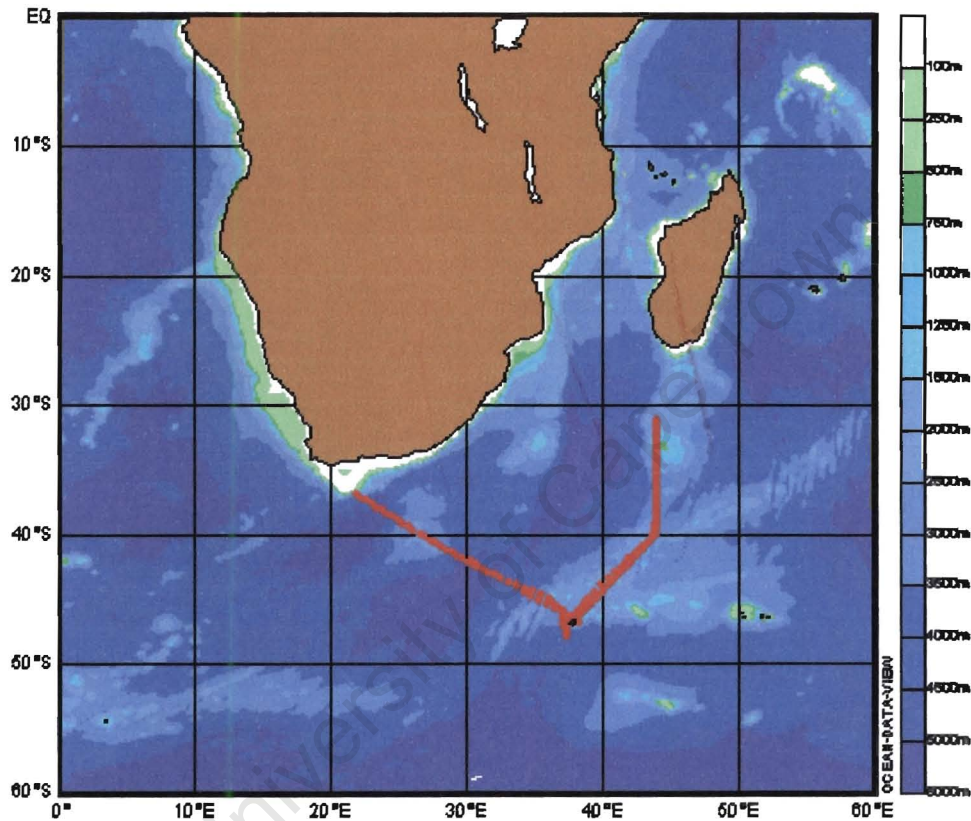


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Phytoplankton Distribution and Nitrogen Dynamics in the Southwest Indian Subtropical gyre and Southern Ocean Waters



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BY

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**Phytoplankton Distribution and Nitrogen Dynamics
in the Southwest Indian Subtropical gyre
and Southern Ocean Waters**

By

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**A thesis submitted to the
Department of Oceanography at the University of Cape Town,
in fulfilment of the requirements for the degree of Master of Science.**

University of Cape Town, South Africa
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DECLARATION

No portion of this thesis has been previously submitted in support of an application for any other degree or qualification in this or any other University.

S. J. Thomalla
September2001

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GENERAL INTRODUCTION

A major unresolved problem in biological oceanography is that of estimating the magnitude, variability and regulation of vertical organic carbon fluxes, which drive CO₂ draw-down from the atmosphere. The exchange of CO₂ from surface waters into the deep ocean is the link between the atmospheric and oceanic carbon cycles, which may ameliorate current increases in atmospheric CO₂. However, our understanding of the oceanic carbon cycle and its response to physical and biological forcing remains incomplete, although it is currently (1995) estimated that the oceans are taking up approximately 2 Gigatonnes (Gt) of anthropogenic carbon per year (Fasham et al., 2001).

Longhurst et al., (1995) recognised the importance of the "biological pump" in driving oceanic CO₂ uptake and attempted to quantify this by making global estimates of primary production based on CZCS-derived fields of surface chlorophyll-a distribution. However, it is not total primary production which is the key to the efficiency of the biological pump, but rather that fraction of total production which has the potential to sink rapidly, and is therefore exported below the seasonal thermocline. Coupled physical-biogeochemical models (e.g. Falkowski et al., 1998; Fasham and Evans, 2000) and more recent models such as the Hadley Centre Ocean Carbon Cycle (HadOCC) model have been used to derive estimates of "export" production on the basis of modelling the losses of particulate carbon and nutrients into the deeper ocean (Palmer and Totterdell, 2001). What sets the export term in this model is the nitrate flux, which proves to be most sensitive to wind stress and the mixed layer depth. In a sensitivity analysis, Palmer and Totterdell (2001) predicted that where mixed depth is increased, increasing the availability of nitrate fuels increased productivity, as long as it is not offset by reducing the light field.

Nevertheless, Palmer and Totterdell (2001) conclude that for the mid-latitude Southern Ocean, changes to the mixed layer depth would not dramatically alter productivity because macro-nutrients are non-limiting. Indeed, in a box-model

simulation of carbon and nitrogen cycling in the ocean, Popova et al. (2000) consider changes to both the mixed layer depth and the degree of iron fertilisation on phytoplankton growth rates in the Southern Ocean, and the impact this might have on ocean-atmosphere regulation of CO₂ via the biological pump. They conclude that only a small (15ppm) reduction in atmospheric pCO₂ would be possible based on the combined effects of iron fertilisation and changes in the mixed layer depth. Such modelled data are however often constrained by the paucity of experimental data available to parameterise the models. More experimental, biogeochemical data are needed to test some of these hypotheses and in particular, to put real numerical values on the magnitude of export production. The recent SOIREE in situ iron-enrichment experiment in the Southern Ocean attempted to provide such data and succeeded in many respects (Boyd and Law, 2001). Their observations demonstrated the positive impact of Fe fertilisation on phytoplankton productivity, and a 10% draw-down of surface CO₂, but could not demonstrate significant particulate export.

Direct measurements of export production in the Southern Ocean have been made by sediment trap (e.g. Honjo et al., 2000) and by thorium isotopes (e.g. Cochran et al., 2000) and indirectly by making the distinction between "new" and "regenerated" production (Eppley and Peterson, 1979). It is the latter technique which has been adopted in this thesis to make estimates of export production and to unravel aspects of nitrogen cycling by phytoplankton in the SW Indian sector of the Southern Ocean.

Regulation of new and regenerated production

Nitrogenous nutrients utilised by phytoplankton are supplied in various chemical forms from a variety of sources. Dugdale and Goering (1967) suggested the partitioning of primary production according to the source and oxidation state of the nitrogen substance utilised. New nutrient input into the euphotic zone (usually NO_3^-) are derived from the deep sea, the land and the atmosphere (e.g. N_2 fixation), while regenerated nutrients (such as ammonium and urea) originate from microbial and metazoan recycling within the euphotic zone.

The new production fraction is described by the f-ratio (new production/total production) (Eppley and Peterson, 1979) and over appropriately long time and space scales is equivalent to the proportion of production available for export. At the same time scale, this is quantitatively equivalent to the re-supply of new nutrients to the euphotic zone. Nitrogen flux into surface waters must ultimately be balanced by corresponding losses, therefore nitrate uptake should yield an indirect estimate of downward carbon flux when Redfield ratio stoichiometry is inferred (Eppley and Peterson, 1979; Minas et al., 1986).

Nitrogen partitioning by phytoplankton and its effect on planktonic community structure has, a sound observational basis (Probyn, 1992), and the interactions between nitrogenous resource, Fe and light can now be readily observed and modelled (Coale et al., 1996; Babin et al., 1996; Flynn et al., 1997; Sunda and Huntsman, 1997; Armstrong, 1999; Boyd et al., 2000; Hannon et al., 2001). The conventional wisdom stemming from such work dictates that in well-lit, nutrient (NO_3^- , Si, Fe) replete systems, fast-growing diatom-dominated communities are typically favoured, leading to a high f-ratio (e.g. $f > 0.5$), high export production and a strong CO_2 "sink". This is particularly true when production and grazing become temporarily uncoupled (Michaels and Silver, 1988 cited Dugdale and Wilkerson, 1991). By contrast, in nutrient rather than light limited oceanic regions (e.g. sub-tropical gyres), the "microbial loop" prevails, dominated by small organisms ($< 20\mu\text{m}$) with low or negligible sinking rates (Hagstrom et al., 1988 cited Detmer and Bathmann, 1997),

and low f-ratios (Probyn and Painting, 1995). In such ecosystems production is based primarily on regenerated nutrients and only weak biological CO₂ draw-down is observed, or there is a net CO₂ source to the atmosphere (for review see Karl, 1999).

Despite the domination of the nitrogenous nutrient pool by nitrate (96%) in sub-Antarctic and Antarctic waters, ammonium and urea are the principle nitrogen resources utilised, and chlorophyll biomass and primary productivity fails to reach levels appropriate to the nutrient status of the system (Dugdale and Wilkerson, 1991; Bathmann et al., 2000). This long-standing puzzle has become known as the high nutrient low chlorophyll (HNLC) “paradox” (Cullen, 1991). A particular feature of HNLC systems is that small eukaryote monads, flagellates and picophytoplankton dominate to the virtual exclusion of diatoms (Detmer and Bathmann, 1997; Karl, 1999). This has profound implications for the global CO₂ budget in which diatoms play a pivotal role (Smetacek, 1998).

Explanations proposed to account for these observations in the Southern Ocean and elsewhere have included grazing pressure by microzooplankton (Froneman and Perissinotto, 1996a,b), mesozooplankton and krill (Razouls et al., 1998, Atkinson et al., 2001), light limitation as a function of seasonality, deep mixing and critical depth relationships (Priddle et al., 1986; Smith and Nelson, 1990; Mitchell et al., 1991; Nelson and Smith, 1991), low temperatures (Jaques, 1983), and more recently limitation of algal growth by iron availability, for which the arguments are now convincing (Martin and Fitzwater, 1988; Martin et al., 1989, 1990a,b, 1991; De Baar et al., 1995; Boyd et al., 2000; Boyd and Law, 2001). In Addition, the oceanic N:P and N:Si nutrient ratios are also important determinants of specific phytoplankton assemblages and species succession which govern biologically driven ocean-atmosphere exchanges of CO₂ (Egge and Aksnes, 1992; Laubscher et al. 1993, Sommer 1994a,b; Tyrrell and Law, 1997). Nevertheless, it is the extent of vertical physical mixing and advective processes which regulate macronutrient and iron supply, the critical depth and light environment as well as water column stability.

It is not surprising therefore that major currents, fronts, eddies and many meso-scale features represent highly dynamic boundaries. These are frequently characterised by significant variability in primary production, which is often diatom dominated over interannual, decadal and seasonal time scales (e.g. Laubscher et al., 1993; Dower and Lucas, 1993; Read and Pollard, 1993; Read et al., 2000a).

The area south of Africa is particularly dynamic. It is characterised by the close juxtaposition of the Agulhas Current, the Agulhas Return Current (ARC), the Subtropical Front (STF) and the Subantarctic Front (SAF), for review see Belkin and Gordon, (1996). Recent work has shown that the prominent topography in the vicinity of the SW Indian Ridge steers geostrophic flow in this region and that this has a considerable impact on biogeochemical zonation (Pollard and Read, 2001; Pollard et al., 2001). Collectively this creates one of the most energetic and important hydrographic regions of the world oceans (Lutjeharms and Ansorge, 2001). It is also a region of complex biogeochemistry, phytoplankton distribution and productivity associated with the transition from oligotrophic and nutrient impoverished subtropical gyres to nutrient replete subantarctic domains (Barange et al., 1998; Bathmann et al., 2000; Read et al., 2000a).

The importance of this survey from 31°S 44°E to the Prince Edward Islands and following the Madagascar and SW Indian ridge is that it seeks to determine the rates of new (export) and regenerated production in this largely unknown region of the ocean. Secondly, by making a careful study of the physical and biogeochemical environment, it is hoped that some key features will emerge which account for the observed distribution of phytoplankton and its productivity. Key questions were:

- What are the rates of new and regenerated production and what therefore is the potential for significant particulate export?

Chapter 1

PHYSICAL AND BIOGEOCHEMICAL CONTROLS ON PHYTOPLANKTON PRODUCTION IN THE SOUTHERN OCEAN: A REVIEW

1.1 Fronts in the Open Ocean

The Southern Ocean is divided into zonal, circum-global bands of quasiuniform water masses, separated by a series of well-defined fronts (for reviews see Belkin and Gordon, 1996, Pollard et al., 2001). Primary control on the north-south zonation of the Southern Ocean is exerted by the strong winds of the roaring forties, which drive the transport of the Antarctic Circumpolar Current (ACC). In order to maintain geostrophic balance within the currents, isopycnals must slope upwards to the south. This tends to occur in narrow frontal bands. At each front, the sloping isopycnals expose different water types to the surface layer, or remove them from it, resulting in a different stratification and surface zonation. This often has profound consequences for production and biological structure of ecosystems (Pollard et al., 2001). Fronts do not only represent physical boundaries for biological communities, but may in themselves, constitute specific areas of enhanced biological activity (Jacques, 1989).

