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**SIZE-FRACTIONATED PHYTOPLANKTON BIOMASS AND PRIMARY  
PRODUCTION IN THE SOUTHERN OCEAN**

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**MASTER OF SCIENCE**

**of**

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**by**

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## TABLE OF CONTENTS

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<b>PREFACE</b>	i
<b>ACKNOWLEDGEMENTS</b>	ii
<b>DECLARATION</b>	iii
<b>LIST OF FIGURES</b>	iv
<b>LIST OF TABLES</b>	viii
<b>ABSTRACT</b>	x
<b>Chapter 1</b> <i>Introduction</i>	1
<b>Chapter 2</b> <i>Materials and methods</i>	25
2.1    Positions of stations	25
2.2    Light measurements	26

2.3	Primary production	26
2.4	Chlorophyll- <i>a</i>	29
2.5	Macronutrients	30
2.6	Hydrological data	30
2.7	Salinity	31
2.8	Data Display System	31
<b>Chapter 3</b>	<i>The Scandinavian/South African Antarctic cruise - December/February</i>	
	<i>1997-1998</i>	32
3.1.	Results	32
3.1.1.	Hydrological conditions	32
3.1.2.	Nutrients	36
3.1.3.	Integrated chlorophyll- <i>a</i>	37
3.1.4.	Integrated primary production	44
3.1.5.	Photosynthetic capacity	46
3.2.	Discussion	50
3.3.	Conclusions	55
<b>Chapter 4</b>	<i>The Third Marion Island Oceanographic Survey (MIOS III) -</i>	
	<i>April/May 1998</i>	57
4.1.	Results	58
4.1.1.	Hydrological conditions	57
4.1.2.	Nutrients	62
4.1.3.	Integrated Chlorophyll- <i>a</i>	63
4.1.4.	Integrated primary production	70
4.1.5.	Photosynthetic capacity	77
4.2.	Discussion	80

	4.3. Conclusions	84
<b>Chapter 5</b>	<i>General conclusions and future perspectives</i>	85
<b>Chapter 6</b>	<i>References</i>	92

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## **PREFACE**

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This study was conducted in two different realms of the Southern Ocean, the high Antarctic and Sub-Antarctic region. The techniques employed were similar for both investigations and are, therefore, described in a single chapter. For clarity, the results and discussion for each cruise are presented in two separate chapters. The results for each cruise have been submitted to peer review journals.

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**DECLARATION**

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The work presented in this thesis was carried out in the Department of Zoology and Entomology (Southern Ocean Group), Rhodes University, under the supervision of Dr. PW Froneman and Prof. CD McQuaid. These studies represent an original work by the author and have not been submitted in any form to another university.

*Fortitudine vincimus*

## LIST OF FIGURES

**Figure 1:** Map of Antarctica and the Southern Ocean showing positions of the major oceanic fronts.

APF = Antarctic Polar Front; SAF = Sub-Antarctic Front; STC = Subtropical Convergence; MIZ = Marginal Ice Zone. (page 8)

**Figure 2:** Positions of production stations during the collaborative Scandinavian/South African Antarctic expedition conducted in the austral summer (Dec./Feb.) 1997 - 1998. MIZ = Marginal Ice Zone; IFZ = Interfrontal Zone; APF = Antarctic Polar Front. (page 21)

**Figure 3:** Primary production stations occupied during the third Marion Island Oceanographic Survey (MIOS III) conducted to the region of the Prince Edward Islands in austral autumn (April/May) 1998. Production station 2 indicates the position of the Sub-Antarctic Front (SAF). (page 23)

**Figure 4.1:** Water column profiles of temperature and density at stations in the Marginal Ice Zone (MIZ) in the Atlantic sector of the Southern Ocean during the Scandinavian/South African Antarctic expedition. (page 34)

**Figure 4.2:** Water column profiles of temperature and density at stations in the APF (Antarctic Polar Front) and IFZ (Interfrontal Zone) in the Atlantic sector of the Southern Ocean during the Scandinavian/South African expedition. (page 34)

**Figure 5:** Total size-fractionated phytoplankton chlorophyll-*a* concentrations at stations in the vicinity of the MIZ, IFZ, and APF during the Scandinavian/South African Antarctic expedition in December 1997-February 1998. All data are integrated to the 1% euphotic depth. Micro = Microphytoplankton (>20  $\mu\text{m}$ ); Nano = Nanophytoplankton (<20 and >2.0  $\mu\text{m}$ ); Pico = Picophytoplankton (< 2  $\mu\text{m}$ ). MIZ = Marginal Ice Zone; IFZ = Interfrontal Zone; APF = Antarctic Polar Front. (page 39)

**Figure 6.1:** Vertical profiles of chlorophyll-*a* concentration at different light depths at the six stations occupied in the MIZ during the Scandinavian/South African Antarctic expedition. (page 40)

**Figure 6.2:** Vertical profiles of chlorophyll-*a* concentration at different light depths at the two stations in the IFZ region during the Scandinavian/South African Antarctic expedition. (page 41)

**Figure 6.3:** Vertical profiles of chlorophyll-*a* concentration at different light depths at the four stations in the vicinity of the APF during the Scandinavian/South African Antarctic expedition. (page 42)

**Figure 7:** Total integrated size-fractionated phytoplankton primary production measurements at stations occupied in the vicinity of the MIZ, IFZ, and APF during the Scandinavian/South African Antarctic expedition in December 1997-February 1998. All data are integrated to the 1% euphotic depth. Abbreviations as in Figure 5. (page 43)

**Figure 8.1:** Vertical profiles of primary production at different light depths at production stations occupied in the vicinity of the Marginal Ice Zone (MIZ) during the Scandinavian/South African Antarctic expedition. (page 47)

**Figure 8.2:** Vertical profiles of primary production at different light depths at production stations occupied in the vicinity of the Interfrontal Zone (IFZ) during the Scandinavian/South African Antarctic expedition. (page 48)

**Figure 8.3:** Vertical profiles of primary production at different light depths at production stations occupied in the vicinity of the Antarctic Polar Front (APF) during the Scandinavian/South African Antarctic expedition. (page 49)

**Figure 9:** Photosynthetic capacity ( $\text{mg C (mg Chl-}a\text{)}^{-1} \text{ h}^{-1}$ ) profiles at production stations occupied in the MIZ, APF and IFZ in the Atlantic sector of the Southern Ocean during the Scandinavian/South African Antarctic expedition. MIZ = Marginal Ice Zone; IFZ = Interfrontal Zone; APF = Antarctic Polar Front. (page 51)

**Figure 10.1:** Water column profiles of temperature and density at production stations in the upstream region of the Prince Edward Islands (Southern Ocean) in late austral summer/autumn (April/May) 1998. (page 59)

**Figure 10.2:** Water column profiles of temperature and density at production stations in the inter-island region of the Prince Edward Islands (Southern Ocean) in late austral summer/autumn (April/May) 1998. (page 60)

**Figure 10.3:** Water column profiles of temperature and density at production stations in the downstream region of the Prince Edward Islands (Southern Ocean) in late austral summer/autumn (April/May) 1998. (page 61)

**Figure 11:** Total integrated size-fractionated chlorophyll-*a* concentrations at stations occupied in the upstream, inter-island and downstream regions of the Prince Edward Islands during April/May 1998. All data are integrated to the 0.1% euphotic depth. Micro = Microphytoplankton ( $>20 \mu\text{m}$ ); Nano = Nanophytoplankton ( $<20$  and  $>2.0 \mu\text{m}$ ); Pico = Picophytoplankton ( $< 2 \mu\text{m}$ ). SAF = Sub-Antarctic Front. (page 65)

**Figure 12.1:** Water column profiles of chlorophyll-*a* concentration at different light depths at the four stations occupied in the upstream region of the Prince Edward Islands in April/May 1998. (page 66)

**Figure 12.2:** Water column profiles of chlorophyll-*a* concentration at different light depths at the six stations occupied in the inter-island region of the Prince Edward Islands in April/May 1998. (page 67)

**Figure 12.3:** Water column profiles of chlorophyll-*a* concentration at different light depths at the six stations occupied in the inter-island region of the Prince Edward Islands in April/May 1998. (page 68)

**Figure 12.4:** Water column profiles of chlorophyll-*a* concentration at different light depths at the three stations occupied in the downstream region of the Prince Edward Islands in April/May 1998. (page 69)

**Figure 13:** Total size-fractionated phytoplankton primary production measurements at stations in the upstream, inter-island and downstream regions of the Prince Edward Islands during April/May 1998. All data are integrated to the 1% euphotic depth. Abbreviations as for Figure 11. (page 72)

**Figure 14.1:** Vertical profiles of primary production at different light depths at the four stations in the occupied in the upstream region of the Prince Edward Islands in April/May 1998. (page 73)

**Figure 14.2:** Vertical profiles of primary production at different light depths at the six stations occupied in the inter-island region of the Prince Edward Islands in April/May 1998. (page 74)

**Figure 14.3:** Vertical profiles of primary production at different light depths at the six stations occupied in the inter-island region of the Prince Edward Islands in April/May 1998. (page 75)

**Figure 14.4:** Vertical profiles of primary production at different light depths at the three stations in the occupied in the downstream region of the Prince Edward Islands in April/May 1998. (page 76)

**Figure 15.1:** Photosynthetic capacity ( $\text{mg C (mg Chl-}a\text{)}^{-1} \text{ h}^{-1}$ ) profiles at stations occupied in the vicinity of the Prince Edward Islands. (page 78)

**Figure 15.2:** Photosynthetic capacity ( $\text{mg C (mg Chl-}a\text{)}^{-1} \text{ h}^{-1}$ ) profiles at stations occupied in the vicinity of the Prince Edward Islands. (page 79)

## LIST OF TABLES

**Table 1:** Comparative results of phytoplankton biomass and production studies conducted in various regions of the Southern Ocean. (ND = no data presented, MIZ = Marginal Ice Zone, PFZ = Polar Front Zone, POOZ = Permanent Open Ocean Zone, SIZ = Seasonal Ice Zone, ACC = Antarctic Circumpolar Current, SAF = Sub-Antarctic Front, APF = Antarctic Polar Front). (page 12)

**Table 2:** Summary of environmental conditions at production stations occupied during the Scandinavian/South African Antarctic expedition within the MIZ, IFZ and APF during austral spring/summer (December/February 1997-1998).

MIZ = Marginal Ice Zone; IFZ = Interfrontal Zone; APF = Antarctic Polar Front. (page 33)

**Table 3:** Nutrient concentrations ( $\mu\text{mol} \cdot \text{L}^{-1}$ ) at stations occupied in the vicinity of the MIZ, IFZ and APF during December 1997/February 1998 Antarctic cruise. (page 36)

**Table 4:** Total integrated chlorophyll-*a* ( $\text{mg chl-}a \cdot \text{m}^{-2}$ ) values during the Scandinavian/South African Antarctic expedition (Dec/Feb) 1997-1998. (page 38)

**Table 5.** Total integrated primary production ( $\text{mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ) at production stations during the Scandinavian/South African Antarctic expedition in the Southern Ocean. (page 45)

**Table 6.** Summary of environmental conditions during the third Marion Island Oceanographic Survey (MIOS III) conducted in the upstream, inter-island and downstream region of the Prince Edward Islands (Southern Ocean) during the late austral autumn (April/May) 1998. (page 58)

**Table 7:** Nutrient concentrations ( $\mu\text{mol} \cdot \text{L}^{-1}$ ) at production stations occupied in the upstream, inter-island and downstream regions of the Prince Edward Islands in April/May 1998. (page 62)

**Table 8:** Total integrated chlorophyll-*a* (mg chl-*a* . m<sup>-2</sup>) during the third Marion Island Oceanographic Survey (MIOS III) conducted in late austral autumn (April/May) 1998. (page 64)

**Table 9:** Total integrated primary production (mg C . m<sup>-2</sup> . d<sup>-1</sup>) measurements during the survey conducted in the region of the Prince Edward Islands (Southern Ocean) in April/May 1998. Data are integrated to the 1% light depth. (page 71)

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**ABSTRACT**

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The factors controlling primary production in the Southern Ocean were investigated over two years during two cruises of the South African National Antarctic Program (SANAP). The first cruise was conducted to the region of the eastern Atlantic sector of the Southern Ocean during the collaborative Scandinavian/South African Antarctic expedition conducted in austral summer (December/February) 1997-1998. Production studies were conducted in the vicinity of the Marginal Ice Zone (MIZ), Interfrontal Zone (IFZ) and Antarctic Polar Front (APF). The second cruise was conducted during the Third Marion Island Oceanographic Survey (MIOS III) to the region of the Sub-Antarctic Prince Edward Islands in austral autumn (April/May) 1998. Size-fractionated production rates were estimated by  $^{14}\text{C}$  incorporation using standard JGOFS protocols. Oceanographic data from the first cruise suggest that the three regions can be divided into two distinct regimes. Stations occupied in the vicinity of the MIZ and the APF were characterised by a shallow mixed layer depth (< 40m) while at the IFZ-stations, the mixed layer depth exceeded the 1% light depth. Microphytoplankton dominated integrated chlorophyll-*a* biomass in the MIZ (total chlorophyll *a* ranged between 15.4 and 41.3 mg Chl-*a* . m<sup>-2</sup>) and at the APF (range between 10.7 and 31.4 mg Chl-*a* . m<sup>-2</sup>), comprising > 50% of total chlorophyll-*a* at all these stations.

Within the IFZ (2 stations), nanophytoplankton dominated total integrated Chl-*a* biomass (range between 5.6 and 8.8 mg Chl-*a* . m<sup>-2</sup>) comprising, on average, 36% of the total. Picophytoplankton comprised an average of 12% of the total Chl-*a* biomass (range between 3.1 and 5.9 mg Chl-*a* . m<sup>-2</sup>) in the MIZ, 36% in the IFZ (range between 6.4 and 7.8 mg Chl-*a* . m<sup>-2</sup>) and 20% in the vicinity of the APF (range between 6.8 and 10.6 mg Chl-*a* . m<sup>-2</sup>). Total integrated primary production ranged between 316 and 729 mg C . m<sup>-2</sup> . d<sup>-1</sup> at stations occupied in the vicinity of the MIZ, and between 292 and 317 mg C . m<sup>-2</sup> . d<sup>-1</sup> within the IFZ. At stations occupied in the region of the APF, total integrated production ranged between 708 and 926 mg C . m<sup>-2</sup> . d<sup>-1</sup>. The contribution of various size fractions to total productivity generally displayed the same pattern as integrated Chl-*a* biomass. Microphytoplankton formed the most important contributor to total production at stations occupied in the MIZ and at the APF. Within the IFZ, nanophytoplankton dominated total daily production. Nutrient data suggest that concentrations of macronutrients within the upper water column were above the threshold where growth would be limited. Preliminary results showed that concentrations of iron (Fe) were highest in the southern region of the MIZ and in the vicinity of the APF. During the second cruise, conducted in the vicinity of the Sub-Antarctic Front (SAF) and in the upstream, inter-island and downstream regions of the Prince Edward Islands, there was evidence of fresh water run-off from the islands, (i.e. decreased salinities and increased concentrations of ammonia and nitrate). Oceanographic data collected at the various production stations indicated that the upper water column was well mixed throughout the survey. Total integrated biomass during the study ranged between 8.5 and 20.1 mg Chl-*a* . m<sup>-2</sup>. No distinct patterns in total Chl-*a* biomass were evident. Picophytoplankton dominated total biomass comprising > 45 % of total pigment at all stations. Nanophytoplankton were the second most important contributor to total integrated biomass. Generally

microphytoplankton contributed  $< 10\%$  of total Chl-*a*. Total daily integrated production was highest ( $442.6 \text{ mg Chl-}a \cdot \text{m}^{-2}$ ) at the single station occupied in the vicinity of the SAF. Outside this region, total areal production was lower, ranging from  $94.5$  to  $353.0 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ . With the exception of the station occupied in the vicinity of the SAF, total productivity was dominated by nanophytoplankton, which comprised between 48 and 66% of the total. Concentrations of macronutrients did not appear to be limiting to phytoplankton growth. The absence of a phytoplankton bloom in the vicinity of the islands appears to have been related to water column stability, which was influenced by the prevailing oceanographic regime during the survey. Previous studies have shown that when the SAF lies in close proximity to the islands, advecting forces prevail, resulting in the islands functioning as a flow-through system. During this study, the SAF lay immediately north of the islands. As a consequence no water was trapped in the leeward side of the islands.

The results of the two cruises suggest that phytoplankton production in the four systems investigated: the Marginal Ice Zone (MIZ), Antarctic Polar Front (APF), Inter Frontal Zone (IFZ) and Prince Edward Islands (PEI), was largely controlled by water column stability. It is probable that the availability of iron, particularly in the region of the MIZ and APF, may have further contributed to the elevated production recorded in these two regions.

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## CHAPTER 1

### *Introduction*

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Climate varies over a wide spectrum of time scales, from interannual changes to the much slower processes that involve the Earth's orbital parameters, continental drift, and solar ageing (Siegenthaler and Sarmiento 1993). Concern now focuses on human activities causing additional climate change through increased concentrations of greenhouse gases, such as carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), and nitrous oxide (NO<sub>2</sub>). The greenhouse gases are generated by agricultural practices, forest clearance and vegetation burning, cement production, and fossil-fuel burning (Siegenthaler and Sarmiento 1993; Kerr 1995; Longhurst 1996; Bird and Cali 1998). Greenhouse gases trap longwave infra-red re-radiation from the earth, thereby reducing heat losses from the atmosphere. The warming effect of greenhouse gases depends on their concentration in the atmosphere and their radiation absorption efficiencies at different wavelengths. Of all the greenhouse gases, the atmospheric concentration of CO<sub>2</sub> has shown the largest increase over the last 200 years. In recent years atmospheric CO<sub>2</sub> concentrations have increased from pre-industrial levels of  $\approx 280$  parts per million by volume (ppmv) to present values of  $\approx 355$  ppm (Neftel *et al.* 1988). It has been suggested that the increases in greenhouse gases have been the main driving force in climate

change in the twentieth century, whereas natural climate forcing by changes in solar radiance and volcanism dominated the pre-industrial climate (Mann *et al.* 1998). Model simulations of the Intergovernmental Panel on Climate Change (IPCC) suggest that the mean global surface temperature will increase by 2.1 °C to 4.6 °C for a doubling of atmospheric CO<sub>2</sub> concentration. Recent measurements made from space showed that the lower-troposphere's temperature (the region of the atmosphere extending from the ground to about 10-15 km) increased by +0.07 K per decade (Wentz and Schabel 1998). A decline in Antarctic sea-ice, commonly predicted as an effect of a warming climate, has also been sourced from whaling records (de la Mare 1997). Such a change in sea-ice extent, estimated to have moved southward by 2.8° latitude, has a global significance because ice-cover of the polar oceans exerts a strong control on the energy exchange between the atmosphere and ocean at high latitudes (de la Mare 1997). Stocker and Schmitter (1997) have shown, in their coupled atmosphere-ocean climate model, which involves heat and fresh water fluxes, that the anticipated future changes in today's climate system due to anthropogenic activities, have the potential to weaken the thermohaline circulation of the North Atlantic Ocean. With an increase of atmospheric CO<sub>2</sub> to 750 parts per million by volume (corresponding approximately to a continuation of today's growth rate) the Atlantic thermohaline circulation, which is driven by North Atlantic Deep Water (NADW) formation, would be reduced. As the thermohaline circulation in the northern hemisphere is coupled with the southern hemisphere, a breakdown in NADW circulation in the Atlantic would have repercussions in the south (Blunier *et al.* 1998).

In an effort to study global climate change, a number of large-scale international global research programmes have been established. The two most prominent are the International

Geosphere-Biosphere Programme (IGBP) and the World Climate Research Programme (WCRP). While the overall objectives of the IGBP and WCRP are to understand the interactive processes that regulate the total global system, for practical reasons a suite of 'core' projects have been formulated. Each of these 'cores' focuses on process linkages for which the current state of understanding is insufficient to predict future changes. The Joint Global Ocean Flux Study (JGOFS) has been established as a core project of IGBP. Its overall aim is to analyse and quantify physical and biochemical processes determining carbon fluxes in the oceans and, ultimately, to predict the response of these processes to climate change. Within this framework, the JGOFS regional study in the Southern Ocean is expected to contribute to the study of the role Antarctic Oceans play in biogeochemical cycles and exchanges, i.e. the sources, sinks, and transport of gases and trace chemicals in the troposphere and stratosphere; exchange of biogenic matter between surface and deep water and sediments; and the response of biogeochemical processes to natural and anthropogenic perturbations. In this context, this study aims to contribute to the understanding of what controls the magnitude and variability of oceanic primary production, and the coupled carbon cycle.

The oceans are the world's largest reservoir of carbon and therefore, exert a considerable influence on the global climate (Mann and Lazier 1991). The sequestration of atmospheric carbon by the world's oceans is mediated by both physico-chemical (**solubility pump**) and biological processes (Siegenthaler and Sarmiento 1993). The solubility pump is driven by diffusion and solubility. (Longhurst and Harrison 1989; Longhurst 1991; Siegenthaler and Sarmiento 1993). The amount of CO<sub>2</sub> (and indeed other gases e.g. nitrogen, oxygen) which can be dissolved in seawater depends on the partial pressure of the CO<sub>2</sub> ( $p\text{CO}_2$ ), and the

temperature, salinity, alkalinity and total carbonate content of the surface waters. Because of low temperatures and high salinities, the cold deep oceans are supersaturated with CO<sub>2</sub> and are reported to contain a huge reservoir 50-60 times that of the atmosphere (Mann and Lazier 1991). From a global perspective, it is well known that the colder, more saline surface waters of the polar regions represent important sinks for CO<sub>2</sub>. The mid latitudes are regarded as sources of CO<sub>2</sub> due to the high surface water temperatures (Siegenthaler and Sarmiento 1993).

Biologically mediated flux of carbon, i.e. the **biological pump** (Longhurst and Harrison 1989; Longhurst 1991), is considered minor when compared to the solubility pump. The surface layer of the ocean is in equilibrium with the atmosphere, while the deeper water masses are oversaturated with dissolved CO<sub>2</sub>. The surface ocean concentrations of CO<sub>2</sub> are ± 12% lower than concentrations in the deeper waters (Sarmiento 1992). Downward flux of carbon (C) is maintained by gravitational settling of organic carbon and carbonate, fixed autotrophically in the surface layers by phytoplankton cells during photosynthesis. The downward flux of dissolved organic carbon (DOC) into deeper waters is fundamentally different to the particle biological pump. (Thinstad *et al.* 1997). DOC may accumulate in the photic zone during the productive season. The non-Redfield behaviour of carbon in this context is of crucial importance as the accumulation of DOC in the surface waters is not stoichiometrically locked to the Redfield carbon : mineral nutrient ratio. Carbon export does not require the import of new nutrients. The transport mechanism is by diffusion and advection rather than by sinking (Sambrotto *et al.* 1993). Longhurst (1991) describes the biological pump as having three components: a *rotary pump* in which material circulates in the microplankton (<200µm) food web of the euphotic zone, an *Archimedean pump*, by

which flux of faecal and aggregate material occurs continually under gravity, and a *reciprocating pump*, by which diel migrants actively carry material down at dawn, to rise again at dusk to feed. The net effect of these processes is a reduction of partial pressure of CO<sub>2</sub> in the surface waters resulting in the drawdown of atmospheric carbon (Longhurst and Harrison 1989; Longhurst 1991; Siegenthaler and Sarmiento 1993). Due to the non-uniform properties of the surface of the ocean, the efficiency of the biological pump demonstrates a high degree of spatial and temporal variability. It is widely accepted that the community structure of the consumers dramatically affects the transfer of carbon within the pelagic subsystem (Roman *et al.* 1993). Legendre and Michaud (1998) assessed the food-web regulation of biogenic carbon fluxes and concluded that short-lived organic C ( $t < 10^{-2}$  yr; 3 to 4 d), comprising organisms with a short turnover time ( $t$ ) and dissolved organic compounds, transits through the microbial loop. In contrast, long-lived organic C ( $10^{-2} < t < 10^2$  yr), consisting of renewable marine resources (fish, marine mammals), transits through a classical food web. Sequestered biogenic C ( $t > 10^2$  yr), which includes organic remains buried in sediments (including petroleum), inorganic deposits of biological origin calcareous ooze, coral reefs, continental limestone), refractory dissolved organic matter, and dissolved CO<sub>2</sub> in deep waters resulting from *in situ* oxidation (respiration) of organic compounds, remain inactive for a considerable time and may, therefore, be regarded as removed from the carbon cycle (Legendre and Michaud 1998).

Marine phytoplankton has a strong influence on the air-sea exchange of CO<sub>2</sub> as it is incorporated into organic matter and calcium carbonate by phytoplankton during photosynthesis. Much of the organic matter is rapidly re-oxidised within the euphotic zone, but a small proportion (~ 10% of net primary production; Holligan 1992) is transferred to

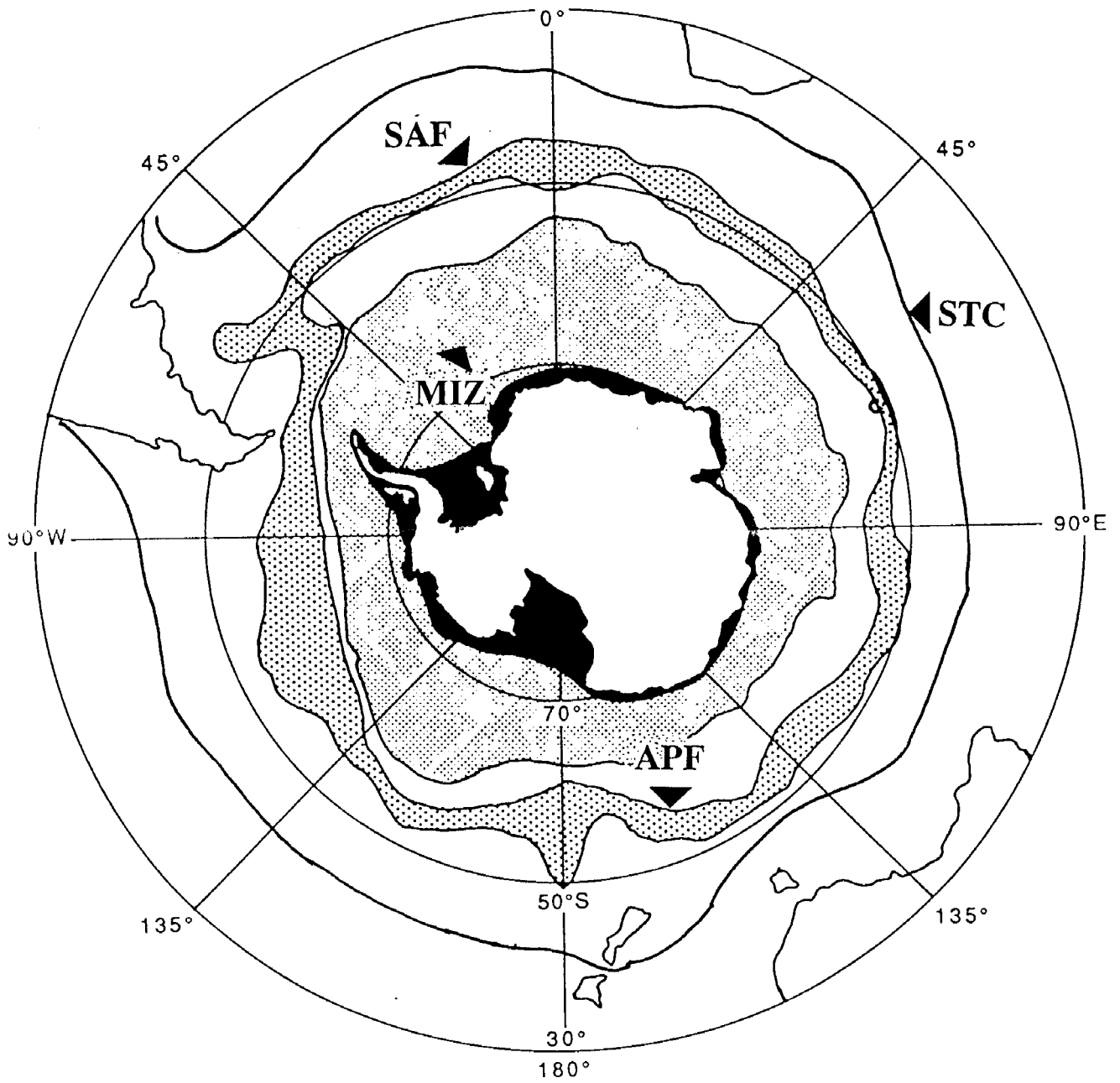
deep water and sediments, so maintaining an atmosphere-to-deep water gradient in CO<sub>2</sub> concentration, which represents the biological carbon pump (Longhurst and Harrison 1989). The flux of sedimentary organic matter on the sea floor generally reflects the magnitude of surface primary productivity. This flux was long thought to represent a very small fraction of exported production, indicating that the overall efficiency for the burial of organic carbon in ocean sediments is very low, <0.1% according to Smith and Mackenzie (1987) or <1.0% according to Berger *et al.* (1989). It should be noted that a small fraction of carbon transported to depth is in fact recycled by bacteria and as a consequence is not buried. However, recent data suggest that up to 10-20% of primary production rapidly reaches the sediments in the Indian sector of the Polar Front region in the Antarctic. This may represent 70-100% of the export production (Rabouille *et al.* 1998). Eventually the particulate organic carbon in deep water is outgassed at the surface in upwelled water as CO<sub>2</sub>.

