control areas. It was found that the bloom extended seaward for approximately 200 km off the ice-edge. Two trends in the horizontal chlorophyll distribution were evident: 1) there was a general decrease in surface chlorophyll away from shore and 2) there was a slight increase from south to north (Figure 2). As a result the bloom exhibited a central region which was higher in surface chlorophyll than most of the bloom. Integrated euphotic zone chlorophyll exhibited similar patterns (Figure 3). Station 30 and Station 41 had the highest surface chlorophyll (5.40 mg m^{-3}) and integrated euphotic zone chlorophyll values (160.73 mg m^{-2}) respectively.

Vertically, the chlorophyll distribution (Figures 4-6) exhibited subsurface maxima at 18 of the 34 stations sampled. These maxima were observed most frequently at the 5% light depth, which corresponded to an average depth of 12 m. The mean chlorophyll concentration of all subsurface maxima was 4.22 $\pm$ 1.45 mg m^{-3}. Chlorophyll concentrations integrated through the euphotic zone (to the 0.1% light depth) averaged 56.27 $\pm$ 26.48 mg m^{-2}, while values integrated through 150 m averaged 102.03 $\pm$ 45.15 mg m^{-2}. Additionally, the difference between integrated euphotic zone chlorophyll values and those integrated through 150 m indicate that a substantial portion of the total chlorophyll concentration was located below the euphotic zone (0.1% light depth).

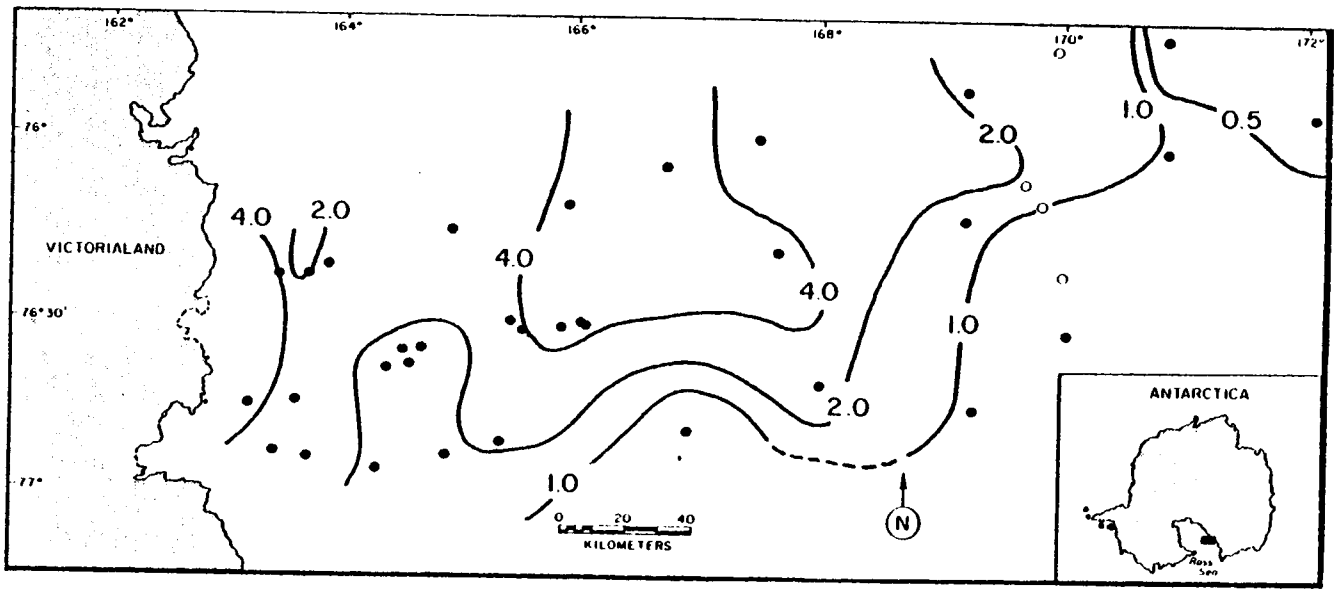

Figure 2. Surface Chlorophyll (mg m^{-3}) Distribution

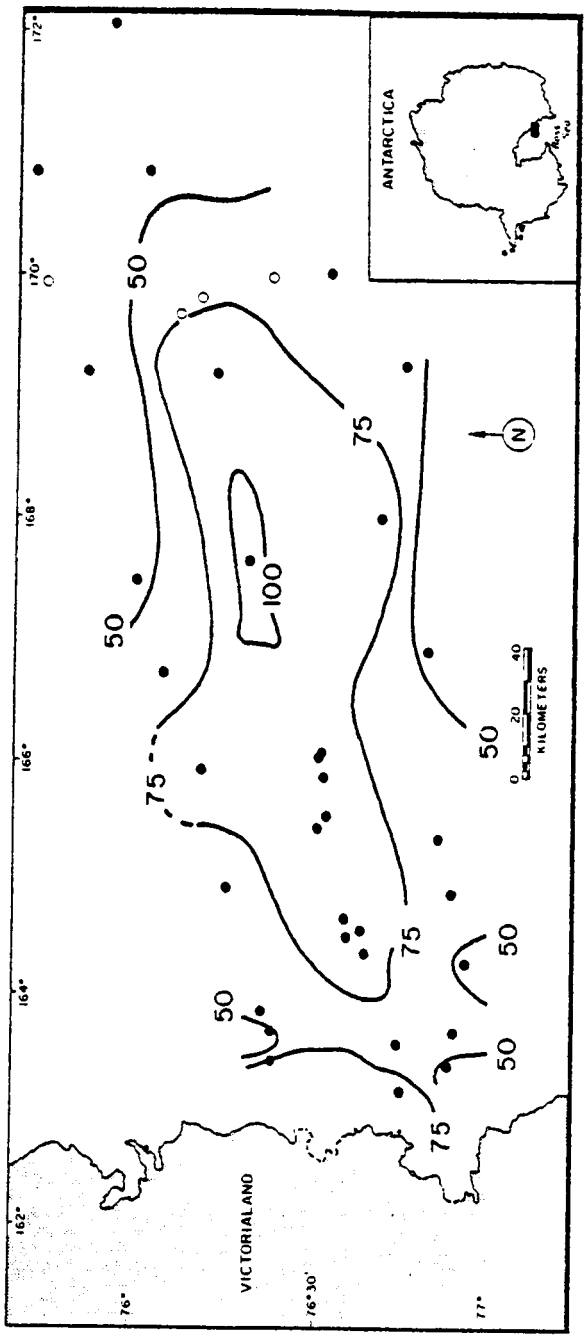

Figure 3. Integrated Euphotic Zone Chlorophyll (mg m^{-2})