The first persistent frontal system to the south of Africa is the Agulhas Front (AF), formed by the Agulhas Return Current (ARC). The ARC lies between longitudes 13.5°E and 25°E. It has a preferential retroflexion at 20°E and a secondary retroflexion at 16°E (Lutjeharms and van Ballegooyen, 1988). The Agulhas Front of the ARC has steeper density gradients than any other front in the Southern Ocean. Its' average width of only 96km covers a temperature range of 21°-15.7°C, an average gradient of 0.102°C.km⁻¹ (Lutjeharms and Valentine, 1984). The ARC is optically clear, warm (18°-25°C) and nutrient depleted with an

- Within the Southern Ocean, why is phytoplankton production, and particularly diatom production, lower than anticipated as well as being fuelled primarily by reduced nitrogen assimilation despite high concentrations of nitrate?
- What accounts for the common observation of elevated chlorophyll concentrations associated with the STF (Dower and Lucas, 1993, Laubscher et al., 1993; Weeks and Shillington, 1994,1996; Barange et al., 1998), when immediately to the south, nutrient concentrations appear to be more favourable?
- What are the mechanisms responsible for enhanced productivity and phytoplankton biomass in the region of the Prince Edward Archipelago?
- And finally, do these areas of enhanced productivity contribute significantly as sinks for atmospheric CO₂ in Southern Ocean waters?

This thesis addresses these questions and hopes to make a contribution to our growing knowledge of export production and phytoplankton regulation of global CO₂ budgets for this region. Particular attention has been given to the density and nutrient structure along the respective transects in order to interpret the observed chlorophyll distribution, nitrogen (NO₃, NH₄ and urea) uptake rates and export production.

observed southern limit of 40° 01'S (Lutjeharms and Valentine, 1984). It can, at times compress closely onto the STF over distances of ~500km, occasionally making the two features difficult to distinguish (Read and Pollard, 1993). Because of the intermittent proximity of the ARC to the STF, the region can be marked by strong temperature gradients of up to 1°C.Km⁻¹.

Further south is the Subtropical Front (STF), also known as the Subtropical Convergence Zone, with pronounced horizontal gradients in temperature and salinity. Directly south of Africa, the STF is a shallow feature of little more than 300m in depth although it's downstream spatial shape is determined by the bottom topography (Weeks and Shillington, 1996). It forms the Poleward boundary of warm, salty, surface waters of the South Atlantic subtropical gyre, and the conventional northern boundary of the Southern Ocean (figure.1). It is the result of cold nutrient-rich Subantarctic Surface Water (SAASW), subducting northwards beneath saline nutrient poor Subtropical Surface Water (SSW), which is thermally enhanced by Agulhas current water (Sverdrup et al., 1942; Lutjeharms et al., 1985).

Lutjeharms and Valentine (1984) note that its location ranges from 40° 35' S to 42° 36' S, with a mean position of 41° 40' S, although there is considerable variability in it's N-S latitudinal position. Whitworth and Nowlin (1987) describe the STF as a surface feature characterised by a southward temperature decrease of 4°C, from 14°C to 10°C and having a southward salinity gradient of 34.9‰ to 34.4‰. Lutjeharms and Valentine (1984) give the mean central temperature of the STF as 14.2°C within a range across the STF of 17.9°C to 10.6°C, a temperature drop of 7.3°C. Salinity decreases are variable but fall by at least 0.5‰ in the range 35.5-35.6‰ to 34.3-34.6‰ (Lutjeharms, 1985, Lutjeharms et al., 1993).

Poleward of the STF is the Subantarctic Front (SAF) and Antarctic Polar Front (APF), which marks the transition between Subantarctic and Antarctic water masses (figure.1). In the meridional region south of Africa, the SAF was described by Lutjeharms et al. (1981 cited Lutjeharms and Valentine, 1984), where it manifested

itself as a subsurface temperature gradient lying between 3-5°C and about 4km north of the Antarctic Polar Front. Definitions of the SAF vary considerably between authors and the front's geographical location. Whitworth and Nowlin (1987) describe the SAF as the northern border of the Polar Frontal Zone, which marks the start of cross-frontal sinking of Antarctic Intermediate Water below 500m. Park et al. (1993) define subsurface expressions of the SAF at 200m with temperature and salinity ranges of 4-8°C and 34.1-34.5. In the Southwest Indian Ocean sector, Read and Pollard (1993) found no evidence of the SAF and concluded that it was merged with the APF into a unique, single structure at 48° S.

1.2 Phytoplankton and the Factors Controlling Primary Production in the Open Ocean

Phytoplankton, are free-floating, unicellular eucaryotes, which may account for up to 90% of the total plant production on earth (Branch and Branch, 1981). Their growth is dependant only on sunlight and the supply of inorganic compounds of carbon, nitrogen, phosphorus, and a certain other elements, such as Si and Fe (Tett and Edwards, 1984).

Because of their important biogeochemical influence on the deep ocean CO₂ reservoir, phytoplankton play an important role in both short and long term climate change (Sarmiento and Bender 1994).

A summary of the major impacts of phytoplankton on climate change is as follows -

- 1) Phytoplankton growth provides a sink for CO₂.
- 2) The biological pump maintains a pCO₂ gradient and prevents the atmosphere from reaching an equilibrium with the deep ocean.
- 3) Synthesis of calcium carbonate coccolithophores removes dissolved bicarbonate, reduces ocean pH and produces a significant difference in the partitioning of CO₂ between the ocean and the atmosphere (Holligan and Robertson, 1996).

4) Both light absorption by chlorophyll and light scattering by coccoliths reduce light and heat penetration into the deeper ocean (Morel and Antoine, 1994; Holligan et al., 1993) which alters the ability of the ocean to accept and retain heat (Sathyendranath et al., 1991).

5) The generation of dimethyl sulphide (DMS) by phytoplankton leads to the release of sulphur compounds to the atmosphere, cloud formation and increased albedo (Charlson et al., 1987). Note that this effect is 20x greater in respect of coccolithophores relative to diatoms (Keller et al., 1989).

The rate at which phytoplankton cells and other particles sink, or are consumed, is largely size-dependant (Probyn, 1992; Hansen et al., 1994 cited Froneman and Perissinotto, 1996a) phytoplankton can therefore be divided into three main size categories based on their cell diameters.

Microphytoplankton (200-20 μ m) consist mainly of diatoms, while nanophytoplankton (20-2 μ m) and picophytoplankton (<2 μ m) consist mainly of small-celled flagellates. For the purposes of this thesis, the term 'diatoms' is synonymous with, and may be used in place of 'microphytoplankton'.

There is an immense literature dealing with phytoplankton and the factors governing their physiology and ecology (for example see: Hart 1934; Bridigare et al., 1986; Holm-Hansen et al., 1977; Tranter, 1982; Witek et al., 1982; Jacques, 1983; Tett and Edwards, 1984; Tilzer et al., 1985; Martin et al., 1990; Cullen, 1991; Dugdale and Wilkerson, 1991; Nelson and Smith, 1991; De Baar et al., 1995; Falkowski and Raven, 1997, Bathmann, 1998, Bracher et al., 1999, Smith et al., 2000, Sharples et al., 2001).

In brief summary, phytoplankton production ultimately depends on the physiological responses of the algae to the sometimes extreme conditions under which they live. Part of what makes the study of phytoplankton ecology and productivity so difficult is the diversity of phytoplankton assemblages. Differences

in species, sizes, the plasticity of their ultra-structure, bulk biochemical composition, pigment type and content, nutrient preferences, assimilation rates and rates of photosynthesis all contribute to the unpredictability of their responses to various physical, chemical and biological conditions.

The Southern Ocean is a physically complex environment in which to investigate phytoplankton distributions. In contrast to most open ocean surface waters, the Southern Ocean is characterised by a unique set of environmental conditions: extreme seasonal variations in irradiance, consistently low temperatures (approximately 4.5 to 1.8°C), small to negligible vertical density gradients, and high nutrient concentrations (5.5 times higher than the global average (Sharp, 1983 cited Koike et al., 1986).

South of the APF, these high nutrient concentrations are maintained by large-scale upwelling and turbulent mixing in the upper water column (Koike et al. 1986). Despite the permanently high nutrient concentrations, primary production in the Southern Ocean is unexpectedly low (Holm-Hansen et al., 1977; Allanson and Parker, 1983), and nevertheless supports large numbers of secondary and tertiary producers. This scenario has become known as the high nutrient low chlorophyll (HNLC) “paradox” (Cullen, 1991). There are other areas of the ocean where relatively low primary production is observed in nutrient rich surface water, most notably the eastern equatorial Pacific, and the central north Pacific (Dugdale and Wilkerson, 1991 for review see Karl, 1999). Lack of biomass over any season, NO_3 concentrations that are never exhausted, and low primary production rates compared to eutrophic regions are characteristics of these HNLC regions (e.g. Holm-Hansen, 1985, De Baar et al, 1990, Chavez and Barber, 1987, Miller et al., 1988 cited Dugdale and Wilkerson, 1991 Wheeler and Kokkinakis, 1990). However, the Southern Ocean differs from these other regions in a way that makes it an area of potentially great importance for the global ocean-atmosphere carbon balance. This is because convergent zones at the APF and STF are the only places in the ocean where globally significant

quantities of surface water down-well to aphotic depths, while still containing high concentrations of pre-formed nutrients (Belkin and Gordon, 1996). It has been suggested that utilisation of these “excess nutrients” might have a substantial impact on the regulation of atmospheric greenhouse gas CO₂ concentrations (Nelson and Smith, 1991).

Furthermore, there are regions in the Southern Ocean, which exhibit high seasonal rates of primary production. These areas are considerably important in terms of their potential as significant atmospheric CO₂ sinks on a global scale. Regions of enhanced production are usually associated with oceanic frontal regions (Allanson et al., 1981; Bridigare et al., 1986; Lutjeharms et al., 1985; Laubscher et al., 1993; Dower and Lucas, 1993) or continental and sub-Antarctic island margins (Boden, 1988; Perissinotto and Duncombe Rae, 1990; Perissinotto et al., 1990,1992). A further exception is the restricted area of the marginal ice-edge zone (Smith and Nelson, 1985, 1990; Waldron et al., 1995; Bury et al., 1995; Rees et al., 1998; Smith et al., 2000).

Although no single factor governing phytoplankton production has been accepted conclusively, the search for underlying causal factors can begin profitably with understanding the factors limiting primary production. There are many physical, chemical and biological explanations proposed to account for the observations in the Southern Ocean and elsewhere. Zooplankton grazing, temperature, solar radiation, water column stability and the availability of macro- and micronutrients are considered to be the more important. Each of these factors will be considered in turn.

Light and Primary Production

The amount of photosynthetically available radiation (PAR) arriving at the sea surface is clearly dependent upon latitudinal, seasonal and diurnal effects while underwater irradiance is controlled by its attenuation co-efficient in sea-water (k_d). Light penetration in the sea determined from k_d nominally defines the

euphotic layer (where light is sufficient to support growth and reproduction by photosynthesis), which of course is related to the surface mixed layer (SML) and the seasonal thermocline boundary, because of the heat input associated with light.

However, wind stress has a profound effect on the deepening or shallowing of the SML and therefore controls the extent to which phytoplankton cells are mixed through the euphotic zone into the aphotic layer. This concept is central to the critical depth models of photosynthesis (Nelson and Smith, 1991). Variations in available light intensity, duration and spectra are also important factors, which influence phytoplankton growth (e.g. Morel, 1991; Falkowski and Raven, 1997).

Total incident radiation is a function of latitude, with higher latitudes experiencing 24 hours of daylight in summer, albeit at lower average insolation than equatorial latitudes (Knox, 1994). During the austral summer months, total daily light flux at higher latitudes can therefore sometimes exceed that of tropical latitudes (Holm-Hansen et al., 1977). Superimposed on the annual patterns of incident radiation, are a number of other factors, which influence the availability of light energy to phytoplankton in the Southern Ocean. Firstly the height of the sun above the horizon is lower for a greater part of the year than in temperate and tropical latitudes. This low angle of the incidence of the sun's rays increases the reflection from the sea surface and reduces the period of effective submarine light per day (Knox, 1994). Secondly, the Southern Ocean is particularly stormy affecting surface reflection, as well as producing bubbles, which considerably reduce transmission through the surface waters (Powell and Clarke, 1936 cited Knox, 1994; Dera and Gordan, 1968 cited Lewis et al., 1984). A combination of low irradiance and high albedo makes it likely that the underwater light field in the Southern Ocean is characterised by low light values which are further diminished by particle backscattering (Strass et al, 2001; Bracher and Tilzer, 2001).