The Southern Ocean is defined as the part of the world ocean situated south of the Subtropical Convergence (STC) and accounts for more than 20% of the world ocean surface area (Tomczak and Godfrey 1994) (Figure. 1). The ocean is not uniform but comprises several distinct bands of water separated by oceanic frontal systems (Tomczak and Godfrey 1994). The major fronts recognised in the Southern Ocean are the STC, which represents the northern boundary of the ocean, the Antarctic Polar Front (APF), which separates the Antarctic and Sub-Antarctic waters and finally the Sub-Antarctic Front (SAF), which separates the subtropical and Sub-Antarctic waters. With the exception of a few Antarctic and Sub-Antarctic Islands, the Southern Ocean is characterised by the absence of significant land masses (Figure 1). The Southern Ocean is also characterised by the presence of extensive seasonal ice-sheets which may extend as far north as 60° S (Sullivan *et al.* 1993).

The sea-ice melt, which begins in early spring, dramatically affects the physical environment, largely through changes in salinity and seawater temperature. The biological consequences of the sea-ice melt are discussed later in this chapter. Due to the continuous upwelling of deep waters south of the APF, the region is characterised by high concentrations of macronutrients (Tomczak and Godfrey 1994).

The large geographic extension of the Southern Ocean suggests that it may play an important role in the global carbon cycle. Unfortunately this ocean is still under-sampled spatially and temporally, thus making it difficult to evaluate the magnitude of air-sea CO<sub>2</sub> exchange (or CO<sub>2</sub> partial pressure) in the region (Metzl *et al.* 1991; Poisson *et al.* 1993). Furthermore, the winds that control the rate of the sea-air gas exchange are not very well known in this area and many more data are needed for a better estimation of sea surface winds. Finally, the relationship between gas transfer velocity and windspeed is not well established and the calculation of fluxes using the relationship between gas transfer velocity and windspeed leads to an uncertainty of a factor of about 2 (Tans *et al.* 1990; Wanninkhof 1992).

Two major regions in the Southern Ocean govern the exchange of CO<sub>2</sub> between the oceans and the atmosphere. These are the Warm Deep Water (WDW) upwelling at the Antarctic Divergence,  $\approx 65^\circ\text{S}$ , (which originates from the North Atlantic Deep Water (Tomczak and Godfrey 1994)) and the Antarctic Bottom Water (AABW) formation, which also governs the cycles of the biogenic elements (Poisson and Chen 1987). At the Antarctic Divergence, upwelling of deep waters (WDW) enriched in CO<sub>2</sub> and in nutrients results in a net flux of CO<sub>2</sub> to the atmosphere interface (Poisson *et al.* 1993). Thermohaline circulation transports



**Figure 1:** Map of Antarctica and the Southern Ocean showing positions of the major oceanic fronts.

APF = Antarctic Polar Front; SAF = Sub-Antarctic Front; STC = Subtropical Convergence; MIZ = Marginal Ice Zone.

this WDW southwards from the low latitudes (Tomczak and Godfrey 1994). As these waters reach the surface, they are subject to intense cooling due to the lower air temperatures. A part of these waters flows southward on the Antarctic shelves, sinking down to abyssal levels. These waters form high density bottom waters, due to low temperatures and increased salinities, resulting from brine rejection during freezing. The areas near the continent, therefore, are huge potential sinks for atmospheric CO<sub>2</sub> (Poisson *et al.* 1993; Robertson and Watson 1995). Due to the wind direction, north of the Antarctic Divergence, a part of the surface waters is entrained northwards to the Antarctic Polar Front, where these waters meet less dense Sub-Antarctic waters. Due to differences in density between the two different water masses, the more dense Antarctic waters sink below the warmer Sub-Antarctic waters to form the cold and relative less saline Antarctic Intermediate waters. As a consequence of the subduction of carbon rich Antarctic waters, the Polar Front zone is also a potential sink for CO<sub>2</sub> (Poisson and Chen 1987).

The role of the biological pump in sequestering atmospheric CO<sub>2</sub> is of particular interest in the Southern Ocean as it is characterised as a high nutrient and low chlorophyll concentration (HNLC) region (Longhurst 1996). It has been suggested (Longhurst 1996) that if primary production in the Southern Ocean could be stimulated to take up excess macronutrients, the increase in production would be sufficient to account for up to 30% of the anthropogenic carbon output. Clearly, an understanding of the processes controlling primary production in the Southern Ocean is of particular importance for the global carbon cycle.

Phytoplankton biomass (chlorophyll-*a* value) in the Southern Ocean, typically shows pronounced geographic and seasonal variability (Table 1). Fukuchi (1980) reported surface

chlorophyll-*a* concentrations at 631 stations south of 35° S ranging from 0.01 to 3.01 mg . m<sup>-3</sup> . The mean surface chlorophyll-*a* concentrations in the open waters recorded for the Pacific, Atlantic, and Indian sectors of the Southern Ocean are usually low, ranging from 0.12 to 0.42 mg . m<sup>-3</sup> (Smith and Nelson 1985; El-Sayed 1988; Jacques 1989). Elevated chlorophyll-*a* levels have , however, been reported from inshore waters, e.g. west of the Antarctic Peninsula (El-Sayed 1968a), near Kerguelen and Heard Islands (El-Sayed and Jitts 1973), and in the southern Ross Sea (El-Sayed *et al.* 1983). Exceptionally high values, in excess of 25 mg . m<sup>-3</sup> have been observed near the Deception Islands during a bloom (Mandelli and Burkholder 1966) and in shelf waters north of the continental shelf break in the Bransfield Strait (> 700 mg Chl-*a* . m<sup>-2</sup>) (Holm-Hansen and Mitchell 1991). High chlorophyll-*a* concentrations have also frequently been associated with frontal systems of the Southern Ocean (Allanson *et al.* 1981; Lutjeharms *et al.* 1985; Laubscher *et al.* 1993; Bradford - Grieve *et al.* 1997), and in the vicinity of the retreating ice, the so called Marginal Ice Zone (maximum 11.3 mg Chl-*a* . m<sup>-2</sup>) (Fukuchi *et al.* 1984; Froneman *et al.* 1995 a, b) (Table 1).

The size structure of Southern Ocean phytoplankton communities demonstrates a distinct temporal and spatial variability. During the austral summer, regions of elevated Chl-*a* biomass (the neritic waters of Antarctica, oceanic fronts and the waters surrounding oceanic islands) are generally dominated by large microphytoplankton (> 20µm) (see reviews of El-Sayed 1988; Jacques 1989). In contrast, the open waters are typically dominated by small nano- (20-2µm) and picophytoplankton (< 2µm) (Jacques 1989). Indeed, at times, microphytoplankton contribution to total biomass in open waters may be < 5% (Weber and El-Sayed 1987; Jacques 1989). The microphytoplankton assemblages are generally

dominated by colonial and chain-forming diatoms of the genera *Thalassiosira*, *Chaetoceros* and *Fragilariopsis* (Priddle 1990). The predominance of colonial and chain-forming taxa appears to be typical of many regions of the Southern Ocean, although species of other genera e.g. *Proboscia*, may at times dominate. Prior to and during ice melts, near the Marginal Ice Zone and shelf waters, the unicellular motile and colonial brown-yellow prymnesiophyte (order Prymnesiales) *Phaeocystis pouchetii* is prominent. The life cycle of this species alternates between free-living flagellate zoospores and gelatinous colonial aggregations of non-motile cells (each cell 3-8 $\mu$ m in size), exceeding 10 mm in diameter. In the colonial form *Phaeocystis pouchetii* produces dense gelatinous blooms.

The principal components of the nanophytoplankton are unicellular green flagellates (Jacques and Panouse 1991), and small diatoms (5 -10 $\mu$ m) such as *Chaetoceros neglectus*, *C. tortissimus* and *Nitzschia curta* (Brandini and Kutner 1987). Siliceous cysts (size range 2.0 - 5.5  $\mu$ m) containing chloroplasts, thought to be cysts in the life cycle of choanoflagellates, are also an important component of the nanophytoplankton in the Southern Ocean (Marchant and McEldowney 1986). The picophytoplankton communities comprise phycoerythrin-rich chroococcoid cyanobacteria and *Chlorella*-like coccoid green flagellates (Knox 1994).

In spite of a large data bank collected over the past decades, our knowledge of the seasonal variability of biomass distribution and productivity is sparse due to the spatial and temporal coverage of sampling and the vastness of the Southern Ocean. Most of the expeditions have been limited to the austral spring and summer and winter observations are rare. The results of these studies have largely demonstrated that Chl-*a* concentrations in winter are generally

**Table 1:** Comparative results of phytoplankton biomass and production studies conducted in various regions of the Southern Ocean. (ND = no data presented, MIZ = Marginal Ice Zone, PFZ = Polar Front Zone, POOZ = Permanent Open Ocean Zone, SIZ = Seasonal Ice Zone, ACC = Antarctic Circumpolar Current, SAF = Sub-Antarctic Front, APF = Antarctic Polar Front).

Author	Location	Season	Chl- <i>a</i>	Primary production
Froneman <i>et al.</i> 1997	MIZ - Lazarev Sea	Austral summer	< 41 mg Chl- <i>a</i> . m <sup>-2</sup> > 50 mg Chl- <i>a</i> . m <sup>-2</sup>	133-356 mg C . m <sup>-2</sup> d <sup>-1</sup> 263-400 mg C . m <sup>-2</sup> d <sup>-1</sup>
El-Sayed & Weber 1982	PFZ in Drake Passage & Scotia Sea	Late winter/early spring Late summer/early fall	12.97 mg Chl- <i>a</i> . m <sup>-3</sup> 2.80 mg Chl- <i>a</i> . m <sup>-3</sup>	73.25-284.38 (max) mg C . m <sup>-3</sup> . d <sup>-1</sup> < 18.82 mg C . m <sup>-3</sup> . d <sup>-1</sup>
Bradford-Grieve <i>et al.</i> 1997	Subtropical Convergence near New Zealand	Austral winter and spring	45.8-137.4 mg Chl- <i>a</i> . m <sup>-2</sup>	249-995 mg C . m <sup>-2</sup> d <sup>-1</sup>
Dower <i>et al.</i> 1996	MIZ Weddell Sea	Austral autumn	7.1-28.0 mg Chl- <i>a</i> . m <sup>-2</sup>	15.6-41.5 mg C . m <sup>-2</sup> d <sup>-1</sup>
Whitehouse <i>et al.</i> 1996	Open ocean Scotia Sea	Summer	0.8-13.5 mg Chl- <i>a</i> . m <sup>-2</sup>	ND
Mengesha <i>et al.</i> 1998	Seasonal Ice Zone POOZ PFZ SIZ POOZ PFZ	Spring  Summer	33 mg Chl- <i>a</i> . m <sup>-2</sup> 28 mg Chl- <i>a</i> . m <sup>-2</sup> 31 mg Chl- <i>a</i> . m <sup>-2</sup> 23 mg Chl- <i>a</i> . m <sup>-2</sup> 13 mg Chl- <i>a</i> . m <sup>-2</sup> 25 mg Chl- <i>a</i> . m <sup>-2</sup>	ND
Jochem <i>et al.</i> 1995	ACC & Weddell gyre	Late winter	20-30 mg Chl- <i>a</i> . m <sup>-2</sup>	200-300 mg C . m <sup>-2</sup> d <sup>-1</sup>
Sharek <i>et al.</i> 1994	Under ice & decreasing ice cover Eastern Weddell Sea	Late winter Spring	2-39 mg Chl- <i>a</i> . m <sup>-2</sup> 10-30 mg Chl- <i>a</i> . m <sup>-2</sup>	ND
Froneman & Pakhomov 1998	SAF between Prince Edward Islands	Late austral summer	1.2-2.0 μg . L <sup>-1</sup> 0.13-1.5 μg . L <sup>-1</sup>	ND
Froneman <i>et al.</i> 1997	MIZ APF Atlantic sector of Southern Ocean	Midsummer	65.8 mg Chl- <i>a</i> . m <sup>-2</sup> 66.9 mg Chl- <i>a</i> . m <sup>-2</sup>	443.0 mg C . m <sup>-2</sup> . d <sup>-1</sup> 356.9 mg C . m <sup>-2</sup> . d <sup>-1</sup>

< 0.3 mg . m<sup>-3</sup> (Table 1). Total biomass in the open waters and in the vicinity of the frontal

systems of the Southern Ocean in winter are dominated by small nano- and picophytoplankton (Garrison *et al.* 1993; Froneman and Perissinotto 1996; Leakey *et al.* 1994; Froneman and Pakhomov 1998). A similar size structure has been reported for phytoplankton communities below the sea-ice (Garrison *et al.* 1993). Further data are, however, required to increase our knowledge on the size structure of plankton communities of the Southern Ocean during winter.

Phytoplankton productivity in the Southern Ocean generally shows a good correlation to biomass (Laubscher *et al.* 1993). The open waters of the Southern Ocean are generally characterized as areas of low production. Here daily integrated production is generally  $< 300 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  (Table 1). Areas of elevated production have been recorded in neritic waters of the Antarctic continent, near oceanic islands, the marginal ice zone (MIZ), and oceanic fronts (Jochem *et al.* 1995; Froneman *et al.* 1997, 1998; and others). El-Sayed (1967) recorded a value of  $3200 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  in the Gerlache Strait, Mandelli and Burkholder (1966) reported  $3600 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  near the Deception Islands. Holm-Hansen and Mitchell (1991), in their Bransfield Strait studies, found low rates in oceanic waters (mean  $340 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ), in contrast to shelf waters during which the austral summer, had rates exceeding  $3000 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ . von Bodungen *et al.* (1986) also observed high primary production rates for the same region, ranging between 230 and  $1660 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ . Many investigators have corroborated these observations and it is clear that, as with phytoplankton biomass, primary production rates vary considerably, geographically and seasonally. The contribution of the different size fractions to total production, both spatially and temporally, generally demonstrates the same pattern as biomass. Generally, microphytoplankton dominates total production in areas of elevated productivity (see reviews of El-Sayed 1988; Jacques 1989),

while nano- and picophytoplankton dominate in the open waters. Winter production is almost entirely dominated by small nano- and picophytoplankton throughout the Southern Ocean.

During the last decade there have been a number of reviews regarding the factors that govern the productivity of Antarctic phytoplankton (Priddle *et al.* 1986; Sakshaug and Holm-Hansen 1986; Jacques 1989). Of the physical and chemical factors which could limit phytoplankton production, water column stability, solar radiation, the availability of macro- and micro nutrients, and temperature are considered to be the most important. Of these factors, the importance of water column stability in controlling phytoplankton production in the Southern Ocean has been most closely studied. The concept that water column stability is important in controlling primary production in the Southern Ocean is largely based on the findings that areas with high primary production (particularly the MIZ and oceanic fronts) are generally characterised by high water column stability (see reviews of El-Sayed 1988; Jacques 1989). The factors responsible for water column stability differ between the various regions. In the case of the MIZ, high water column stability is the result of freshwater input during sea-ice melt (Jacques 1989; Froneman *et al.* 1997) and thermal stratification resulting from the summer capping of cold winter waters. In the vicinity of the frontal systems, the convergence of water masses with different physico-chemical properties confers localised water column stability (Laubscher *et al.* 1993). The net result of high water column stability is that phytoplankton cells are retained in a light environment that allows for net energy gain (Fogg 1991). Recent model simulations have shown that water column stability for more than 14 days is required for phytoplankton blooms in the high Antarctic. In contrast, the open waters of the Southern Ocean are often characterised by a deep mixed layer (up to 200 m in depth) which exceeds the 1% light depth. In these regions, total production is limited due to an

unfavourable light environment. The deep mixed layer depths in these regions are largely the consequence of high wind activity, which results in a well mixed upper water column (Tomczak and Godfrey 1994).

Variations in photo period, light intensity, and spectral composition are also regarded as important in influencing phytoplankton growth in the Southern Ocean. The total incident radiation is a direct function of latitude, with regions at high latitudes experiencing a period of complete darkness in winter (60 days at 70°S, 100 at 75°S) (Heywood and Whitaker 1984). Ice and associated snow cover, cloud cover, the low angle of incidence of the sun's rays, surface disturbance by storms, are all factors affecting the intensity and spectral composition of the total radiation entering the water. Some Antarctic marine plants appear to be adapted to low light levels, although the enzymatic content of the cell does not seem to differ from other non-polar species (Heywood and Whitaker 1984). Sakshaug and Holm-Hansen (1986) have shown that the photochemical apparatus of Antarctic phytoplankton is 'saturated' at between 100-180  $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ . They pointed out that the incident light flux on a sunny day is about 1500  $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , and phytoplankton in the surface waters are either 'saturated' or photoinhibited. A high degree of correlation exists between the intensity of solar radiation and photosynthetic rates in the euphotic zone. When incident light is high, photosynthetic rates are low in the surface waters and increase with depth. On the other hand, when incident light is low, photosynthetic rates remain constant in the upper water of the euphotic zone, or are highest in the surface waters. It is thought that these effects are probably due to photoinhibition, the calculated threshold being in the range of 40-50  $\text{cal m}^{-2} (\text{half light day})^{-1} (\approx 100 - 180 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1})$  ( Sakshaug and Holm-Hansen 1986).

Surface concentrations of macronutrients such as nitrate ( $\text{NO}_3$ ), phosphate ( $\text{PO}_4$ ) and silicate ( $\text{SiO}_4$ ) remain above limiting values south of the APF largely because continuous upwelling results in an abundance of macronutrients (Tomczak and Godfrey 1994). These facts suggest that phytoplankton growth south of the APF is not nutrient limited. North of the APF, seasonal decreases of surface nutrients do, however, occur in summer, especially during phytoplankton blooms, when nutrient levels may be depressed to  $<1.0 \text{ mg-at P} \cdot \text{L}^{-1}$ ,  $< 10 \text{ mg-at Si} \cdot \text{L}^{-1}$ , and  $< 16 \text{ mg-at N} \cdot \text{L}^{-1}$  (Satoh *et al.* 1986). Under these conditions, nutrients may be limiting. Whitaker (1977) showed that  $\text{PO}_4$  was rate limiting below  $0.59 \text{ mg-at P} \cdot \text{L}^{-1}$  for a natural mixed population of phytoplankton dominated by *Thalassiosira antarctica*. Similarly, Walsh (1971) and Allanson *et al.* (1981) found that silicates may be the most limiting of the major nutrients for phytoplankton growth in the region north of the APF. It has been suggested that the particular molecular species of the inorganic nutrients and the ratios in which they are present in the environment are of importance in relation to the observed preferential uptake of the phytoplankton organisms. For instance, N-uptake (Nitrogen) experiments with Antarctic phytoplankton have shown that ammonia, or occasionally urea, is the preferred nitrogen substrate, with between 50-80% of all nitrogen assimilated in the form of ammonium (Probyn and Painting 1985). The limiting nutrient for phytoplankton production in most oceanic regions is believed to be nitrogen, which originates from a variety of sources, including eddy driven nitrate fluxes as discussed by McGillicuddy *et al.* (1998), and Oschlies and Garçon (1998), and which is supplied in various chemical forms, e.g. as nitrates in the oxidised form, ammonia and ammonium ions. In the open ocean, outside the photic zone, the dominant contribution to the externally supplied nitrogen is in the form of nitrates (Fogg 1982) on which new production depends. Reduced nitrogen compounds, in particular ammonia, originate from rapid remineralization

of organic matter in the euphotic zone by biological and chemical processes in which microbial organisms are involved (microbial loop). Regenerated primary production is intimately related to the rate of remineralization. Rönner *et al.* (1983) states that nitrogen is recycled up to eight times before it is lost from the euphotic zone. The sum of regenerated production and new production is referred to as total production. Ammonium appears to play an important role in Antarctic phytoplankton in the open ocean and is generally present in high concentrations, increasing in late winter to early spring from  $0.1 \mu\text{M}$  to over  $1.0 \mu\text{M}$  (Rönner *et al.* 1983). Rönner *et al.* (1983) also showed that Antarctic phytoplankton generally derive at least 50% of their nitrogen from ammonium, and in spite of high concentrations of nitrate present ( $19\text{-}21 \mu\text{M}$ ) in coastal waters in the Scotia Sea, up to 93% was assimilated in the form of ammonium. Ammonium and nitrate were associated with nanophytoplankton, while microphytoplankton assimilated mostly nitrates (Rönner *et al.* 1983). In contrast, during bloom conditions, ammonium concentrations were reported frequently to be below detection limits ( $<0.1 \mu\text{M}$ ) (Nelson and Smith 1986).

A range of trace metals have been shown to be important in phytoplankton growth: i.e. molybdenum, magnesium (Volkovinski 1966), cobalt, zinc, copper, vanadium (El-Sayed 1968b), and iron (Fogg 1977; Sunda 1994). Iron is of particular importance as it is instrumental in the biosynthesis of chlorophyll. Ferric iron (Fe), the main component of ferredoxin, is present in the active centres of cytochromes and iron-sulphur proteins which are critical components of photosynthetic and respiratory electron transport chains (Sunda 1994). Oceanic concentrations of iron in the Southern Ocean are within the submicromolar range. The low concentrations are due to the isolated nature of the ocean as inputs of iron are largely derived from aeolian and volcanic inputs (Donaghay *et al.* 1991). Martin *et al.*

(1990a,b) hypothesized that Antarctic phytoplankton suffered from iron deficiency which prevented them from blooming and using up the plentiful supply of macronutrients. They found that the highly productive inshore waters of the Gerlache Strait have an abundant supply of iron ( $7.4 \text{ nmol} \cdot \text{L}^{-1}$ ) which facilitates blooming ( $3 \text{ g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ), whereas in the offshore Drake Passage waters ( $0.1 \text{ g C} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ ) the dissolved Fe levels are so low ( $0.16 \text{ nmol} \cdot \text{L}^{-1}$ ) that the phytoplankton can use less than 10% of the available nutrients. The importance of iron to phytoplankton growth has been challenged by several researchers, e.g. Peng and Broecker (1991); de Baar *et al.* (1995) and others. Recently Hutchins and Bruland (1998), and Takeda (1998) have shown that iron affects diatom uptake of silica relative to both nitrate and phosphorus. Antarctic diatoms exhibited increased cellular silicon or decreased cellular nitrogen and phosphorus in response to iron limitation. Iron limitation, therefore, increases the export of biogenic silicon, relative to nitrogen and phosphorus, from the surface to deeper waters. This result suggests that Fe has a much broader role in regulating oceanic biogeochemical cycle and biological pumping of carbon into the deep sea than has been previously appreciated (Takeda 1998). Recently, Löscher *et al.* (1997) reported that the major inputs of Fe in the regions of the Antarctic ocean originate from upward transport from shelf sediments, as well as aeolian inputs. The effect of sea-ice melting and iceberg melting on Fe concentrations is thought to be relatively small. Sunda (1994) points out that dimethyl sulfide (DMS), produced by certain plankton groups particularly dinoflagellates and prymnesiophytes, enhances the supply of iron to phytoplankton by promoting iron's solubilization from atmospheric mineral aerosols and by facilitating rainfall, the primary mechanism for the delivery of atmospheric iron to the ocean. This process in turn enhances productivity.