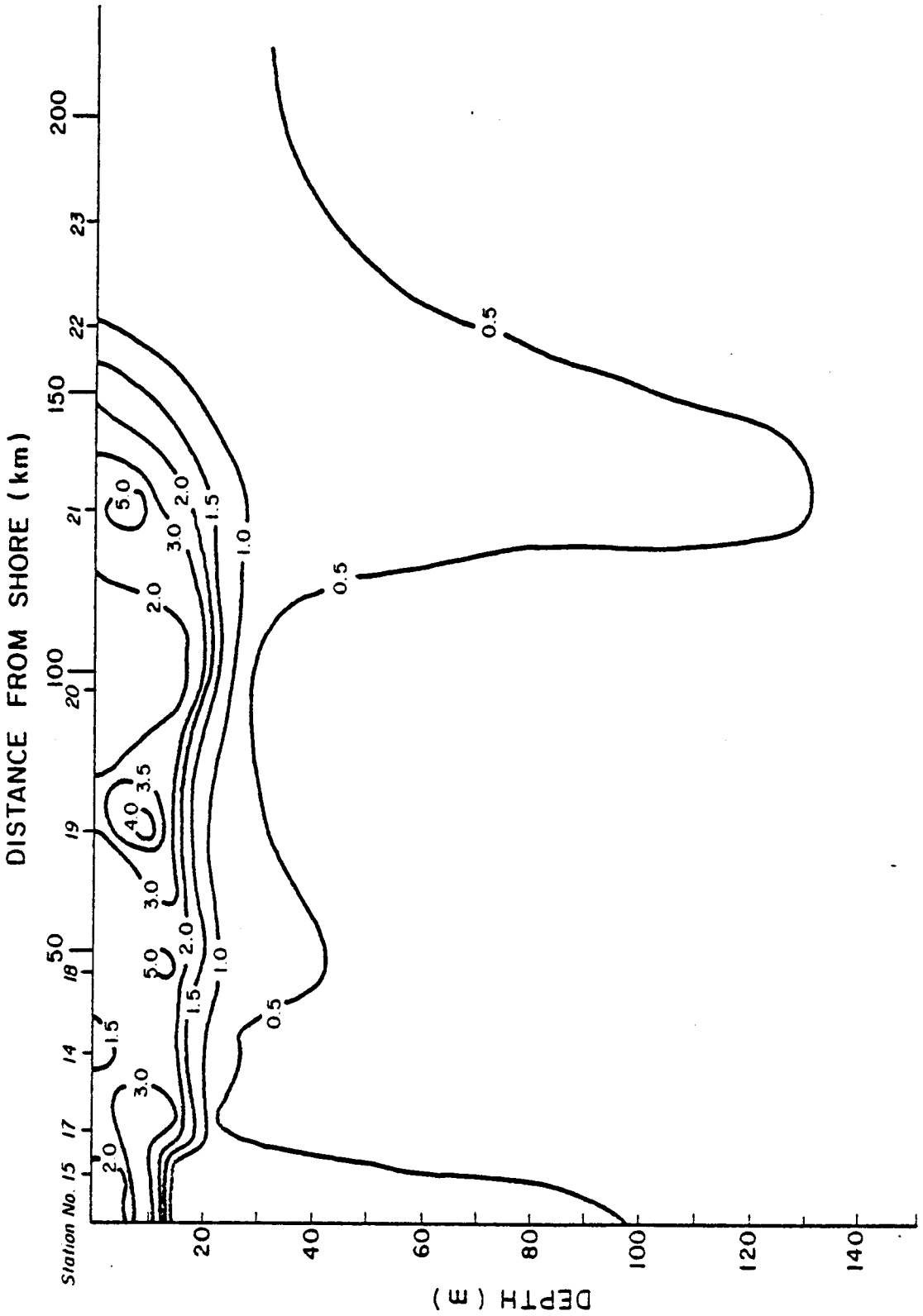

Figure 4. Vertical Section of Chlorophyll (mg m^{-3}): Stations 15-23

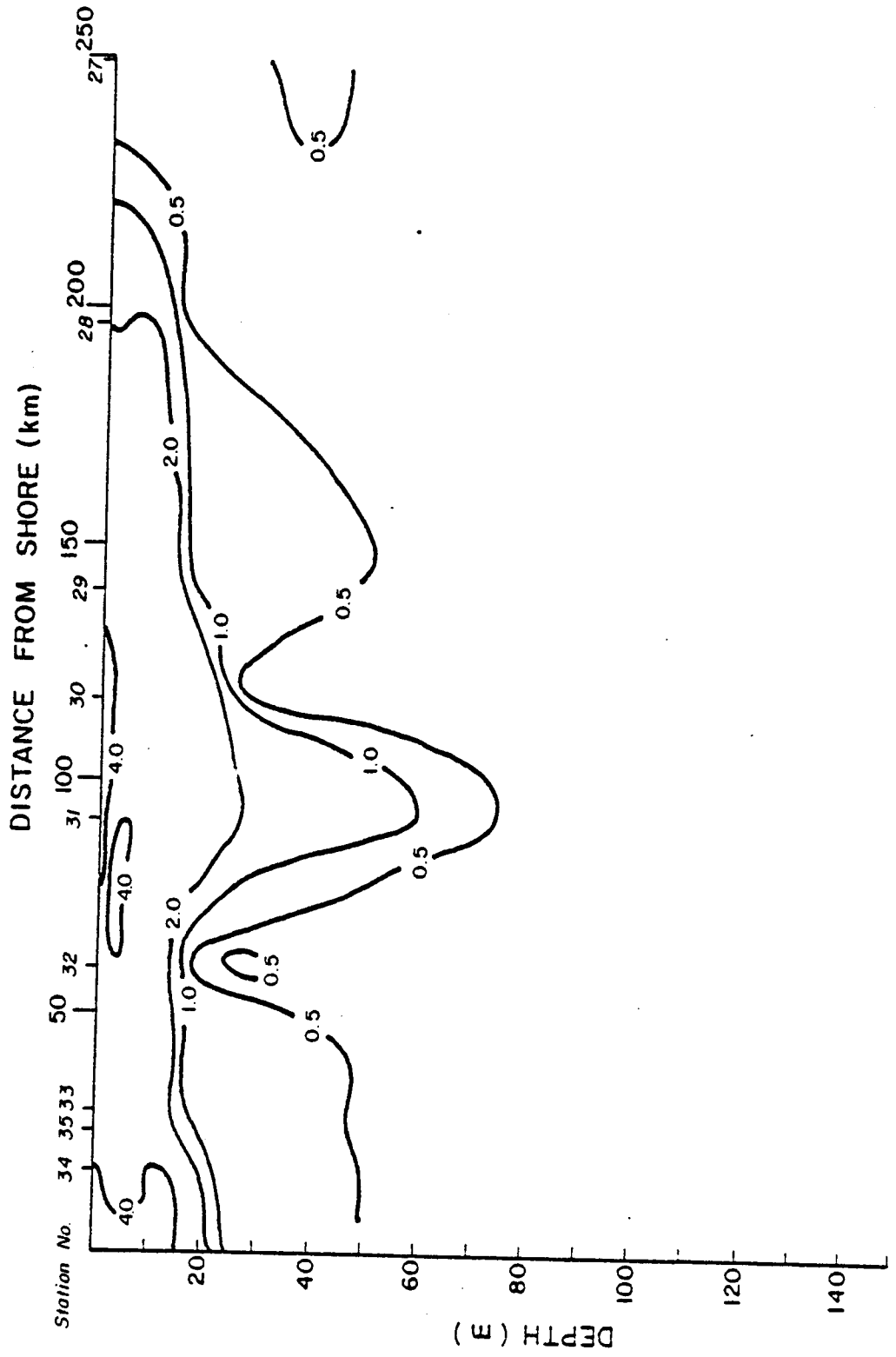

Figure 5. Vertical Section of Chlorophyll (mg m^{-3}): Stations 34-27

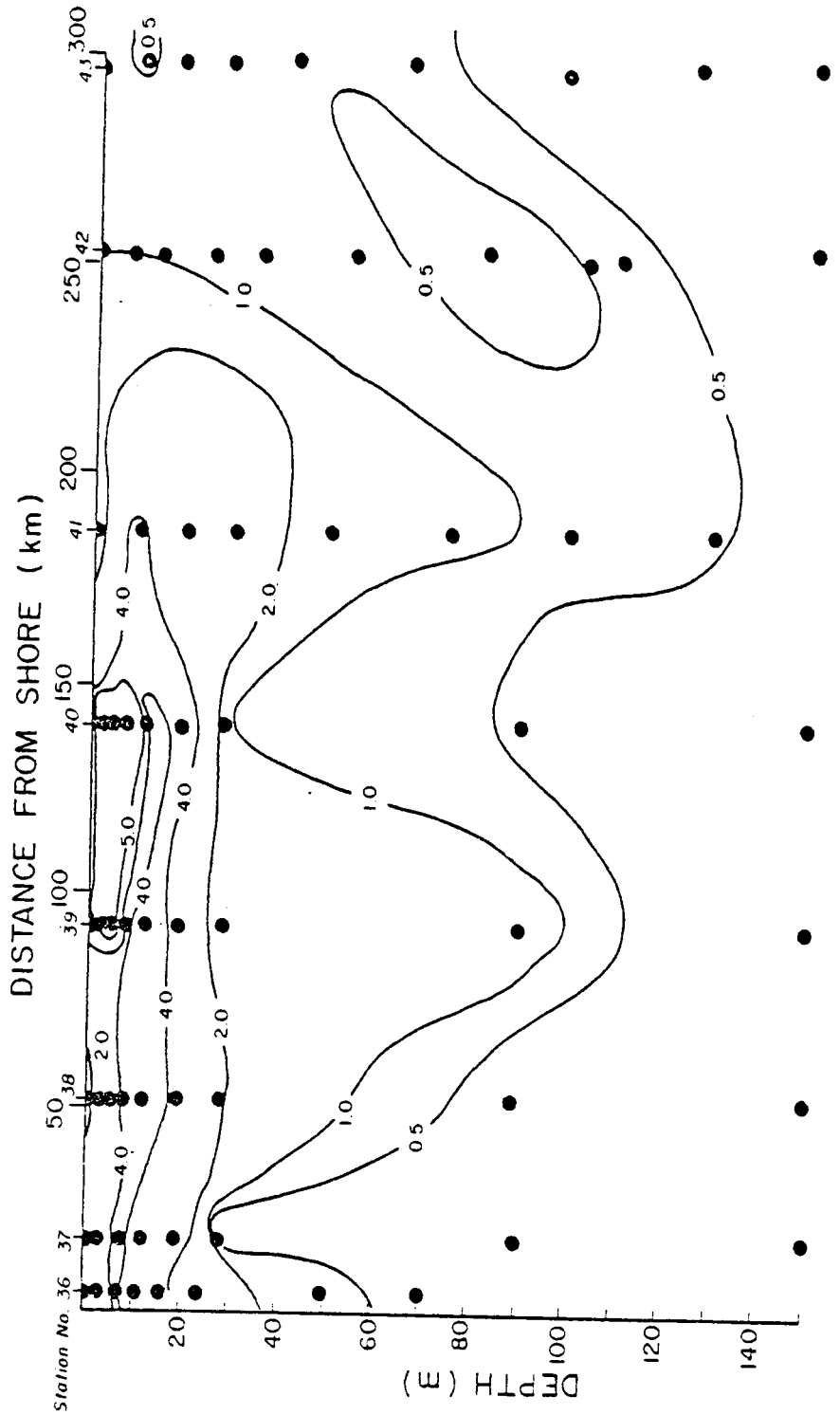

Figure 6. Vertical Section of Chlorophyll (mg m^{-3}): Stations 36-43

Productivity

The horizontal distribution of productivity was similar to that of chlorophyll. Specificially, surface productivity was highest at the center of the bloom (7.0 $mgCm^{-3}h^{-1}$); (Figure 7), and gradually decreased seaward. There was an abrupt decrease in productivity west of Stations 23 and 27. The mean surface productivity for stations measured within the bloom was 3.02 $mgCm^{-3}h^{-1}$. The highest surface value (6.92 $mgC\ m^{-3}h^{-1}$) was recorded at station 39 while the lowest surface value (1.73 $mgCm^{-3}h^{-1}$) associated with the bloom was recorded at station 21. The mean surface productivity for stations outside the bloom was $0.68 \pm 0.14\ mgCm^{-3}h^{-1}$.