The key question then is to ask if phytoplankton of the Southern Ocean are light limited or whether they are photo-adapted to low ambient irradiance?

Part of the answer to this question depends on light attenuation (k_d), the mixed layer depth and the critical depth (D_{cr}), which has been addressed for the Southern Ocean by Nelson and Smith (1991).

The compensation depth (D_c) is defined as the depth at which a cell's respiration during 24 hours exactly consumes the organic material fixed by photosynthesis during the same period (i.e. $P_c=R_c$), and this can be used to set the lower limit of the euphotic zone (figure.2) which varies from 20-100m over much of the Southern Ocean (Jaques, 1983; Knox, 1994).

The depth at which photosynthesis throughout the water column is balanced by phytoplankton respiration throughout the water column ($P_w=R_w$) is termed the critical depth, D_{cr} (figure.2). Sverdrup (1953) demonstrated theoretically that when the critical depth is less than the depth of mixing, no net production takes place (i.e. $R_w>P_w$ over 24 hours). Net production ($P_w>R_w$) only occurs when the critical depth lies below the depth of mixing.

The Southern Ocean is well known for its rough weather and turbulent seas. Wind stress is frequently so great that a homogeneous (isothermal and isohaline) water column develops which reaches depths of 50-100m (Nelson and Smith, 1991; Knox, 1994). In these circumstances, phytoplankton cells, being without independent powers of movement, are mixed well below the critical depth where gains by photosynthesis are lost in respiration. This may hinder the development of blooms and contribute to the low primary productivity of Antarctic waters. There is now large-scale spatial information to suggest that high winds are coincident with low phytoplankton biomass. Satellite-derived composite distributions of annual mean winds show a zone of high wind stress in the Indian Ocean. This area is also one from which ocean colour images from Nimbus 7

coastal zone colour scanner (CZCS) show virtually no chlorophyll (Nelson and Smith, 1991).

However, it has been argued that the critical depth in the Southern Ocean is generally deeper than the usual summer mixed layer (>100m), and that Sverdrup's hypothesis cannot explain the low phytoplankton production of these waters (Jacques, 1983,1989; Priddle et al., 1986; El Sayed, 1988 cited Perissinotto et al., 1990; Figueiras et al., 1999). Nelson and Smith (1991) reformulated Sverdrup's equation for the critical depth by substituting terms that are more consistent with present-day optical and biological data, with the purpose of eliminating or significantly reducing the source of error. Using the reformulated equations, they found that in winter the entire region seemed to be mixed beyond the critical depth, and in late spring through summer, the irradiance mixing regime appeared to be favourable for the initiation and early development of a phytoplankton bloom. However, as chlorophyll increases in the surface layer, the critical depth shoals, making any bloom self-limiting. This self-limitation may keep chlorophyll levels below $\sim 1\text{mg}\cdot\text{m}^{-3}$.

It has been reported that phytoplankton blooms in the Southern Ocean occur predominantly in conjunction with a shallow mixed layer (Holm-Hansen and Foster, 1981 cited Perissinotto et al., 1990; Mitchell and Holm-Hansen, 1991). An increase in water stability may help maintain phytoplankton in the euphotic zone, thus promoting growth and subsequent biomass accumulation (Marra and Boardman, 1984 cited Bridigare et al., 1986). This is thought to occur at the ice edge, at the STF and surrounding sub-Antarctic islands, where local stabilisation of the upper water diminishes to significantly less than the critical depth and permits high phytoplankton biomass to accumulate (Allanson et al., 1981; Lutjeharms et al., 1985; Nelson and Smith, 1991; Dower and Lucas, 1993).

However, given that phytoplankton have evolved with the development of the Southern Ocean over the last 15million years, it would not be unreasonable to

expect that phytoplankton growth ought to be conditioned to a low light regime through adaptive physiological responses. When physiological parameters of *P.* vs. *E.* curves are examined (Sakshuag et al., 1997) Southern Ocean phytoplankton can show high degrees of photo-adaptation to low ambient underwater irradiance (e.g. Dower and Lucas, 1993; Dower et al., 1996; Bracher et al., 1999; Strass et al., 2001)

In experiments on Antarctic diatoms, increased light utilisation was found in environments characterised by fluctuating light conditions. This is likely to be an adaptation of the microphytoplankton in overcoming such constraints and enabling them to attain a higher than expected productivity (Knox, 1994). In the APF region of the south Atlantic sector of the Southern Ocean, Bracher et al., (1999) determined that light saturation (E_k) at the 1% light depth ranged from 8-139 mg-at.q m⁻² s⁻¹ and at the surface, was higher; 34-246 mg-at.q m⁻² s⁻¹. Consistently low E_k values (8-83 mg-at.q m⁻² s⁻¹) were only evident within ACC waters. These values are nevertheless considerably lower than are typical for phytoplankton in temperate regions indicating a degree of photo-adaptation to a low light environment.

Temperature and Primary Production

The temperature dependence of light-saturated photosynthesis has been well established (e.g. Knox, 1994) and is expected because the photosynthetic capacity is controlled by enzymatic processes. The metabolic machinery of a phytoplankton cell is complex, and there is no reason to suppose that its' component parts could adjust to changes in irradiance and temperature at the same rate (Lewis et al., 1984). Results from Tilzer and Dubinsky (1987) suggest that under the nutrient-saturated conditions of the Antarctic Ocean, the temperature dependence of both photosynthesis and algal respiration are key factors in controlling phytoplankton productivity. Their studies show that when energy supply is low due to short days and/or deep mixing, mass balance of phytoplankton is mainly controlled by respiration rates, which are more

temperature sensitive than photosynthesis (Tilzer and Dubinsky, 1987). Low temperatures enable the algae to efficiently conserve carbon and stored energy. However, if the temperature were to rise even slightly, the maintenance of biomass would no longer be possible due to increased respiratory losses.

Despite the adaptations of Antarctic phytoplankton to variable light conditions and low light intensities, the photosynthetic capacity (photosynthesis per Chl-a at optimum light) and maximum quantum yield of photosynthesis (moles CO₂ assimilated per mole light quantum absorbed) are on average smaller by a factor of 7 and 4 respectively, than in phytoplankton at lower latitudes. This suggests that in Antarctic waters, constraints on the efficiency of photosynthetic energy conversion imposed by low temperature take over as rate limiting steps in otherwise light limited situations, and ultimately restrict phytoplankton productivity (Tilzer et al., 1985).

Macronutrients and Phytoplankton Production

The mechanisms of supply and the kinetics of utilisation of dissolved nitrogen are believed to play a critical role in determining the productivity, size structure and species succession of phytoplankton communities in much of the world's oceans (Dugdale and Goering, 1967; Carpenter and Capone, 1983; Probyn 1992; Bronk et al; 1994; Harrison et al., 1996; Karl 1999; Tremblay et al., 2000).

Following the pioneering work of Dugdale and Goering (1967), it became possible to partition primary production into "new" and "regenerated" production according to the source and oxidation state of the nitrogen resource. This partition is based on whether the nitrogen is supplied from within the euphotic zone (regenerated production), or from outside the euphotic zone (new production). Regenerated production is based on the uptake of reduced nitrogenous compounds; ammonium (NH₄), urea, or dissolved organic nitrogen (DON). Their uptake is related to the rates of remineralisation of organic matter by biological and chemical processes within the euphotic zone. New production

on the other hand, is based on nutrients introduced into the euphotic zone (NO_3 , N_2 fixation) and can be derived from the deep sea, the land and the atmosphere (Dugdale and Goering, 1967).

The partitioning between new and regenerated nitrogen uptake can be summarised in the form of f-ratios, a quantitative measure of the proportion of phytoplankton growth dependant upon NO_3 relative to total N (Eppley and Peterson, 1979). Implicit in this therefore, is a measure of that fraction of primary production, which is available for export to the deep ocean or to higher trophic levels (new production); which is surplus to phytoplanktonic community maintenance requirements (regenerated production)(Tremblay et al., 1997). The f-ratio is important in that it provides an index of coupling between the photic zone and the rest of the water column, being directly related to the rates of vertical NO_3 flux from below over suitable time scales (Probyn et al., 1996). As nitrogen flux into surface waters must ultimately be balanced by equivalent losses, nitrate uptake yields an indirect estimate of downward carbon flux when Redfield ratio stoichiometry is inferred (Eppley and Peterson, 1979; Minas et al., 1986).

Qualitative relative preference indices (RPI) for the individual nitrogenous nutrients follow the sequence ammonium > urea > nitrate. This preferential uptake of reduced over oxidised forms of inorganic nitrogen by phytoplankton has been reported in various marine environments (Dugdale and Goering, 1967; McCarthy et al., 1977; Probyn, 1985; Probyn and Painting, 1985). The preference is based on energy expenditure, the active uptake of nitrate being energy expensive. NO_3 first has to be reduced to NH_4 before it can be utilised by the cell and this reduction phase costs energy (Tett and Edwards, 1984). Ammonium and urea on the other hand have already been reduced and their uptake can be considered as energy saving (Losado and Guerrero, 1979; Syrett, 1981 cited Dortch, 1990). Raven's (1988,1990) calculations demonstrated the high cost of N_2 fixation and the more moderate cost of NO_3 assimilation relative to least expensive growth based on NH_4 uptake.

However, quantitative demands for nitrogen may not follow the RPI if supply and demand do not match. Ammonium and urea regeneration and uptake rates are based largely on the close coupling between microzooplankton grazers and uptake by nano- and picophytoplankton (Probyn 1987, 1992) within the "microbial loop". Regeneration of nitrogen and its turnover rate is not fast enough to support the demand of fast growing microphytoplankton populations which can therefore dominate the uptake of NO_3 at high concentrations of this nutrient (Malone, 1980; Chisholm, 1992 cited Tremblay et al., 2000).

By contrast, the smaller size-classes typically exhibit slower growth rates. Nano- and picophytoplankton nitrogen requirements are therefore satisfied by the preferred assimilation of regenerated nitrogen without resorting to nitrate uptake. The smaller pico- and nanophytoplankton also have a higher surface area to volume ratio and are therefore more efficient (per unit chlorophyll) than microphytoplankton at scavenging nitrogen at low ambient concentrations (Koike et al., 1981,1986; Holm-Hansen, 1985; Probyn and Painting, 1985). In low nutrient conditions small cell sizes will therefore typically out-compete the larger microphytoplankton. Thus for a particular water body, decreasing f-ratio and decreasing cell size within the phytoplankton community are likely to be closely related (Probyn and Painting, 1985, Probyn, 1992).

In summary, it can be said that in well-lit nutrient replete systems, fast-growing microphytoplankton communities are typically favoured, leading to high f-ratios, high export production and a strong CO_2 "sink". By contrast, in nutrient rather than light limited oceanic regions (e.g. sub-tropical gyres), regenerated production prevails, dominated by small organisms ($<20\mu\text{m}$) with low or negligible sinking rates (Hagstrom et al., 1988 cited Detmer and Bathmann, 1997). In such ecosystems, the f-ratio is low and only weak biological CO_2 draw-down is observed or there is a net CO_2 source to the atmosphere (Karl, 1999).

The limiting elemental resource for plant production in most oceanic regions is believed to be nitrogen (Carpenter and Capone, 1983 cited Knox, 1994).

However, the characteristic features of large scale upwelling and turbulent mixing in the upper water column of the Southern Ocean south of the APF enhances and maintains the supply of nutrients, particularly NO_3 and Si, into surface waters. This region of the Antarctic marine ecosystem is thus almost unique amongst the world's oceans, where NO_3 is non-limiting while Si only becomes limiting towards the northern boundary of the APF (Read et al., 2000a).

High nutrient concentrations notwithstanding, algal growth may still be restricted by the nutrient regime. Dugdale (1967 cited Harrison et al., 1996) was the first to propose that the acquisition of nitrogen by phytoplankton be dependant on a relationship between the concentration of NO_3 or NH_4 and the uptake of that nutrient. The preference of phytoplankton for NH_4 over NO_3 extends over the full spectrum of nitrogen concentration (Harrison et al., 1996). It is generally believed that NH_4 recycling and high ambient NH_4 concentrations can inhibit or repress nitrate uptake by phytoplankton. This together with a low light environment may set upper limits to new production in nutrient rich grazing-balanced environments (Wheeler and Kokkinakis, 1990). The inhibitory effects of NH_4 on NO_3 uptake in natural phytoplankton assemblages have been investigated on numerous occasions. Some results confirm that extremely low concentrations of NH_4 are capable of significant inhibition of NO_3 uptake, although complete inhibition was a rarity (Eppley and Renger, 1988; Wheeler and Kokkinakis, 1990; Harrison et al., 1996). These results highlight the important role NH_4 plays in regulating new production and the f-ratio even at nanomolar concentrations. These results are based on the simplified assumption that NO_3 and NH_4 uptake are regulated solely by kinetics (Harrison et al., 1996). A study by Rees et al. (1999) challenged these results and found no direct evidence for NH_4 inhibition. They concluded that the greatest influence on NO_3 uptake was the large decrease in NO_3 concentration.