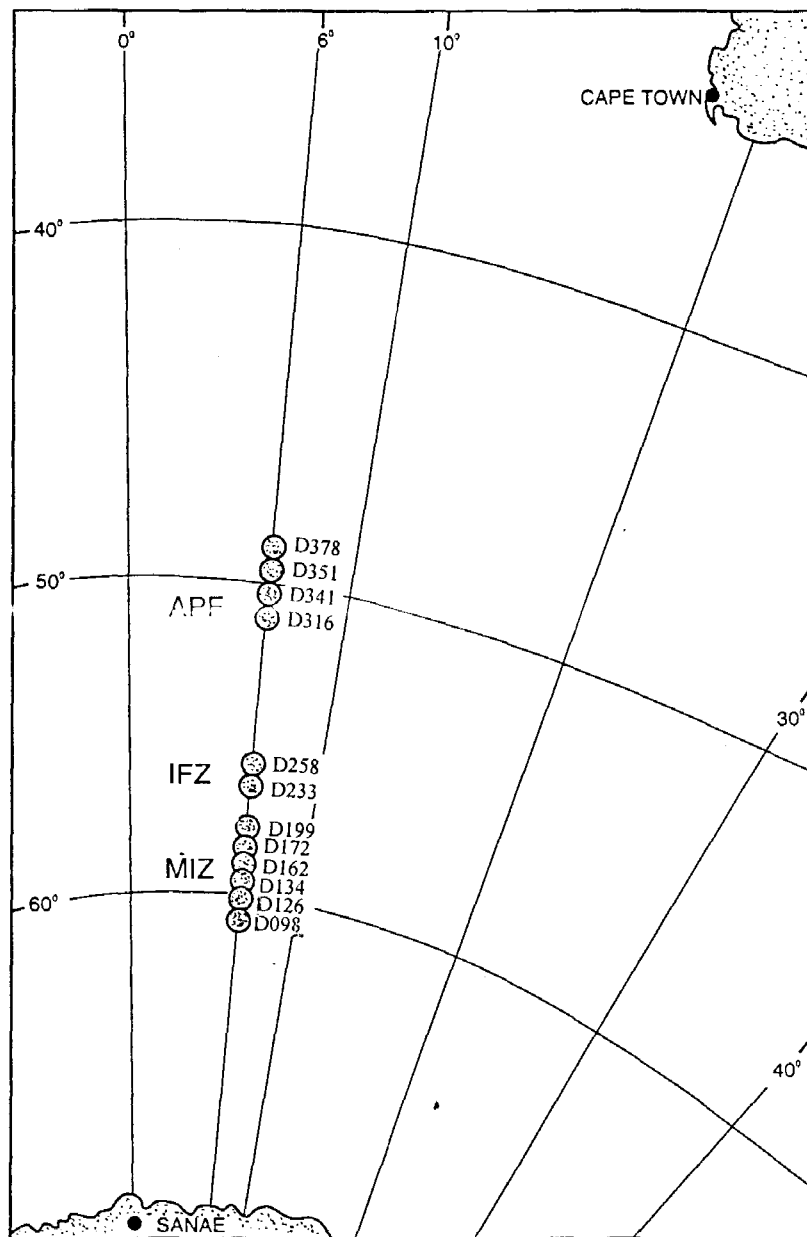
The effects of temperature on photosynthetic carbon uptake by phytoplankton have been investigated for a number of Antarctic species (Tilzer *et al.* 1985, 1986; Tilzer and Dubinsky 1987). Maximum uptake of inorganic carbon generally fell within the temperature range of 7-12 °C. Variable positive and negative relationships between temperature and chlorophyll have been noted by Hayes *et al.* (1984) and Tilzer *et al.* (1986). These authors found that the rates of both light-saturated and light-induced photosynthesis were temperature dependent in the range of -1.5 to 5.0°C, and concluded that Antarctic phytoplankton had not evolved mechanisms to overcome the inhibiting effects of low temperatures on photosynthesis. Optimum temperatures for growth may be close to ambient temperatures. Growth rates in the order of 0.1 to 0.3 doublings per day were recorded in the Ross Sea (Holm-Hansen *et al.* 1977), and of 0.5 to 2.1 in the Indian sector of the Southern Ocean (Miller *et al.* 1985). There is thus a wide variation in recorded growth rates of Antarctic phytoplankton in response to temperature.

The Southern Ocean is a major repository of surface macronutrients, an important region of deep water formation and a major sink for dissolved carbon dioxide (Siegenthaler and Sarmiento 1993). As a consequence, the importance of the Southern Ocean in the global carbon cycle is presently a leading concern in oceanographic studies. Fundamental to our understanding of the biochemical cycles of the Southern Ocean, is the process of photosynthesis (Falkowski *et al.* 1998). The factors controlling phytoplankton production in the Southern Ocean are, therefore, of particular interest in understanding the global carbon cycle. Despite a number of studies that have investigated factors controlling growth of phytoplankton within the different regions of the Southern Ocean, it is well documented that the Southern Ocean demonstrates a high degree of spacial and temporal variability. Further

studies examining the control of phytoplankton in the Southern Ocean are, therefore, required.

During 1998, the main factors controlling primary production in the Southern Ocean were investigated during two cruises of the South African National Antarctic Program (SANAP). The first cruise was conducted in the eastern Atlantic sector of the Southern Ocean, during a collaborative Scandinavian/South African Antarctic expedition. Production stations were occupied within three regions: the Marginal Ice Zone (MIZ), interfrontal region (IFZ) and Antarctic Polar Front (APF) in austral summer (Dec./Feb.) 1998 (Figure 2). It is well documented that phytoplankton production in the vicinity of the MIZ and APF are elevated suggesting that they are important in the Southern Ocean carbon cycle (Laubscher *et al.* 1993; Froneman *et al.* 1997). The elevated production associated with these regions is thought to be due to localised water column stability and availability of macronutrients. In contrast, the interfrontal waters are generally characterised by low water column stability and phytoplankton production (Jacques 1989; Laubscher *et al.* 1993; Bradford-Grieve *et al.* 1997). The data collected during this cruise would allow comparison of the factors controlling primary production in three different regions of the Southern Ocean.

The second cruise was conducted in the region of the Sub-Antarctic Prince Edward Islands. (Figure 3). The Prince Edward Islands (46° 50'S and 37° 50'E), comprising Marion Island and Prince Edward Island, are located in the Indian Ocean sector of the Southern Ocean



**Figure 2:** Positions of production stations during the collaborative Scandinavian/South African Antarctic expedition conducted in the austral summer (Dec./Feb.) 1997 - 1998. MIZ = Marginal Ice Zone; IFZ = Interfrontal Zone; APF = Antarctic Polar Front.

(Pakhomov and Froneman 1998). The islands, which rise from a depth of 3000m, lie to the east of the Southwest Indian Ridge and west of the Del Cano Rise, and are separated by a shallow plateau 40 to 200m in depth (Ansorge *et al.* 1998). Oceanographic investigations have shown that the islands are situated in the direct path of the easterly flowing Antarctic Circumpolar Current (ACC), between the Sub-Antarctic (SAF) and the Antarctic Polar Fronts (APF) (Lutjeharms *et al.* 1985; Pakhomov and Froneman 1998). The islands thus lie in the nutrient impoverished Polar Frontal Zone waters (PFZ). Due to the continuous current flow, the islands have an upstream (west) and downstream (east) region. The easterly flow of the ACC is markedly disturbed by the Southwest Indian Ridge resulting in the formation of large-scale meanders and eddies (Lutjeharms *et al.* 1985). The formation of these features in the region downstream of the islands results in a complex hydrology, including the presence of warm and cold-core eddies (Pakhomov and Froneman 1998; Ansorge *et al.* 1998). These eddies dramatically affect the exchange of water masses in the region, resulting in the intrusion of Antarctic and Sub-Antarctic surface waters into the immediate vicinity of the islands (Ansorge *et al.* 1998).

Seasonally occurring phytoplankton blooms, with enhanced primary productivity relative to the surrounding ocean, have been observed in the inter-island and downstream regions of the islands on several occasions (Allanson *et al.* 1981; 1985; Boden 1988; Perissinotto and Duncombe Rae 1990). Here, daily production rates in excess of  $1 \text{ g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  have been recorded ( El-Sayed *et al.* 1979 a; b; Allanson *et al.* 1985; Perissinotto and Duncombe Rae 1990; Pakhomov and Froneman 1998). It is thought that this high productivity is related to an "island mass effect", which involves the stability of the mixed-layer and the availability

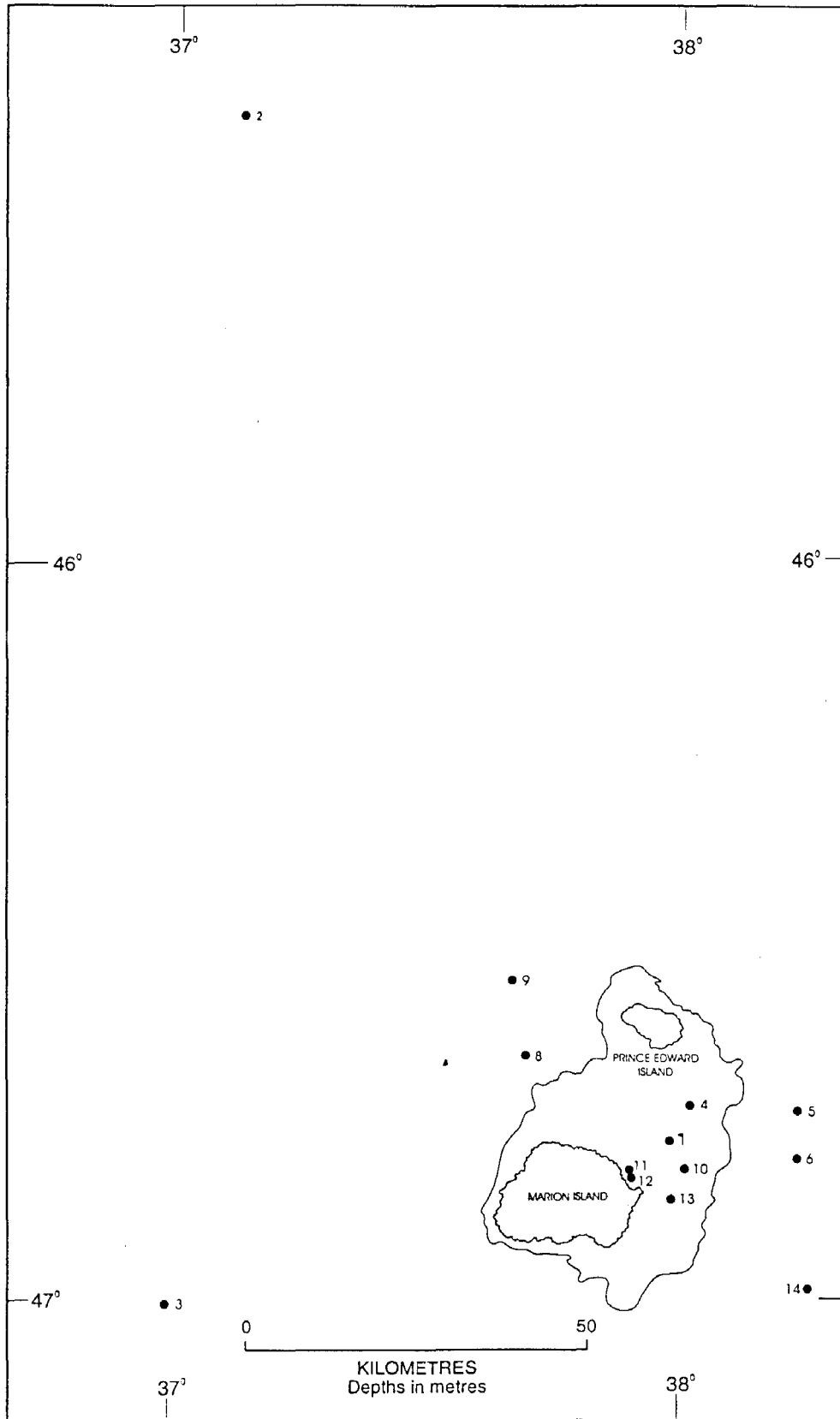


Figure 3: Primary production stations occupied during the third Marion Island Oceanographic Survey (MIOS III) conducted to the region of the Prince Edward Islands in austral autumn (April/May) 1998. Production station 2 indicates the position of the Sub-Antarctic Front (SAF).

of reduced forms of nitrogen (Perissinotto *et al.* 1990) and other nutrients (Ismail 1990) resulting from freshwater run-off from the islands (Allanson *et al.* 1985). Several other hypotheses have, however, been suggested to account for the elevated phytoplankton production generally recorded in the waters surrounding the Prince Edward Islands. Perissinotto and Duncombe Rae (1990) suggested that elevated production in the vicinity of the islands was the result of a combination of both freshwater run-off and increased stabilisation due to the presence of a low-density core eddy analogous to a Taylor Column. In contrast, Attwood (1991) proposed an alternative hypothesis to explain the elevated production recorded in the vicinity of the islands. Here it was suggested that the elevated Chl-*a* concentrations generally recorded in the shallow waters between the islands were the result of seeding by dormant stocks of diatom spores from the shallow sediments around the islands. This was largely based on the facts that the elevated phytoplankton biomass generally recorded in the waters between the islands was dominated by the diatom, *Chaetoceros radicans* (Attwood 1991). It is well documented that the SAF and APF exhibit a large degree of latitudinal variability and may at times lie in the immediate vicinity of the islands (Froneman and Ansorge 1998; Pakhomov and Froneman 1998; Pakhomov *et al.* 1998; Ansorge *et al.* 1998). Most recently it has been suggested that the elevated production associated with the frontal systems to the north and south of the islands may be transported directly to the Prince Edward Islands when the fronts lie in close proximity to the islands (Pakhomov and Froneman 1998). The actual mechanisms responsible for the elevated Chl-*a* concentrations and production in the waters surrounding the islands are presently unknown.

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## CHAPTER 2

### *Materials and methods*

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#### **2.1 Positions of stations**

During the first survey, water samples for chlorophyll-*a* and size-fractionated primary productivity were collected in the three zones along a south-north transect between 60° 24.57' S and 49° 49.51' S along the 6° 00' E meridian aboard the *MV SA Agulhas*, during December/February 1997-1998. The transect in the Marginal Ice Zone (MIZ) was occupied from 4-10 January, the transect in the Inter Frontal Zone (IFZ) over the period 14-16 January, while the transect in the vicinity of the Antarctic Polar Front (APF) was occupied from 28 till 31 January 1998 (Figure 2).

During the second cruise, size-fractionated production studies were conducted in the vicinity of the Sub-Antarctic Front (SAF) and in the upstream, inter-island and downstream regions of the Prince Edward Islands aboard the *MV SA Agulhas* during April/May 1998. In total, four stations were occupied in the upstream region, six within the inter-island region and three in the downstream region (Figure 3). A single station was occupied in the vicinity of the SAF (Figure 3).

## 2.2 Light measurements

Incident photosynthetic radiation (PAR) was measured at 08.00 each morning using a Li-Cor quantum meter so that water samples could be collected at 6 standard depths. These corresponded to 100, 50, 25, 10, 5 and 1% of surface irradiance. Unfortunately, due to mechanical failure during the second cruise, the Li-Cor quantum sensor could not be used to determine light depths. As a consequence, a Secchi disc was used to estimate the light depths. A 50kg weight was attached to the lower eye of the Secchi disc on the hydrowire so that the disc was horizontal and wire angle was negligible. The Secchi disc was raised and lowered until the depth of disappearance was obtained. A comparison from previous cruises conducted in the region of the islands showed that the estimated light depths were in agreement with a previous study conducted in the vicinity of the Prince Edward Islands. Sampling depths were calculated using the following formula (Tyler 1968; Holmes 1970):

$$\text{Sampling depth in meters} = \left( \ln \frac{\% \text{ light depth}}{100} \right) \times \left( \frac{\text{Secchi depth in metres}}{-1.7} \right) \quad (1)$$

## 2.3 Primary production

Size-fractionated primary production, defined as the uptake of inorganic carbon into particulate matter was measured with a method adapted from Evans *et al.* (1987) and JGOFS Protocols (1994). The purpose of this method is to estimate the uptake of dissolved inorganic carbon (DIC) from the water by planktonic algae as they photosynthesize in the light. The carbon taken up either remains in the algae as particulate organic carbon (POC) or is excreted into the water as dissolved organic carbon (DOC). There has been much debate as to exactly

what is measured by the  $^{14}\text{C}$  method, as the results are difficult to interpret (see Dring and Jewson 1979; and Peterson 1980 for a detailed overview). A number of workers consider that the method generally underestimates primary production (Gieskes *et al.* 1979). However, it is currently the only technique sensitive enough to measure the low rates of production encountered in the Southern Ocean. The  $^{14}\text{C}$ -uptake method remains the standard against which all other methods are compared (Peterson 1980).

Water samples for the measurement of primary production were obtained from each of the standard depths using a 12/24 bottle rosette mounted to a teflon coated stainless steel frame carrying a CTD. Once on board, triplicate water samples were decanted into 250 mL polycarbonate bottles from each Niskin bottle. These polycarbonate bottles were used for the production studies. A further litre was removed from each corresponding Niskin bottle for the determination of chlorophyll-*a* concentrations. All manipulations were conducted in the dark to prevent light shock. Water samples were immediately placed in plastic sleeves to exclude light and then taken to the radio-isotope laboratory where further manipulations were conducted. Immediately, 50  $\mu\text{L}$  of sodium carbonate ( $\text{H}^{14}\text{CO}_3$ ) were added to each polycarbonate bottle. This gave a specific activity of 50  $\mu\text{Ci} \cdot \text{mL}^{-1}$ . Once the bottles had been sealed, they were gently inverted to ensure that the  $^{14}\text{C}$  was well mixed. Following the inoculation with the radioactive isotope, the bottles were placed on the helideck in light-gradient incubators for 24 hrs. Again great care was taken to prevent light shock and all manipulations were carried out in the dark. The incubators consisted of perspex sleeves covered with neutral density screens to simulate light intensity at the depth of collection. The neutral density screens were calibrated using a Biospherical Instruments quantum meter (Model QSP- 170) probe. The incubators were cooled with running surface water obtained

from the scientific seawater supply. Temperatures within the incubators were maintained to within 1°C of the sea surface temperatures. The incubation of deep water samples at sea surface temperatures suggests that the results obtained may be subject to error due increased phytoplankton growth rates associated with higher temperatures (Jacques 1983) However, given that the difference in temperature was less than 1°C, the error associated with the temperature discrepancy would be minimal. As a consequence, we have not corrected the value to account for temperature differences.

After incubation, a 50mL water sample from each production bottle was gently serially filtered ( $\approx$  710mm Hg) onto Nitex mesh (20  $\mu$ m pore size) and isopore membrane (Millipore) filters (2.0 $\mu$ m and 0.2 $\mu$ m pore size). Incubations were terminated by the addition of 0.5 mL 3M HCl to each sample. Following acidification, the samples were placed in a shaker under a fume hood for 2 hrs. Time-zero controls were treated in the same manner, except that the samples were not acidified. 10 mL of Packards UltraGold XR fluor were added to each sample and the radioactivity determined on a Beckman LS-133 liquid scintillation system after 24 hrs. All counts (cpm) were converted to disintegrations per minute (dpm) by the external standard ratio method.

Total areal production at each station was estimated employing the following equation:

$$(\text{mg C} \cdot \text{m}^{-3} \cdot \text{d}^{-1}) = ((\text{SDPM}/V) \cdot (W \cdot 0.25 \times 10^{-4}) / \text{TDPM}) \cdot (1.05/T) \quad (2)$$

where

SDPM = DPMs in filtered samples

V	=	volume of filtered sample (Litres)
TDPM	=	Total <sup>14</sup> C DPMs (in 0.05L)
W	=	DIC concentration in samples
0.25 x 10 <sup>-4</sup>	=	conversion of pipette volumes to litres
1.05	=	correction for the lower uptake of <sup>14</sup> C compared to <sup>12</sup> C
T	=	time (days)

## 2.4 Chlorophyll-*a*

Size-fractionated chlorophyll-*a* concentrations at each standard depth were determined by gently (< 710 mm Hg) filtering 250 mL water samples through 20 $\mu$ m (Nitex), 2.0 $\mu$ m (Millipore) and Whatman GF/C filters. The filters were then placed into 10 mL polycarbonate tubes and 10 mL of 90% acetone was added. Extraction of the pigment was allowed to take place in the dark at -20°C. After 24 hrs. the contents of the polycarbonate tubes was centrifuged and the clear supernatant liquid was decanted into a fluorometer cuvette (13 x 100 mm). The fluorescence was measured before and after acidification with 2% HCl on a Turner Designs 10 AU fluorometer (Holm-Hansen and Riemann 1978). The fluorometer was calibrated against a Chl-*a* standard prior to the cruise, using pure chlorophyll-*a* purchased from Sigma Chemical Company, USA. The chlorophyll-*a* concentrations were expressed either as value per cubic meter or the total amount in the water column beneath a square meter of the water surface.

Areal production and chlorophyll-*a* (corresponding to 1% surface irradiance) were obtained by trapezoidal integration (Legendre and Legendre 1983). Photosynthetic capacity (mg C (mg Chl-*a*)<sup>-1</sup> h<sup>-1</sup>) was calculated by dividing production values of incubation bottles by the

chlorophyll-*a* concentrations from corresponding depths.

## **2.5 Macronutrients**

Triplicate 20 mL water samples obtained from each standard depth were used for the determination of major macronutrients (nitrate, nitrite, phosphorous, silicate and ammonia (second cruise only)). A Technicon II Autoanalyser was employed to determine the concentrations of the macronutrients following the methods of Windt *et al.* (1997) and Kirkwood (1994). Dissolved inorganic carbon was determined using the Gran titration method of Monteiro (1997). Unfortunately, the nutrient analyses for the second cruise were conducted by CSIR in Durban. The values presented in Table 7 are the lower limits of detection.

## **2.6 Hydrological Data**

Conductivity, temperature and pressure (CTD) measurements were obtained from the Neil Brown MKIII data logger. The following laboratory calibrations were carried out before and after the cruise by the Sea Fisheries Research Institute: The pressure sensor was calibrated against a Budenberg Dead Weight Tester 0-60 Mpa (serial number 13917/280D). The temperature sensor was calibrated against a Hewlett Packard 2804A quartz thermometer with probes 1812A and 18119A. The Hewlett Packard was calibrated against an Automatic Systems Laboratories Precision Thermometry Bridge Model F700 (serial number 1328-009-437). Finally, the conductivity sensor was calibrated against a Guildline Autosal Model 8400B (serial number 61 284) using IAPSO Standard Sea Water K15 = 0.99986 and salinity 34.994. The conductivity to salinity conversion described in UNESCO (1983) was applied, using the corrected CTD temperatures (Froneman *et al.* 1998).

## **2.7 Salinity**

Bottle salinities were collected from each Niskin bottle in order to calibrate the CTD. The conductivity ratio was determined using a Guildline Autosal Model 8400A salinometer, following the methods described in the Guildline Autosal Operating Manual. The conductivity was converted to salinity using equations described by UNESCO (1983). Wormley Standard Sea water batch P119 was used to standardise the salinometer at the start and end of every batch of stations. All data were logged using the SIS Softsal software, which automatically calculated corresponding salinity values from conductivity data (Froneman *et al.* 1998).

## **2.8 Data Display System**

The Data Display System (DDS) on the *MV SA Agulhas* was operational from the beginning of each cruise. The system was driven by a 486 DX 33 PC with a 120 MB hard-drive and 4M ram. Parameters logged by the DDS included: Position (Latitude and Longitude), Wind Speed (relative and true), Wind Direction (relative and true)), Air Temperature and Pressure, Humidity, and Thermosal (sea surface temperature and salinity), The average parameters for each value recorded was saved on file every hour (Ansorge *et al.* 1998).

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## CHAPTER 3

### *The Scandinavian/ South African Antarctic cruise - December/February 1997-1998*

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#### 3.1 RESULTS

##### 3.1.1 Hydrographical conditions

Broadscale hydrological regimes during the study are discussed elsewhere (Froneman *et al.* 1998). Here the hydrological data at the production stations are presented in Table 2. Sea surface temperatures in the MIZ ranged between  $-0.28$  and  $0.09^{\circ}\text{C}$ , between  $1.2$  and  $1.3^{\circ}\text{C}$  in the IFZ and between  $3.52$  and  $3.74^{\circ}\text{C}$  in the region of the APF. Surface salinities displayed a distinct trend at stations occupied within the MIZ. At the four most southern stations (D 98; D126; D134 and D 162), salinity concentrations were  $\pm 33.8^{\text{‰}}$  in the top 30m while at the northerly stations (D172 and D199), the concentrations were  $> 34.0^{\text{‰}}$  throughout the euphotic zone (depth 40m). At stations in the IFZ (D233 and D258) salinities ranged between  $34.2^{\text{‰}}$  and  $34.3^{\text{‰}}$  in the euphotic zone (up to 140m depth). In the vicinity of the APF (stations D316, D341, D351, D378) the salinity values of  $33.7^{\text{‰}}$  were virtually uniform at the different depths in the euphotic zone (up to 81m). Throughout the

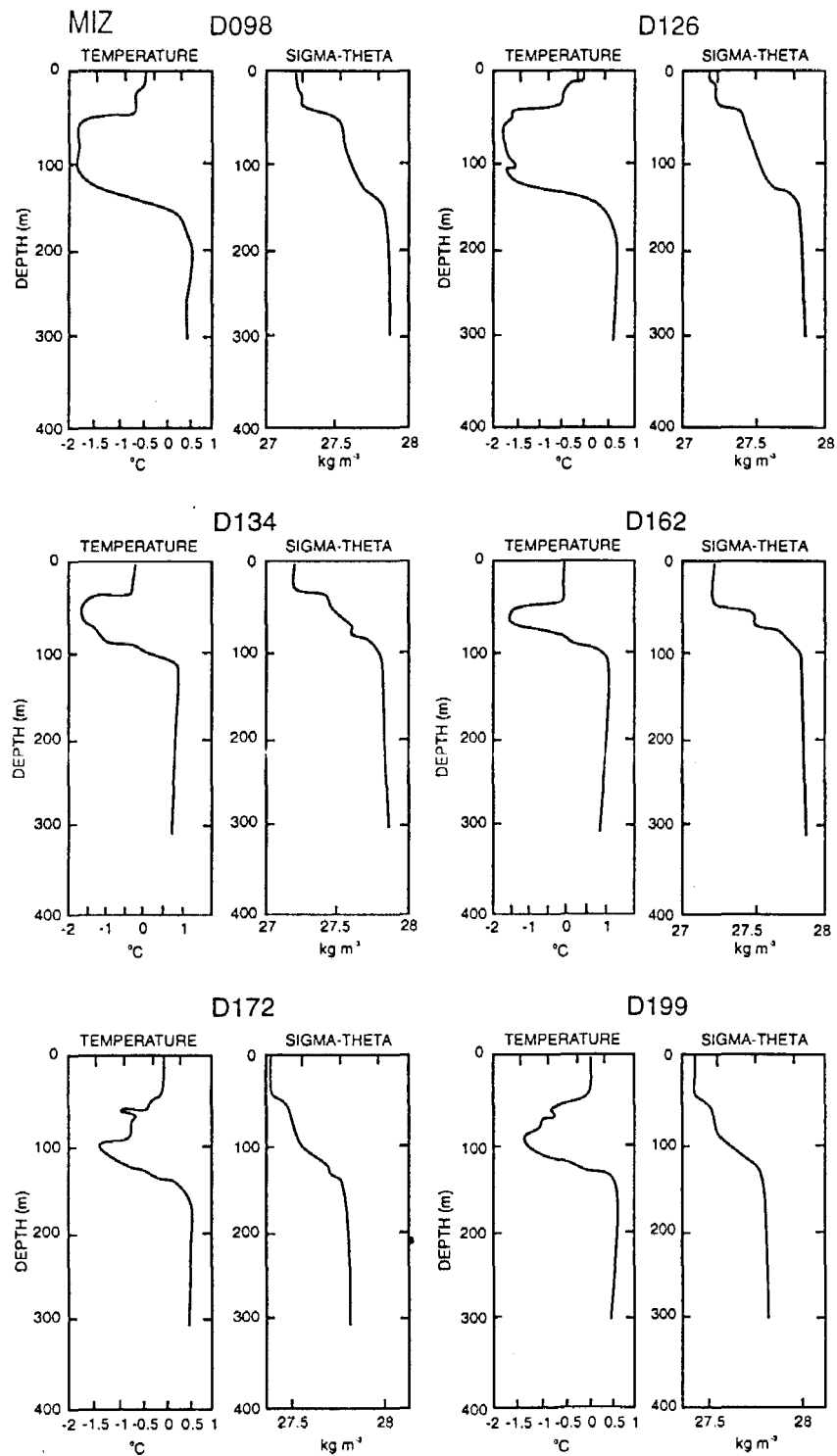
**Table 2:** Summary of environmental conditions at production stations occupied during the Scandinavian/South African Antarctic expedition within the MIZ, IFZ and APF during austral summer (December/February 1997-1998).