Integrated euphotic productivity corresponded closely with surface productivity (Figure 8). It is evident that production increased from nearshore seaward and from north to south resulting in a distinct central region of high productivity (70-80 $mgCm^{-2}h^{-1}$). However, the highest integrated productivity (97.26 $mgCm^{-2}h^{-1}$) occurred at station 18. The mean integrated productivity within the bloom was 44.19 ± 22.80 mg $C^{-3}h^{-1}$ while stations outside the bloom had a mean value of $24.06 \pm 10.63\ mgCm^{-2}h^{-1}$.

Like chlorophyll, the vertical distribution of productivity was characterized by subsurface maxima. Of the 31 stations sampled, 11 exhibited maxima at the 50% light depth (average depth = 3.0 m). The mean value of the subsurface maxima was $3.41 \pm 1.83\ mgCm^{-3}h^{-1}$. Vertical sections (Figures 9 and 10) clearly illustrate that productivity was confined to relatively shallow depths within the bloom

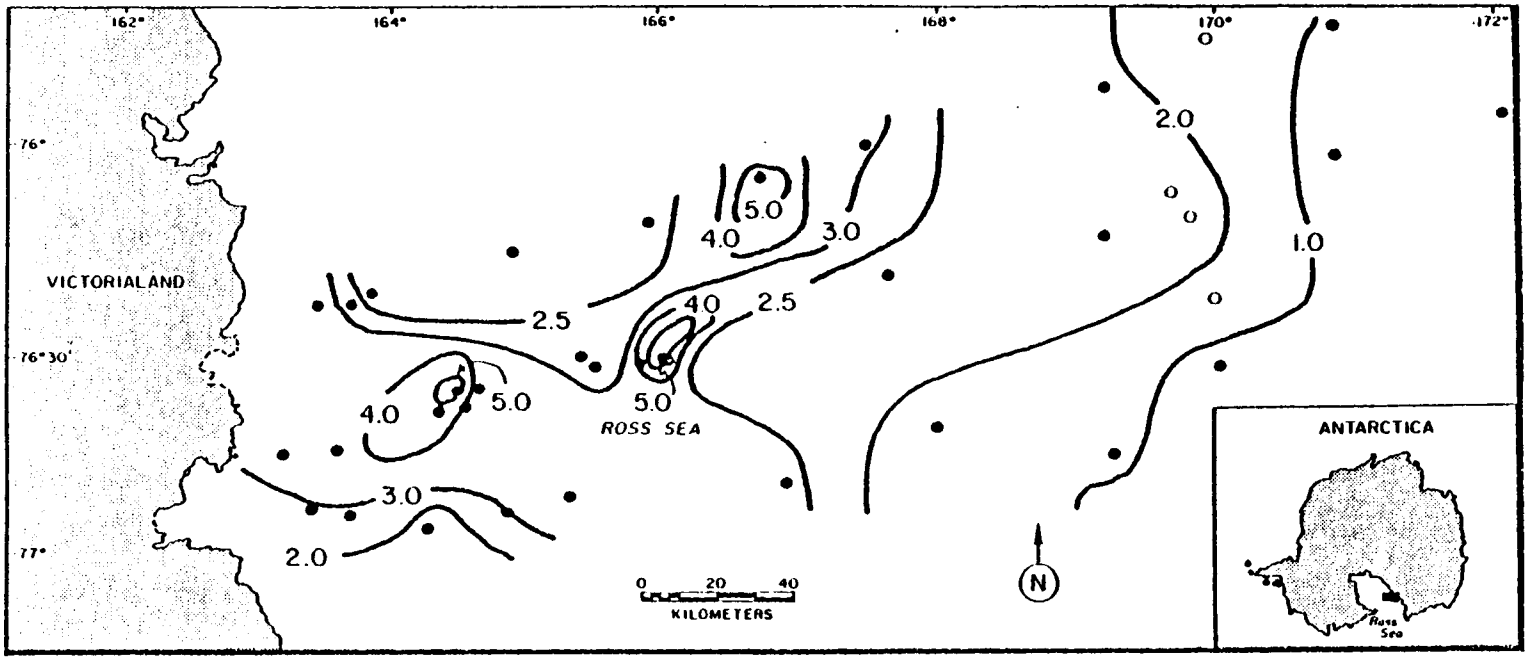

Figure 7. Surface Productivity (mg C m^{-3} h^{-1}) Distribution

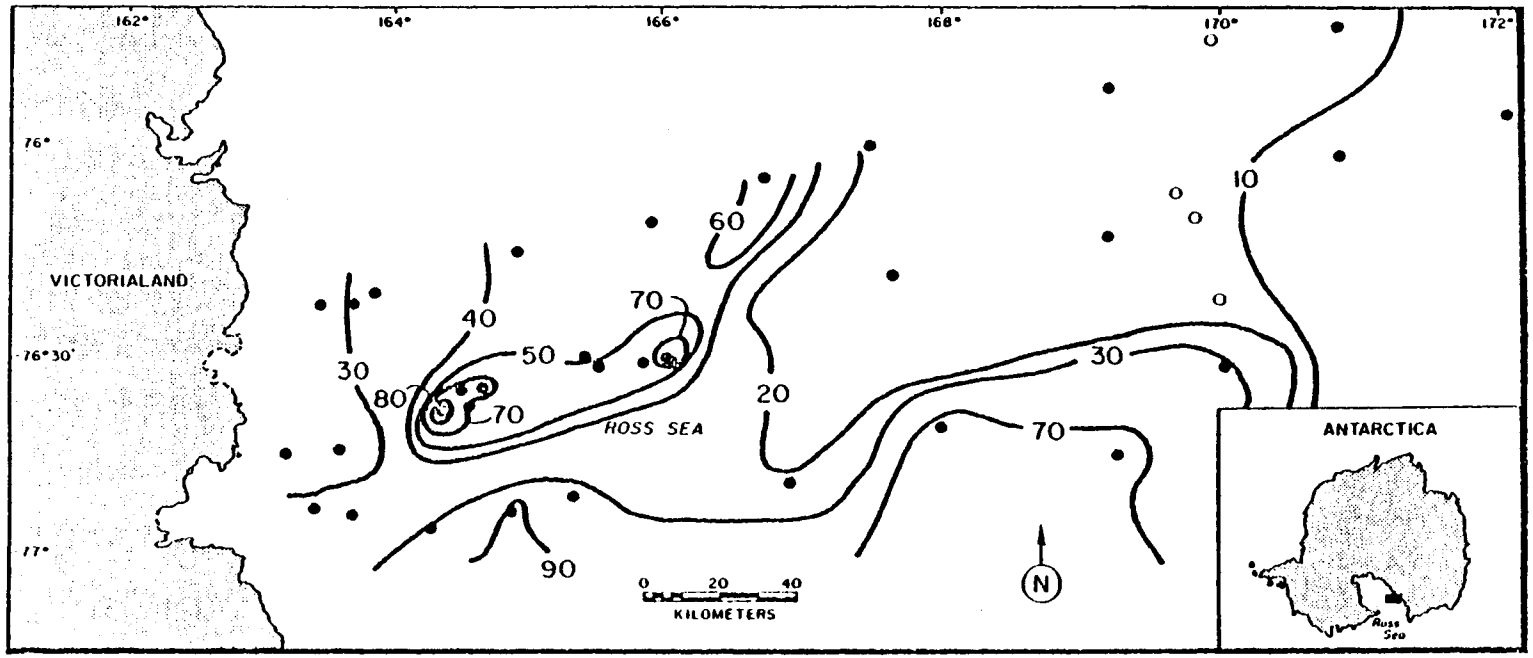

Figure 8. Integrated Euphotic Zone Productivity (mg C m^{-2} h^{-1})