Dortch (1990) has separated the interaction between NO_3 and NH_4 into preference for ammonium (indirect interaction) and inhibition of nitrate uptake by ammonium (direct interaction). Preference and inhibition are two interactions, which are not mutually exclusive and are influenced differently by environmental conditions. Preference is hypothesised to be maximal at low light and nutrient deficiency, whereas inhibition will be maximal under conditions of low light and nitrogen sufficiency (Dortch, 1990). In its most extreme form, it is believed to result in no NO_3 uptake above a threshold NH_4 concentration of $\sim 1\mu\text{M}$. A thorough review of the literature, however, indicates that 'inhibition' or 'preference' is neither as universal nor as severe a phenomenon as is generally believed (Dortch, 1990).

Another macronutrient, which is potentially responsible for setting upper limits to new production within some regions of the Southern Ocean is silicate (Si), which may be present in concentrations below the threshold for phytoplankton growth (Allanson et al., 1981; Jacques, 1989; Verleucar et al., 1990 cited Laubscher et al., 1993). Nevertheless, the Southern Ocean is associated with the greatest rates of biogenic silicate deposition in any of the world oceans, particularly at the APF (Treguer et al., 1995, Queguiner et al., 1997) where large and highly silicified diatoms such as *Fragilariopsis kerguelensis* often dominate community biomass (Bathmann et al., 1997). Since Antarctic diatoms have high cellular ratios Si:C and Si:N, they require high silicate concentrations to achieve their optimal growth (Jacques, 1989). Dugdale and Wilkerson (1998) note that nitrate uptake appears to cease when silica concentrations are less than $\sim 2\text{mg-at.m}^{-3}$. The results of Laubscher et al. (1993) showed positive relations between diatom abundance and silicate concentrations, supporting the suggestion that silicate limitation influences diatom distribution in the Southern Ocean.

In open ocean waters, Redfield et al (1963 cited De Baar et al., 1997) and Dugdale and Wilkerson (1998) have demonstrated that the nutrients nitrate, silicate and phosphate are typically released in constant atomic proportions N : Si : P of 16 : 16 : 1. Nevertheless, for the Southern Ocean there are

significant deviations to the Redfield ratio due to anomalies in N : Si : P uptake by diatoms and N : Si recycling rates (Queguiner et al, 1997 cited Read et al 2000; De Baar et al, 1997). Strong phytoplankton species-specific preferences also exist for different nutrients. Diatoms prefer high Si:N (Sommer, 1994a,b cited Read et al., 2000a), blue-green algae prefer low N:P (Howarth, 1998 cited Read et al., 2000a) and dinoflagellates prefer low N and low P (Margalef, 1978).

In surface waters, N : Si : P will be due largely to uptake by phytoplankton, while in deeper waters, N : Si : P largely reflects re-mineralisation processes and can signify differing water masses (Read et al, 2000). The NO_3 : Si ratio in particular significantly effects the driving of the diatom/non-diatom community succession, with implications for food chains and CO_2 sequestration.

Using field data and a Si-cycle model for the HNLC eastern equatorial Pacific. Dugdale and Wilkerson (1998) showed that there was a differential export of Si relative to N. Zooplankton grazing on diatoms resulted in much greater regeneration of N than Si in euphotic waters, so that the NO_3 : Si ratios were <1 and as low as 0.25 in Southern Ocean surface waters. These systems are eventually driven into Si limitation by the rate of supply of Si.

More recently however it is clear that silicate concentrations alone cannot be the sole determinant of algal biomass or productivity. Algal biomass appears to be co-limited by nitrate, silicate, iron and light coupling (Sunda and Huntsman, 1997; Boyd et al., 1999, Francke et al., 2000) as well as by silicate distribution (Read et al., 2000a)

Micronutrients and Primary Production

The eastern Equatorial Pacific, the Subarctic North Pacific Ocean and the Southern Ocean are all recognised to be HNLC regions in which macronutrient abundance is very evident, but where productivity is nevertheless limited. A range of mineral micronutrients (Mo, Mn, Co, Zn, Cu, N, B, Cl, Mg, Fe), have

been recognised as important for algal growth. In addition a number of organic substrates, especially vitamins, are required for sustained plant growth (Knox, 1994).

Amongst the first to recognise that these HNLC systems might be micro-nutrient (iron) limited were Martin and Fitzwater (1988), Coale (1988), Martin (1990) and Martin et al., (1989, 1990). Martin's (1990) "Iron Hypothesis" was based on the theory that the lowered atmospheric CO₂ concentration observed during the Last Glacial Maximum was due to increased phytoplankton production and sequestration of atmospheric CO₂, which he proposed was a result of increased iron supply to the Southern Ocean at that time.

Iron is a particularly important micronutrient because it is instrumental in the biosynthesis of chlorophyll. It is a main component of ferredoxin, which facilitates the intracellular transfer and storage of photosynthetically incorporated energy and occurs in both nitrate and nitrite reductase (Verstraete et al., 1980 cited De Baar et al., 1990). These Fe dependent enzymes serve to readily reduce nitrate via nitrite into ammonium, which is required for synthesis of amino acids and proteins (Raven, 1988, 1990). Nitrate assimilation and reduction increases the iron requirement for growth by 60% and N₂ fixation increases the requirement by about 100 fold (Raven, 1988; Geider and La Roche, 1994; De Baar, 1994 cited De Baar et al., 1997). However assimilation of ammonium does not require extra iron. Hence at open ocean sites with extremely low iron (<0.2nM) one may expect a recycling ecosystem, mostly utilising ammonium. Under these conditions biomass build up and export into deeper waters would be limited (De Baar et al., 1997). The unused excess of major plant nutrients, and low ambient iron concentrations supports the "Fe hypothesis" which severely limits the "biological pump" and thus contributes to the raised atmospheric CO₂ concentrations typical of previous and present interglacial periods (Martin et al., 1990).

Fe has been found to sequentially stimulate net chlorophyll increase, carbon build up, nitrate uptake and PO₄ uptake in that order (De Baar et al., 1990; Scharek et al., 1997 cited Bathmann et al., 1997; Martin et al., 1990 cited Nelson and Smith, 1991). Other experimental studies by Price et al. (1991,1994) in the HNLC region of the west equatorial Pacific showed that Fe additions stimulated NO₃ reduction and CO₂ fixation in cells >3µm but not in picophytoplankton. They concluded that Fe limitation adversely affected NO₃ uptake and reduction in large (diatom) cells. However, Greene et al (1994) using fast repetition-rate fluorometry (FRRF) in the high NO₃ equatorial Pacific concluded that all size-classes were Fe limited, including the ubiquitous picophytoplankton. Changes in community structure have also been observed in which diatom cell (and red tide) division rates have been elevated (Di tullio, 1993) thereby increasing the biomass - but in the absence of grazers, which was a point of departure for those (e.g. Banse, 1991) who questioned the ecological significance of such bottle experiments (for review, see De Baar and Boyd, 1999).

An alternative approach was to relate ambient Fe concentrations in the ocean with phytoplankton distribution, biomass and size-structure, for example in the Southern Ocean (De Baar et al., 1995, 1999). It was noted that the greatest phytoplankton abundance in the Southern Ocean was located downwind and downcurrent of the major continental land masses, where trace metal input is greatest, and within the fast-flowing, iron-rich jet of the Polar Front, where spring blooms produced phytoplankton biomass an order of magnitude higher than that in Fe deficient Southern Ocean waters. This hypothesis is further supported by composite ocean colour images of the Southern Ocean from Nimbus 7 CZCS. These images show areas immediately east (i.e. downwind) of South Africa, Australia, and Argentina to have pigment concentrations higher than those in most other areas of the Antarctic Ocean. These observed pigment distributions are consistent with the hypothesis that airborne dust from the continents provides an iron source that stimulates phytoplankton growth (Nelson and Smith, 1991).

These surveys provided strong circumstantial evidence for the link between Fe concentrations and phytoplankton abundance. However, it was not until mesoscale Fe fertilisation experiments in HNLC environments of the equatorial Pacific (Martin et al., 1994 - IronEx I and Coale et al., 1996 - IronEx II) and the Southern Ocean (Boyd et al., 2000, Boyd and Law, 2001 - SOIREE), that convincing *in situ* evidence emerged for the Fe dependence of phytoplankton growth (particularly by diatoms).

However, despite Fe-mediated increases in chlorophyll biomass (from 0.2 to ~2 $\mu\text{g l}^{-1}$) and productivity (up to 1.3g C m⁻² d⁻¹) occurring concurrently with a 10% draw-down of surface CO₂ over the 40 day period of the bloom, no downward export of particulate carbon was observed (Boyd and Law, 2001).

It seems plausible that the time-lag between the observations made during SOIREE and direct evidence of particulate export may well have exceeded the observation period. This in itself may place some constraints on the evidence from sediment trap (e.g. Honjo et al., 2000) and thorium (²³⁴Th, ²³⁸Th) measurements (e.g. Cochran et al., 2000) which are frequently associated with relatively short term observation periods. Estimates of potential export based on measurements of new production may overcome some of these difficulties if integrated over appropriate time scales.

Grazing controls on primary production

Many studies have documented the existence of an inverse relationship between phytoplankton biomass and zooplankton. Peaks of zooplankton density generally coinciding with troughs in phytoplankton biomass; this relationship has been ascribed to grazing (Jacques, 1989). Although grazing has a direct impact on phytoplankton, the indirect impact is to promote growth through ammonium excretion by both micro- and mesozooplankton as well as by krill (Glibert et al., 1992, Atkinson and Whitehouse, 2001 and Atkinson et al., 2001). Because of the inhibitory effects of NH₄ on NO₃ utilization, an important consequence of grazing

is that it sets an upper limit on NO_3 uptake in nutrient-rich, grazing balanced ecosystems (Wheeler and Kokkinakis, 1990).

There are two pathways (Hewes et al., 1985 cited Jacques, 1989), which coexist in all ecological situations, but the magnitude of the flow passing through each of them varies (Jacques, 1989). In the first instance, mesozooplankton (~3-5mm in length) feeding on microphytoplankton typifies a short food chain where carbon may be efficiently passed to higher trophic levels (e.g. diatoms to zooplankton to fish) with minimal respiratory CO_2 losses. This path is based principally on new production and a large fraction of the organic matter is exported into deep water and the sediments through the rapid sinking of large diatoms and faecal pellets (Jacques, 1989; Tremblay et al., 2000).

The second pathway involves the small nano- and picophytoplankton, and microzooplankton of the “microbial loop”. By contrast, to the efficient diatom-dominated food chains, the “microbial loop” is characterised by many steps in the food chain (e.g. phytoflagellates to microzooplankton to mesozooplankton to larval/adult fish) and inefficient energy transfer, but a tight coupling between ammonium excretion and ammonium uptake by phytoplankton (Gifford and Dagg, 1988, 1991 cited Froneman and Perissinotto, 1996; Gifford, 1991; Glibert et al., 1992). In conditions such as these, a high degree of phylogenetic, functional and genetic diversity exists, particularly with regard to nutrition and inter-relationships between the autotrophs, heterotrophic bacteria and microzooplankton consumers (for review, see Karl, 1999). This food web is representative of oligotrophic and HNLC conditions in which a sizeable fraction of the production is achieved through rapid recycling of inorganic carbon in surface waters (Jacques, 1989; Tremblay et al., 2000) and export production is insignificant.

Over large areas of the Southern Ocean, mesozooplankton have a generally low biomass and low grazing impact on phytoplankton productivity (egg Schnack et

al., 1985, Atkinson, 1996, Razouls et al., 1998). For example in spring 1992, the dominant species in the Polar frontal zone of the S. Atlantic were *Calanoides acutus* and *Rhincalanus gigas*, while *Calanus propinquus* was dominant at the ACC-Weddell Gyre boundary, yet in neither case did their grazing impact account for more than 1% of the primary production (Dubischar and Bathmann, 1997). There are exceptions of course, and it is apparent that strong grazing pressure by mesozooplankton and krill may be apparent locally, for example around South Georgia where diatoms frequently dominate (for review, see Atkinson et al., 2001), by mesozooplankton around the Prince Edward Islands (Perissinotto and Boden, 1989) and by krill within the Marginal Ice Zone (Perissinotto et al., 1997). These and other studies suggest that up to 80% of the net production is channelled into these larger herbivores (for review see Bathmann et al., 2000).