MIZ = Marginal Ice Zone; IFZ = Interfrontal Zone; APF = Antarctic Polar Front.

Station	Sea surface temp. (°C)	Air temp. (°C)	Surface Salinity ‰	PAR $\mu\text{E m}^{-2} \text{s}^{-1}$	Wind speed (knots)	Cloud cover	Sea state Beaufort scale
<b>MIZ</b>							
D098	-0.28	0.2	33.788	510.8	11.6	6/8	3
D126	0.09	-0.2	33.775	946.8	7.4	5/8	2
D134	-0.05	0.2	33.735	808.4	22.9	8/8	5
D162	-0.06	0.9	33.711	441.4	28.7	5/8	7
D172	0.03	1.4	34.019	203.6	16.9	3/8	2
D199	0.06	-0.2	34.058	1016.9	27.5	8/8	6
<b>IFZ</b>							
D233	0.12	1.2	34.266	374	20.2	8/8	5
D258	0.27	1.3	34.208	353	13.3	7/8	4
<b>APF</b>							
D316	3.72	3.2	33.772	555	32.6	7/8	7
D341	3.74	2.7	33.788	405	14.3	8/8	3
D351	3.52	4.7	33.812	1326	15	4/8	3
D378	3.56	6.4	33.792	430	30.3	8/8	7

survey, cloud cover ranged from 4/8 to 8/8. Wind speeds varied considerably during the study, ranging from 7.4 to 32.6 knots (Table 2).

Based on water column profiles, stations occupied within the three regions could be divided into two distinct regimes. A well defined pycnocline was observed at stations occupied in the vicinity of the MIZ and APF (Figure 4.1 and 4.2). Here the mixed layer depth corresponded to light depths equivalent to  $\pm 5\%$  of the surface irradiation. In contrast, within



**Figure 4.1:** Water column profiles of temperature and density at stations in the Marginal Ice Zone (MIZ) in the Atlantic sector of the Southern Ocean during the Scandinavian/South African Antarctic expedition.

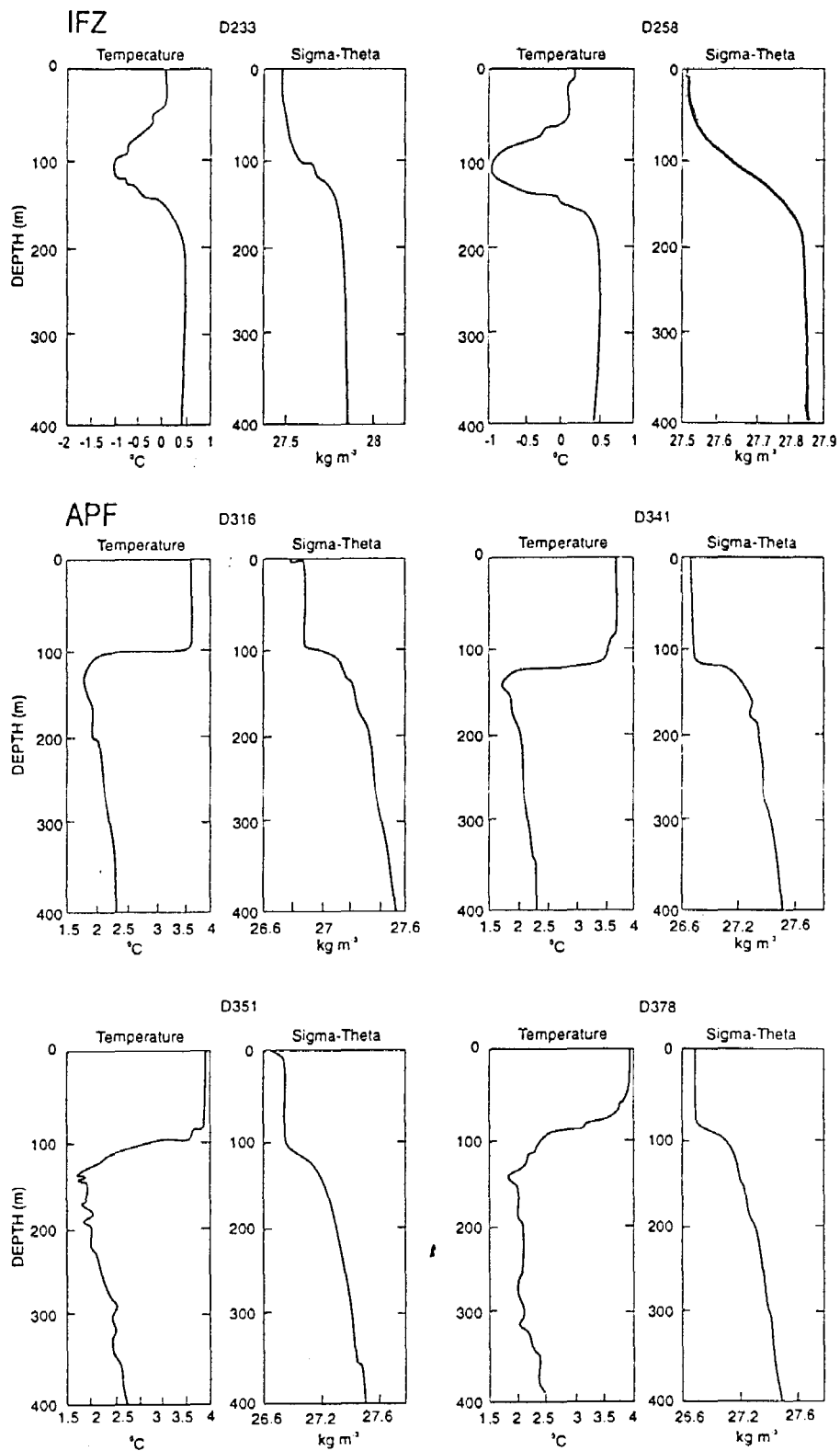


Figure 4.2: Water column profiles of temperature and density at stations in the APF (Antarctic Polar Front) and IFZ (Interfrontal Zone) in the Atlantic sector of the Southern Ocean during the Scandinavian/South African expedition.

**Table 3:** Macronutrient concentrations ( $\mu\text{mol} \cdot \text{L}^{-1}$ ) at stations occupied in the vicinity of the MIZ, IFZ and APF during the Scandinavian/South African December 1997/February 1998 Antarctic cruise.

MIZ = Marginal Ice Zone; IFZ = Interfrontal Zone; APF = Antarctic Polar Front

Station	NO <sub>3</sub>			NO <sub>2</sub>			PO <sub>4</sub>			SiO <sub>4</sub>		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
<b>MIZ</b>												
D098	17.89	17.32	18.85	0.12	0.12	0.18	1.52	1.39	1.58	35.21	34.2	36.33
D126	22.67	21.35	25.26	0.16	0.12	0.23	3.55	3.17	4.06	41.64	42.9	45.57
D134	20.13	19.96	20.48	0.63	0.6	0.69	2.35	2	2.8	35.52	35.66	35.52
D162	19.55	19.12	19.88	0.48	0.42	0.54	1.15	1	1.2	33.54	33.02	33.78
D172	20.77	19.93	21.7	0.57	0.54	0.63	3.32	1.9	2.9	36.76	35.2	37.2
D199	21.18	20.43	22.58	0.6	0.51	0.66	2.1	1.9	2.2	36.88	36.51	37.34
<b>IFZ</b>												
D233	23.29	22.81	24	0.74	0.72	0.74	4.33	4.1	4.7	42.61	41.56	45.35
D258	30.85	30.5	31.2	0.19	0.18	0.23	2.12	1.8	3.5	42.88	42.03	43.67
<b>APF</b>												
D316	22.44	21.32	22.83	0.17	0.12	0.23	5.48	4.4	6.6	7.95	7.95	7.95
D341	22.22	21.53	22.54	0.23	0.23	0.23	4.6	3.4	5.2	7.95	7.95	7.95
D351	22.66	21.88	22.24	0.19	0.12	0.29	4.32	3.6	5.6	12.12	11.36	12.73
D378	22.69	22.12	23.5	0.23	0.18	0.29	5.81	5.28	6.2	13.49	13.49	14.55

the IFZ the upper water column appeared well mixed and mixed layer depth exceeded the 1% light depth (> 50m) (Figure 4.2).

### 3.1.2 Nutrients

The average, minimum and maximum macronutrient concentrations within the upper 100m in the three regions of investigation are shown in Table 3. Throughout the investigation, macronutrient concentrations were highest at stations within the IFZ. An exception was recorded in the case of phosphates for which the highest concentrations were recorded at stations in the vicinity of the APF. Nitrate concentrations at stations in the vicinity of the MIZ ranged from 17.3 to 25.3  $\mu\text{mol} \cdot \text{L}^{-1}$  and between 21.3 and 23.5  $\mu\text{mol} \cdot \text{L}^{-1}$  at the APF.

Within the IFZ, nitrate concentrations ranged between 22.8 and 31.2  $\mu\text{mol} \cdot \text{L}^{-1}$ . Nitrite concentrations varied between 0.12 and 0.7  $\mu\text{mol} \cdot \text{L}^{-1}$  in the MIZ, between 0.19 and 0.74  $\mu\text{mol} \cdot \text{L}^{-1}$  at the IFZ, and between 0.17 and 0.29  $\mu\text{mol} \cdot \text{L}^{-1}$  at stations occupied in the vicinity of the APF. Phosphate concentrations ranged between 1 and 3.6  $\mu\text{mol} \cdot \text{L}^{-1}$  in the MIZ, between 3.4 and 5.8  $\mu\text{mol} \cdot \text{L}^{-1}$  at the APF, and between 1.8 and 4.7  $\mu\text{mol} \cdot \text{L}^{-1}$  in the IFZ. Silicate ( $\text{SiO}_4$ ) concentrations in the MIZ ranged between 33.5 and 41.6  $\mu\text{mol} \cdot \text{L}^{-1}$  and between 7.95 and 13.5  $\mu\text{mol} \cdot \text{L}^{-1}$  in the APF. At stations occupied within the IFZ, Si concentrations were always  $> 41 \mu\text{mol} \cdot \text{L}^{-1}$  (Table 3).

### 3.1.3 Integrated chlorophyll

Total areal chlorophyll-*a* (Chl-*a*) concentrations in the MIZ ranged from 21.2 to 55.4 mg Chl-*a*  $\cdot \text{m}^{-2}$  (Table 4). Within the MIZ, total integrated Chl-*a* biomass decreased along the south-north transect (Figure 5). Microphytoplankton formed the most important contributor to total pigments at all stations comprising between 68% and 76% of the total (Figure 5). Microphytoplankton integrated biomass ranged from 15.4 to 39.7 mg Chl-*a*  $\cdot \text{m}^{-2}$  in the MIZ. Nanophytoplankton biomass ranged between 2.6 and 8.7 mg Chl-*a*  $\cdot \text{m}^{-2}$  and picophytoplankton between 3.1 and 5.9 mg Chl-*a*  $\cdot \text{m}^{-2}$  (Table 4). At all stations occupied within the MIZ, maximum Chl-*a* concentrations were recorded at depths greater than the 5% light depth (Figure 6.1).

In the IFZ, total chlorophyll concentrations were lower ranging between 16.7 and 23.3 mg Chl-*a*  $\cdot \text{m}^{-2}$  (Table 4). A considerable shift in the size composition of the phytoplankton assemblages was evident with the smaller nano- and picophytoplankton cells contributing between 71 and 73 % of the total pigment (Figure 5). Integrated pico- and nanophytoplankton

values ranged between 6.5 and 7.8 mg Chl-*a* . m<sup>-2</sup> and between 5.7 and 8.8 mg Chl-*a* . m<sup>-2</sup>, respectively (Table 4). Microphytoplankton comprised

**Table 4:** Total integrated chlorophyll-*a* (mg Chl-*a* . m<sup>-2</sup>) during the Scandinavian/South African Antarctic expedition (Dec./Feb.) 1997-1998.

Station	Phytoplankton size-fraction			total
	micro >20 $\mu\text{m}$	nano 2-20 $\mu\text{m}$	pico <2 $\mu\text{m}$	
<b>MIZ</b>				
D098	37.55	8.74	3.82	50.11
D126	32.11	7.48	4.71	44.3
D134	41.34	8.58	5.43	55.36
D162	39.67	6.69	5.9	52.26
D172	18.43	4.26	4.36	27.05
D199	15.42	2.65	3.12	21.19
<b>IFZ</b>				
D233	6.73	8.8	7.77	23.3
D258	4.57	5.65	6.47	16.7
<b>APF</b>				
D316	22.96	15.45	10.57	48.99
D341	10.71	9.93	7.25	27.89
D351	31.41	11.57	7.48	50.47
D378	17.69	11.5	6.76	35.96

< 29% of the total pigment at all stations occupied within the IFZ. Maximum Chl-*a* concentrations at stations occupied within the IFZ occurred at light depths corresponding to 1% surface irradiation. An exception was presented in the nanophytoplankton fraction at station D233 where maximum chlorophyll-*a* concentration was observed at the 0.1% light depth (Fig. 6.2).

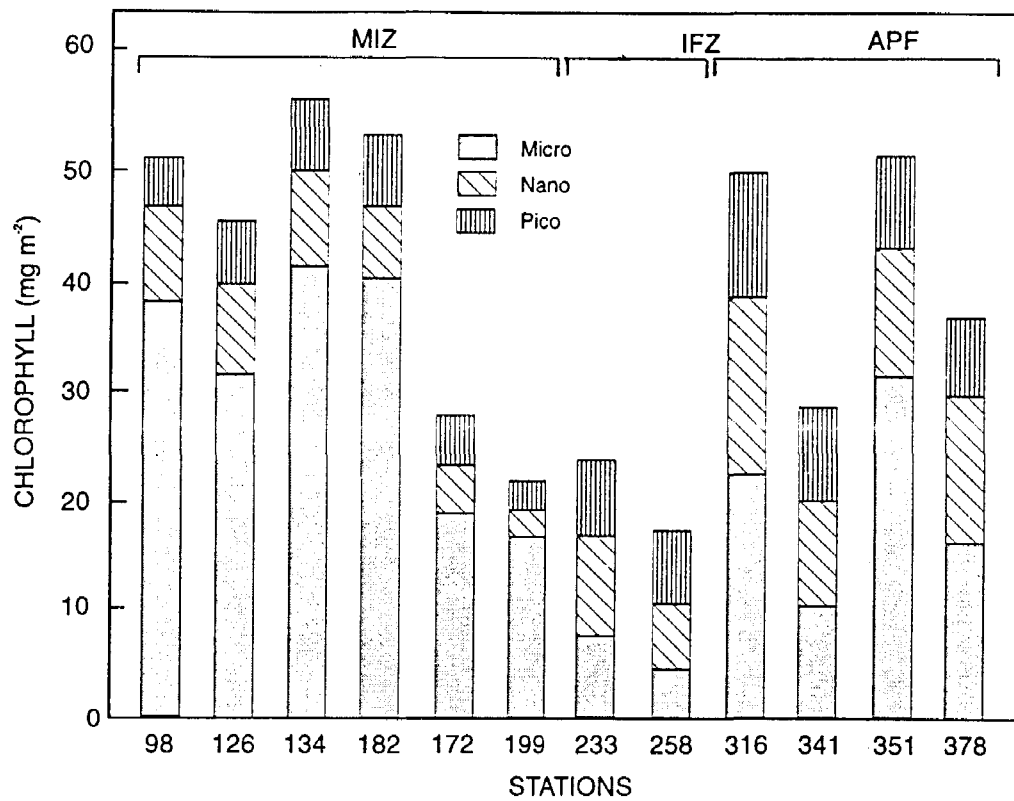
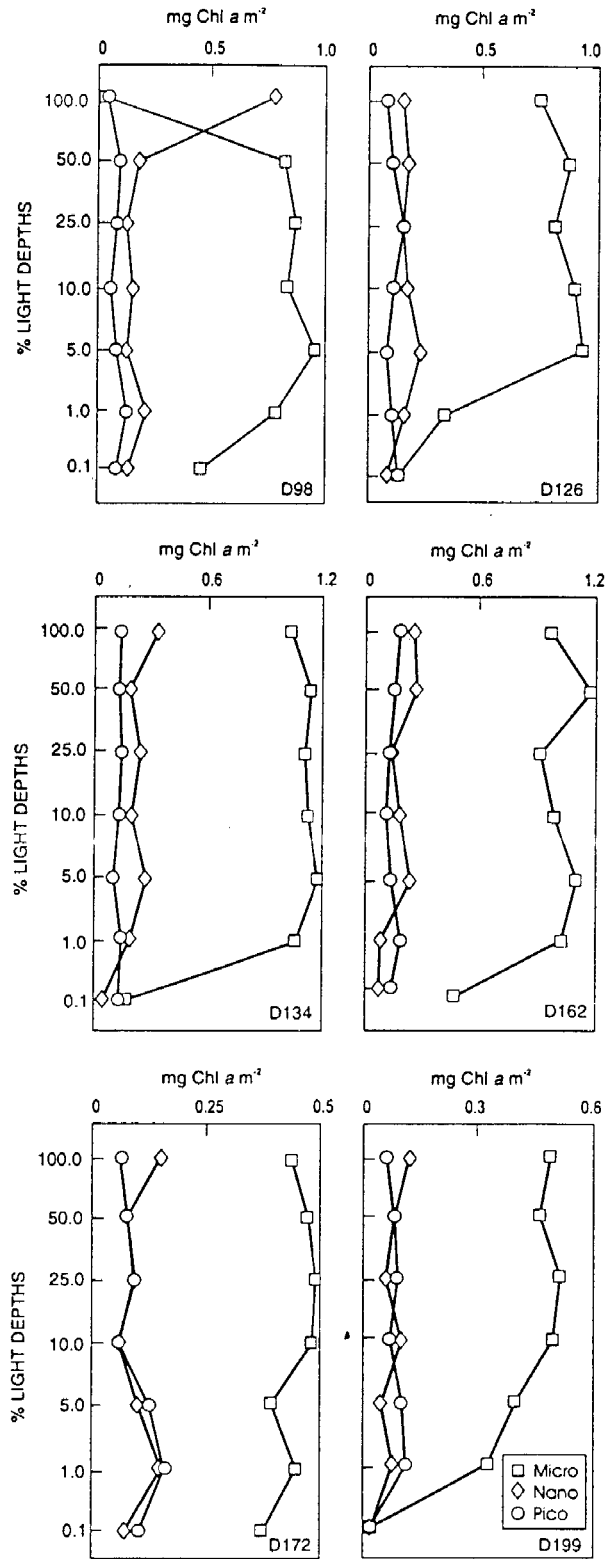


Figure 5: Total size-fractionated phytoplankton chlorophyll-*a* concentrations at stations in the vicinity of the MIZ, IFZ, and APF during the Scandinavian/South African Antarctic expedition in December 1997-February 1998. All data are integrated to the 1% euphotic depth. Micro = Microphytoplankton (>20  $\mu\text{m}$ ); Nano = Nanophytoplankton (<20 and >20  $\mu\text{m}$ ); Pico = Picophytoplankton (< 2  $\mu\text{m}$ ). MIZ = Marginal Ice Zone; IFZ = Interfrontal Zone; APF = Antarctic Polar Front.



**Figure 6.1:** Vertical profiles of chlorophyll-*a* concentration at different light depths at the six stations occupied in the MIZ during the Scandinavian/South African Antarctic expedition.

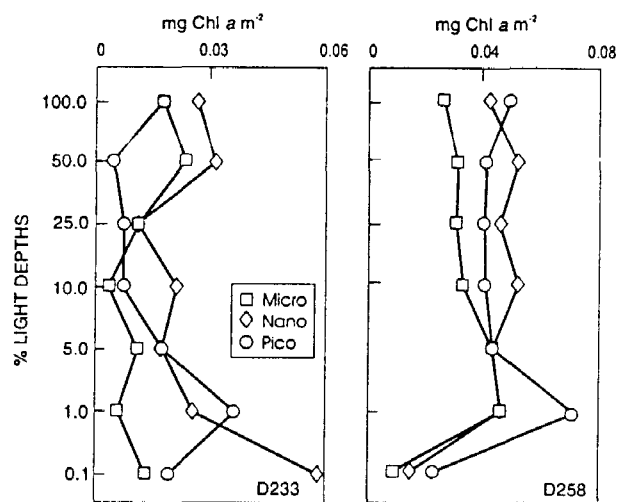
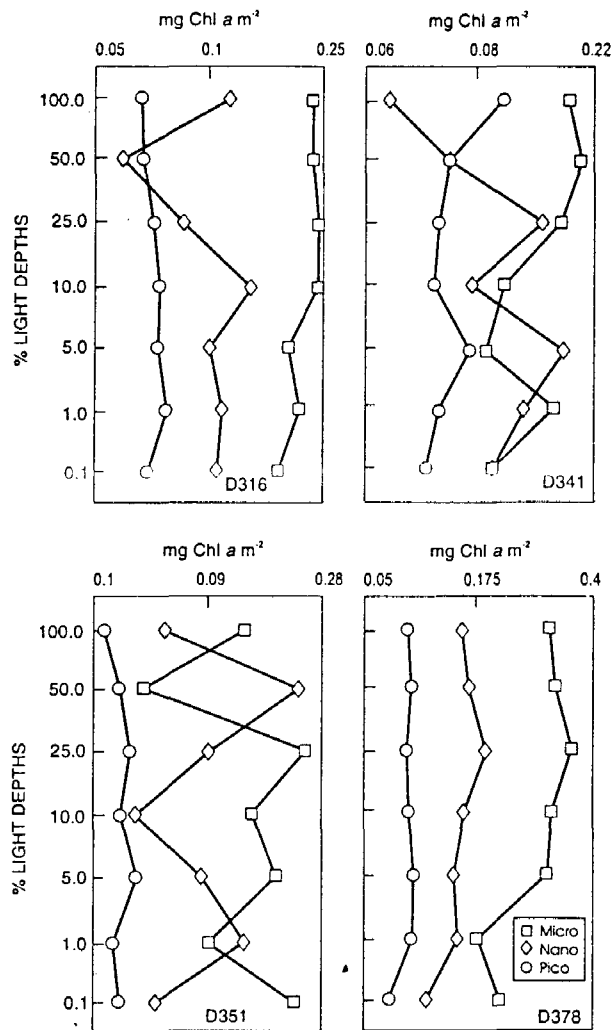
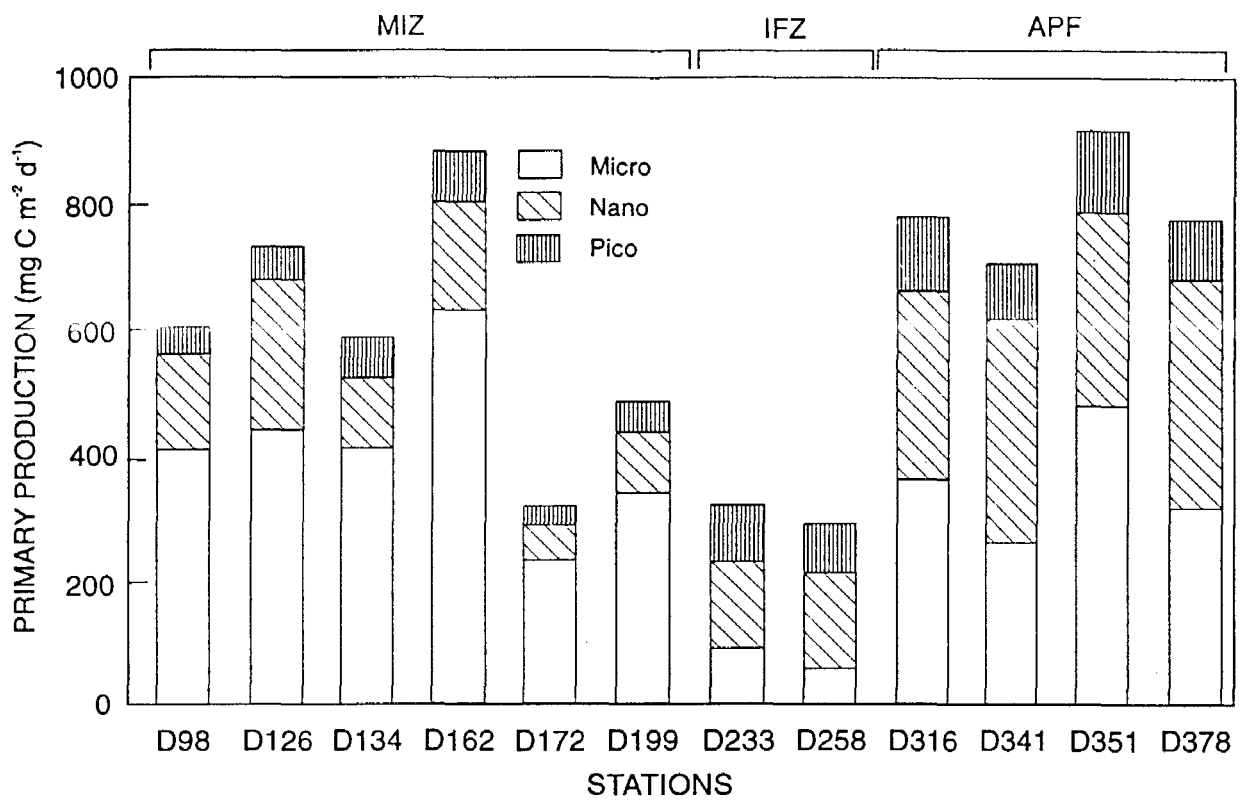


Figure 6.2: Vertical profiles of chlorophyll-*a* concentration at different light depths at the two stations in the IFZ region during the Scandinavian/South African Antarctic expedition.



**Figure 6.3:** Vertical profiles of chlorophyll-*a* concentration at different light depths at the four stations in the vicinity of the Antarctic Polar Front (APF) during the Scandinavian/South African Antarctic expedition.



**Figure 7:** Total integrated size-fractionated phytoplankton primary production measurements at stations occupied in the vicinity of the MIZ, IFZ, and APF during the Scandinavian/South African expedition in December 1997-February 1998. All data are integrated to the 1% euphotic depth. Abbreviations as in Figure 5.

Total integrated Chl-*a* biomass at stations in the vicinity of the APF ranged between 27.9 and 50.5 mg Chl-*a* . m<sup>-2</sup> (Table 4). Microphytoplankton integrated biomass ranged between 10.8 and 23.0 mg Chl-*a* . m<sup>-2</sup> or between 35 and 45% of the total pigment (Figure 5). Nanophytoplankton represented the second most important fraction (Figure 5). Integrated nanophytoplankton biomass ranged between 9.9 and 15.5 mg Chl-*a* . m<sup>-2</sup> (Table 4). Picophytoplankton always contributed < 25% of the total integrated biomass at all stations (Figure 5). Maximum Chl-*a* concentrations at stations occupied within the APF occurred at light depths greater than 1% except at station D351 (Figure 6.3).