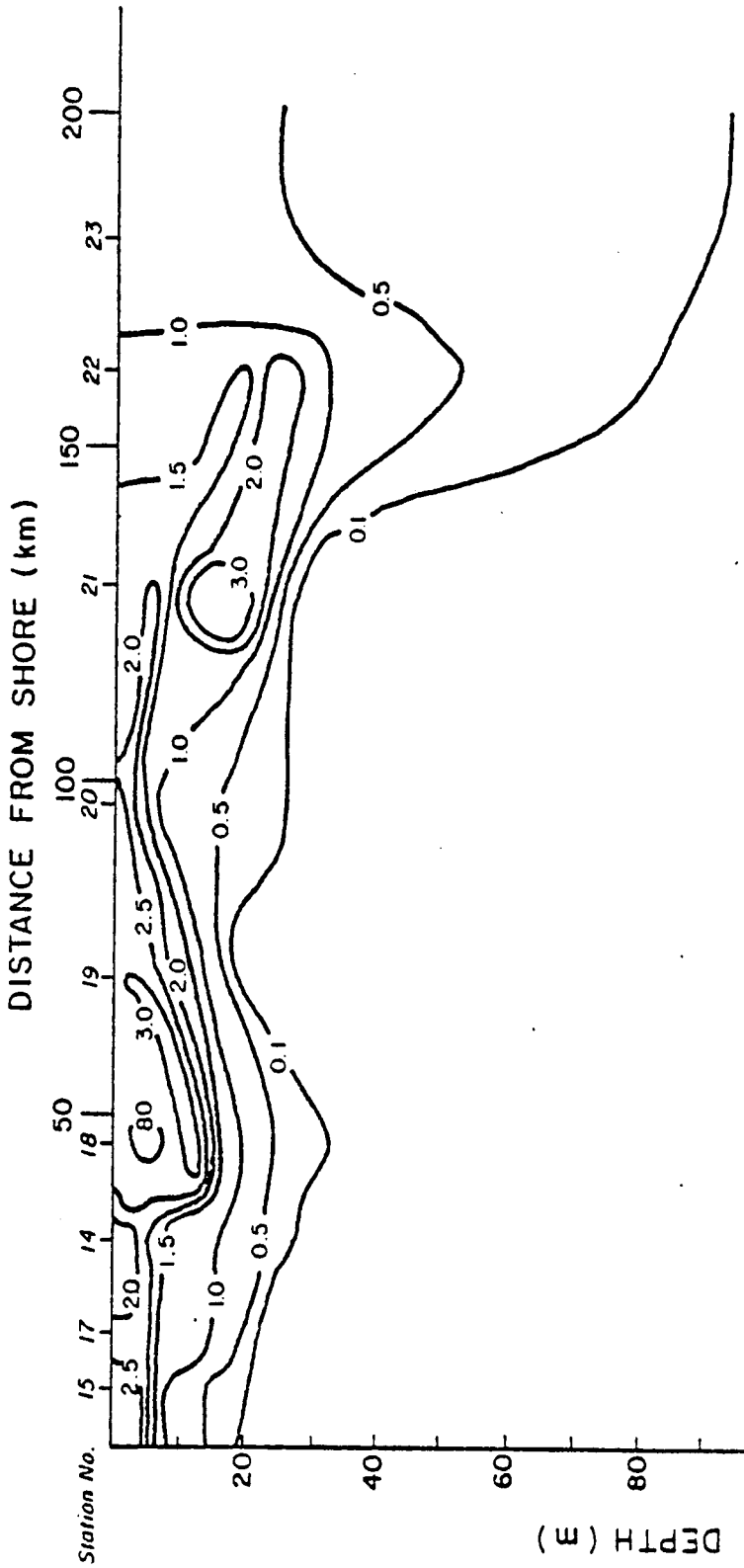

Figure 9. Vertical Section of Productivity (mg C m^{-3} h^{-1}): Stations 15-23

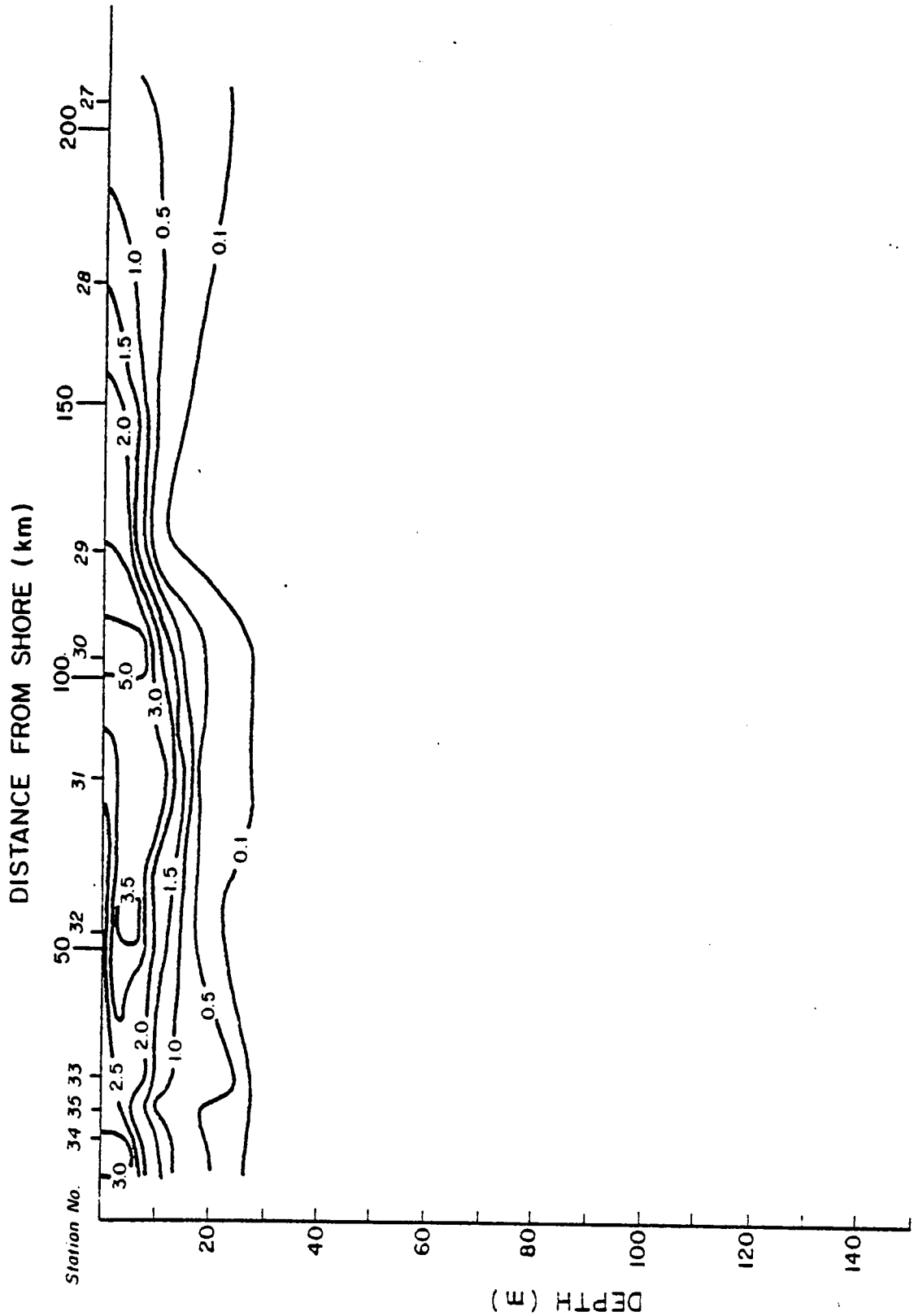

Figure 10. Vertical Section of Productivity (mg C m^{-3} h^{-1}): Stations 34-27

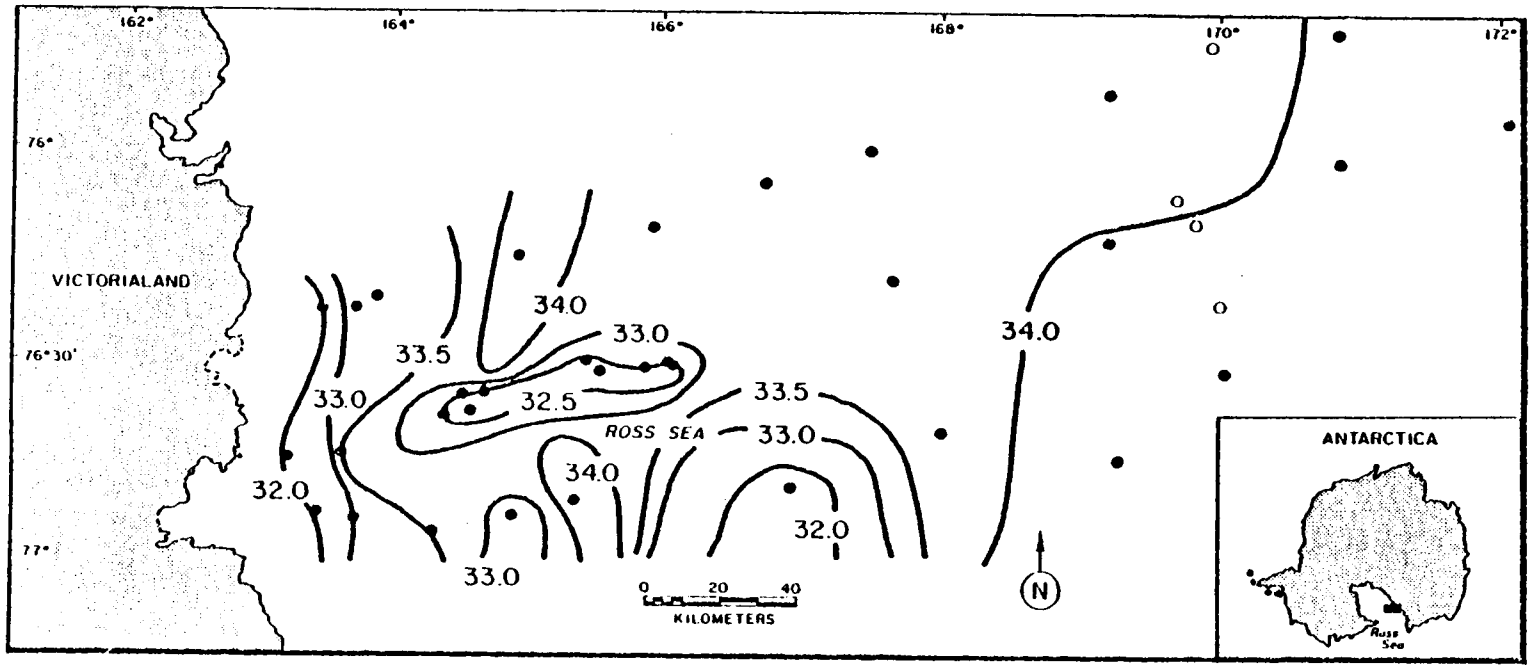

Figure 11. Surface Salinity (parts per thousand)

(approximately 25 m). In contrast, stations outside the bloom (i.e. station 23) had reduced productivity but had much deeper euphotic zones (approximately 90-100 m).