However, where small phytoplankton cells dominate in the ACC, microzooplankton constitute a significant proportion of total zooplankton biomass and may readily consume more than 100% of the phytoplankton productivity (Froneman and Perissinotto, 1996). In a review, Bathmann et al. (2000) concluded that microzooplankton grazing removed between 52-82% of the primary production on a daily basis in all subantarctic regions. Similarly, where salps (e.g. *Salpa thompsonii*) dominate, they too can remove close to 100% of the productivity (Perissinotto and Pakhomov, 1998). Due to the inefficient energy transfer of the “microbial loop”, these microzooplankton grazing rates may be sufficiently high to account for the generally low phytoplankton biomass in the Southern Ocean (Bjornsen and Kuparinen, 1991 cited Froneman and Perissinotto, 1996). Some field studies also suggest that microzooplankton not only control the size of the phytoplankton population, but may also control the growth of certain species by selective grazing (Reynolds et al., 1982; Burkhill et al., 1987; Strom and Welschmeyer, 1991 cited Froneman and Perissinotto, 1996).

It seems that essentially, there is no either/or pathway in subantarctic waters. However, it is clear, that planktonic food webs have strong size-based relationships. It is therefore likely, that where phytoplankton communities undergo seasonal or inter-annual shifts in community structure (Murphy et al, 1998), the relative importance of micro- and macrozooplankton grazing communities will shift accordingly. This in turn will influence the biogeochemical cycling of both carbon and nitrogen, but in relatively predictable ways based on allometric relationships (e.g. Moloney and Field, 1989, 1991).

1.3 The Prince Edward Islands and primary production

Sub-Antarctic Marion and Prince Edward Islands are volcanic outcrops of the Prince Edward Island Fracture Zone. The islands lie 28km apart and are S.E of the African continent (47°S, 38°E). The bathymetry to the west of the islands deepens rapidly to 5000m while the saddle between and to the east of the islands is shallow (<250m)(Lucas and Probyn, 1987).

Similar to most subantarctic islands, the Prince Edward Islands have a particular ecological importance. They support a rich benthic invertebrate community of mainly filter feeders in the shallow island seas (Branch et al., 1993 cited Lucas and Probyn, 1987), whilst a very large community of marine birds and mammals (Williams et al., 1979) depend on the primary production supported by these islands through meso- and macrozooplanktonic intermediary steps in the food chain (Perissinotto et al., 1992). A certain level of controversy surrounds the oceanographic and biological processes responsible for the levels of enhanced phytoplankton production and biomass typically observed in the vicinity of these islands.

It has been argued that the enhanced productivity and phytoplankton biomass associated with the Prince Edward archipelago is due to an "island mass effect" (Doty and Oguri, 1956). The "island mass effect" has been associated with two

main causes: (1) micronutrient (iron) availability (Martin 1990; Martin et al., 1990) and (2) dynamic interactions between oceanic circulation and shelf topography (Heywood and Priddle, 1987; Perissinotto and Duncombe Rae, 1990).

There is increasing evidence that bloom development associated with subantarctic islands is triggered by stabilization of the water column (e.g. Mitchell and Holm-Hansen, 1991; Perissinotto et al., 1990, 1992, 2000). Smith (1987 cited Ismail, 1990) stated that due to the high annual rainfall, guano is dissolved and carried into the sea via run-off, spreading out from the islands. The flux of fresh water is of particular importance for the development of phytoplankton blooms as it provides a significant input of buoyancy into the surface layer, and a consequent increase in water column stability and shoaling of the mixed layer depth (Perissinotto et al., 1990; Duncombe Rae, 1989). When mixed layer depths are shallower than euphotic depths, the ratio of carbon fixation to respiratory losses improves (Tilzer and Dubinsky, 1987). However, bloom generation requires favourable environments, such as a stable mixed layer and high concentrations of ambient NH_4 , to persist long enough for the accumulation of excess biomass.

Previous studies have shown that the SAF and APF display extreme meridional variability around the Prince Edward islands and in adjacent waters, either combining together to form an intensive single feature, or remaining separate (Read and Pollard, 1993; Park and Charriaud, 1997; Froneman et al., 1999 cited Pakhomov et al., 1999). The latitudinal position of the SAF and APF plays an important role in controlling the conditions of inter-island productivity. When the SAF is separate and further north of the islands, ambient current speeds are low. The complex bathymetry and topographically modified disturbances to the zonal currents associated with these fronts can create low density eddies, which may be retained in the immediate downstream vicinity of the islands. Trapped circulations over the plateau prolong the residence time of the water mass, thus retaining the fresh water and reduced nitrogen within the inter-island region and

allowing blooms of large diatoms to develop on the islands' shelf (Perissinotto et al. 1990).

When the SAF migrates south and combines with the APF, a faster flowing system is set up through the islands preventing the retention of eddies. In consequence, the latitudinal variability of the SAF and APF sets up a conveyor-like system where waters rich in nutrients and primary production are being continually replenished both upstream and downstream of the islands (Pakhomov, personal communication).

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Chapter 2

INTRODUCTION

Phytoplankton biomass and photosynthesis provide the basis for transporting fixed carbon into the deep ocean by the process of direct sedimentation of cells and through particle transformation into rapidly sinking faecal pellets as a result of krill and mesozooplankton grazing on larger microphytoplankton cells. This is the “biological pump” (Volk and Hoffert, 1985; Longhurst, 1991). It provides the link between atmospheric and oceanic carbon cycles, which may ameliorate current increases in atmospheric CO₂. A major unresolved problem in biological oceanography is that of estimating the magnitude and variability of the “biological pump” which drives CO₂ draw-down from the atmosphere. Our incomplete understanding of the specific factors controlling phytoplankton distribution and nitrogen dynamics on broad spatial and temporal scales, constrains our predictive ability.

A feature of the Southern Ocean generally is that primary production is typically based on regenerated uptake by pico- and nanophytoplankton, and much lower than might be expected on the basis of available nutrients, particularly nitrate and silicate. This long-standing puzzle has become known as the high nutrient low chlorophyll (HNLC) “paradox” (Cullen, 1991). Explanations proposed to account for these observations in the Southern Ocean and elsewhere have included low surface temperatures (Jaques, 1983), light and critical depth considerations (Mitchell et al., 1991; Nelson and Smith, 1991), strong grazing pressure (Froneman and Perissinotto, 1996; Razouls et al., 1998, Atkinson et al., 2001), and the availability of macro- and micronutrients, in particular iron (de Baar et al., 1997, Boyd et al., 2000; Boyd and Law, 2001). In addition, the oceanic N:P and N:Si nutrient ratios are also important determinants of specific phytoplankton assemblages which govern biologically driven ocean-atmosphere exchanges of

CO₂ (Egges and Asknes, 1992; Laubscher et al. 1993, Sommer 1994a,b; Tyrrell and Law, 1997).

However, there are open ocean regions, which exhibit high seasonal rates of primary production; frequently in a diatom dominated fraction (Boden, 1988 cited Lucas and Probyn, 1987; Tremblay et al., 2000). These regions are usually associated with particular topographic and hydrographic features, for example, oceanic frontal regions (Dower and Lucas, 1993; Laubscher et al., 1993; Bracher et al., 1999; Tremblay et al., 2001), continental and sub-Antarctic island margins (Boden, 1988; Perissinotto and Duncombe Rae, 1990; Perissinotto et al., 1990, 1992; Atkinson et al., 2001), and at marginal ice-edge zones (Smith and Nelson 1985, 1990; Waldron et al., 1995; Bury et al., 1995; Rees et al., 1998). Such regions are associated with the greatest rates of biogenic silicate deposition in any of the world oceans. As a result, the Southern Ocean is the oceanic province which exports (to 1000m) the highest proportion (~3%) of its total production (Honjo et al., 2000), thus making it disproportionately important as a biologically mediated sink for atmospheric CO₂ in its more productive regions.

The area south of Africa is one of the most energetic and important hydrographic regions of the world oceans (Lutjeharms and Ansorge, 2001), it is characterised by the close juxtaposition of the Agulhas Front (AF), the Subtropical Front (STF), and the Subantarctic Front (SAF). This study has addressed the phytoplankton community structure surrounding Marion and Prince Edward Island, and along two transects: one from Cape Town to the Prince Edward Islands, and another northbound and reciprocal southbound transect along the Southwest Indian and Madagascar Ridge, between the Prince Edward Islands and 31°S. Particular attention has been given to the density and nutrient structure along these transects in order to interpret the observed chlorophyll distribution and export production, as a function of new production based on ¹⁵N stable isotope tracers.

METHODS

A five year Marion Island Oceanographic Survey (MIOS) has been run concurrently with the annual Marion Island relief cruise, carried out by the MV SA Agulhas. Routine annual underway transects (Marion Underway) are done between April and May of each year between Cape Town and the Prince Edward Islands to determine the variability of meandering fronts in the Southern Ocean (Pakhomov et al., 1998). During the 1999 logistics cruise (MIOS 4), an additional northbound and a reciprocal southbound transect were taken along the Southwest Indian and Madagascar Ridge, between the Prince Edward Islands and 31°S. The section crossed a number of major fronts and smaller, mesoscale features. The aim of this survey was to study the physico-biological interactions at the frontal regions. Associated with the physical survey, measurements of chlorophyll, nutrients and nitrogen uptake were made. The third component of this cruise involved a mesoscale oceanographic survey in the upstream region of the islands (along 37°E) and within the inter-island region.

The Marion Underway Transect

During the Marion Underway transect, Sippican T - 7 (760m) XBT's (expendable bathythermograph's) were deployed at 15' intervals. The XBT's were launched from a Sippican hand launcher and the data were captured using a Sippican Mk12 data acquisition system. Each probe was placed in a water bath for 5 minutes before deployment in order to minimise the difference between the probe's storage temperature and that of the sea surface temperature. The profiles were converted into two-dimensional sections in Ocean Data View (ODV) and used to determine the geographical positioning of the fronts and physical characteristics of the water column. Surface water samples at each station were taken for size fractionated chlorophyll determinations. The method used to determine chlorophyll concentration is explained later in the methods.

Northbound transect

During the northbound transect, 68 XBT's were deployed at 15' intervals (figure.3c). The temperature section obtained from this transect was used to provide a first estimate of the geographical positioning of the fronts and hence plan the CTD station spacing of the southbound leg. To identify the major features along the Madagascar Ridge section, the definitions of the frontal positions outlined by Park et al. (1993) were adopted. They defined these features using the subsurface (200m) cross frontal ranges of temperature as well as their axial values. The Agulhas Front (AF) was identified by a temperature range of 12°-16°C with a median temperature of 14°C the Subtropical Front (STF) by 8°-12°C and 10°C and the Subantarctic Front (SAF) by 4°-8°C and a median temperature of 6°C. Surface water samples at each station were taken for total and size fractionated chlorophyll determinations.

Southbound transect

The southbound section was close to the crest of the ridge running south from Madagascar to the crest of the Southwest Indian Ridge then turning south-west terminating west of the Prince Edward Islands (figure.3.d). The positioning of the frontal regions obtained from the northbound XBT transect was used to plan the CTD station spacing for the reciprocal southbound transect during which a line of 33 (2000m) CTD stations was conducted. Station spacing varied from 1° over the subtropical gyre between 31° and 37°S to every 20' over the frontal regions. The CTD rosette consisted of 12 Niskin bottles. Water samples were collected at 12 standard depths between 2000m and the surface. Bottles were triggered at 2000m, 1500m, 1000m, 750m, 500m, 250m, 150m, 100m, 75m, 50m, 25m and surface (~5m). Pressure, depth, temperature, salinity and density were available to facilitate examination and quality control of the bottle data as the sampling and laboratory analyses progressed. Productivity stations were carried out at selected locations (table.1) where a second CTD cast was performed. At each station,

light attenuation was estimated by Secchi disk. The extinction coefficient K_d was used to calculate the 100, 50, 25, 10, 1 and 0.1% light depths. The use of a Secchi disk resulted from a malfunctioning light sensor. The light depths were determined from Secchi depth estimates according to the equation:

$$Z(x\%) = \frac{Z(sd)}{1.44(-\ln(x/100))}$$

Where: $Z(x\%)$ is the depth (m) of a particular light level ($x\%$), $Z(sd)$ is the Secchi depth (m) and x is the light level to be determined.

The Inter-island Survey

XBT profiles obtained from the transect along 37°E from 47°20'E northwards were used to identify the position of the SAF in relation to the Prince Edward Islands. Within the inter-island region, XBT profiles were obtained at 20 stations together with surface size fractionated chlorophyll data (figure.3b). Ocean Data View was used to create interpolated images of temperature at the sea surface and at 200m for the Prince Edward Island region and surrounding ocean. SURFER was used to plot surface contours of temperature and size fractionated chlorophyll-a for the inter-island region.

Chlorophyll a

At the end of each CTD deployment, water was drawn from the Niskin bottles for a number of routine hydrographic analyses. A 250ml sample was obtained from those bottles at depths 0, 25, 50, 75, 100 and 150m for the determination of total and size fractionated chlorophyll-a concentrations.