### **3.1.4 Integrated primary production**

Total daily integrated production within the three regions of investigation displayed the same spatial pattern as integrated biomass. Generally the highest integrated production rates were recorded at stations occupied in the vicinity of the MIZ and APF (Figure 7). Integrated primary production at stations in the MIZ ranged from 317 to 887.3 mg C . m<sup>-2</sup> . d<sup>-1</sup> (Table 5). In this zone microphytoplankton were the most important contributor to total production comprising between 60 and 73% of the total. Total daily integrated microphytoplankton ranged from 230.6 to 633.1 mg C . m<sup>-2</sup> . d<sup>-1</sup> (Table 5). Nanophytoplankton integrated production ranged between 62.3 and 246.7 mg C . m<sup>-2</sup> . d<sup>-1</sup>, while the picophytoplankton production ranged between 24.1 and 77 mg C . m<sup>-2</sup> . d<sup>-1</sup> (Table 5). Water column productivity at stations occupied in the vicinity of the MIZ displayed a distinct pattern. At two of the most southern stations (stations D098 and D134) maximum production occurred at depths corresponding to 25-10% surface irradiation. In contrast, at the northern stations, maximum production corresponded to light depths > 50% of the surface radiation (Figure 8.1).

One-way Analysis of Variance showed that within the IFZ the total primary production was significantly ( $P > 0.05$ ) lower ranging between 292.8 and 317.9 mg C . m<sup>-2</sup> . d<sup>-1</sup> (Table 5). In this region, nanophytoplankton was the most important contributor to total productivity comprising between 44 and 52% of total (Figure 7). Picophytoplankton was the second most important contributor to total production comprising ≈26% of total. Daily integrated picophytoplankton values ranged between 76.5 and 83.6 mg C . m<sup>-2</sup> . d<sup>-1</sup> while nanophytoplankton production ranged from 141.1 to 152.7 mg C . m<sup>-2</sup> . d<sup>-1</sup> (Table 5).

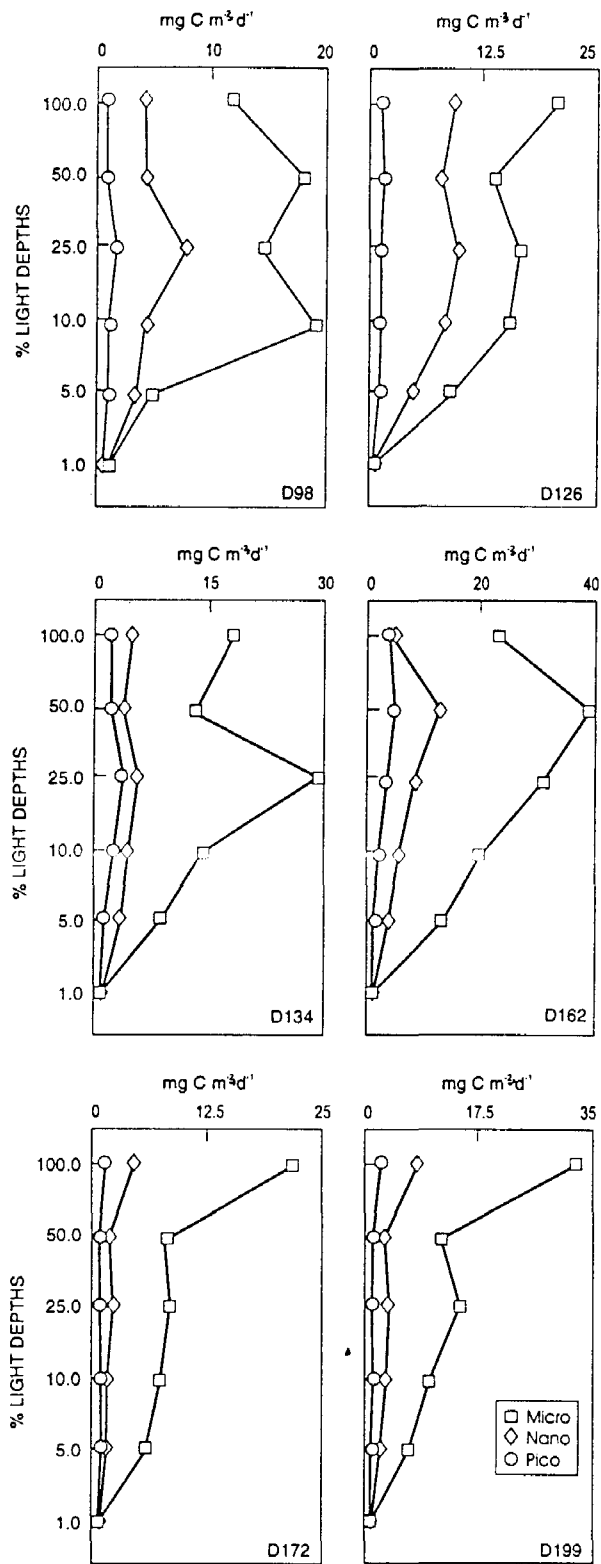
**Table 5.** Total integrated primary production (mg C . m<sup>-2</sup> . d<sup>-1</sup> ) at production stations during the Scandinavian/South African Antarctic expedition in the Southern Ocean.

Station	Size classes of phytoplankton			total
	micro >20 μm	nano 2-20 μm	pico <2 μm	
<b>MIZ</b>				
D098	405.69	155.38	38.73	599.8
D126	437.25	246.71	45.98	729.94
D134	414.26	115.29	59.2	588.76
D162	633.09	177.32	76.85	887.27
D172	230.61	62.26	24.08	316.95
D199	341.29	99.95	42.81	484.06
<b>IFZ</b>				
D233	93.16	141.11	83.62	317.9
D258	63.58	152.69	76.55	292.83
<b>APF</b>				
D316	362.59	304.46	117.42	784.48
D341	264.68	359.12	84.71	708.51
D351	483.49	311.01	132.26	926.77
D378	320.26	364.12	95.47	779.85

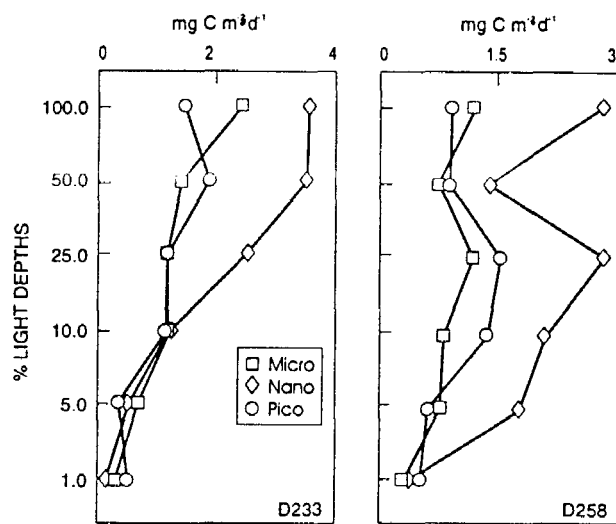
Water column production for all three fractions displayed the same trend with maximum production occurring at light depths greater than 50% of the surface irradiance (Figure 8.2). At stations occupied in the vicinity of the APF total daily integrated production ranged from 708.5 to 926.8 mg C . m<sup>-2</sup> . d<sup>-1</sup>. Microphytoplankton was the most important contributor to total production at stations D316 and D351 while nanophytoplankton dominated total production at two stations, D341 and D378. Total daily integrated microphytoplankton production ranged from 264.7 and 483.5 mg C . m<sup>-2</sup> . d<sup>-1</sup> while nanophytoplankton production ranged between 304.5 and 364.1 mg C . m<sup>-2</sup> . d<sup>-1</sup>. Picophytoplankton production ranged from 84.7 to 132.3 mg C . m<sup>-2</sup> . d<sup>-1</sup> (Figure 8.3). Water column production at stations occupied in the vicinity of the APF displayed the same pattern for all three fractions. Generally, the highest production occurred at light depths corresponding to 10-25% light penetration. An exception was found at station D316 where maximum production occurred at the light depth corresponding to 25% surface irradiation (Figure 8.3).

### **3.1.5 Photosynthetic capacity**

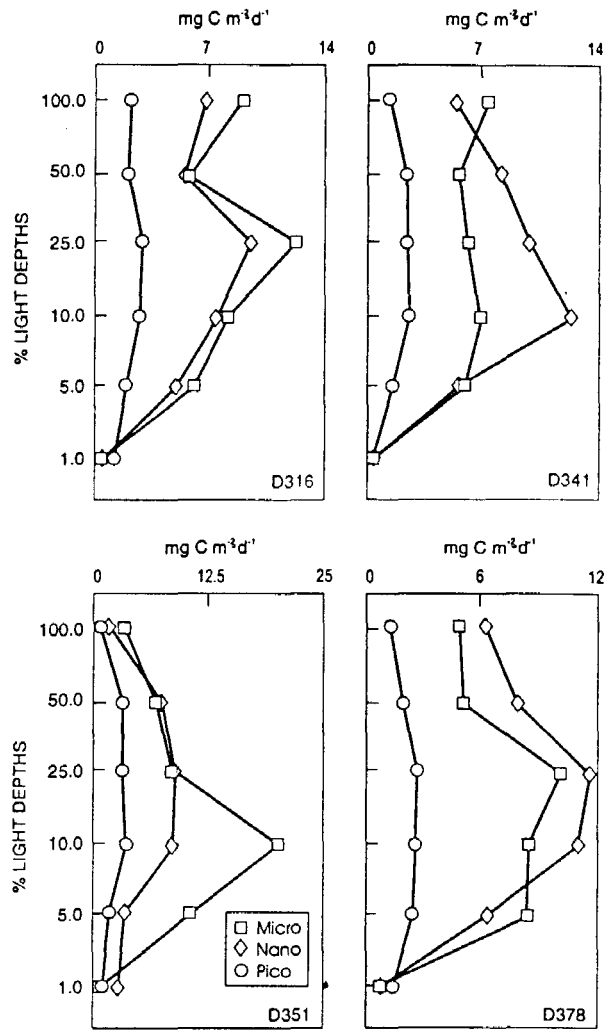
Photosynthetic capacities ( $P_B$  max) of phytoplankton assemblages displayed a high degree of spatial variability during the study (Figure 9). Within the MIZ, a shallowing of the maximum photosynthetic capacity values was observed along the south-north transect. At the three most southern stations, maximum values (range 3.1 to 4.3 mg C (mg Chl-*a*)<sup>-1</sup> h<sup>-1</sup>) were recorded at light depths corresponding to 25% of surface radiation. In contrast, at the three remaining stations, maximum values (ranging from 2.9 to 4.3 mg C (mg Chl-*a*)<sup>-1</sup> h<sup>-1</sup>) were recorded in the surface waters (Figure 9). At stations occupied within the IFZ, a general decrease in  $P_B$  max values was recorded with depth. An exception occurred at station 8, where a dramatic decrease in  $P_B$  max was recorded at a depth corresponding to 50% surface



**Figure 8.1:** Vertical profiles of primary production at different light depths at production stations occupied in the vicinity of the Marginal Ice Zone (MIZ) during the Scandinavian/South African Antarctic expedition.



**Figure 8.2:** Vertical profiles of primary production at different light depths at production stations occupied in the vicinity of the Interfrontal Zone (IFZ) during the Scandinavian/South African Antarctic expedition.



**Figure 8.3:** Vertical profiles of primary production at different light depths at production stations occupied in the vicinity of the Antarctic Polar Front (APF) during the Scandinavian/South African Antarctic expedition.

light. In the vicinity of the APF, maximum  $P_B$  max values were generally highest at the 10% light depth. An exception was recorded at station 9, situated at the southern region of the front, where the highest  $P_B$  max value was recorded at 25% light depth (Figure 9).

### 3.2 DISCUSSION

The general oceanographic conditions during the survey can be summarised as follows. Stations in the Marginal Ice Zone (MIZ) and near the Antarctic Polar Front (APF) were generally characterised by relatively high water column stability and a shallow mixed layer depth (see also Froneman *et al.* in press). Within the MIZ, the factors responsible for the high water column stability appeared to differ between the southern and northern stations. The low surface salinity values recorded at the southern most stations in the MIZ, suggest the water column stability was related to the sea-ice melt, which imparts stability in the vicinity of the retreating ice (Table 2). In contrast, the increase in surface water temperature at the northern stations suggests that water column stability there was the result of the summer capping of the colder winter waters (Table 2). At stations occupied in the vicinity of the APF, water column stability appeared to be related to interaction between colder saline Antarctic waters and the warmer Sub-Antarctic waters, which confers localised stability in the region of the front (Froneman *et al.* in press). In contrast to the APF and MIZ stations, stations occupied in the Interfrontal Zone (IFZ) were characterised by low water column stability with a deep mixed layer (Froneman *et al.* in press).

The integrated chlorophyll-*a* biomass and primary production observed in the MIZ during this investigation is in agreement with previous studies conducted in the MIZ in different

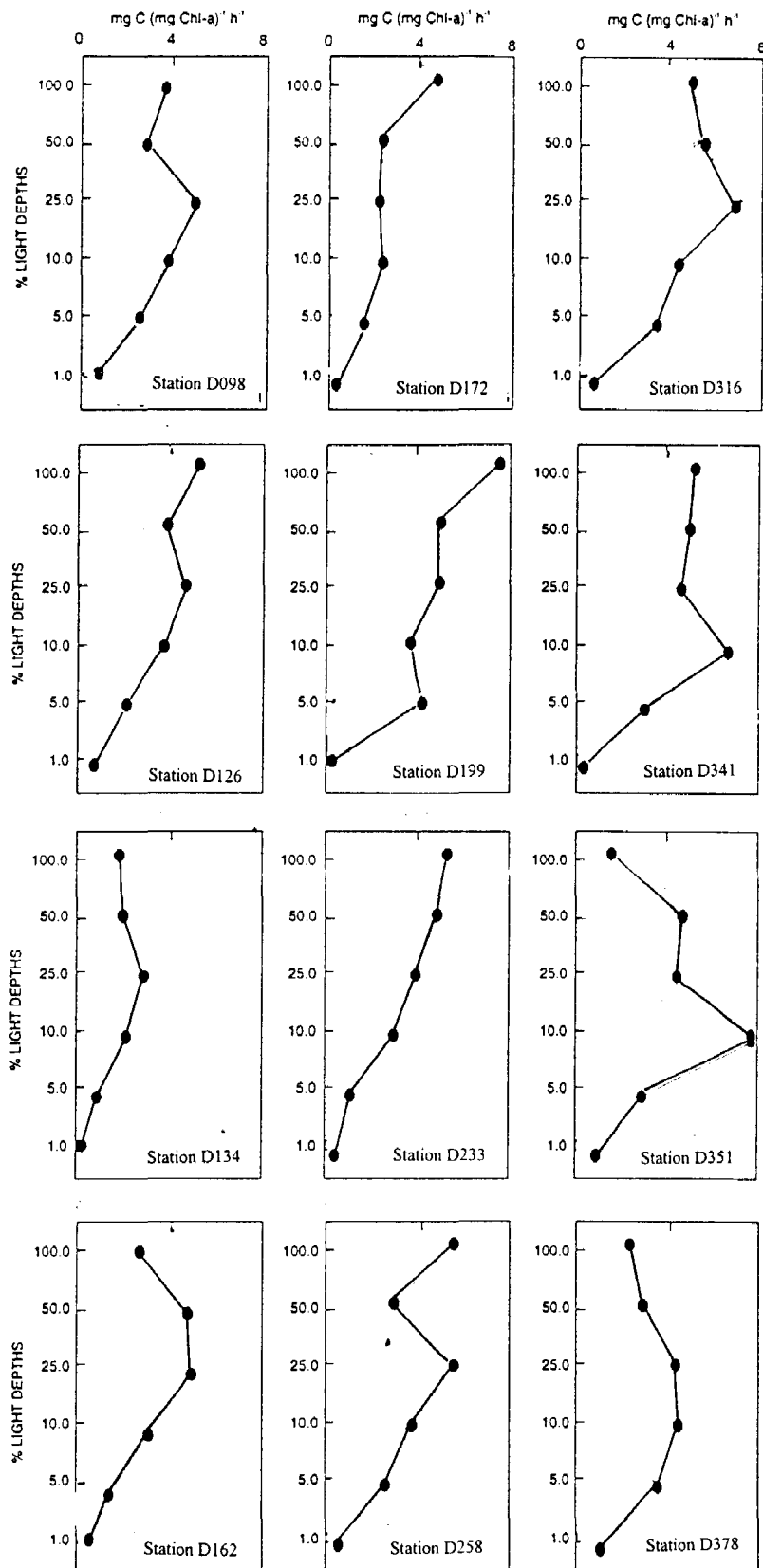


Figure 9: Photosynthetic capacity ( $\text{mg C (mg Chl-}a\text{)}^{-1} \text{ h}^{-1}$ ) profiles at stations occupied in the MIZ, APF and IFZ in the Atlantic sector of the Southern Ocean. MIZ = Marginal Ice Zone; IFZ = Interfrontal Zone; APF = Antarctic Polar Front.

sectors of the Southern Ocean (von Bodungen *et al.* 1986; Boyd *et al.* 1995; Froneman *et al.* 1997). At stations within the MIZ, total integrated biomass and productivity decreased along the south-north transect. At the four stations furthest south, the mean integrated biomass and productivity was  $50 \text{ mg Chl-}a \cdot \text{m}^{-2}$  and  $701 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ , respectively (Tables 4 and 5). In contrast, at the northern most stations integrated chlorophyll-*a* biomass and productivity were substantially lower ranging between 21 and 27  $\text{mg Chl-}a \cdot \text{m}^{-2}$  and between 316 and 484  $\text{mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  (Tables 4 and 5). The decrease in chlorophyll-*a* biomass and productivity along the south-north transect is consistent with recent studies conducted in the Bellingshausen Sea (Boyd *et al.*, 1995). The pattern observed during this study can probably be related to differences in oceanographic conditions along the MIZ transect. At the southern-most stations a shallow pycnocline was evident at all stations (Figure 4). In contrast, at stations located in the northern section of the transect a deepening of the pycnocline was observed. The higher salinity concentrations recorded at the northern stations suggest that the stability imparted by sea-ice melt had been eroded (Table 2). These data suggest that higher productivity recorded at stations occupied at the southern-most stations within the MIZ was largely determined by water column stability. This is consistent with both theoretical and field studies conducted in the MIZ of the Southern Ocean (de Baar *et al.* 1995; Boyd *et al.* 1995; Froneman *et al.* 1997). Lewis *et al.* (1984) suggested that the photoadaptation index, including the maximum photosynthetic rate and *in vivo* fluorescence, should provide some indication of response of algae to turbulence. Under conditions where turbulence is low, the photosynthetic index of algae should produce variations with depth. During this investigation, photosynthetic capacity values of stations within the MIZ demonstrated a distinct trend (Figure 9). At the southern stations  $P_{B\text{max}}$  values were highest at light depths corresponding to 25% surface irradiance, while at the northern stations, the maximum values

were recorded in the surface waters. This result suggests that the patterns observed were indicative of the physiological status of the algal communities and were not due to vertical mixing. Thus, different phytoplankton communities were probably encountered along the MIZ transect. At southern stations the profile was typical of the ice-associated community, while at northern stations the profile resembled typical open water communities. Indeed, analyses of phytoplankton communities of the two regions showed typical ice-associated species e.g., *Phaeocystis* species dominated at the southern stations, while at the northern stations, typical open water species of the genera *Corethron* and *Proboscia* dominated (Froneman, unpublished data). The importance of iron in determining the spatial pattern in productivity cannot be discounted. Iron concentrations during this investigation were highest at stations located in the southern region of the MIZ (P. Croot unpublished data).

The levels of primary production within the interfrontal region (IFZ) contrasted dramatically with those observed in the MIZ to the south and the APF to the north. Integrated Chl-*a* biomass and primary production were  $< 25 \text{ mg Chl-}a \cdot \text{m}^{-2}$  and  $< 320 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  respectively. (Tables 4 and 5). At all stations integrated Chl-*a* biomass and productivity was dominated by the nano- and picophytoplankton size fractions (Figures 5 and 7). Similar observations in the interfrontal regions have been reported in the literature (El-Sayed 1988; Jacques 1989; Laubscher *et al.* 1993; Froneman *et al.* 1995a,b) suggesting that the results obtained here are typical for open waters of the Southern Ocean. Several hypotheses have been proposed to explain the phenomenon of low phytoplankton biomass in the open waters of the Southern Ocean despite high concentrations of macro-nutrients (i.e. phosphate, nitrate and silica) (Chisholm and Morel 1991; Priddle *et al.* 1992). Froneman *et al.* (1995a) suggested that silicate availability may limit the importance of microphytoplankton in the

open waters of the Southern Ocean. During this investigation, silicate concentrations within the IFZ appeared above the threshold where growth would be limiting (Jacques 1983). A more likely explanation for the low productivity within the IFZ, is low water column stability. At stations occupied within this region, a poorly developed pycnocline was evident suggesting a high degree of vertical mixing. The high degree of vertical mixing was evident from Chl-*a* profiles which were evenly distributed (Figure 6.2). These data suggest that production in the open ocean stations was limited due to an unfavourable light environment conferred by low water column stability (Lewis *et al.* 1984).

The total integrated Chl-*a* biomass at stations occupied within the vicinity of the APF ranged between 27 and 50 mg Chl-*a* . m<sup>-2</sup> while daily integrated primary production ranged between 784 and 926 mg C . m<sup>-2</sup> . d<sup>-1</sup> (Tables 4 and 5). Although these values are in the same range as those reported by El -Sayed and Weber (1982) ( mean = 805.2 mg C . m<sup>-2</sup> . d<sup>-1</sup>) in spring in the Scotia Sea , they are substantially higher than that reported by Froneman *et al.*(in prep.), 357 mg C . m<sup>-2</sup> . d<sup>-1</sup>, for the same region. Similarly, de Baar *et al.* (1995) recorded primary production rates of up to 3000 mg Chl-*a* . m<sup>-2</sup> . d<sup>-1</sup> during spring bloom conditions in the vicinity of the APF. These results indicate that production at the front exhibits a high degree of spatial/ temporal variability. The highest production within the region of the APF during this study was associated with the northern edge of the front which is in contrast with the findings of Laubscher *et al.* (1993) who showed that the highest production rates at the front were associated with its southern boundary. At stations 341 and 378 nanophytoplankton represented the most important contributor to total daily production (Figure 7). This result is surprising as previous studies have largely demonstrated that microphytoplankton dominate total Chl-*a* biomass and production when production is enhanced in the vicinity

of the front (Laubscher *et al.* 1993; Lancelot *et al.* 1993; Froneman *et al.* 1997). The predominance of small nanophytoplankton at these two stations can be related to both the oceanographic conditions and nutrient availability. Jacques (1983) suggested that silica concentrations  $< 40 \mu\text{mol} \cdot \text{L}^{-1}$  may cause a reduction in growth rates of some Antarctic diatom species. Nutrient data indicate that silica concentrations at station 341 were the lowest along the entire transect (Table 3). Here, the availability of silicate may have limited microphytoplankton production. Oceanographic data collected at stations occupied at the northern region of the front, showed strong vertical movement of water (Froneman *et al.* in press). Indeed, analysis of chlorophyll profiles at these stations showed that Chl-*a* was evenly distributed within the upper water column (Figure 6). Under conditions of high vertical mixing, the growth of small nanophytoplankton would be promoted (Fogg 1991).

### 3.4 CONCLUSIONS

The results of the investigation in the Atlantic sector of the Southern Ocean clearly demonstrated that elevated production rates were associated with stations occupied in the MIZ and APF. At these stations the upper water column was relatively stable. Enhanced production in the vicinity of these features is well documented (Jacques 1989; Laubscher *et al.* 1993; Boyd *et al.* 1995; Froneman *et al.* 1997). In contrast, in the IFZ, total production was significantly lower, which appears to reflect the low water column stability. Nutrient availability did not appear to limit total production although there is some evidence to suggest that the availability of  $\text{SiO}_4$ , particularly in the vicinity of the APF, may have limited the growth of the microphytoplankton. There is also some evidence to suggest that the availability of iron may have contributed to increased production associated with the MIZ

and APF. Unfortunately, we do not have any direct evidence to support this hypothesis.

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## CHAPTER 4

### *The Third Marion Island Oceanographic Survey (MIOS III) - April/May 1998*

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#### 4.1 RESULTS

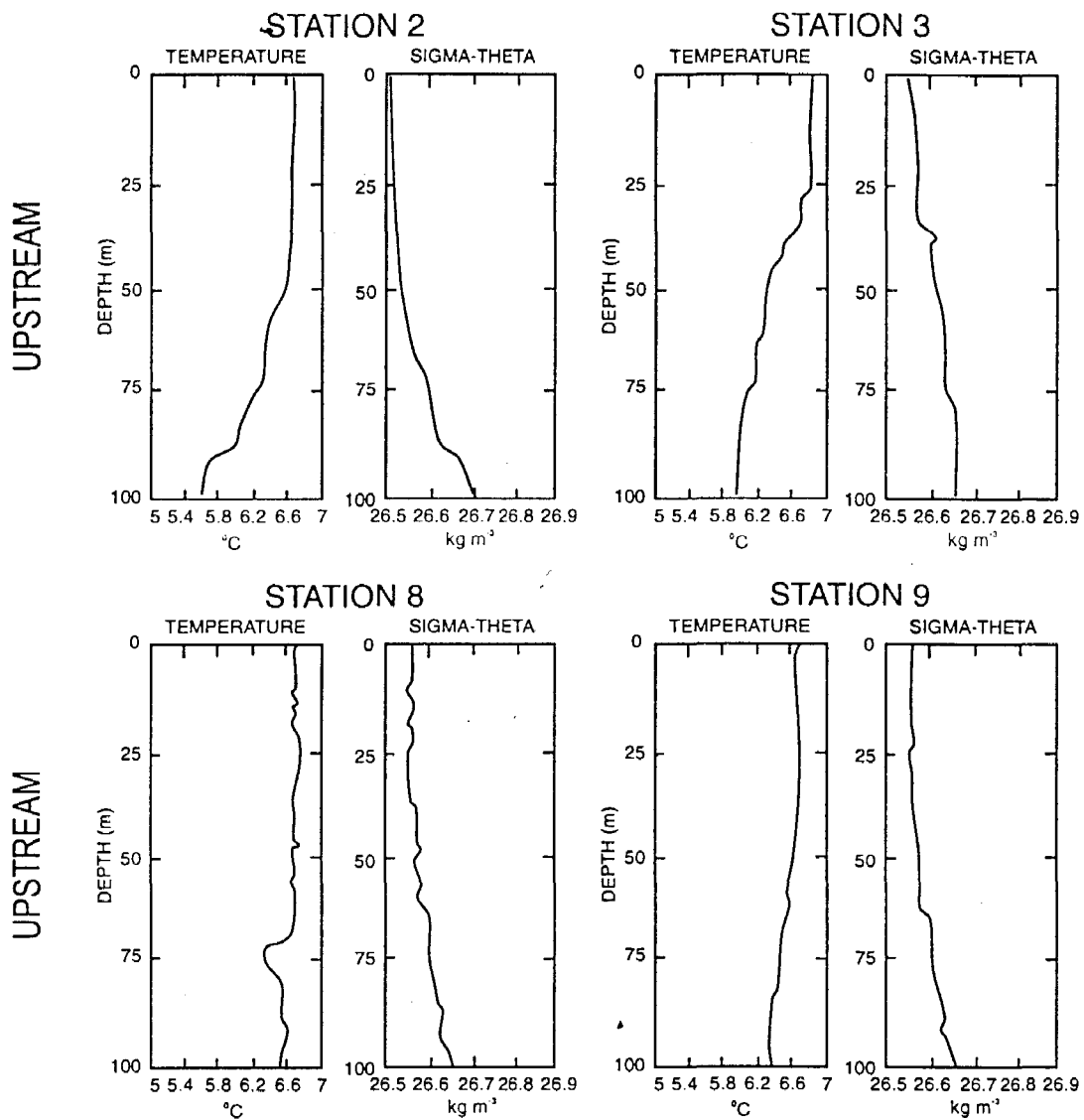
##### 4.1.1 Hydrological conditions

A summary of the experimental conditions at the primary production stations within the upstream, inter-island and downstream regions of the islands is given in Table 6. Sea surface temperatures in the upstream region ranged between 6.64 and 6.75°C, between 6.52 and 6.75°C in the inter-island region and between 5.84 and 6.74°C in the downstream region. At all stations the salinity values in the upper 100m of the water column were virtually uniform. Surface salinities upstream of the islands varied from 33.7 ‰ to 34.2 ‰. At stations in the inter-island region the salinities ranged between 33.7 ‰ to 33.8 ‰, while in the downstream region (stations 5, 6, 14) salinity values ranged between 33.8 and 34.0 ‰. The salinity value at the station occupied in the vicinity of the SAF (station 2) was 33.8 ‰. Throughout the investigation, the upper surface layer (up to 100 m) appeared to be well mixed with no clear thermocline evident. This is confirmed by the density profiles at the various primary production stations, which indicate that the upper water column was well

mixed (Figure 10.1 - 10.3).