Salinity

The pattern of salinity distribution was tightly coupled with the distribution of chlorophyll and productivity. The bloom region was characterized by reduced surface salinity values which ranged from 31.8690 ppt at station 16 to 34.4084 ppt at station 43. The lowest surface values (32.0 - 32.5 ppt) occurred near shore (stations 15, 16, 34, and 36) and in the central region of the bloom (stations 2-13) (Figure 11).

Every station sampled exhibited reduced surface salinity and increased salinity at depth (Figures 12 and 13). Stations within the bloom exhibited strong vertical salinity gradients while control stations outside the bloom exhibited weak gradients. For example, salinity values at station 36 ranged from 32.281 ppt at the surface to 33.529 ppt at the 1% light level and 34.5774 ppt at 150 m. In contrast, values at station 43 ranged only from 34.4084 ppt at the surface to 34.6091 ppt at 150 m.

Density

The vertical density structure closely resembled that of salinity, since salinity is the major determinant of density at low temperatures (Pickard, 1963). Vertical sections of density, expressed as sigma-t, along two transects (Figures 14 and 15) clearly illustrated that the surface

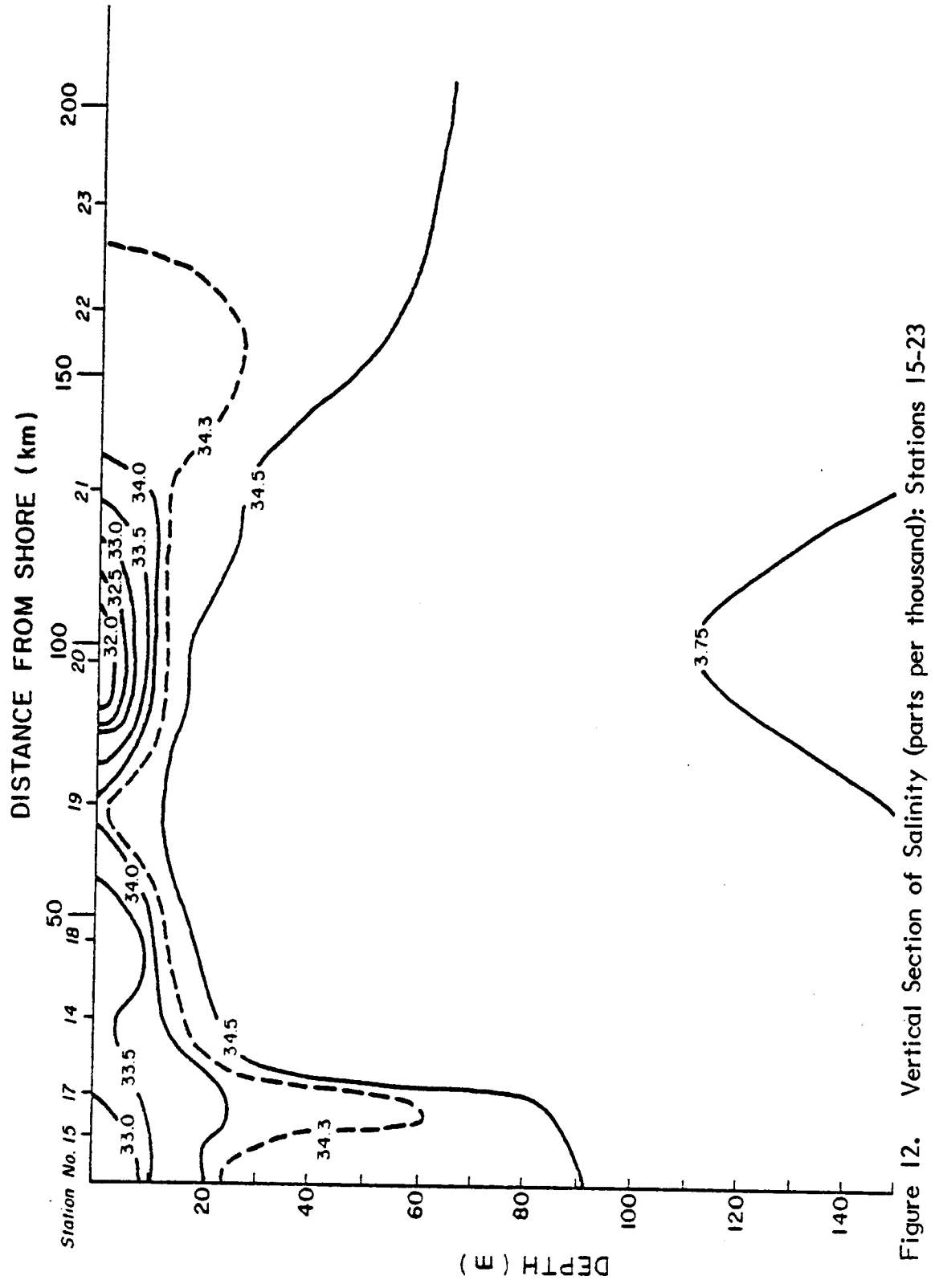

Figure 12. Vertical Section of Salinity (parts per thousand): Stations 15-23

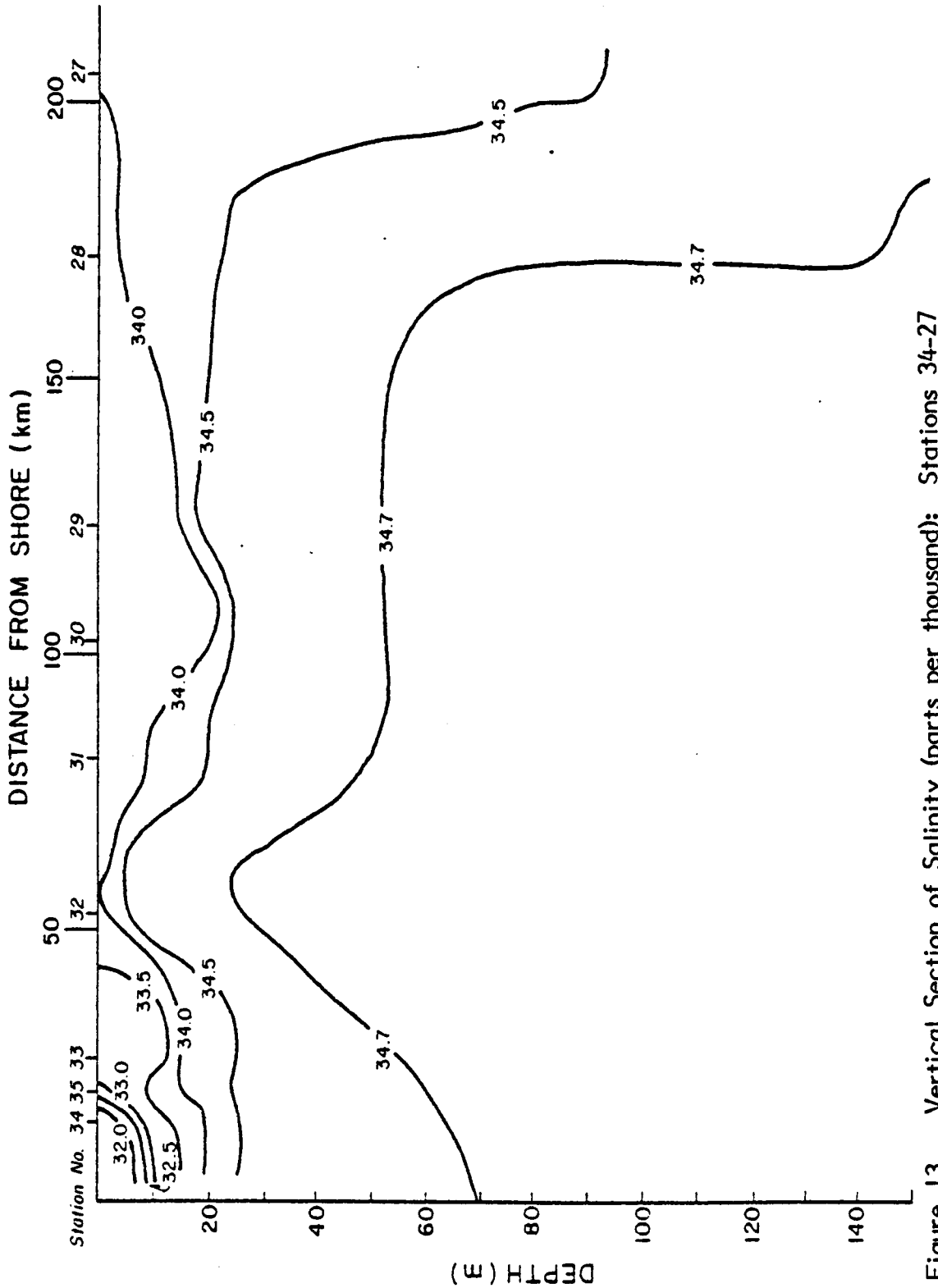

Figure 13. Vertical Section of Salinity (parts per thousand): Stations 34-27

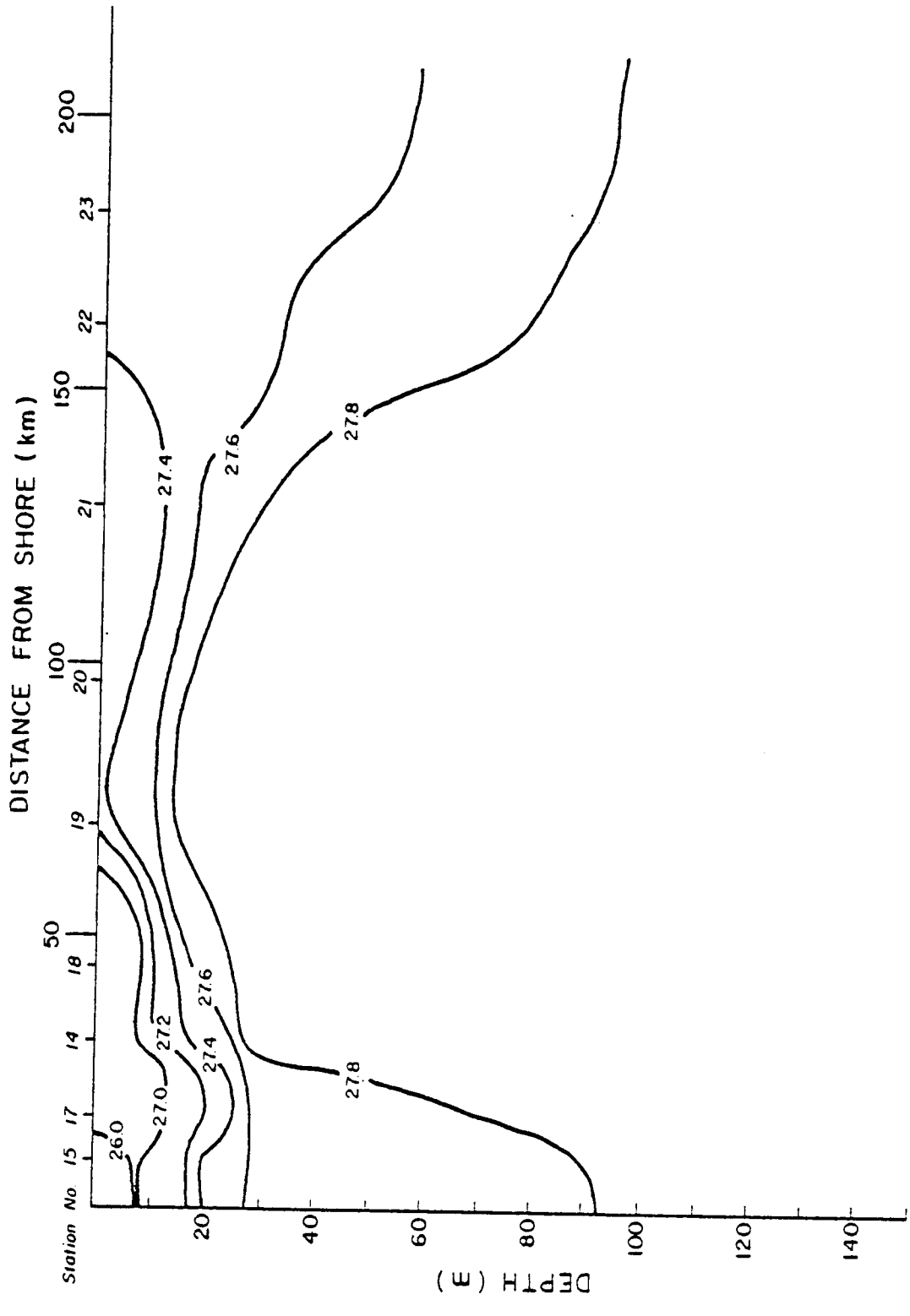

Figure 14. Vertical Section of Sigma-t: Stations 15-23

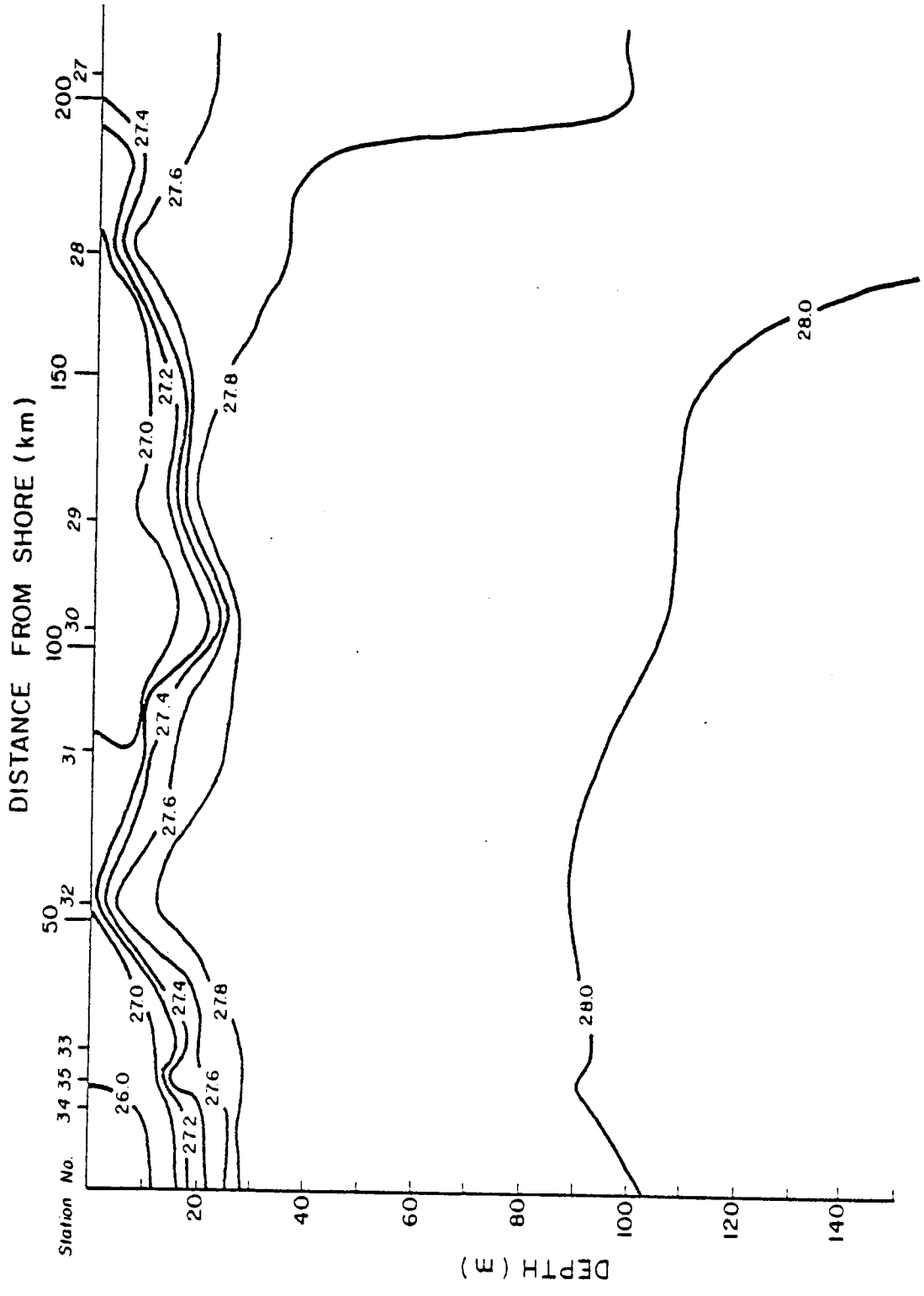

Figure 15. Vertical Section of Sigma-t: Stations 34-27