Samples were screened for the >200µm fraction to exclude grazers, after which they were gently filtered (5cm Hg) through a serial filtration unit and fractionated into pico- (2.0µm), nano- (2-20µm) and micro- (>20µm) size fractions and

collected on 25mm GF/F Whatman filters. After extraction in 90% acetone for 24 hours (Holm-Hansen and Riemann, 1978), chlorophyll a was measured on an AU-10 Turner Designs fluorometer calibrated against a standard chlorophyll-a solution (Sigma).

Nutrients

For every CTD cast along the Southbound transect, 15ml samples for every set depth were stored frozen for later analysis at the UCT laboratory. Manual analyses were performed for NO_3 and Si according to the methods described in Grasshoff et al. (1983) and Parsons et al. (1984), but scaled to a 5ml sample size. Nitrate samples were diluted three times with distilled water to make up sufficient sample size for running through the cadmium column. ODV was used to create nutrient (NO_3 and Si) sections of the transect.

For each productivity station, on board analyses of ammonium and urea were carried out for each light depth in triplicate according to the manual method described in Grasshoff et al. (1983), scaled down to 5ml sample volumes.

^{15}N Incubations

Bulk water samples were obtained from each light depth and 2-litre volumes of this water were dispensed into 2-litre acid cleaned polycarbonate bottles. Spikes estimated to be 10% of ambient concentration of $^{15}\text{N-NO}_3$, $^{15}\text{N-NH}_4$ and $^{15}\text{N-urea}$ were added to one of each of the three 2-l incubation bottles. These were transferred into on-deck perspex tube incubators, which were screened with neutral density filters to simulate *in situ* light levels at the appropriate depths. Near ambient *in situ* temperatures were maintained by pumping surface seawater through the system. The samples were incubated for between 10-24 hours, centred round local midday. A more optimum strategy would generally be to employ relatively shorter incubation periods, so as to minimise bottle effects. Our objectives however, were to quantify the daily rates of nutrient uptake and since day and night incubations were not possible, longer incubation periods had

to suffice. Isotope-dilution, resulting from the production (recycling) of the traced substance *in vitro*, may lead to underestimates in the computed uptake rates (Harrison and Harris, 1986). Isotope dilution and recycling errors may be more important in the oligotrophic oceans where substrate concentrations are lower and regenerative fluxes are of proportionally greater importance (Harrison and Harris, 1986). Uptake experiments were terminated by filtration onto 47mm GF/F filters (Whatman Ltd), which were retained and stored frozen. These filters were later oven dried and analysed at the Plymouth Marine Laboratory (PML) for particulate nitrogen and atom% ¹⁵N. The analyses were performed on a Europa Tracermass continuous flow mass spectrometry (Europa Scientific Ltd.) using methods described by Barrie et al. (1989), and Owen and Rees (1989).

Nitrate urea and ammonium uptake rates were calculated according to the equations of Dugdale and Goering (1967) and expressed as rates per day:

$$PNO_3, pNH_4 \text{ and } purea \text{ (mg-at. N. l}^{-1}\text{.h}^{-1}\text{)} = (PE \times PN) / (Ro \times T)$$

Where PE = % ¹⁵N enrichment of the PON fraction in excess of the natural abundance; PN = particulate N concentration (mg-at N.l⁻¹); T = experimental duration (hrs) and Ro is the calculated aqueous ¹⁵N enrichment at time zero.

Relative preference index (RPI)

Using the nutrient data, a relative preference index (RPI) was calculated for each nutrient assimilated, e.g. for ammonium: $RPI = \frac{pNH_4}{\sum pN} / \frac{[NH_4]}{[\sum N]}$

$$\frac{\sum pN}{[\sum N]}$$

Where pNH₄ and $\sum pN$ are the uptake rates for ammonium and the sum of the uptake rates for the three nitrogen sources, and [NH₄] and [ΣN] are their ambient nutrient concentrations. RPI values of <1 reflect a relative rejection while RPI values >1 show a relative preference for that particular nitrogen resource (McCarthy et al., 1977).

RESULTS

The data obtained on the cruise have been divided into three main components. The underway transect from Cape Town to the Prince Edward Islands (figure.3a), the Northbound and southbound legs of the Northern Transect along the Madagascar Ridge (figure.3c and d), and the Inter-island survey between Marion and Prince Edward Island (figure,3b).

The Underway Transect

Temperature Distribution and Frontal Positions

The thermal characteristics of the upper 760m were established by regular expendable Bathythermograph (XBT) deployments. From this information and from the sea-surface temperature distribution, the locations of the three major fronts were established (figure.4) according to the definitions of Park et al. (1993). The Agulhas Front (AF) lay at approximately 40°S, while the STF was situated at around 43°S. The subsurface expression (200m) of the SAF was found at 45°45'S (Pakhomov et al.,1999), while the surface expression was found further north at 45° S (Ansorge, personal communication). The STF was found unusually far south compared to its mean latitudinal position of 41°40' S (Lutjeharms et al., 1985). This uncharacteristic position was most likely as a result of it being pushed further south by the warm Agulhas meander centred at approximately 42°S. This meander may have been formed by the Agulhas current, which retroflects eastward just south of the Agulhas Bank, and then meanders around the Agulhas Plateau.

Sea Surface Temperature and Chlorophyll Concentration

North of the AF, total surface chlorophyll remained low ($\sim 0.2\text{mg}\cdot\text{m}^{-3}$). Enhanced chlorophyll concentrations show a latitudinal correlation to surface temperature; enhanced concentrations coinciding with the positions of frontal systems. These fronts are marked by a large change in surface temperature over a relatively

small distance (figure.5a). Enhanced chlorophyll concentrations are found at both the northern and southern extremities of the AF, and are dominated by pico- and nanophytoplankton (figure.5b). The highest concentrations of surface chlorophyll ($0.66\text{mg}\cdot\text{m}^{-3}$) are found just south of the STF at $43^{\circ}30'S$. This population is once again dominated by the smaller pico- and nanophytoplankton (95%). Moving further south, the size structure of the population changes with a steady rise in the contribution of microphytoplankton. At the SAF, these larger cells dominate the chlorophyll peak and contribute $\sim 41\%$ to the total biomass. Microphytoplankton also dominate the peak in chlorophyll ($>56\%$) found at the most southerly station, which is in the vicinity of the Prince Edward Islands.

Northbound transect

Temperature Distribution and Frontal Positions

The track of the northbound transect along the south west Indian and Madagascar Ridge from the Prince Edward Islands to $31^{\circ}S$ and the positions of the XBT deployments (68) is shown in figure.3c). The temperature section (figure.6), which also shows bottom topography, illustrates the extent to which the ridge shallows in certain places ($<1000\text{m}$). The Agulhas Front was positioned at approximately $40^{\circ}S$ while further south, the STF was located at $43^{\circ}30'S$, further south than the range given by Lutjeharms and Valentine (1984). The AF and STF were present on this occasion as discrete fronts, most likely separated by a warm core eddy. It is probable that this feature was propagated downstream from the Agulhas retroflection zone. The suggested eddy was centred at $41^{\circ}45'S$ and the physical variables associated with this feature ($>17^{\circ}C$ and surface salinity >35.20) fell between subtropical and subantarctic water values. The presence and position of the eddy may account for the more southerly position of the STF on this transect. The SAF was located at $45^{\circ} 30'S$.

Sea Surface Temperature and Chlorophyll Concentration

Surface temperature and surface chlorophyll-a concentrations for the Northbound leg are shown in figure.7a). Within the subtropical waters north of the AF, chlorophyll concentrations did not exceed $\sim 0.2\text{mg.m}^{-3}$. To the south of the AF, maximum concentrations were 0.4mg.m^{-3} and were associated with the STF region. There was no marked change in the chlorophyll concentrations of the SAF region, although at $\sim 46^{\circ}\text{S}$, chlorophyll concentrations rose sharply to $\sim 1.6\text{mg.m}^{-3}$. This may be a result of entering the shallow water, ($<1000\text{m}$) of the Prince Edward Island plateau. Nano- and picophytoplankton dominate the surface chlorophyll biomass throughout the transect, except for the phytoplankton bloom over the Prince Edward Island plateau which was dominated by microphytoplankton; probably diatoms (figure.7b).

Southbound transect

General Hydrography

The section running from $31^{\circ}\text{S } 43^{\circ}58.55'\text{E}$ to the Prince Edward Islands once again crossed major frontal features and smaller, mesoscale features. In comparison to the earlier northbound leg, the fronts had migrated during the intervening ten days. The STF had migrated equator ward, and although the position of the AF was similar to that in the northbound leg, it had now merged with the STF. The northward shift in the position of the STF may have been the result of the eastward movement of the warm eddy feature observed previously at $41^{\circ} 45'\text{S}$.

Sloping isopycnals in the 2000m sections (figures.8,9 and 10a) at about 38°S and 40.5°S showed westwards and eastwards flow concentrated in relatively narrow bands. The westward flow at 38°S is thought to be part of a recirculation associated with a gap in the topography of the ridge (Pollard and Read, 2001). The concentrated eastward flow at 40.5°S separated Subtropical Surface Water, which is defined as lying along the TS line $15^{\circ}\text{C}-35.5$ to $24^{\circ}\text{C}-34.6$ (Darbyshire,

1966 cited Read and Pollard, 1993), from slightly fresher water found in the Agulhas Return Current. According to the Read and Pollard (1993) criteria, this would identify the position of the AF. Alternatively, according to criteria suggested by Park et al. (1993), the AF could be positioned at 40°S.

The depth of the surface mixed layer (SML) is defined by the steepest temperature gradient found at the base of the thermocline. North of the AF, surface waters exhibited relatively little temperature variability (19.5 – 22°C) and were isothermal to ~75m, which marked the upper boundary of the strong seasonal thermocline. Below this the temperature dropped sharply to <17°C at 150m (figure.8b). Water between 40.5-42.5°S is typical Agulhas Water, however to the south, from 42.5°S to 43.25°S, is a transitional region. In this region the surface layer is fresh (an Ekman layer driven north from the subantarctic zone) (figure.9b), while the central water beneath is lower in temperature (figure.8b). Temperatures at the base of the mixed layer (~80m) (about 12°C) are significantly less than those of Agulhas (15°C) or subtropical (19-20°C) water but more than Subantarctic waters (<9°C). The TS relation of this transitional region is indicative of a mixture of Agulhas Water and Subantarctic Surface Water, which has probably mixed in the retroflexion zone (Read, personal communication).

On this transect the Subtropical Front (STF) could be placed at the northern (42.5°S) or southern (43.25°S) edge of the transitional region. Both locations lie within a broad band of eastwards flow (41°S – 46°S) indicated by upward sloping isopycnals, and neither is associated with any concentration of that flow. The more northerly edge marks the greatest change in water mass characteristics and concurs with the definitions outlined by Park et al. (1993). Hence the STF is placed at 42.5°S (Pakhomov et al.1999). South of the STF, surface temperatures decrease to 8°C and the depth of the seasonal thermocline deepens to ~90m at ~45°30'S.

South of 43°S no frontal features were obvious. The water masses are typical of the subantarctic region, but potential temperature and salinity showed considerable structure superimposed on the general regime (figures.8 and 9b). There is a sequence, from north to south, of cold, fresh (44.5°S); warm, salt (45.33°S); cold, fresh (45.75°S); and warm, salt (46°S) features. Whether these were mesoscale eddies, filaments, or larger frontal structures, is not possible to determine from a single section. Such structures have been observed previously (Read and Pollard, 1993) and attributed to eddies, which often give rise to double step frontal features (e.g., Pollard and Regier, 1992 cited Read and Pollard, 1993) that can be important in driving vertical motions that bring nutrients into the surface layer (Pollard et al., 2001) enhancing primary production. South of 46°S the mesoscale structures were no longer present and the temperature and salinity characteristics were those of Subantarctic Surface Water.

North of 45°S there is a subsurface salinity minimum (~300m) associated with subducting Antarctic Intermediate Water (AAIW). However, south of 45°S the lowest salinity water is in the surface layer and continues to decrease reaching a minimum at the southern end of the section (figure.9a). According to Whitworth and Nowlin (1987), this change in vertical structure is the major identifier of the SAF and hence, for this transect it is placed at 45°S. The positioning of the SAF agrees with that of Pakhomov et al. (1999), who used definitions outlined by Park et al. (1993). Although the position of the subsurface salinity minimum appears easy to identify and label as the SAF, the lack of sloping isopycnals implies that there is no current jet associated with it.

In contrast, and according to the criteria in Read and Pollard (1993), the most likely location of the SAF is about 46°S i.e. the southern edge of the field of mesoscale structures and of the broad eastward flow. However there is no compelling evidence in the water mass Temperature and salinity structure for this location and the only clue is in the density field (figure.10b), which shows greatly

reduced stratification of the pycnocline which is a typical feature of the Subantarctic Frontal region (Read, personal communication).