**Table 6.** Summary of environmental conditions at production stations during the third Marion Island Oceanographic Survey (MIOS III) conducted in the upstream, inter-island and downstream region of the Prince Edward Islands (Southern Ocean) during the late austral autumn (April/May) 1998.

	Sea	Air temp.	Surface	Wind speed	Cloud cover	Sea state
Station	surface temp. (°C)	(°C)	salinity ‰	(knots)		Beaufort scale
<b>Upstream</b>						
2	6.75	10.2	33.793	22.8	8/8	6
3	6.75	10.5	34.176	26.3	8/8	6
8	6.73	5.1	33.771	8.1	7/8	2
9	6.64	8.8	33.679	17.2	7/8	4
<b>Inter-island</b>						
11	6.52	8.9	33.663	11.7	6/8	3
12	6.73	6.4	33.807	26.4	0/8	6
7	6.75	8	33.708	9.6	0/8	3
13	6.6	7	33.813	9.2	7/8	3
4	6.67	10.9	33.891	12.3	8/8	3
10	6.69	7.2	33.829	21.2	5/8	5
<b>Downstream</b>						
5	6.33	7.7	34.009	7.7	8/8	3
6	6.74	7.9	33.899	26.3	7/8	6
14	5.84	6.27	33.788	9.7	2/8	3



**Figure 10.1:** Water column profiles of temperature and density at production stations in the upstream region of the Prince Edward Islands (Southern Ocean) in late austral autumn (April/May) 1998.

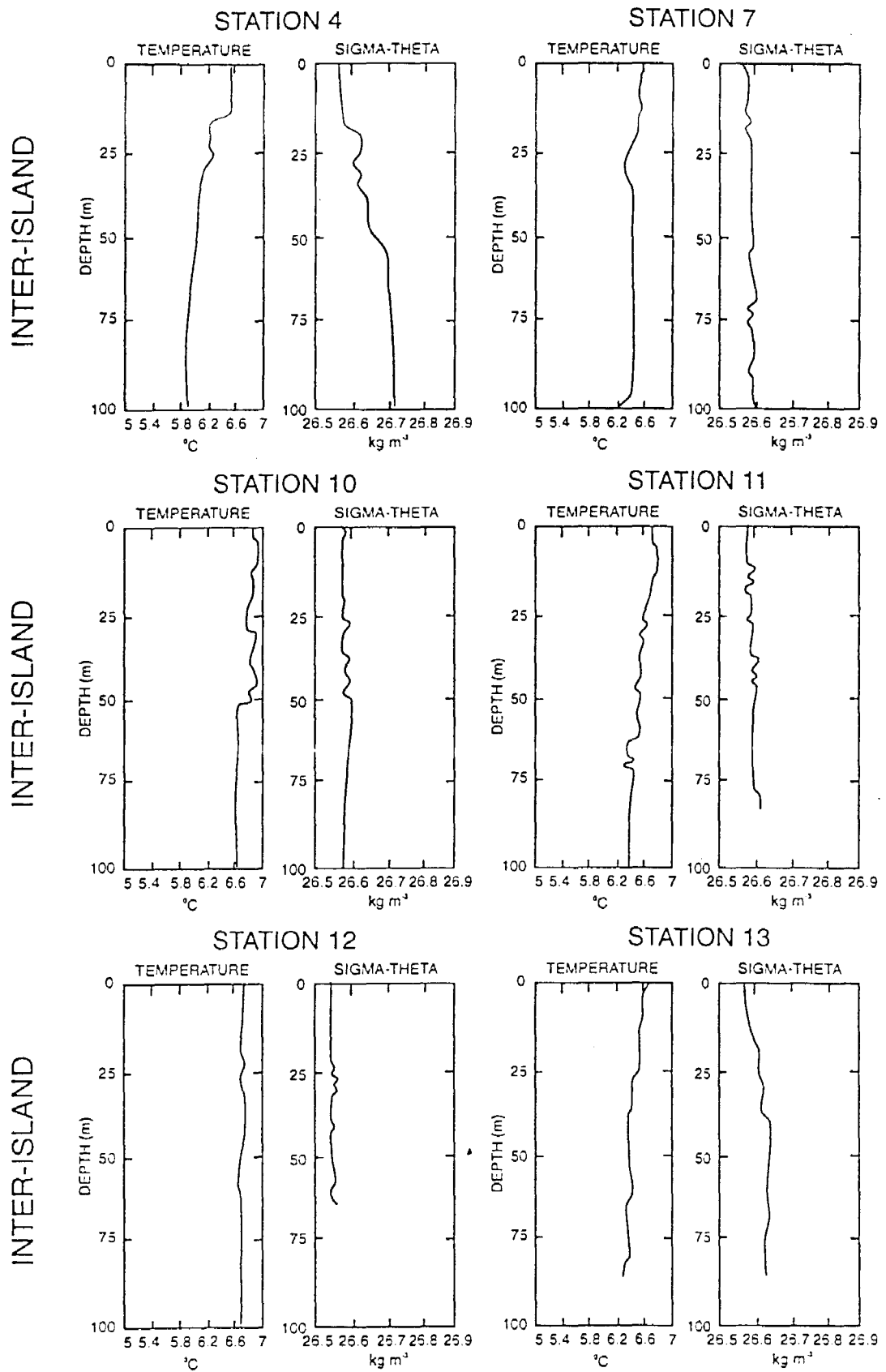


Figure 10.2: Water column profiles of temperature and density at production stations in the inter-island region of the Prince Edward Islands (Southern Ocean) in late austral autumn (April/May) 1998.

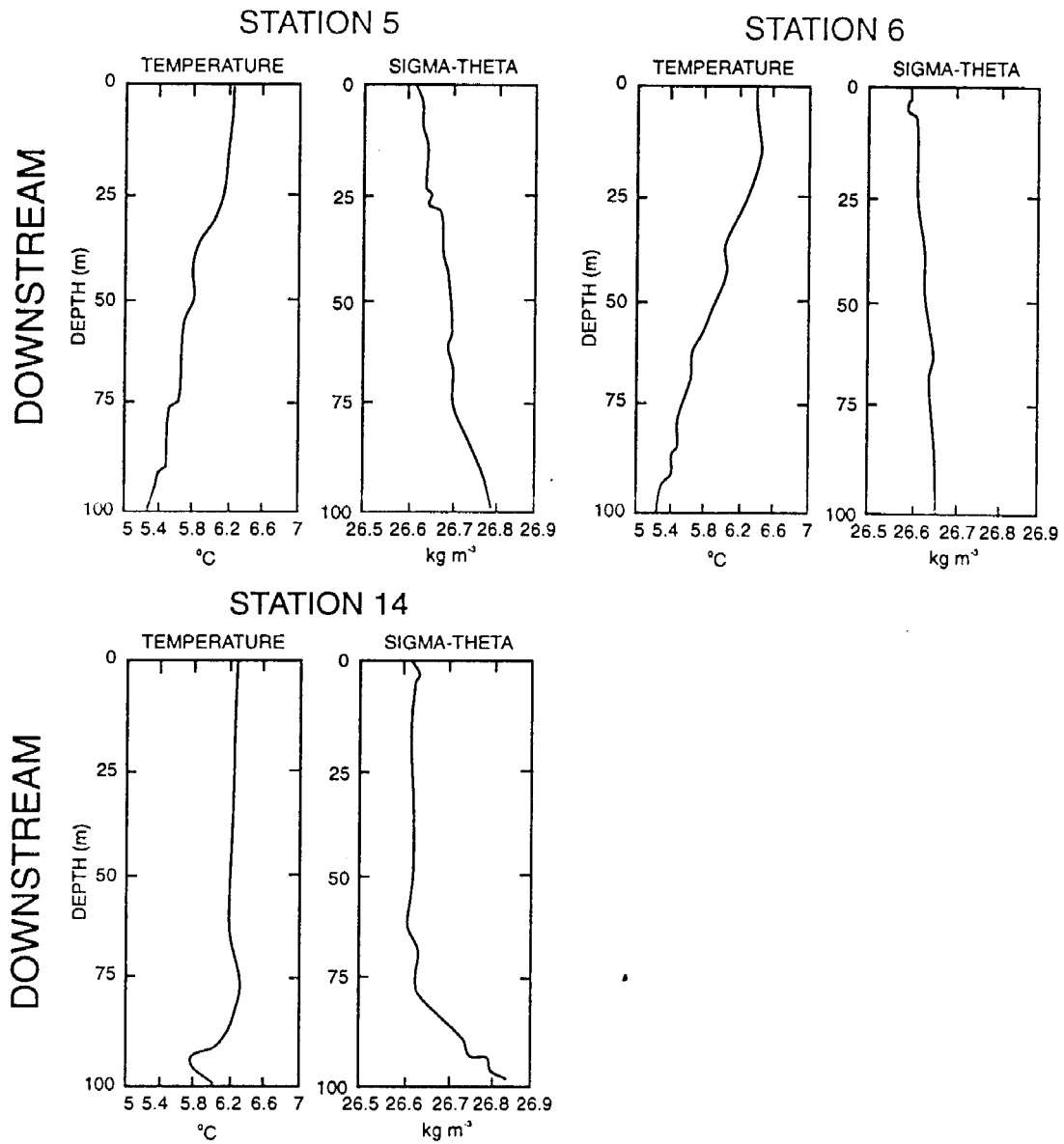


Figure 10.3: Water column profiles of temperature and density at production stations in the downstream region of the Prince Edward Islands (Southern Ocean) in late austral autumn (April/May) 1998.

**Table 7:** Nutrient concentrations ( $\mu\text{mol} \cdot \text{L}^{-1}$ ) at production stations occupied in the upstream, inter-island and downstream regions of the Prince Edward Islands in April/May 1998.

Station	Light depth %	Silica $\mu\text{mol} \cdot \text{L}^{-1}$	Phosphate $\mu\text{mol} \cdot \text{L}^{-1}$	Ammonia $\mu\text{mol} \cdot \text{L}^{-1}$	$\text{NO}_2$ $\mu\text{mol} \cdot \text{L}^{-1}$	$\text{NO}_3$ $\mu\text{mol} \cdot \text{L}^{-1}$
<b>Upstream</b>						
3	100	<1.8	0.74	<0.71	<0.71	13.9
	50	2.58	1.09	<0.71	<0.71	7.4
	25	<1.8	0.79	0.71	<0.71	14.4
	5	<1.8	0.87	<0.71	<0.71	16
	1	<1.8	0.82	1.41	<0.71	14.8
<b>Inter-island</b>						
7	100	<1.8	0.75	<0.71	<0.71	16.2
	50	<1.8	0.74	0.82	<0.71	17
	25	<1.8	0.83	1.12	<0.71	19.7
	5	<1.8	1	1.84	<0.71	21.8
	1	<1.8	0.92	1.12	<0.71	21.1
<b>Downstream</b>						
5	100	<1.8	0.87	0.71	<0.71	20.1
	50	2.5	1.05	0.82	<0.71	22.3
	25	3.3	1.09	<0.71	<0.71	23.6
	5	<1.8	0.87	1.12	<0.71	19.7
	1	<1.8	0.57	<0.71	<0.71	13.9

#### 4.1.2 Nutrients

The concentrations of the macronutrients at stations within the three zones were similar throughout the region of investigation. As a consequence, the results of only a single station within each region are presented here (Table 7). Silica concentrations within the euphotic zone were generally  $< 1.8 \mu\text{mol} \cdot \text{L}^{-1}$  in the three regions. Exceptions were recorded at the 50% light depth in the upstream region of the islands and at the 50% and 25% light depth in the downstream region. Here Si concentrations were  $> 1.8 \mu\text{mol} \cdot \text{L}^{-1}$ . Ammonium concentrations were lowest ( $< 0.71 \mu\text{mol} \cdot \text{L}^{-1}$ ) at stations occupied in the upstream region

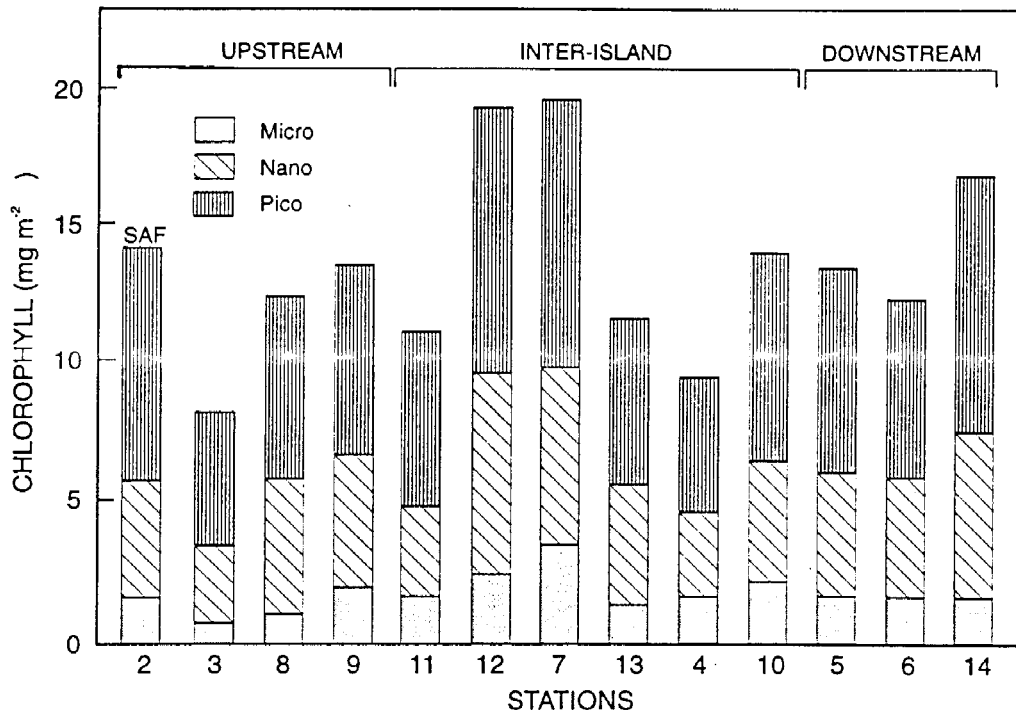
of the islands. Within the inter-island and downstream regions ammonia levels were higher, ranging between 0.71 and 1.84  $\mu\text{mol} \cdot \text{L}^{-1}$  and between 0.71 and 1.12  $\mu\text{mol} \cdot \text{L}^{-1}$  respectively (Table 7). Nitrate values within the three regions were highest at stations occupied within the inter-island and downstream regions. Here, concentrations of nitrate within the euphotic zone ranged between 16.2 and 21.8  $\mu\text{mol} \cdot \text{L}^{-1}$  in the inter-island region and between 13.9 and 23.6  $\mu\text{mol} \cdot \text{L}^{-1}$  in the downstream region. Upstream of the islands, nitrate concentrations ranged between 7.4 and 16.0  $\mu\text{mol} \cdot \text{L}^{-1}$ . Nitrite concentrations within the three zones of investigation were similar and were always  $< 0.8 \mu\text{mol} \cdot \text{L}^{-1}$  (Table 7).

#### **4.1 3 Integrated Chlorophyll-*a***

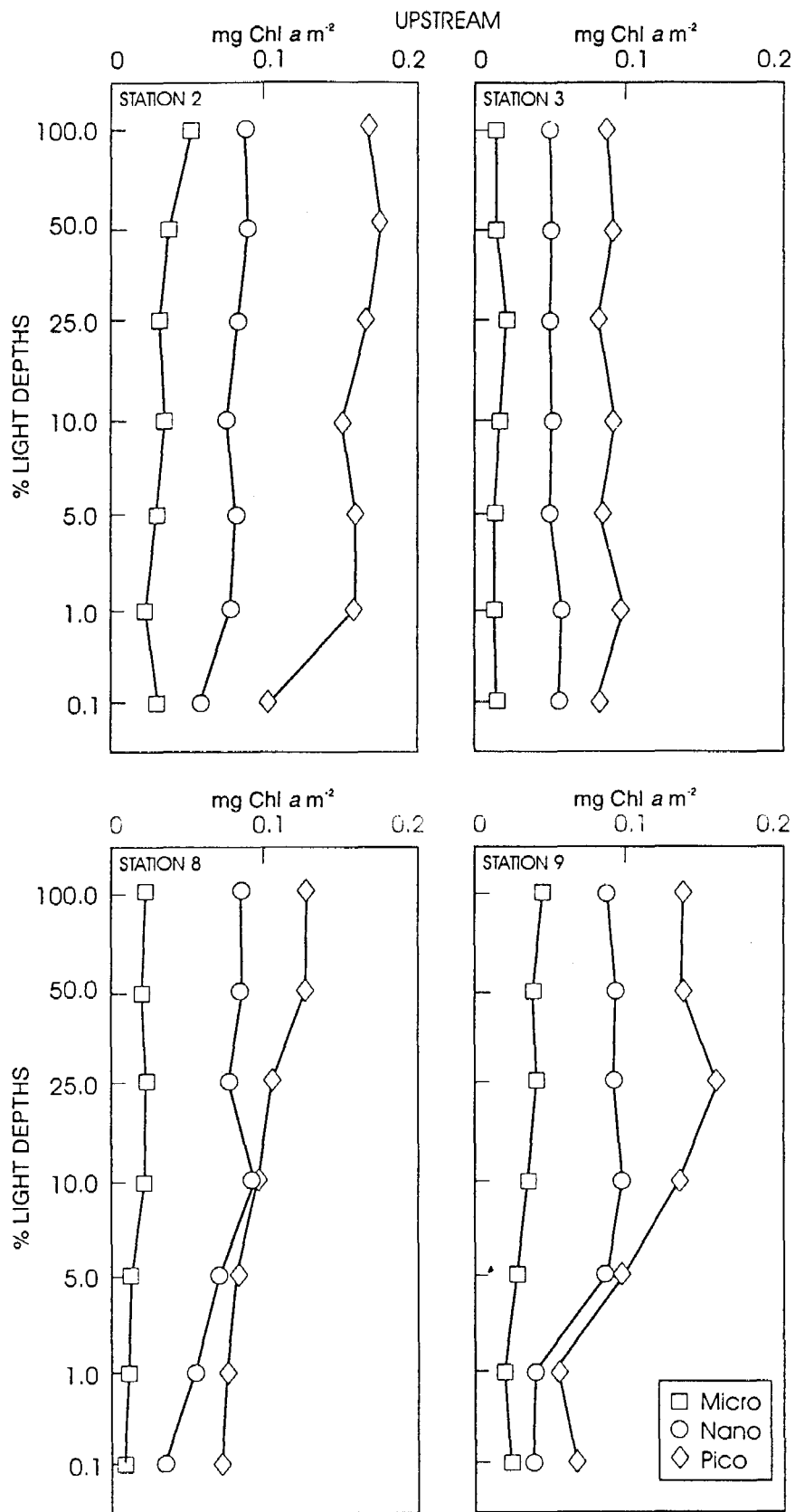
Total areal chlorophyll-*a* distribution within the three regions of investigation were uniform (Table 8; Figure 11). No clear sub-surface chlorophyll-*a* maxima were evident at any of the stations (Figure 12.1 - 12.4). Total areal chlorophyll-*a* concentrations at stations in the upstream region ranged from 8.5 to 14.7 mg Chl-*a*  $\cdot \text{m}^{-2}$ , between 12.8 and 17.4 mg Chl-*a*  $\cdot \text{m}^{-2}$  in downstream, and between 9.8 and 20.1 mg Chl-*a*  $\cdot \text{m}^{-2}$  in the inter-island region (Table 8). The highest integrated biomass was recorded at stations 7 and 12 in the inter-island region with 20.1 and 19.8 mg Chl-*a*  $\cdot \text{m}^{-2}$  respectively (Table 8). Picophytoplankton dominated total pigment concentrations throughout the three zones comprising between 49% and 58% of the total (Figure 11). Picophytoplankton integrated biomass ranged from 5 to 9.9 mg Chl-*a*  $\cdot \text{m}^{-2}$  within the three regions (Table 8). Nanophytoplankton represented the second most important fraction comprising between 29 and 38% of total pigment. Integrated nanophytoplankton biomass ranged between 2.9 and 7.4 mg Chl-*a*  $\cdot \text{m}^{-2}$  (Table 8). Microphytoplankton integrated biomass ranged between 0.7 and 3.6 mg Chl-*a*  $\cdot \text{m}^{-2}$  (Table 8).

**Table 8:** Total integrated chlorophyll-*a* (mg chl-*a* . m<sup>-2</sup>) during the third Marion Island Oceanographic Survey (MIOS III) conducted in late austral autumn (April/May) 1998.

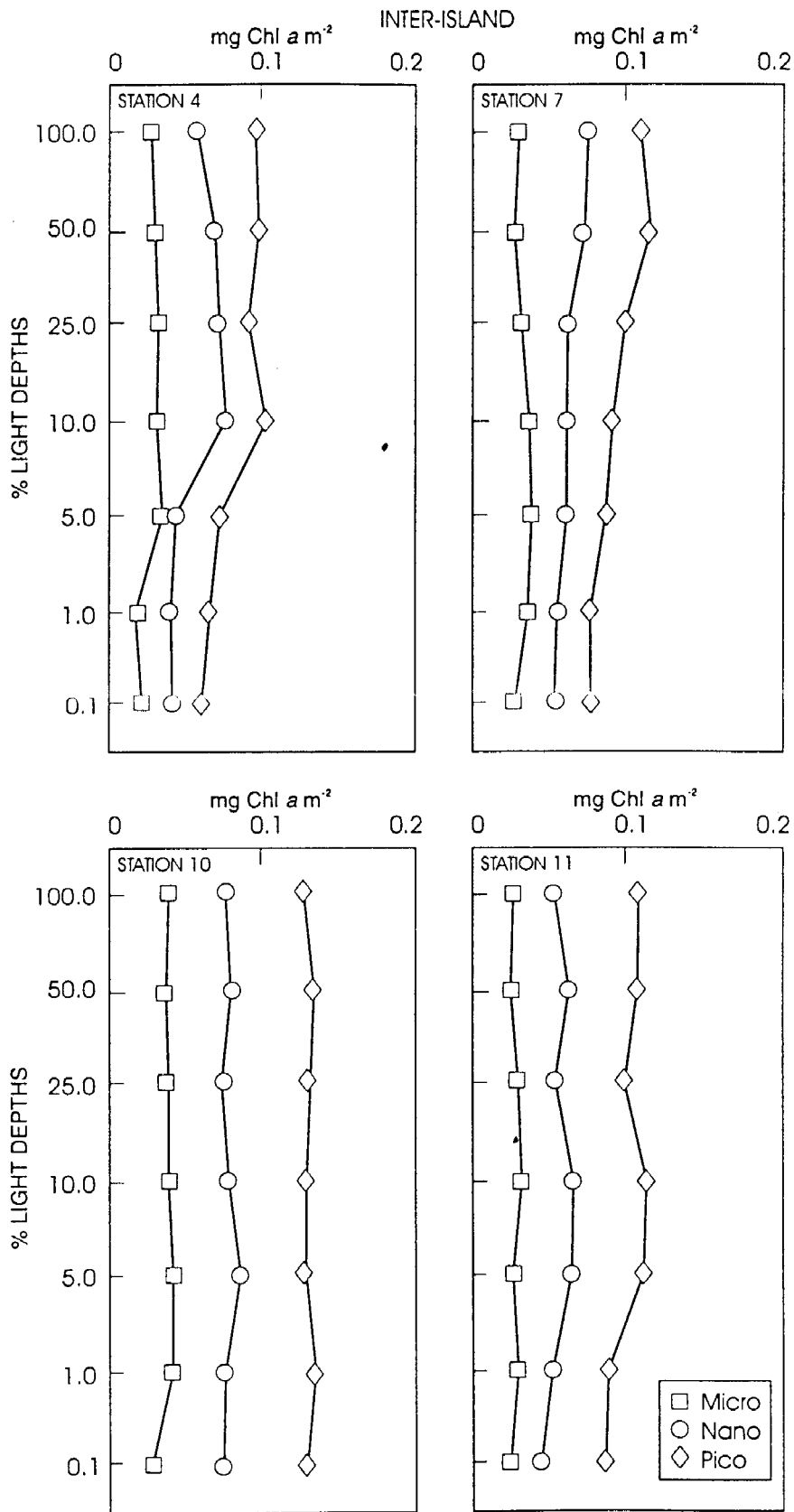
Stations	micro >20 μm	nano 2-20 μm	pico <2 μm	Total Chl- <i>a</i> mg Chl- <i>a</i> . m <sup>-2</sup>
<b>Upstream</b>				
2	1.74	4.35	8.57	14.66
3	0.74	2.91	4.89	8.53
8	1.15	4.96	6.75	12.87
9	2.11	4.91	7.08	14.08
<b>Inter-island</b>				
11	1.71	3.47	6.38	11.56
12	2.59	7.37	9.85	19.8
7	3.64	6.62	9.88	20.14
13	1.41	4.55	6.04	12
4	1.61	3.27	4.95	9.84
10	2.21	4.54	7.71	14.44
<b>Downstream</b>				
5	1.72	4.61	7.57	13.91
6	1.73	4.44	6.61	12.79
14	1.71	6.15	9.53	17.38



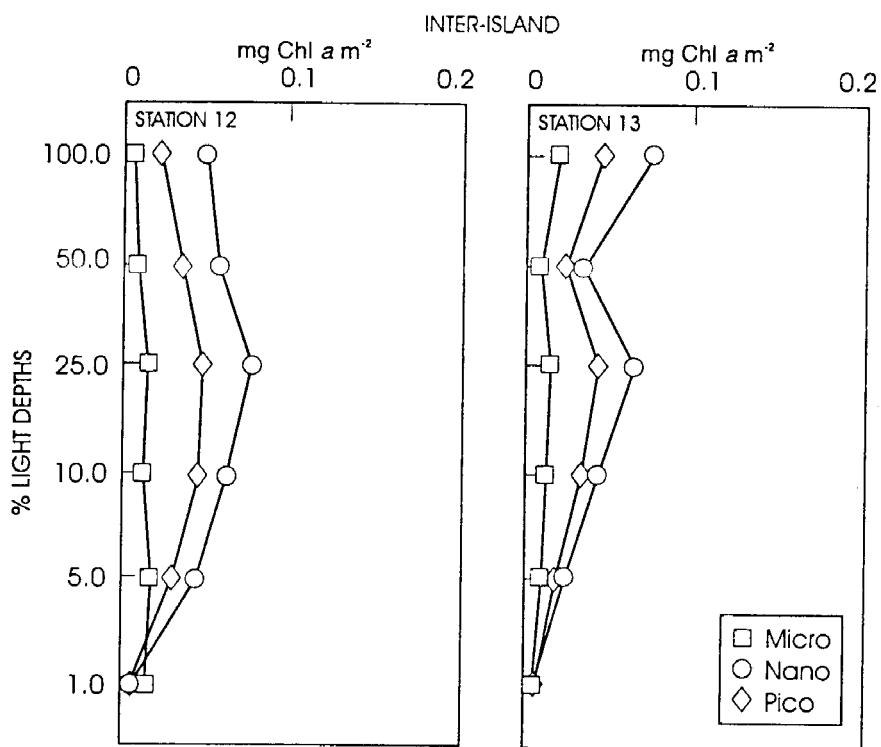
**Figure 11:** Total integrated size-fractionated chlorophyll-*a* concentrations at stations occupied in the upstream, inter-island and downstream regions of the Prince Edward Islands during April/May 1998. All data are integrated to the 0.1% euphotic depth. Micro = Microphytoplankton (>20  $\mu\text{m}$ ); Nano = Nanophytoplankton (<20 and >2.0  $\mu\text{m}$ ); Pico = Picophytoplankton (< 2  $\mu\text{m}$ ). SAF = Sub-Antarctic Front.