layers within the bloom are highly stratified. Contrasting those seaward to the bloom, bloom stations had sigma-t values which ranged from approximately 25.8 at the surface to approximately 28.0 at 150 m. Values for control stations (i.e. station 42) ranged from approximately 27.5 at the surface to approximately 28.0 at 150 m. Additionally, the seaward extent of vertical stability was very tightly coupled with the occurrence of elevated chlorophyll and productivity values.

Species Specific Productivity

The bloom was dominated by a single species, Nitzschia curta (section Fragilariopsis). This species comprised an average of 63.13 ± 5.44% of the standing stock at the surface, 67.56 ± 7.88% at the 30% light depth, and 78.16 ± 12.98% at the 5% light depth. Similarly, N. curta accounted for an average of 86.06 ± 12.40% of the productivity at the surface, 87.23 ± 10.74% at the 30% light depth, and 93.58 ± 7.03% at the 5% light depth.

A second species, Nitzschia closterium, was found to contribute to the overall productivity along transect #1 while being somewhat less prevalent within transect #2. For transect #1, this species accounted for 16.04 ± 10.95, 19.55 ± 11.28, and 5.89 ± 4.41% of the standing stock and 17.55 ± 13.88%, 17.43 ± 12.29%, and 4.77 ± 7.53% of the productivity at 100%, 30%, and 5% light depth respectively. In contrast, this species accounted for less than 5.0% of the standing stock and less than 2.0% of the productivity in transect #2.

Finally, a third diatom species, Nitzschia cf. curta var. minima, contributed to the total productivity of the bloom region. This species accounted for 10.29 ± 8.02% of the standing stock along transect #1 and 6.47% of the standing stock along transect #2. With regard to relative productivity, N. curta var. minima contributed 1.83 ± 1.5% of the overall productivity along transect #1 and 1.71 ± 0.78% along transect #2. For both transects, N. curta var. minima accounted for 8.38 ± 6.6% of the standing stock and 1.77 ± 1.2% of the productivity.