Phytoplankton Distribution

Surface chlorophyll-a concentrations for the southbound transect are shown in figure.12a). In agreement with the northbound leg, chlorophyll concentrations in subtropical waters north of the AF are low (max $\sim 0.23 \text{mg chl.m}^{-3}$) but increase over the Agulhas and Subtropical Fronts to ~ 0.27 and 0.38mg.m^{-3} respectively, and to $\sim 0.74 \text{mg.m}^{-3}$ at the SAF. The bloom present at 46°S during the northbound transect was no longer evident at the same location, 10 days later.

Total chlorophyll for the water column to (150m) along the southbound transect is shown in figure.11. The section shows low chlorophyll concentrations in subtropical waters north of the STF with a deep subsurface maxima ($\sim 0.2 \text{mg.m}^{-3}$) at $\sim 75\text{m}$. This marks the upper boundary of the seasonal thermocline as can be seen in the temperature section (figure.8b). A slight increase in chlorophyll just north of the AF at $\sim 38^\circ\text{C}$ corresponds with the sloping isopycnals of the westward flow that is thought to be part of a recirculation associated with a gap in the topography of the ridge (Pollard and Read, 2001). Enhanced chlorophyll concentrations showed strong correlations with all three of the frontal regions. In the STF region, maximum chlorophyll concentrations were found in the surface waters south of the front and only reached $\sim 0.4 \text{mg.m}^{-3}$. At the SAF, maximum concentrations of $\sim 0.7 \text{mg.m}^{-3}$ were attained at subsurface depths of $\sim 50\text{m}$. The highest concentrations ($\sim 0.74 \text{mg chl.m}^{-3}$) were found over relatively shallow waters in the proximity of the Prince Edward Island plateau. South of the STF chlorophyll distribution showed considerable variation with a series of high and low concentrations. These changes in chlorophyll appear to be related to the potential temperature and salinity structure, with enhanced biomass coinciding with cold, fresh waters and visa versa. Such structures have been observed previously (Read and Pollard, 1993) and attributed to eddies.

Integrated pigment concentrations to 150m for the southbound transect (figure.12b) show peaks in the concentration of all three size classes coinciding with the latitudinal positions of the frontal regions. Picophytoplankton dominate chlorophyll distribution north of the STF by >81%, followed by nanophytoplankton (~16%) and low concentrations of microphytoplankton (2.75%) (table.2). However, south of the STF (~44°S) the phytoplankton community structure shifts in favour of the larger microphytoplankton cells, which dominate total pigment concentrations south of the SAF.

A summary of chlorophyll distribution by size-class is given in table.2. South of the SAF microphytoplankton are the dominant size class by ~53%. By contrast, between the STF and SAF, pico- (57%) and nanophytoplankton (31%) together account for ~88% of total pigment concentration, rising to >97% further north of the AF. Nano- (~15%) and microphytoplankton (3%) are largely absent in subtropical waters north of the AF. Apart from around the P.E. Island plateau, picophytoplankton are ubiquitous and the dominant fraction everywhere, extending their distribution to greater than 100m depth.

Nutrient Distribution

The nutrient distributions for nitrate and silicate are shown in figures.13a) and b). A strong horizontal gradient in the nitrate concentration is exhibited with the progression from north to south across the transect (figure.13.a), concurrent with the decreasing temperature gradient (figure.8a). Nitrate values in subtropical surface waters are low (<1mg-at⁻³) and intensify southwards, with sharp increases in concentration across the Subtropical (2-4mg-at⁻³) and Subantarctic (8-11mg-at⁻³) Fronts.

In contrast, the spatial distribution of silicate (figure.13b) is noticeably different to that of nitrate. The surface silicate values remain low throughout the transect (<2mg-at.m⁻³), with minimum concentrations at the Subtropical and Subantarctic Fronts (<1mg-at.m⁻³). However, in deeper water, and in particular between the

STF and the SAF, NO_3 and Si contours do correspond and are associated with colder water, both depicting the advection of nutrient rich bottom water into the surface layer ($\sim 43.75^\circ\text{S}$ see figures.13a) and b).

The introduction of nutrients into the surface can be attributed to upward sloping isopycnals towards the south. Moving polewards, a sequence of high and low concentrations is observed in both the silicate and to a greater extent in the nitrate concentrations. This sequence in the nutrient data matches the structure observed in the potential temperature (figure.8b) and salinity (figure.9b) sections, and supports the suggestion that mesoscale eddies may be driving the vertical motions responsible for the advection of these nutrients into the surface.

Nutrient Ratios

In open ocean waters, Redfield et al. (1963) and Dugdale and Wilkerson (1998) have demonstrated that the nutrients nitrate, silicate and phosphate are typically released in constant atomic proportions N : Si : P of 16 : 16 : 1. The NO_3 : Si ratio in particular significantly affects the driving of the diatom/non-diatom community succession, with implications for food chains and CO_2 sequestration.

In surface waters, N : Si : P will be due largely to uptake by phytoplankton in the euphotic zone. An attempt to ensure that samples came from within this zone was made by setting the sample depth at 100m north of the STF and at 75m south of the STF. Stations are grouped into different water mass regions on the basis of their temperature and salinity characteristics, giving NO_3 : Si ratios for Subtropical water (north of the AF), typical Agulhas water (between the AF and the STF), and Subantarctic water (south of the STF) (figure.14a-c).

According to the regression method used by Redfield et al. (1963), nitrate and silicate concentrations are plotted for each region and fitted with linear regressions. The slope of the regression line gives the ratio of the difference in concentration of the elements in question. However these ratios do not represent

the proportions in which the elements are available in seawater, but rather the ratios of change in their concentration resulting from biological activity. In surface waters, this ratio of change will indicate the uptake of the various nutrients during photosynthesis. The intercept of the regression line is also important. According to the relative uptake and availability of NO_3 and Si, it shows which of the two nutrients will be totally depleted before the other, and hence become limiting. This has particular special relevance to diatom production (Waldron, 1985; Smetacek, 1998).

Subtropical water north of the AF (figure.14a) and Agulhas water between the AF and the STF (figure.14b) have a NO_3 : Si regression slope of ~ 0.7 and ~ 0.5 respectively. Both are less than the predicted Redfield slope of 1, indicating a higher uptake of nitrate relative to silicate.

In subtropical surface water north of the AF (figure.14a) the NO_3 : Si regression intercept lies on the x-axis close to the origin, and gives some evidence that when NO_3 is exhausted, there remains a low concentration of Si ($\sim 0.33\text{mg-at.m}^{-3}$). (Data from two of the stations in this region (NP1 and NT_69) have been excluded as outliers. These stations had abnormally high Si concentrations and low surface NO_3 concentrations).

In Agulhas water (figure.14b), as with Subtropical water, the intercept of the regression line lies close to the origin, however, the position of intercept now lies on the Y axis, and the nutrient regime has switched to one, which is limited by Si. Once south of the STF (figure.14c) the intercept increases to $\sim 6\text{mg-at.m}^{-3} \text{NO}_3$. This high intercept value implies that Si will be exhausted before NO_3 , and provides strong evidence for the support of silicate limitation of diatom growth south of the STF. Dugdale and Wilkerson (1998) noted that nitrate uptake appears to cease when silicate concentration is $< 2\text{mg-at.m}^{-3}$. For subantarctic surface waters south of the STF this was the case (with one exception).

The $\text{NO}_3 : \text{Si}$ regression slope for the subantarctic surface water (figure.14c) is ~ 3.5 . This is much greater than Redfield's predicted slope and implies an excess of silicate uptake relative to nitrate uptake.

Phytoplankton Production

Data are presented for the nominal euphotic zone to the 0.1% light depth for six productivity stations (NP1-NP6) undertaken during the southbound transect. An exception is station NP1, which only has data up to the 1% light depth. The locations of these stations within hydrographic regions are given in Table.1. The 0.1% light depth was used to define the base of the euphotic zone because previous studies have found N uptake below the 1% light depth (Probyn et al., 1996).

Ambient Nutrient Concentrations

Ambient nutrient profiles for the six productivity stations are shown in figure.15a-f). The NO_3 profiles for stations NP1 to NP4 show minimum concentrations within the surface waters, and a rapid increase with depth once below the surface mixed layer. Stations NP5 and NP6 on the other hand have subsurface peaks in NO_3 concentration, just above the mixed layer depth at station NP5, and at 32m at station NP6. Vertical profiles for both ammonium and urea are variable, at the three subtropical stations (NP1-NP3) surface and subsurface peaks occur, but generally, their concentrations tend to be higher in surface waters than at the 0.1% light depth. At stations NP5 and NP6 the profiles are noticeably more uniform from the surface through to the 0.1% light depth.

The ambient nutrient concentrations integrated over the photic zone are shown in figure.16a-f), together with their percentage of the total nutrient concentration. Changes in the nutrient regime occur with the latitudinal progression from north to south. This phenomenon is most evident from the large nitrate concentration differentials between subtropical water in the north and subantarctic water further

south. In subtropical waters (NP1-NP3) integrated NO_3 ranges from ~20 to 60mg-at.m^{-2} and comprises between 20% and 30% of the total ambient nutrients. Its concentration continues to increase with latitude to a maximum of $1074.94\text{mg-at.m}^{-2}$ at the southern most station (NP6), where it constitutes 93.8% of the total. The only interruption in the continuity of this increase with latitude is station NP1, which has a higher integrated nitrate concentration than station NP2 and NP3. However, it is important to note that the surface mixed layer at station NP1 is very shallow (63m). Looking at the nutrient profile for this station (figure.16a) it is clear that the nitrate concentrations responsible for the high, integrated value are only present below the mixed layer depth, and surface concentrations remain characteristically low.

Ambient urea was also latitude dependant, however in this case the concentration tended to decrease with latitude. From a maximum at station NP1 ($130.15\text{mg-at.m}^{-2}$), where it comprised 68.3% of the total, to a minimum at station NP6 (11.47mg-at.m^{-2}), where it only contributed 1% to the total ambient nutrients. Unlike NO_3 and urea, ambient ammonium concentrations are variable, and do not display any obvious spatial trends. Station NP1 had the least amount of ambient ammonium (2.24mg-at.m^{-2}), and comprised only 1.2% of the total N nutrients. The highest integrated concentrations of 39.23mg-at.m^{-2} and 59.92mg-at.m^{-2} were found at the AF (stations NP3) and in the vicinity of the Prince Edward Island Plateau (station NP6). Between these two high ammonium stations were stations NP4 and NP5, which showed low amounts of ammonium (15.28mg-at.m^{-2} and 11.56mg-at.m^{-2}).

Temperature and Total Chlorophyll Profiles

Temperature and total chlorophyll profiles for each of the production stations are shown in figure.17a-f), together with the position of the surface mixed layer (SML) and euphotic depth. The profiles of the most northerly stations show a stratified water column with strong thermoclines and shallow surface mixed layers (~60-75m), which lie above the euphotic depths. To the south, the SML

deepens to below the 0.1% light depth (>80m), and the thermocline weakens. At the most southerly station (NP6) the profile has become almost isothermal. Total chlorophyll profiles for stations NP1 to NP3 show subsurface maxima that coincide with the depth of the surface mixed layer. At stations NP4 to NP6, the chlorophyll maxima are found at the surface and decline rapidly below the 0.1% light depth.

Size Fractionated Chlorophyll Distribution within the Euphotic Zone

Chlorophyll profiles for stations NP1 to NP3 (figure.18a-c) show a general decrease in concentration with depth for all three of the size classes. Subsurface peaks in concentration coincide with the depth of the surface mixed layer at each of the three stations. At stations NP4 to NP5 (figure.18d-f) the surface mixed layer is deeper than the 0.1% light depth, and has no effect on chlorophyll distribution within the euphotic zone. At station NP4, the size fractionated chlorophyll profiles are fairly uniform to the 0.1% light depth, while at station NP5 and NP6 they tend to decrease with depth. At station NP6 a subsurface peak in the concentration of micro, nano, and picophytoplankton is observed at 50m depth.

Integrated and size fractionated chlorophyll data for the productivity stations is shown in figure.19a-f). These graphs depict how the overall biomass and community structure changed with progression from north to south. Within subtropical waters of the ARC (NP1,2) total biomass was low (7.5 and $8.6\text{mg}\cdot\text{m}^{-2}$) and picophytoplankton dominated total chlorophyll by around 80%. The microphytoplankton on the other hand only accounted for 2-4% of the total. The AF (NP3) was marked by a sharp increase in biomass to $19.6\text{mg}\cdot\text{m}^{-2}$ but showed little change in the community structure. At the STF (NP4), the biomass increased slightly, but there was a shift towards nanophytoplankton (~33%), the highest percentage of the entire transect. Further south however at stations NP5 and NP6 the biomass rose to ~26 and $45\text{mg}\cdot\text{m}^{-2}$ respectively, which is attributable to the larger microphytoplankton $>20\mu\text{m}$ which dominated the

community with 58.6% and 61.4% of the total chlorophyll. These are followed by the pico- (~22%) and nanophytoplankton (~16%) size classes in terms of relative biomass.