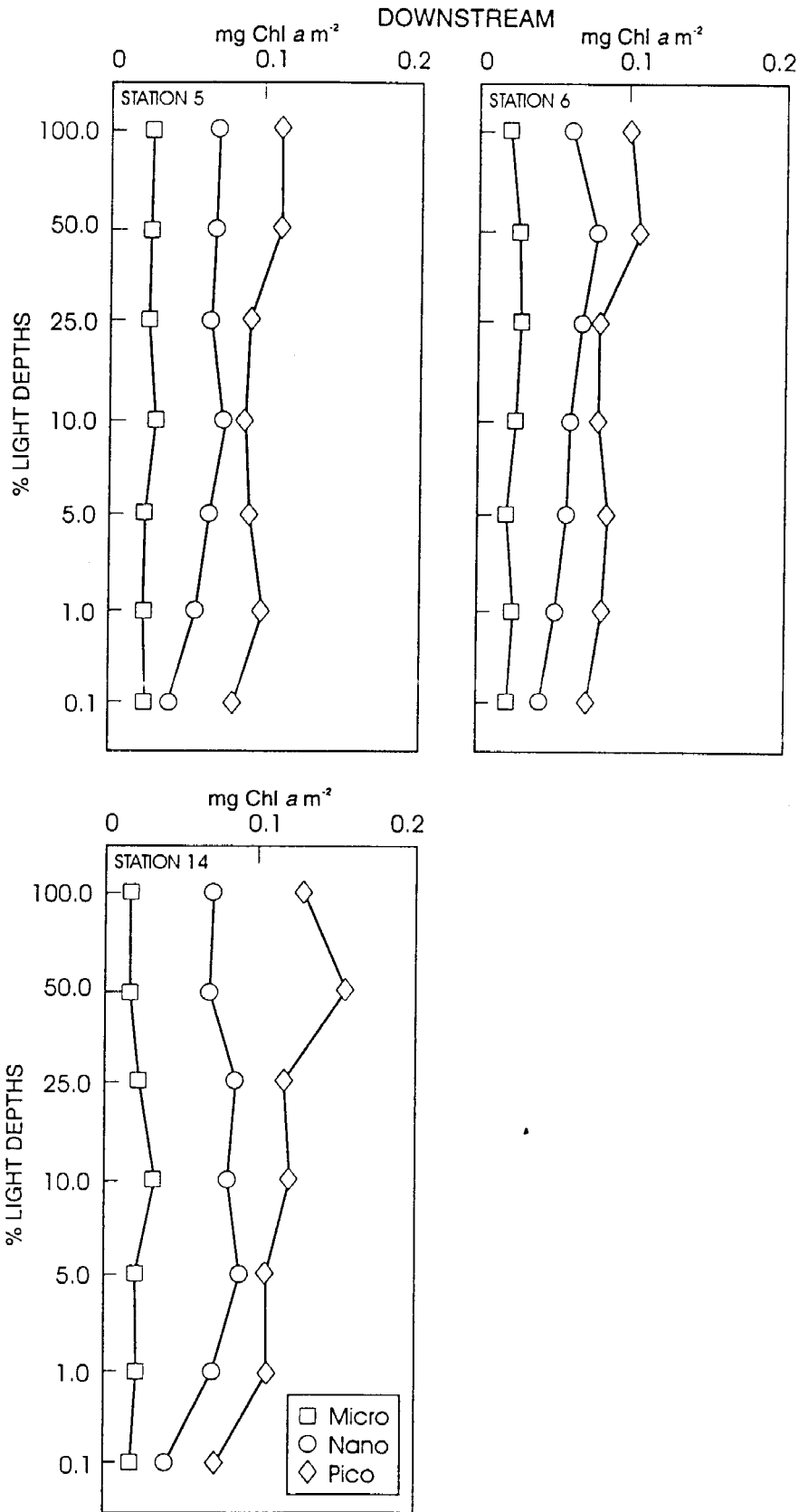
**Figure 12.1:** Water column profiles of chlorophyll-*a* concentration at different light depths at the four stations occupied in the upstream region of the Prince Edward Islands in April/May 1998.



**Figure 12.2:** Water column profiles of chlorophyll-*a* concentration at different light depths at the six stations occupied in the inter-island region of the Prince Edward Islands in April/May 1998.



**Figure 12.3:** Water column profiles of chlorophyll-*a* concentration at different light depths at the six stations occupied in the inter-island region of the Prince Edward Islands in April/May 1998.



**Figure 12.4:** Water column profiles of chlorophyll-*a* concentration at different light depths at the three stations occupied in the downstream region of the Prince Edward Islands in April/May 1998.

Vertical profiles of pigment concentration within the three regions of investigation indicate that the distribution of chlorophyll-*a* in the upper water column was uniform. An exception was recorded at station 9 in the upstream region of the islands where maximum pigment concentrations were recorded at light depths > 10% of the surface irradiance (Figures 12.1).

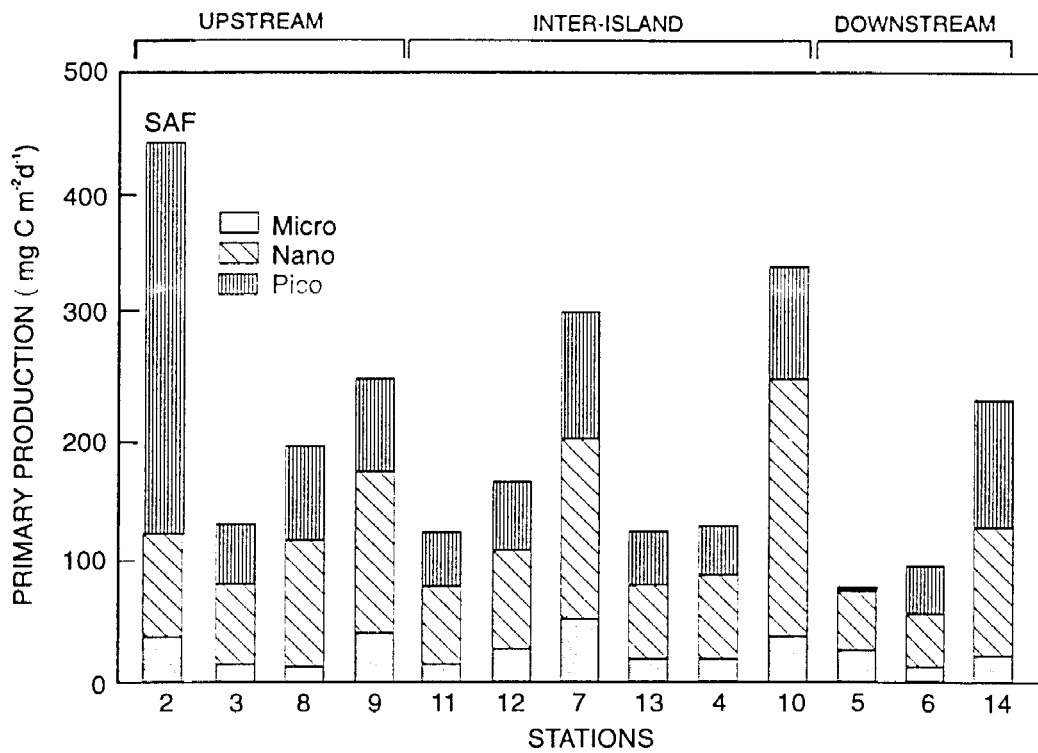
#### **4.1.4 Integrated primary production**

The total daily integrated production, although highly variable, displayed the same spatial pattern as integrated biomass (Table 9). An exception was presented at station 2 in the vicinity of the SAF (443 mg C . m<sup>-2</sup> . d<sup>-1</sup>), where the highest productivity during the entire survey was measured. Integrated primary production at the stations occupied within the upstream region of the Prince Edward Islands ranged from 131 to 251 mg C . m<sup>-2</sup> . d<sup>-1</sup> (Table 9). Within the inter-island and downstream regions, total areal production ranged between 120 and 353 mg C . m<sup>-2</sup> . d<sup>-1</sup> and between 94 and 229 mg C . m<sup>-2</sup> . d<sup>-1</sup>, respectively (Table 9). One-way Analysis of Variance showed that integrated production within the three regions were not significantly different ( $P > 0.05$ ).

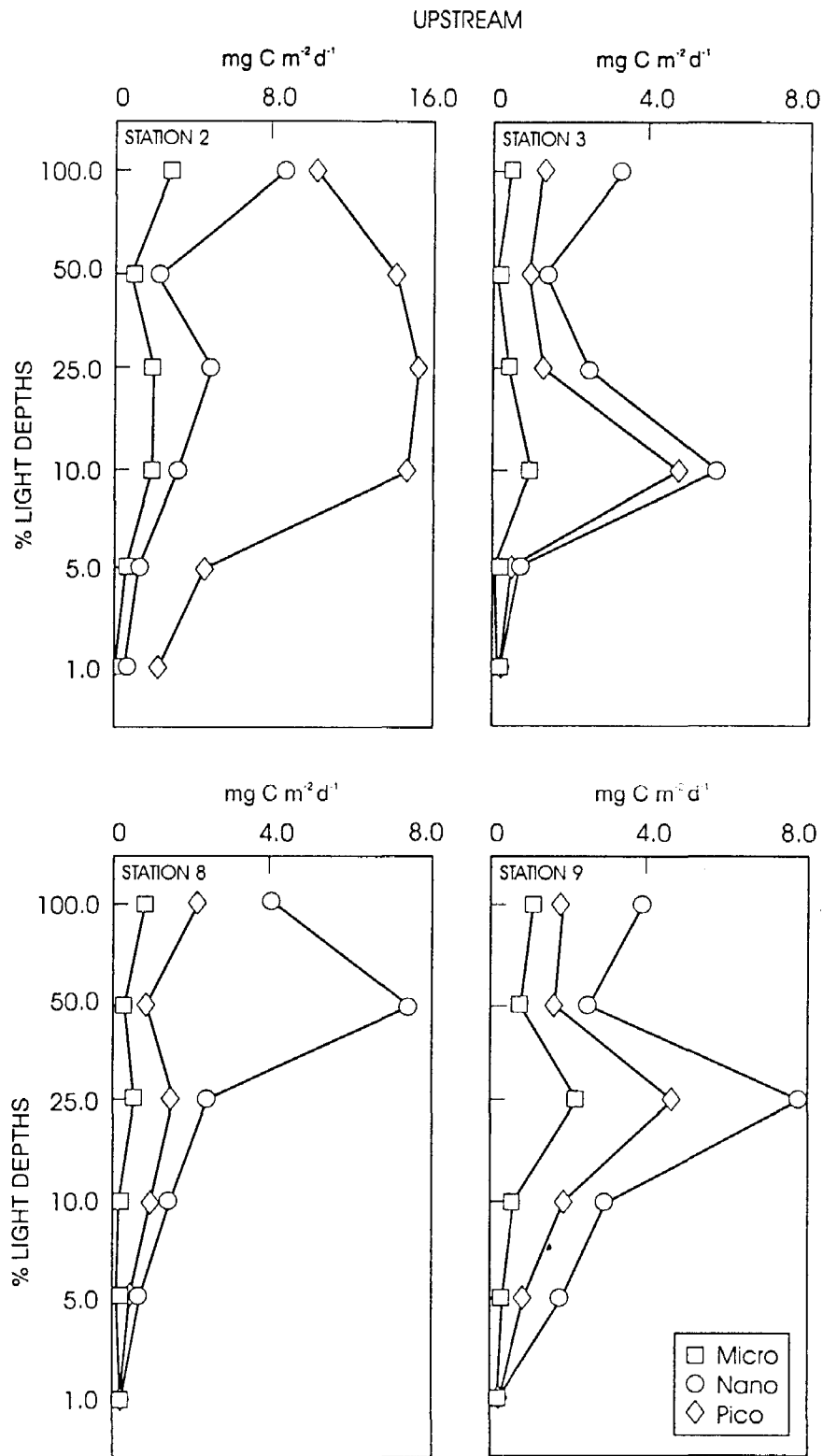
Throughout the survey, nanophytoplankton formed the most important contributor to total production comprising up to > 45% of the total (Figure 13). An exception was found at station 2 located in the vicinity of the SAF where picophytoplankton represented the most important contributor to total production. Daily integrated nanophytoplankton production at stations in the upstream region ranged between 69 and 136 mg C . m<sup>-2</sup> . d<sup>-1</sup>, between 60 and 205 mg C . m<sup>-2</sup> . d<sup>-1</sup> within the inter-island region, and between 45 and 106 mg C . m<sup>-2</sup> . d<sup>-1</sup> in the downstream region (Table 9).

**Table 9:** Total integrated primary production ( $\text{mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ) measurements during the survey conducted in the region of the Prince Edward Islands (Southern Ocean) in April/May 1998. Data are integrated to the 1% light depth..

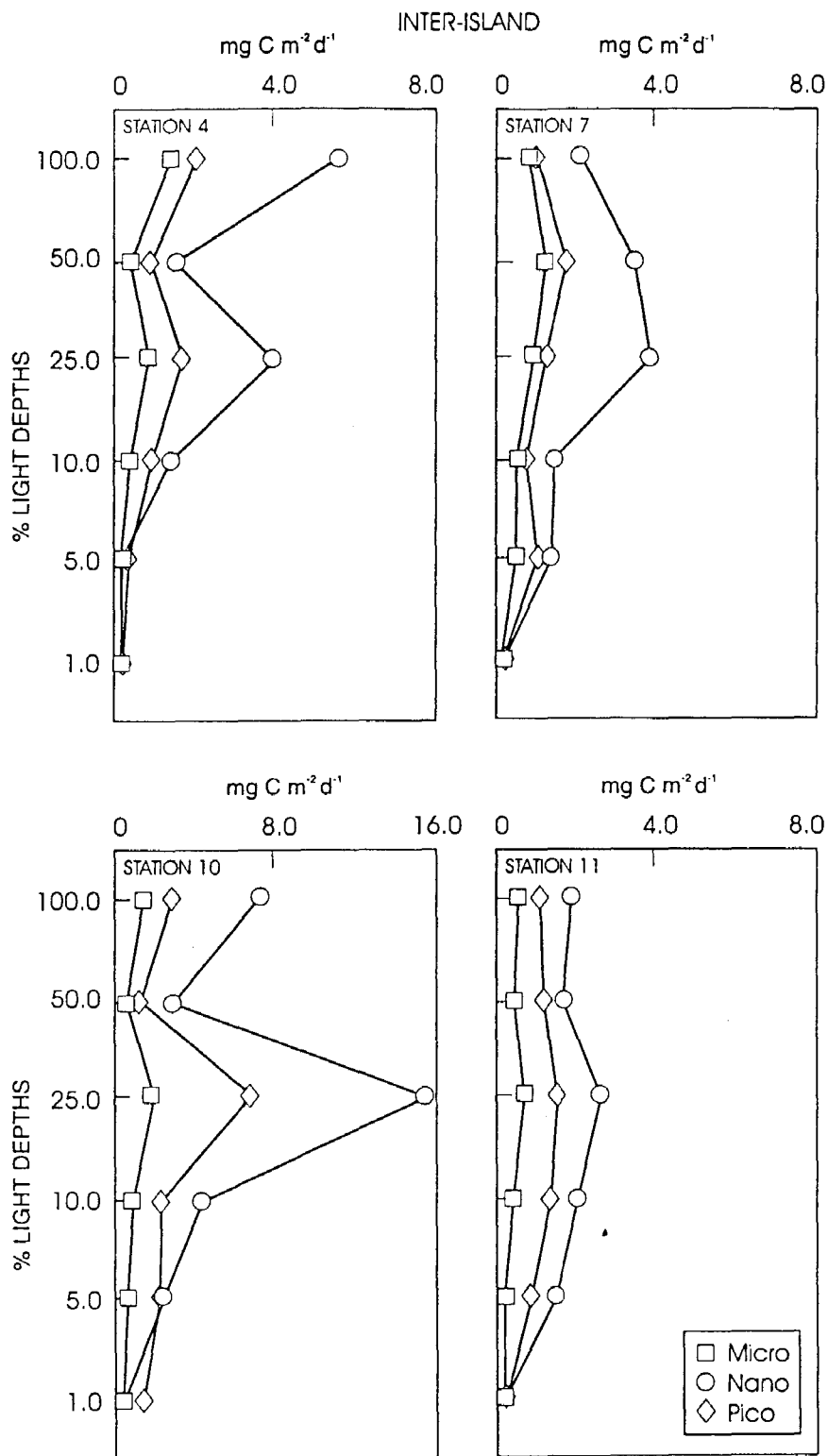
<b>Production Stations</b>	<b>micro &gt;20 <math>\mu\text{m}</math></b>	<b>nano 2-20 <math>\mu\text{m}</math></b>	<b>pico &lt;2 <math>\mu\text{m}</math></b>	<b>Total primary prod. <math>\text{mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}</math></b>
<b>Upstream</b>				
2	33.97	86.75	321.91	442.63
3	11.03	69.35	50.39	130.78
8	11.87	104.05	40.99	156.91
9	36.71	135.87	78.5	251.08
<b>Inter-island</b>				
11	14.23	63.28	42	119.51
12	24.02	83.56	56.83	164.41
7	48.44	153.52	74.8	276.76
13	17.65	59.95	45.8	123.4
4	17.77	71.04	39.26	128.07
10	32.21	205.54	115.3	353.04
<b>Downstream</b>				
5	22.48	60.46	39.18	122.12
6	10.56	45.31	38.61	94.48
14	20.54	106.12	103.03	229.69



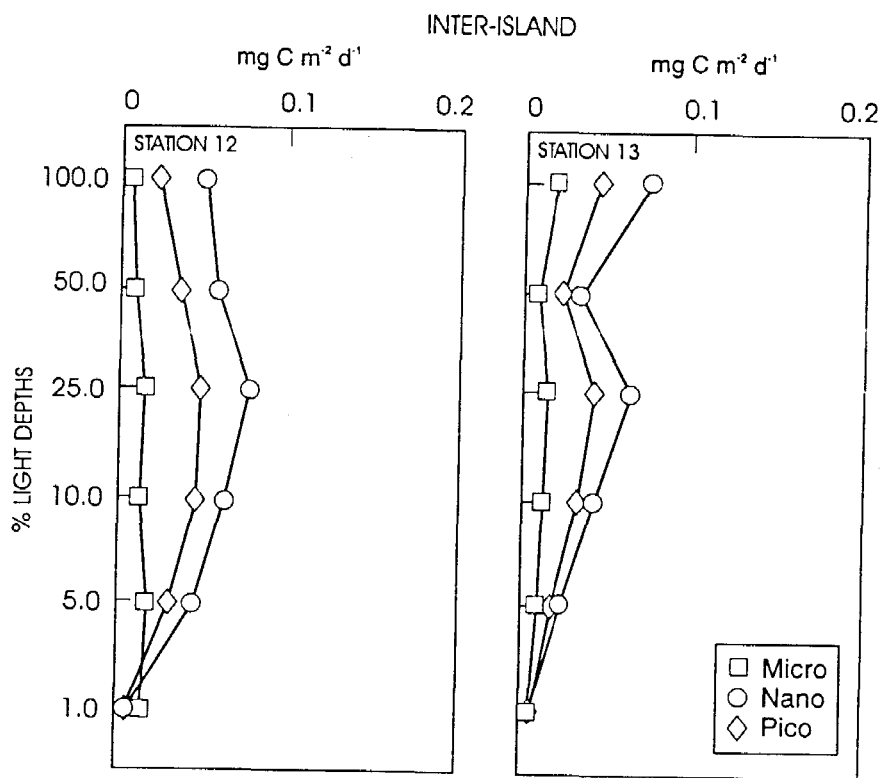
**Figure 13:** Total integrated size-fractionated phytoplankton primary production measurements at stations occupied in the upstream, inter-island and downstream regions of the Prince Edward Islands during April/May 1998. All data are integrated to the 1% euphotic depth. Abbreviations as for Figure 11. SAF = Sub-Antarctic Front.



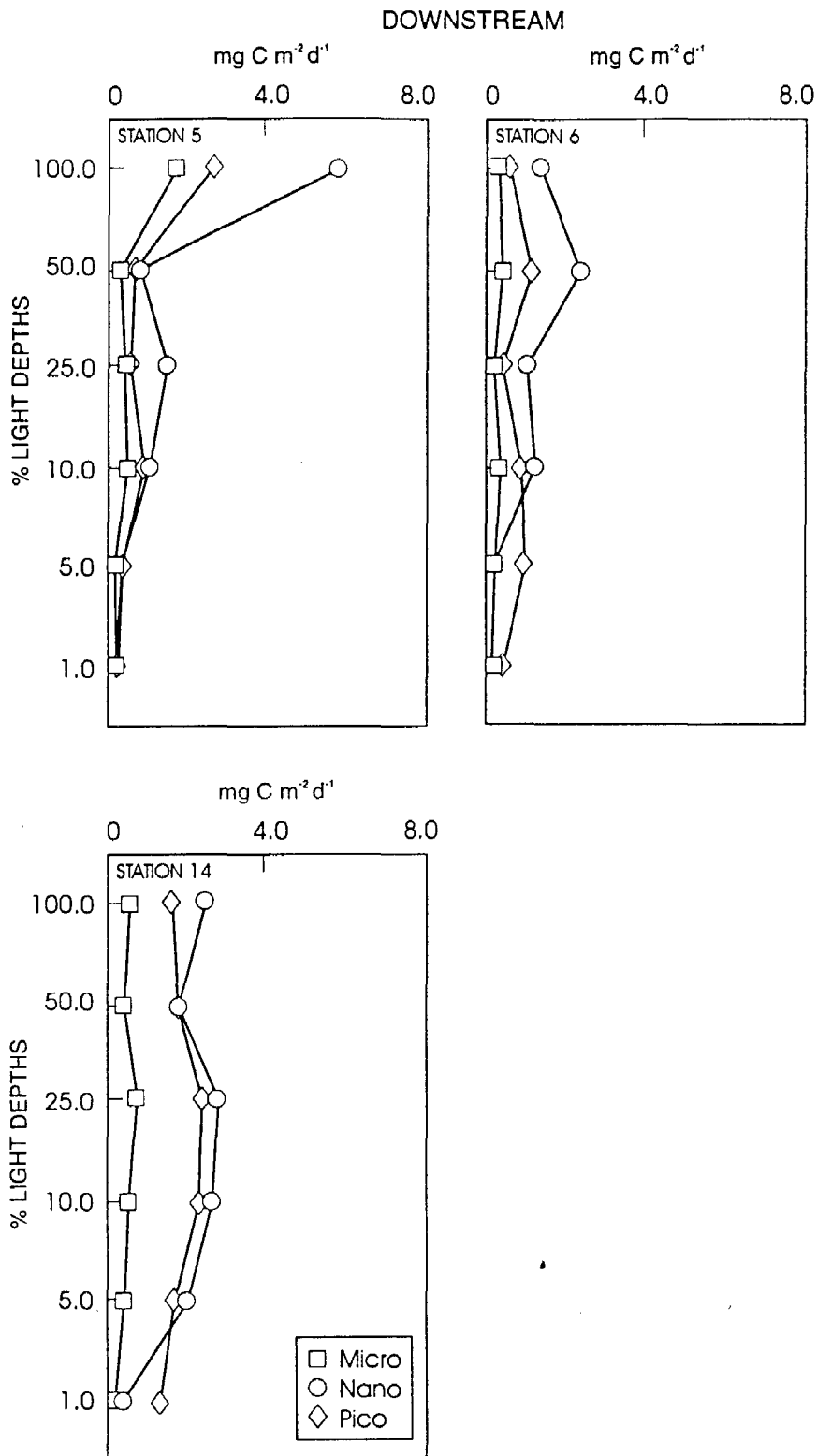
**Figure 14.1:** Vertical profiles of primary production at different light depths at the four stations occupied in the upstream region of the Prince Edward Islands in April/May 1998.



**Figure 14.2:** Vertical profiles of primary production at different light depths at the six stations occupied in the inter-island region of the Prince Edward Islands in April/May 1998.



**Figure 14.3:** Vertical profiles of primary production at different light depths at the six stations occupied in the inter-island region of the Prince Edward Islands in April/May 1998.