"ANCOVA" (see Materials and Methods) analysis of the data indicated that there were no significant differences between depths along each transect for the "productivity index versus station" regression relationship of N. curta. However, a significant difference was detected between transects for the same regression relationship. Specifically, N. curta showed a strong increase in relative productivity at all depths along transect #1 with surface populations showing the greatest increase. In contrast, along transect #2, N. curta exhibited slight decreases in relative productivity at the 30% (slope = -.001) and 5% (slope = -.008) light depths while showing a slight increase (slope = .023) at the surface. Additionally, the relative productivity of N. curta was significantly ($P < .001$) higher along transect #2 (94.95 ± 3.89%) than transect #1 (82.96 ± 11.67%).

"ANCOVA" analysis of the "relative productivity versus station" regression for Nitzschia closterium indicated that there was significant variation in relative productivity between transects ($p < .001$) as well as indicating a slightly significant ($p < .05$) interaction between depth

and transect. Specifically, the relative productivity of N. closterium showed a general decrease seaward at all depths along both transects. Transect #1 showed the most drastic reduction, while transect #2 showed a much more gradual decrease. Additionally, increases in the relative productivity of N. closterium corresponded closely with decreases in the relative productivity of N. curta along each transect.

As with N. curta, "ANCOVA" analysis indicated that there was no significant variation between depths for the "relative productivity versus station" regression for N. curta var. minima; however, a moderately significant variation between transects was indicated (Table 1). Yet, the regression analysis indicated a slight increase in relative productivity for all depths along both transects with the exception of the 100% and 30% light depth along transect #2.

The cell specific activity (grains $cell^{-1}$) of Nitzschia curta and Nitzschia closterium did not vary greatly while standing stock for the two species was often separated by an order of magnitude. Specifically, the N. curta x N. closterium cell-specific activity ratio ranged between 2-4 for both transects. Additionally, N. curta averaged 1.452×10^9 cells m^{-3} along transect #1 and 1.929×10^9 cells m^{-3} along transect #2 while N. closterium averaged 3.045×10^8 cells m^{-3} and 1.071×10^8 cells m^{-3} for transect #1 and transect #2 respectively. This indicated that species population was more important than cell-specific activity in governing the relative productivity of these two species.

Although the remaining phytoplankton species accounted for less than 1% of the total population of the bloom, many of these species

TABLE 1. ANCOVA Tables for the PI versus Station Regression for Nitzschia curta, Nitzschia closterium, and Nitzschia cf. curta var. minima.

ANOVA	Source	DF	SS	MS	F_s[1]	F_s[2]
N. curta	Depth	4	385.60	96.40	1.37	2.36
	Transect	2	1614.98	807.49	19.77**	19.77**
	Depth x Transect	4	280.48	70.12	1.72	1.72
	Error	18	735.27	40.85		
	Total	28	3016.33			
N. closterium	Depth	4	382.78	95.70	1.03	3.10*
	Transect	2	1497.92	748.96	24.28**	24.28**
	Depth x Transect	4	371.63	92.91	3.01*	3.01*
	Error	18	555.26	30.85		
	Total	28	2780.31			
N. cf. curta var. minima	Depth	4	9.57	2.39	1.10	2.69
	Transect	2	7.04	3.52	3.26*	3.96*
	Depth x Transect	4	8.72	2.18	2.45	2.45
	Error	18	15.98	0.89		
	Total	28	41.31			

*Significant, $P < 0.05$
**Highly significant, $P \leq 0.001$.
[1]Where transects arre considered "random" effects.
[2]Where transects are considered "fixed" effects.

were characterized by cell specific activities (grains cell^{-1}) which were often ten fold greater than that of either Nitzschia curta or Nitzschia closterium. For example, Chaetoceros atlanticus often produced 200-300 grains cell^{-1} and Distephanus speculum often produced 100-200 grains cell^{-1}. In contrast, Nitzschia curta typically produced 10-20 grains cell^{-1}. Regression analyses were not performed on these and the remaining species because the sample population was insufficient to yield statistically significant results.

"ANCOVA" analysis of the data (Table 1) with transects considered as "fixed" effects did not yield drastically different results. As before, transects were significantly different ($p < 0.001$) for all three species. The results were also very similar for depths, with the exception of N. curta, which showed a slightly significant difference between depths.

CHAPTER 6

DISCUSSION

The chlorophyll concentrations observed during this study were high when compared with previously reported values from the Antarctic pack-ice zone. For example, El-Sayed and Taguchi (1981) found mean chlorophyll values of 4.36 ± 1.75 mg m^{-2} for the northern and central regions of the Weddell Sea and 31.6 ± 9.5 mg m^{-2} in the Southern region. El-Sayed (1970) reported mean integrated euphotic zone (through the 0.1% light depth) chlorophyll values of 15.94 mg m^{-2} and 12.62 mg m^{-2} for the Atlantic and Pacific sectors respectively. Recent studies, covering a wider geographical range, have provided a composite of the biomass of the Southern Ocean. For example, El-Sayed and Turner (1977) reported an overall mean chlorophyll concentration for the Pacific sector of 0.26 mg Chl a m^{-3} and 1.22 mg Chl a m^{-2} for surface and integrated euphotic zone (through 0.1% surface radiation).

The vertical distribution of chlorophyll found during this study was similar to those previously reported for the Southern Ocean. Holm-Hansen et al. (1977) found maximum chlorophyll values at or near the surface of the subtropical and subantarctic regions of the Atlantic and Pacific Oceans. However, waters south of the Antarctic convergence were characterized by subsurface chlorophyll maxima between the depths of 25% and 12% light penetration. Maximum chlorophyll values in the area of the Ross Ice Shelf were found at an average depth of 30 m while, seaward of the shelf, no prominent chlorophyll maxima were observed. Additionally, Holm-Hansen et al. (1977) reported the presence

of high chlorophyll concentrations well below the euphotic zone (average depth = 43 m) of the Ross Sea. However, this was not a prominent feature along transects in the Pacific and Indian Oceans.

The levels of productivity measured during this study were also relatively high when compared to the Southern Ocean as a whole. El-Sayed and Turner (1977) reported an overall average of 0.134 g C m^{-2} d^{-1} while pointing out that, because of the considerable geographic variations in productivity, this value could be misleading. Additionally, data are still lacking from both oceanic and coastal regions, as well as from different seasons. Thus, it is very difficult to describe the Southern Ocean in terms of average values with any certainty and it is even more difficult to make an assessment of annual production.

The vertical distribution of productivity was similar to that previously reported for the Ross Sea. Specifically, El-Sayed and Turner (1977) found maximum values for productivity to be located between the depth of 50% and 25% light penetration. Holm-Hansen et al. (1977) demonstrated a good correlation between the intensity of incident solar radiation and photosynthetic rates in the euphotic zone. They found that on bright days (ca. 100-160 cal cm^{-2} half-light-day^{-1}), photosynthetic rates were low in the surface water and increased with depth. However, when incident light intensities were low (20-30 cal. cm^{-2} half-light-day^{-1}) during the incubation period, they found that photosynthetic rates either remained constant or were highest in surface waters. This indicated that Antarctic phytoplankton are somewhat adapted to reduced light intensities and that surface populations might often experience photoinhibition.

During our study, the amount of available light varied considerably and most probably had some affect on the distribution of productivity. However, this variability was not such that it affected the overall resolution of the bloom.

Several studies have drawn attention to the importance of water column stability in controlling production (Sverdrup, 1953; Hasle, 1956; El-Sayed and Mandelli, 1965; El-Sayed and Taguchi, 1981). The salinity and density (σt) data from the present study indicates that a stable surface layer was present and, as the vertical sections indicate, this stability was tightly coupled with the occurrence of elevated chlorophyll concentrations and primary productivity. This is in agreement with previous reports which attributed low productivity in the Southern Ocean to reduced stability of surface waters, while suggesting that high primary productivity occurs in areas of comparative stability (El-Sayed et al., 1974; El-Sayed, 1978). Thus, it is probable that the high levels of primary productivity measured during this study were, at least in part, due to meltwater induced stability of the water column.

Although water column stability is indicated as a primary factor in bloom initiation, additional factors may have been important. From the analysis of species composition and phytoplankton standing stock it appeared that the bloom was dominated by pennate diatoms, most notably Nitzschia curta (section Fragilariopsis). In contrast, those stations seaward of the bloom were characterized by greater relative numbers of characteristically planktonic species (i.e. Corethron sp., Chaetoceros

sp., and Distephamous sp.). This serves as indirect evidence that seeding of the ice-edge bloom may have been important factor in its initiation. Unfortunately, only one sample of the epontic community was available for analysis. However, N. curta was well represented in this sample. Additionally, several other species were observed from both the ice-algae sample and the bloom (see Appendix A).

Further evidence of the importance of ice-algae seeding of the bloom system comes from the autoradiographic analysis. Autoradiography provided direct evidence that N. curta as well as other typically epontic species (Burkle, personal communication) may produce viable populations upon their release from the sea ice. Despite the fact that N. curta had only a moderate cell specific activity, it is probable that its growth rate (i.e. doubling time) was greater than those of the larger more active species. That is, cell specific activity (grains $cell^{-1}$) did not serve as an accurate index of growth rate because it does not take into account differences in cell size and cell volume. These values are at best extremely difficult to determine and, to date, few studies have reported data on cell volumes of Antarctic species. In addition, comparison of data on the same species, calculated by different authors (i.e. Paasche, 1960; Bernhard and Rampi, 1967) indicated that estimates of specific cell volumes are only applicable to the material from which the data were derived (Halse, 1969). Therefore, it is impossible to compare the differing species on the basis of volume and/or carbon-specific activity. However, it is well established that cell division rates

of unicellular algae are size dependent with growth rates being directly and linearly related to the square root of the ratios of cell surface area to cell volume (Eppley, 1966). Respiration rate has also been shown to decline with increasing size in the same manner (Banse, 1976). Finally, growth efficiency (net divided by gross photosynthesis) has not been shown to be size dependent (Banse, 1976). Thus, it seems likely that N. curta had a relatively high growth rate and comparable growth efficienty (discounting inherent species differences) when compared to the larger species (i.e. Chaetoceros) in the bloom.