**Figure 14.4:** Vertical profiles of primary production at different light depths at the three stations occupied in the downstream region of the Prince Edward Islands in April/May 1998.

Picophytoplankton were identified as the second most important contributor to total production. At stations occupied within the upstream and downstream regions, total daily integrated picophytoplankton production ranged from 50 to 78 mg C . m<sup>-2</sup> . d<sup>-1</sup> and from 39 to 103 mg C . m<sup>-2</sup> . d<sup>-1</sup>, respectively. At stations located within the inter-island region, integrated picophytoplankton production ranged from 39 to 115 mg C . m<sup>-2</sup> . d<sup>-1</sup>. Microphytoplankton integrated production throughout the survey was < 37 mg C . m<sup>-2</sup> . d<sup>-1</sup>. This comprised < 20% of the total production at all stations.

Water column production profiles of the different size fractions in the three regions of investigation were generally similar throughout the survey (Figures 14.1 to 14.4). Maximum production occurred at light depths corresponding to 10-25% of the surface irradiation. Exceptions were recorded at stations 4 and 5, located in the inter-island and downstream region respectively, where the maximum production occurred at light depths greater than 50% of the surface irradiation. Below the 10% light depth, a dramatic decrease in production was generally observed (Figure 14.2).

#### **4.1.5 Photosynthetic capacity**

No clear patterns in photosynthetic capacities of the phytoplankton communities within the water column were evident in the three regions of investigation (Figures 15.1 and 15.2 ). Generally, the photosynthetic capacities were low, < 1.0 mg C (mg Chl-*a*)<sup>-1</sup> h<sup>-1</sup>. Exceptions were recorded at stations 2 and 3 where the photosynthetic capacity in the upper water column was > 1.0 mg C (mg Chl-*a*)<sup>-1</sup> h<sup>-1</sup> (Figure 15.1).

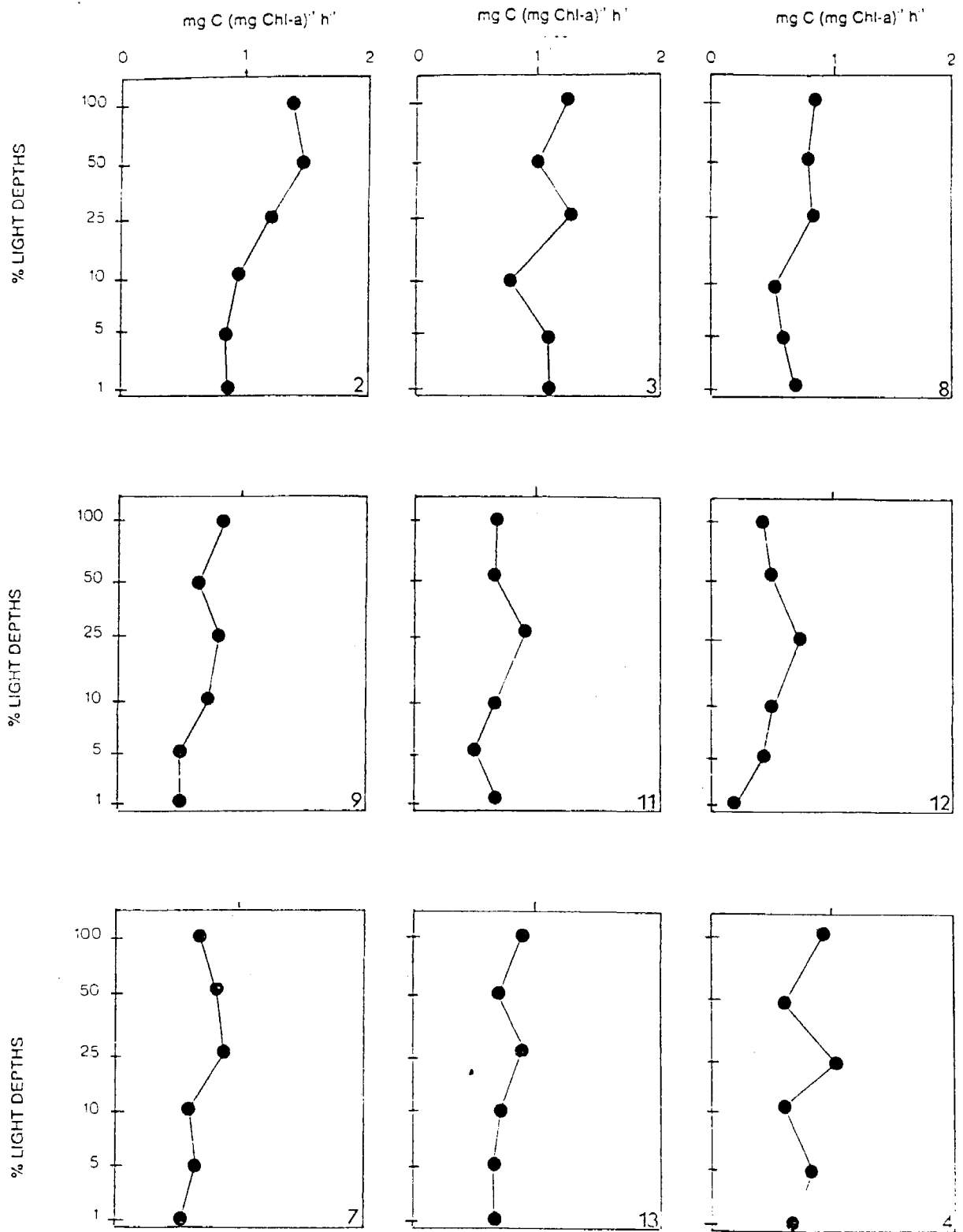


Figure 15.1: Photosynthetic capacity ( $\text{mg C (mg Chl-a)}^{-1} \text{ h}^{-1}$ ) profiles at stations occupied in the vicinity of the Prince Edward Islands.

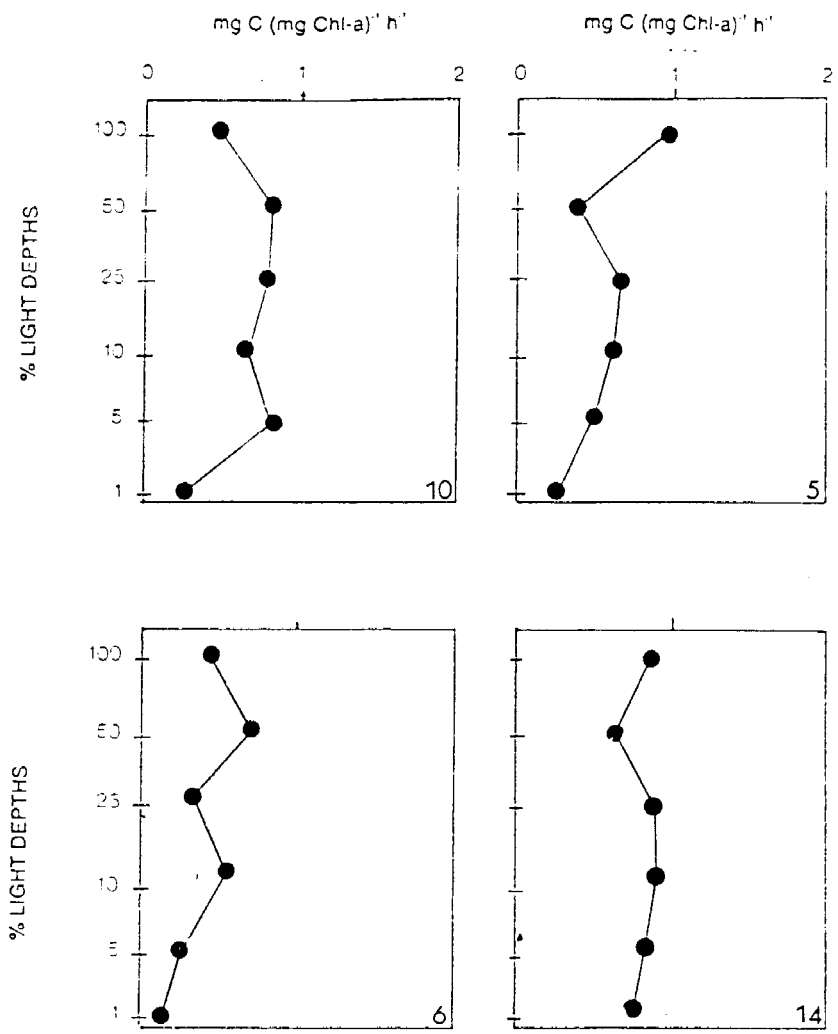


Figure 15.2: Photosynthetic capacity ( $\text{mg C (mg Chl-}a\text{)}^{-1} \text{ h}^{-1}$ ) profiles at stations occupied in the vicinity of the Prince Edward Islands.

## 4.2 DISCUSSION

Macroscale surveys conducted in the off-shore environment of the Prince Edward Islands have shown that the oceanographic regime in the vicinity of the islands exists in two distinct forms (Perissinotto and Duncombe Rae 1990; Pakhomov and Froneman 1998). Under conditions when the Sub-Antarctic Front (SAF) lies far to the north of the islands, the weak interaction of the Antarctic Circumpolar Current (ACC) with the archipelago leads to the domination of frictional forces with resultant trapping of water within the inter-island region (Perissinotto and Duncombe Rae 1990). In contrast, when the front lies in close proximity of the islands, advecting forces prevail, which results in the system being a flow-through system (Pakhomov and Froneman 1998). During the present cruise, the SAF migrated from its initial position of  $46^{\circ} 00' S$  at the onset of the investigation, to  $46^{\circ} 30' S$  (Froneman and Anson 1998). As a consequence, the SAF lay in close proximity to the islands when the production stations were occupied in the vicinity of the islands (Froneman and Anson 1998). These facts suggest that little water was retained on the shelf region and that the island system represented a flow-through system. This is supported by the water column profiles at the various production stations within the three regions of investigation. At all stations the upper water column appeared well mixed suggesting that no trapping of water occurred in the inter-island or downstream region (Figures 10.1 to 10.3). The absence of water column stability is not surprising as the islands lie within a belt of strong, persistent, westerly winds leading to the formation of a well mixed upper water column (Tomczak and Godfrey 1994).

Total integrated biomass during the survey ranged between 8 and 20 mg Chl-*a* . m<sup>-2</sup> and was always dominated by small nano- and picophytoplankton (Figure 11). These results are in agreement with previous studies conducted in the vicinity of the islands (Froneman and

Ansorge 1998; Froneman and Balarin 1998; Froneman and Pakhomov 1998; Pakhomov and Froneman 1998) and indeed, the Polar Front Zone proper (Froneman *et al.* 1995a; 1995b; Laubscher *et al.* 1993). No enhancement in total pigment concentration was recorded at the station occupied within the vicinity of the SAF. Although this result is in agreement with a recent study conducted in 1997 (Froneman and Pakhomov 1998), it is in contrast to several previous investigations, which have shown that the SAF is a region of elevated Chl-*a* (Laubscher *et al.* 1993; Froneman *et al.* 1995a; b). While it is possible that the absence of a Chl-*a* signal at the front may be due to seasonality, the data suggest that biomass at the front varies between periods of high and low concentration. This result is consistent with the findings of studies conducted in the vicinity of the other major oceanic fronts (Subtropical Convergence and Antarctic Polar Front) in the Southern Ocean (Laubscher *et al.* 1993; Weeks and Shillington 1994).

Total daily integrated production in waters surrounding the islands ranged between 95 and 353 mg C . m<sup>-2</sup> . d<sup>-1</sup> and was always dominated by small nano- and picophytoplankton (Figure 13). These production rates fall among the lower rates reported in the literature (El-Sayed *et al.* 1979a; Miller 1982; Allanson *et al.* 1985; Perissinotto 1992). In contrast to several previous studies, no phytoplankton bloom was recorded at stations occupied within the inter-island and downstream region (Allanson *et al.* 1985; Perissinotto and Duncombe Rae 1990). It has been suggested that phytoplankton blooms around the islands are the result of increased *in situ* phytoplankton production rates, resulting from a combination of water column stability and the increased availability of macronutrients from freshwater run-off (Allanson *et al.* 1985; Ismail 1990; Pakhomov and Froneman 1998). Although there was clear evidence during this study of enhanced NO<sub>3</sub> and PQ concentrations in waters

surrounding the islands (Table 7), no increase in phytoplankton production rates were recorded at stations in the vicinity of the islands (Figure 13). Throughout the study, the upper water column appeared well mixed (Figures 10.1 to 10.3). The high degree of mixing is evident in the distribution of Chl-*a* and the photosynthetic capacities of the phytoplankton which were uniform throughout the upper water column (Figures 12 and 15). Under conditions where vertical mixing is high, photosynthetic indices of phytoplankton will be evenly distributed throughout the upper water column (Lewis *et al.* 1984). The absence of a phytoplankton bloom in the waters surrounding the islands during this study can, therefore, probably be related to low growth rates of the phytoplankton resulting from low water column stability. These data are consistent with the findings of Perissinotto *et al.* (1990), who showed that water column stability and mixed layer depth accounted for most of the variability associated with potential productivity and photosynthetic capacity in the vicinity of the islands. The unfavourable light environment may also partially account for the predominance of the contribution of small phytoplankton cells to total production (Fogg 1991). Possibly, the low silica concentrations recorded in the region (ranging between <1.8 and 3.3  $\mu\text{mol} \cdot \text{L}^{-1}$ ; mean = 1.9), may also have contributed to the low contribution of the larger microphytoplankton to total production (Allanson *et al.* 1981; Nelson and Trequer 1992). The role of iron in promoting production in the vicinity of the islands cannot be discounted in the light of recent studies which have shown that production within the Southern Ocean may be limited by iron availability (Martin *et al.* 1990a, b; Miller *et al.* 1991; Sunda 1994; de Baar *et al.* 1995; Hutchins and Bruland 1998).

The highest production during the entire investigation was recorded at the station occupied in the vicinity of the SAF (Figure 13). Here total areal production was estimated at 442.6 mg

$C \cdot m^{-2} \cdot d^{-1}$ . Although only a single station was occupied in the vicinity of the front, the results indicate that production in the vicinity of the front is enhanced relative to the open ocean waters. This result is consistent with a previous study conducted in the region of the SAF (Laubscher *et al.* 1993). Unfortunately it is not possible to identify the mechanism/s responsible for the elevated productivity in the region of the front. Laubscher *et al.* (1993) suggested that elevated production in the vicinity of oceanic fronts in the Atlantic sector of the Southern Ocean was largely the result of locally increased water column stability. No evidence of this was found at the SAF during this study. Rather, the upper water column (< 100 m) appeared well mixed. While it is possible that the well mixed upper layer may have resulted from high wind activity encountered at the onset of the survey, the low photosynthetic capacities of the phytoplankton at the station occupied at the front suggest a history of destabilisation within the region (Sakshaug and Holm-Hansen 1986). Possibly, the elevated productivity in the vicinity of the SAF may reflect increased iron availability resulting from the divergent nature of the front which transports iron into the surface waters (P Croot pers. comm.). Unfortunately, no data is available to support this hypothesis.

Throughout the investigation, a discrepancy between the contributions of the various phytoplankton size fractions to integrated biomass and production was observed (Figures 11 and 13). In a previous study, Perissinotto (1992) showed that the dominant zooplankton in the vicinity of the islands preferentially consumed phytoplankton within the nanophytoplankton size fraction. More recently, Froneman and Balarin (1998) showed that protozooplankton in the waters surrounding the islands consume phytoplankton smaller than  $20\mu m$ . These facts suggest that grazing by zooplankton may determine the size structure of the phytoplankton communities in the waters surrounding the islands. The grazing activities

of the larger zooplankton may be an important mechanism coupling the open ocean production to the benthic community on the island shelf through the production of faecal pellets which are subsequently consumed (Fortier *et al.* 1993; Pakhomov and Froneman 1998).

### **4.3 CONCLUSIONS**

Previous studies have shown that under conditions when the SAF lies far to the north of the islands a combination of both mesoscale processes, which retain water on the island shelf (Pakhomov and Froneman 1998), and a so called 'island mass effect' (Allanson *et al.* 1985) are responsible for the elevated production recorded in the waters surrounding the islands. Throughout this investigation the upper water column was well mixed, which appears to be the effect of the close proximity of the SAF to the islands. The low water column stability results in an absence of any phytoplankton bloom. The results of this investigation, therefore, suggest that mesoscale oceanographic conditions, in particular the position of the SAF relative to the islands, largely controls phytoplankton production in the waters surrounding the islands through its effect on water column stability. It is possible that the availability of Si may have limited the growth of the larger microphytoplankton during this study. Although it is highly probable that the waters surrounding the islands would be rich in iron, no increase in production was recorded. It appears therefore, that water column stability controls growth of phytoplankton production in waters surrounding the Prince Edward Islands.

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## CHAPTER 5

### *General conclusions and future perspectives*

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The Southern Ocean, particularly in the region south of the Antarctic Polar Front, is characterised by nutrient concentrations in excess of the threshold values necessary for phytoplankton growth. Despite high concentrations of nutrients, production in the open waters are generally low. As a consequence, the Southern Ocean is regarded as a high nutrient, low chlorophyll (HNLC) area (El-Sayed *et al.* 1983; Codispoti *et al.* 1991 and others). High productivity regions have, however, been observed in coastal areas, ice-edge margins and near oceanic frontal zones. The mechanisms suggested as responsible for the low productivity in the open waters are low vertical stability of the upper water column, whereby plankton are mixed below the photic zone (Smith and Sakshaug 1990; Mitchell *et al.* 1991; Smith and Nelson 1990; Mitchell and Holm-Hansen 1991), irradiance limitation (Parsons *et al.* 1990), nutrient availability (El-Sayed *et al.* 1983), and trace metal deficiency, particular iron deficiency (Martin *et al.* 1990 a,b; de Baar *et al.* 1990, 1995; Sullivan *et al.* 1993; Holm-Hansen *et al.* 1994).

During this study, water column stability appeared to be the main factor controlling primary

productivity. High phytoplankton biomass and production were associated with relatively high water column stability and a shallow mixed layer depth in the vicinity of the MIZ and APF region during the Scandinavian/South African Antarctic expedition. In the region of the MIZ, water column stability was related to the fresh water input during the ice-melt. There is also some evidence of summer water capping of winter waters at more northern stations within the MIZ. At the APF, water column stability was related to the convergence of Antarctic and Sub-Antarctic water masses in the region of the front. Different physico-chemical properties confer localised water column stability in the vicinity of frontal systems (Laubscher *et al.* 1993). In contrast, productivity in the IFZ was found to be considerably lower. There, the mixed layer depth exceeded the 1% light depth. Similarly, in the vicinity of the Prince Edward Islands, total production also appeared to be related to water column stability. Low water column stability appeared largely to be the result of oceanographic conditions, particularly the position of the SAF relative to the islands. When the SAF is in close proximity to the islands, no water is trapped in between the islands, resulting in the islands representing a flow-through system (Pakhomov and Froneman 1998). The low biomass recorded in the IFZ during the Antarctic cruise and the Marion Island cruise appear, therefore, to reflect low productivity resulting from low water column stability.

During the Antarctic cruise, total production did not appear to be limited by nutrient availability as concentrations of macronutrients appeared to have been above the threshold for phytoplankton growth. The importance of iron in promoting primary production in the Southern Ocean has recently been the subject of intensive investigation (Sunda 1994; de Baar *et al.* 1995). Although we do not have any direct evidence for the importance of iron in primary production studies during the Antarctic cruise, total production may have been

further enhanced by iron availability. Preliminary data collected during the cruise suggested that iron concentrations in the vicinity of the MIZ and APF were enhanced (P. Croot pers. comm.) Since these two regions were characterised by high water column stability, it is impossible to determine the role of iron in promoting primary productivity. However, during the second cruise conducted in the vicinity of the Prince Edward Islands, total production was low despite possibly elevated iron concentrations resulting from freshwater run-off from the islands (Pakhomov and Froneman 1998) in the waters surrounding the islands. These facts suggest that, while iron availability may determine the magnitude of a bloom, water column stability is required for the onset of phytoplankton blooms. Macronutrient availability did not appear to limit total production during the two cruises. However, the very low  $\text{SiO}_4$  concentrations recorded in the vicinity of the APF ( $>8 \mu\text{mol} \cdot \text{L}^{-1}$ ) during the Antarctic cruise and in the vicinity of the Prince Edward Islands may have contributed to the dominance of small pico- and nanophytoplankton to total production.

In view of the importance of primary production in the carbon cycle of the Southern Ocean, there are several areas where our knowledge requires further investigation. These are:

- (1) The role Fe plays in controlling primary production;
- (2) The effect of low temperatures on nutrient uptake by algae, particularly the mechanism involved in the uptake of nitrate compared to ammonium;
- (3) The effect of parasitism by protists and viral infections on phytoplankton production.

I will discuss the importance of each of these points below:

- (1) The importance of iron (Fe) availability in the Southern Ocean is currently of great interest (de Baar *et al.* 1990,1995; Sunda 1994). The uptake of iron by phytoplankton cells

is regulated by an active process whereby iron is bound to a ligand. Once bound to the ligand, the ion is either dissociated back into the medium or transported across the cell membrane and released into the cytoplasm. The cell's ability to maintain constant uptake rates of iron in spite of decreasing availability of Fe and other nutrients will ultimately be subjected to physical limits relating to: firstly, the maximum rate of metal binding on ligands, secondly, the space on the outer membrane that can be made available for transport ligands, and thirdly the rate of diffusion of labile inorganic species to the cell's surface. At low available iron concentrations, all three factors simultaneously limit uptake rates (Sunda 1985). Results of studies with individual phytoplankton species and enrichment experiments at sea, have shown that the addition of trace metals has both a positive and a negative effect on the productivity and species composition of marine phytoplankton in the Southern Ocean (de Baar *et al.* 1990; Miller *et al.* 1991). The results of iron enrichment experiments are thus, inconclusive. To adapt to low concentrations of available iron, smaller oceanic species with lower maximum growth rates and reduced cellular growth requirements have evolved (Sunda 1994). It is known that many species of phytoplankton are able to replace some portion of ferredoxin, (an iron-sulphur protein), with flavodoxine, a non-metalloprotein. Cells also economize by avoiding metabolic pathways that utilize large amounts of iron, i.e. the reduction of nitrate to ammonia (Sunda 1994). The preferential uptake of ammonium in low temperature regions by small cells suggests that pico- and nanophytoplankton play an important role in primary production in iron limited regions. The involvement of iron in nitrogen metabolism has led to the hypothesis that oceanic productivity is often simultaneously limited by both iron and nitrogen supply (Morel *et al.* 1991). This hypothesis may explain the relatively high productivity of phytoplankton in the vicinity of the SAF near the Prince Edward Islands where high nitrate and elevated iron (P. Croot, pers. comm.)

concentrations were noted in the surface waters. Unfortunately, we do not have any data to test this hypothesis. However, the importance of iron in phytoplankton growth is difficult to assess as areas characterised by high iron concentrations may support relatively low production as demonstrated in the waters surrounding the Prince Edward Islands. This suggests that iron in conjunction with other factors is responsible for elevated primary production.

Current evidence indicates that phytoplankton has a beneficial effect on trace metal chemistry. The release of dimethyl sulphide (DMS), which was particularly noted in the bloom conditions in the MIZ during the Antarctic survey (K Abrahamson pers. comm.), represents an important feedback mechanism which enhances the supply of iron to phytoplankton by promoting iron's solubilization from the atmospheric mineral aerosols and by facilitating rainfall. This volatile compound is derived from dimethylsulphoniopropionate (DMSP), which occurs in large amounts in phytoplankton groups, particularly dinoflagellates and prymnesiophytes (e.g. *Phaeocystis spp*). DMSP is released following cell death (e.g. during grazing) and forms DMS and acrylic acid. The DMS diffuses into the atmosphere where it is photochemically oxidised to  $\text{SO}_3$  which hydrates to sulphuric acid. which in turn adsorbs to mineral aerosols. Since it is highly hygroscopic the mineral surfaces become bathed in  $\text{H}_2\text{SO}_4$  which acts as a leaching agent solubilizing iron and other trace metals (Sunda 1994). Cloud condensation nuclei are thus formed, facilitating rainfall and providing a mechanism whereby trace metal nutrients are delivered to the ocean and onto ice sheets. The elevated iron values recorded in the vicinity of the MIZ during this survey (P. Croot pers. comm.) may have been the result of these mineral aerosols which are particularly important cloud nucleators in remote oceanic regions (Charlson *et al.* 1987). The production of DMS

represents indirectly, therefore, a positive feedback mechanism by which the phytoplankton community enhances the delivery of biologically available iron and other nutrients, thereby promoting higher productivity (Duce and Tindale 1991).

(2) Recently, interest has been focussed on the effects of low temperatures on metabolic processes and photosynthesis. The low seawater temperatures in the high Antarctic may affect the uptake of some nutrients. For example, uptake of nitrogen is both an active transport process (e.g.  $\text{NH}_4^+$  uptake) and a passive, diffusion process ( $\text{NH}_3$  uptake). The rate of nutrient uptake, particularly the uptake of  $\text{NH}_4^+$ , is temperature dependent (Hayes *et al.* 1984; Tilzer *et al.* 1986). The diffusion process is less affected by low temperatures. These facts suggest that temperature may limit total production by limiting the rate of nutrient uptake, particularly during active processes. It is not improbable that the effect of temperature may also limit the uptake of trace metals. To date, however, the effect of temperature on nutrient uptake by phytoplankton cells is poorly studied.

(3) Recently, interest has been focussed on the susceptibility of algae to viral and parasitic protist infections, which may affect abundance, composition and primary production (van Donk 1989; Suttle 1991; Kühn 1995). Also, invasive pathogenic bacteria have been reported to cause mortality among diatoms (Peterson *et al.* 1993). Already in the last century researchers reported that diatoms can be infected by several taxa of protists (i.e. invasive amoebae and phycomyces). In aquatic ecosystems, infective viruses or bacteria that cause algal mortality are generally referred to as 'pathogens' (Peterson *et al.* 1993), whereas infective protists have traditionally been regarded as 'parasites' (van Donk 1989). Parasitism is defined as an association of different species where one organism lives at the expense of

a larger organism (Begon *et al.* 1990). Available evidence to date suggests that the host diatoms infected with parasitoids, the parasitic protists, are not able to reproduce. Epidemic infections occur sporadically, generally occurring during late summer/autumn, when between 3 and 20% diatom cells were found to be infected (Sen 1987; Drebes and Schnepf 1988). Wetsteyn and Peperzak (1991) reported that infection rates appear to be temperature dependant. Similarly, turbulence decreased the encounter rates between hosts and parasites resulting in less infestation of hosts. Present knowledge about parasitoid-host associations has, however, mainly been obtained from freshwater ecosystems. To date, little is known of the importance of parasites in limiting primary production in the Southern Ocean. However, the available data in the literature suggest that they may be important in limiting primary production in the warmer waters north of the SAF, as infection rates appear to be temperature dependent. Further investigations are, however, required before the importance of these organisms can be determined in the Southern Ocean carbon cycle.

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