From the available data it appears that several factors combined to favor the dominance of N. curta within the bloom: 1) It was probably released from the sea ice into the water column in relatively large numbers, 2) meltwater-induced stability provided a favorable light environment for phytoplankton growth regardless of species and 3) it most likely had a relatively high growth rate when compared to the larger species. If, however, vertical stability and heavy "seeding" interacted to allow an accumulation of Nitzschia curta within the bloom, it is difficult to account for the relatively low numbers of other small epontic species. It is possible that these species were lost via sinking, however, it is unclear how N. curta could escape a similar fate. One explanation might be that N. curta responded more rapidly to the improved growth conditions encountered upon release from the sea-ice and thus better maintain its abundance within the upper water column. Unfortunately, little or no data are available on the metabolic responses

metabolic responses of the various epontic species to release from the ice. Furthermore, the relative activities of the various epontic species prior to release are not known. Finally, no data are available on the vertical flux of biogenic material from the euphotic zone in ice-edge blooms in the Southern Ocean.

CHAPTER 7

SUMMARY

1. The input of relatively fresh (hence less dense) meltwater imparted vertical stability to the water column in the study area

2. Elevated levels of chlorophyll and primary productivity were tightly coupled with the occurrence of a vertically stable surface layer, indicating its primary importance in initiating a phytoplankton bloom.

3. Taxanomic analysis of both the planktonic and epontic communities indicate that a significant overlap occurred between the ice and bloom flora, but not between ice and non-bloom planktonic flora.

4. Autoradiographic analysis indicated that Nitzschia curta (section Fragilariopsis) dominated the bloom with respect to both standing stock (cells m^{-3}) and relative primary productivity. Nitzschia closterium and Nitzschia cf. curta var. minima also contributed to the overall productivity within the bloom.

5. "ANCOVA" (see Materials and Methods) analysis of the relationship between relative productivity and station (as distance from shore) indicated that there was generally little difference between depth along each transect for the three species analyzed; however, transects 1 and 2 were shown to be significantly different.

6. It appears that vertical stability of the euphotic zone and a strong "seeding" influence from the epontic community combined to produce the observed dominance of Nitzschia curta within the bloom. However, no data are available with respect to the fate of other epontic species.

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APPENDICES

APPENDIX A

PARTIAL LIST OF OBSERVED SPECIES

Diatoms:

1. *Actinocyclus* sp.
2. *Amphipleura* sp.*
3. *Asteromphalus parvulus*
4. *Chaetoceros atlanticus*
5. *C.* spp.
6. *Charcotia actinochilus*
7. *Corethron criophilum*
8. *Coscinodiscus* sp.
9. *Dactyliosolen antarcticus*
10. *Dactyliosolen antarcticus**
11. *Nitzschia closterium**
12. *N. cylindrus**
13. *N. curta**
14. *N.* cf. *curta* var. *minima*
15. *N.* spp.*
16. *Rhizosolenia styliformis*
17. *Schimperiella antarctica*
18. *Thalassiosira tomida*
19. *T.* spp.
20. *Thalassiothris* sp.*
21. *Tropidoneis* sp.*
22. *Pleurosigma* sp.*

Flagellates:

1. *Ceratium* sp.
2. *Gymnodinium* sp.
3. *Peridininum* sp. (Also observed cysts)

Silicoflagellates:

1. *Distephanus speculum*

*Observed as components of both the "bloom" and the epontic communities.

APPENDIX B

STATION	2	3	4	5	11	12	13	14	15	16
Depth of Euphotic Zone (meters)	36	25	33	29	34	34	30	29	22	30
Surface Productivity (mg C m^{-3} h^{-1})	4.46	3.53	2.56	2.45	2.49	3.46	1.90	1.94	2.48	3.30
Integrated Euphotic Productivity (mg C m^{-2} h^{-1})	88.04	69.09	22.10	19.64	37.61	54.51	35.85	32.26	19.08	28.97
Surface Chlorophyll (mg Chl -a m^{-3})	2.04	1.14	1.68	1.74	1.66	1.76	1.16	1.52	2.00	2.78
Integrated Euphotic Chlorophyll (mg Chl -a m^{-2})	44.66	54.09	27.28	36.29	64.55	48.59	53.23	57.78	35.51	54.90
Integrated Chlorophyll 150 m (mg Chl -a m^{-2})	90.06	77.71	48.07	78.75	84.70	75.97	74.23	76.08	111.88	140.40
Mean Euphotic Zone Chlorophyll-Specific Productivity (mg C mg Chl^{-1}-a h^{-1})	1.97	1.28	0.81	0.54	0.58	1.12	0.67	0.56	0.54	0.53
Mean Euphotic Zone Carbon-Specific Growth Rate (per day)	0.281	0.340	0.168	0.047	0.087	0.095	0.097	0.082	0.087	0.094

STATION	17	18	19	20	21	22	23	24	25	26
Depth of Euphotic Zone (meters)	24	25	20	28	28	89	98	108	24	32
Surface Productivity (mg C m^{-3} q^{-1})	2.15	2.85	2.57	2.57	1.73	1.08	0.69	1.7	2.5	***
Integrated Euphotic Productivity (mg C m^{-2} q^{-1})	23.10	91.08	31.11	17.78	54.10	65.10	28.58	***	***	***
Surface Chlorophyll (mg Chl -a m^{-3})	2.77	1.92	3.28	0.86	3.10	0.96	0.79	0.61	1.41	2.2
Integrated Euphotic Chlorophyll (mg Chl -a m^{-2})	52.14	58.84	49.89	27.93	69.56	37.71	45.45	***	***	***
Integrated Chlorophyll 150 m (mg Chl -a m^{-2})	111.66	98.27	95.82	62.86	166.15	61.08	79.51	***	***	***
Mean Euphotic Zone Chlorophyll-Specific Productivity (mg C mg Chl^{-1} -a h^{-1})	0.44	1.55	0.62	0.64	0.78	1.73	0.63	***	***	***
Mean Euphotic Zone Carbon-Specific Growth Rate (per day)	0.055	0.212	0.183	0.069	0.143	0.179	0.081	***	***	***

STATION	27	28	29	30	31	32	33	34	35
Depth of Euphotic Zone (meters)	53	80	18	28	28	28	28	30	24
Surface Productivity (mg C m^{-3} h^{-1})	0.67	***	2.99	5.41	2.63	2.30	1.96	3.01	3.04
Integrated Euphotic Productivity (mg C m^{-2} h^{-1})	15.67	***	17.08	66.41	46.23	43.47	32.81	35.68	13.68
Surface Chlorophyll (mg Chl. -a m^{-3})	0.30	1.97	2.77	5.40	4.16	2.91	3.46	4.02	1.97
Integrated Euphotic Chlorophyll (mg Chl. -a m^{-2})	15.84	39.60	35.71	56.47	65.89	53.37	50.93	71.97	34.20
Integrated Chlorophyll 150 m (mg Chl. -a m^{-2})	41.70	53.40	87.38	85.69	158.39	80.15	93.27	112.77	75.23
Mean Euphotic Zone Chlorophyll-Specific Productivity (mg C mg $Chl.^{-1}$ -a h^{-1})	0.99	***	0.48	1.18	0.70	0.81	0.64	0.50	0.40
Mean Euphotic Zone Carbon-Specific Growth Rate (per day)	0.124	***	0.066	0.128	0.136	0.182	0.104	0.104	0.048

STATION	36	37	38	39	40	41	42	43
Depth of Euphotic Zone (meters)	24	28	28	28	28	81	81	98
Surface Productivity (mg C m^{-3} h^{-1})	5.04	3.69	5.42	6.92	***	***	***	***
Integrated Euphotic Productivity (mg C m^{-2} h^{-1})	35.52	30.38	54.17	75.06	***	***	***	***
Surface Chlorophyll (mg Chl. -a $^{-3}$)	4.57	3.60	1.73	4.85	4.71	1.20	0.99	0.72
Integrated Euphotic Chlorophyll (mg Chl. -a m^{-2})	79.12	70.71	90.16	87.30	102.02	160.73	46.71	52.62
Integrated Chlorophyll 150 m (mg Chl. -a m^{-2})	123.52	112.28	191.38	212.35	179.58	203.00	70.03	56.53
Mean Euphotic Zone Chlorophyll-Specific Productivity (mg C mg $Chl.^{-1}$ -a h^{-1})	0.45	0.43	0.60	0.86	***	***	***	***
Mean Euphotic Zone Carbon-Specific Growth Rate (per day)	0.137	0.089	0.192	0.169	***	***	***	***

VITA

David Lee Wilson was born in Chattanooga, Tennessee, on July 20, 1958. He attended primary and secondary schools in Dunlap, Tennessee and graduated from Sequatchie County High School in May 1976. The following September he began studies at The University of Tennessee, Knoxville. He graduated cum laude in March 1981 with a Bachelor of Arts degree in Biology. After receiving a graduate research assistantship at The University of Tennessee, Knoxville in September 1982, he began work towards a Master of Science degree in the Department of Botany. He received this degree in December 1983.