Nitrogen Uptake

Profiles of the nutrient (NO_3 , NH_4 , urea) uptake rates for the six stations are shown in figure.20a-f). Nitrogen uptake rates were typically highest in surface waters or at the 25% light depth and decreased with depth. An exception is at station NP5 (in the vicinity of the SAF), where significant ammonium uptake at ~60m contributed to a total uptake rate at depth which was only exceeded at the 25% light depth of (9m).

The highest total nitrogen uptake rate occurred in the surface water of station NP2 ($1.49\text{mg-at.m}^{-3}\cdot\text{d}^{-1}$). Total uptake at the surface was more than six times higher than at any depth in the water column, and was dominated by ammonium uptake (~70%). From table.3 we see that the ambient NH_4 concentration in the surface water of this station is 2 to 4 times greater than its neighbouring stations and is indeed the highest concentration of NH_4 from all of the productivity stations.

Station NP3 (50% light depth, 9m) has the second highest total uptake rate ($1.39\text{mg-at.m}^{-3}\cdot\text{d}^{-1}$). Urea uptake dominated the total uptake at 60%. The only other station with comparable total uptake rates is in the surface water of station NP6 ($1.22\text{mg-at.m}^{-3}\cdot\text{d}^{-1}$) in the vicinity of the Prince Edward Islands. Here, the maximum total uptake rate is 2.5 and 5 times higher than at the previous two stations, and is once again dominated by regenerated uptake with, ammonium uptake accounting for 70% of the total N uptake. Surface and subsurface maximum uptake rates, coincide with peaks in chlorophyll concentration.

f-ratio

The relative contribution of NO_3 to total nitrogen uptake for each station can be expressed by the f-ratio, profiles (return to figure.15a-f). At subtropical stations NP1-NP3, the f-ratio coincided with the availability of ambient NO_3 , and generally increased with depth. Subsurface peaks in the f-ratio at 15m coincided with increases in ambient NO_3 and with minimum concentrations of regenerated nutrients. However, at the subtropical stations NP4 and NP5 the situation is reversed and f-ratio's decreased with depth, indicating a shift from nitrate uptake in surface waters to reduced nitrogen uptake at depths with a lower light environment. The profile for NP6, in relatively close proximity to the PE Islands and situated over the PE Island plateau may be anomalous for a subantarctic station. Here the f-ratio increased from a surface value of ~ 0.09 to a maximum of ~ 0.492 at the 0.1% light depth of 96m.

When the f-ratio is calculated for the entire water column (figure.22), a southbound latitudinal increase in the f-ratio is evident, although this too remains low. The low f-ratios for stations NP1 (~ 0.06) and NP2 (~ 0.036) are indicative of regeneration based production. A shift from regeneration production toward new production is evident from an increase in f-ratio to a maximum of 0.14 in waters adjacent to the PE Islands (NP6). Increasing nitrate utilisation with latitude is attributable to an overall increase in chlorophyll biomass, together with an increase in the proportion of microphytoplankton cells, which are more likely to utilise NO_3 (especially at the SAF and in the region of PE Islands).

Integrated Nitrogen Uptake

The integrated nitrogen uptake rates in figure.21a-f) illustrate the overall significance and percent contribution of each nutrient throughout the euphotic layer. Despite having the lowest mean total chlorophyll concentrations ($\sim 8\text{mg}\cdot\text{m}^{-2}$), the mean integrated total uptake rate at stations NP1 and NP2 in subtropical waters, was surprisingly high; $26.82\text{mg}\cdot\text{at}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (figure.21a-b). Urea and NH_4 dominated uptake, together contributing on average $\sim 95\%$ to total N assimilation.

Nitrate was relatively unimportant, contributing on average ~4.77% to the total. The AF (NP3) was marked by a tripling in water column productivity to 84.61mg-at.m⁻².d⁻¹ but was still dominated by regenerated nutrient assimilation with urea and NH₄ contributing ~46% and ~44% respectively to the total. The increased productivity is consistent with a doubling of the chlorophyll biomass to 19.6mg.m⁻² relative to stations NP1 and NP2.

The STF station (NP4) did not fit the interpretive trend. In spite of having similar chlorophyll biomass (20.7mg.m⁻²) to that at NP3, and an increase in ambient NO₃ concentration (104.1mg-at.m⁻²), integrated total uptake was low (18.23mg-at.m⁻².d⁻¹). Station NP5 within the SAF was also seemingly inconsistent having the lowest rate of integrated total uptake (7.11mg.N m⁻².d⁻¹). This was in spite of higher total chlorophyll biomass (25.8mg.m⁻²) and a higher ambient nitrate concentration (422.42mg-at.m⁻²) than at NP4.

Integrated total uptake over the PE Island plateau (NP6) revealed an increase in uptake rate (55.18mg-at.m⁻².d⁻¹), similar to that of station NP3 at the AF. These high rates are consistent with the highest integrated chlorophyll value (45.3mg.m⁻²) dominated by microphytoplankton (~61%)(table.4). Despite having the highest microphytoplankton abundance, and the highest NO₃ assimilation of all the stations (~14%), total nutrient assimilation was still dominated by NH₄ uptake (~70.6%). Urea assimilation accounted for ~15% of the total uptake and was therefore of the same order as NO₃ uptake.

Chlorophyll-a Normalised N Assimilation (pN^{*})

Following the JGOFs protocol (Sakshaug et al., 1997) chlorophyll-a normalised N uptake is denoted as pN^{*}. This provides a tenuous photophysiological link to photosynthetic efficiency although it should not be forgotten that cellular carbon:chl-a ratios and packaging is species-specific and is influenced by light and nutrient regimes (Sakshaug et al., 1997).

Chlorophyll-a normalised N uptake rates are shown in figure.24a-f. There is a general decrease in pN^* with depth for all productivity stations. This is most noticeable in stations NP1 and NP2 where the pN^* values decreased rapidly from the highest pN^* values of all the stations in the surface waters (~ 14.5 and ~ 16 mg-at N $[\text{mg chl.}]^{-1} \cdot \text{d}^{-1}$), to (~ 6.14 and 2.52 mg-at N $[\text{mg chl.}]^{-1} \cdot \text{d}^{-1}$) at the 50% light depth. Stations NP3 to NP5 on the other hand have subsurface maximum pN^* values at the 50% and 25% light depths.

Integrated pN^* values for each of the productivity stations are shown in figure.23. The contrast in chlorophyll-specific photosynthetic efficiency between subtropical and subantarctic phytoplankton assemblages is outstanding. For stations NP1 to NP3, north of the STF, the mean integrated pN^* value was approximately 5 times that of the three subantarctic stations (NP4-NP6). The highest integrated pN^* value ($3.97 \text{ mg-at N}(\text{mg chl})^{-1} \text{m}^{-2} \text{d}^{-2}$) was in the region of the AF (NP3), whereas extremely low pN^* values were associated with the subtropical and subantarctic frontal regions (NP4 and NP5).

Relative Preference Index

The relative preference index (RPI) provides a qualitative insight into the preference of a particular phytoplankton assemblage for a particular nitrogen source. This index incorporates aspects of the relative uptake rate and relative concentration of a particular nutrient and gives an indication of the physiological preference of phytoplankton for that nutrient (McCarthy et al., 1977; Probyn, 1985). An $\text{RPI} > 1$ indicates a relative preference while an $\text{RPI} < 1$ indicates relative discrimination against that nutrient. The RPI results in figure.25 confirmed the typical hierarchy of $\text{NO}_3 < \text{urea} < \text{NH}_4$, and reflects the relative energetic costs of using oxidized as opposed to already reduced sources of nitrogen.

Inter-Island Region

The contoured interpolated surface temperature in and around the Prince Edward Islands (figure.28a), and at 200m (figure.28b), give an indication of the positioning of the SAF, which lies between 46.8 and 46.9°S. The SAF is characterised by 6°C water at 200m depth, and forms the northern most boundary of the polar frontal zone. Figure.28a) reveals the SAF deflecting northwards around the islands.

The Antarctic Polar Front (APF) is distinguished by 2°C water at 200m and forms the northern boundary of the polar frontal zone. The APF was not observed on either of the Madagascar transects, however cold temperatures <2.65°C at 200m indicative of Ataractic Surface Water were encountered at 47°20'S 14 days previously during a Marion Island survey (Ansorge personal communication). The northern edge of the front can be seen in figure.28b) at 47.3°S, with 2.6°C water at 200m.

Figure.29 provides a closer view of the surface temperatures between the islands. A relatively warm body of water (surface temperatures >7°C) in the inter-island region, and to the east, in the lee of Marion and Prince Edward island was evident. Offshore, of the islands domain, colder waters (<7°C) were present. Surface temperature was closely coupled with the distribution of total surface chlorophyll (figure.30a). High chlorophyll concentrations were found in areas of warmer water.

The inter-island region had surface chlorophyll concentrations, which varied over a range of 0.11mg.m⁻³ to 2.4mg.m⁻³. This maximum concentration was four times the maximum value found in the region south of the STF. Microphytoplankton dominated the inter-island region accounting for nearly 58% of the total pigment concentration. The larger microphytoplankton dominated offshore chlorophyll distribution (figure.30b). In the shelf region to the east of Marion Island (depth

>1000m), a phytoplankton bloom was observed (Pakhomov et al., 1999) with microphytoplankton concentrations of $2.2\text{mg}\cdot\text{m}^{-3}$. The smaller nano- and picophytoplankton size classes dominated the inter-island and near shore regions (figure.30c) and d).

The temperature depth profile of station.11 between Marion and Prince Edward Island (figure.31a) illustrated a well-mixed surface layer to 60m. This surface layer had a temperature of approximately 8°C . In contrast, the profile of station.10 in the shelf region offshore from Marion Island (figure.31b) showed a much shallower surface mixed layer (30m), and a slightly cooler surface temperature (7.5°C).

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DISCUSSION

For studies of general distribution it is convenient to divide a diverse sampling area into similar provinces. A broad-scale view of the world's oceans identifies two main region types: the less productive oligotrophic regions of the open oceans, which approximate to the central parts of the oceanic gyres and the more productive eutrophic regions, coincident with the shelf seas, coastal upwelling zones and some parts of the polar oceans. In accordance with this view, and based on an analysis of the data acquired from our respective transects, two contrasting marine provinces were identified within this study, each with distinctive physical, chemical and biological characteristics. The two provinces identified are: the subtropical region north of the STF and the subantarctic region south of the STF.

Chlorophyll distribution and primary production within the various regions, requires careful explanation and revolves around four main questions. These are:

1. What are the rates of new and regenerated production and what therefore is the potential for significant particulate export?
2. How do we account for the low chlorophyll concentrations north of the STF?
3. Why chlorophyll concentrations south of the STF are lower than anticipated despite high concentrations of nitrate?
4. What mechanisms account for the elevated chlorophyll values found within the frontal regions and in the region of the Prince Edward Islands?

Interpretation of the observed chlorophyll biomass distribution and differences between the regions can result from a consideration of hydrographic influences and potentially limiting combinations of factors which include grazing control, light limitation, nutrient and iron limitation (Read et al. 2000). Even partial answers to the questions will provide a better understanding of the biophysical forcing of new and export production, together with the magnitude and variability of CO₂ draw

down from the atmosphere. Such information will contribute to the effectiveness of ocean-atmosphere Global Carbon Models (e.g. Palmer and Totterdell, 2001), and increase the predictive ability to assess climate change.

Chlorophyll distribution north of the STF

Chlorophyll concentrations in subtropical waters are low, with maximum concentrations not exceeding $0.27\text{mg}\cdot\text{m}^{-3}$. Throughout this region picophytoplankton dominate chlorophyll distribution by $>81\%$, followed by nanophytoplankton ($\sim 16\%$) and exceptionally low concentrations of microphytoplankton (2.75%) (table.2). Subsurface chlorophyll maxima are found at depths of $\sim 75\text{m}$ (figure.11), which roughly coincide with the depth of the surface mixed layer (SML) (figure.8b).

Since total incident radiation is a function of latitude (lower latitudes experiencing high light intensity throughout the year), the availability of sufficient light is not considered a limiting factor for phytoplankton production north of the AF. Our study confirms this statement for the region north of the STF, as surface mixed layer depths are shallower than the (0.1%) euphotic depths, which vary from 90 to 150m (figure.17a-c).

North of the STF is the region of warm and salty subtropical water with low nitrate ($<1\text{mg}\cdot\text{at}\cdot\text{m}^{-3}$) concentrations. However, maximum concentrations of ammonium and urea were observed in the surface waters of this region. The presence of regenerated nutrients in the euphotic zone is related primarily to *in situ* metabolic recycling by zooplankton, microzooplankton and bacteria. These high concentrations of regenerated nutrients imply, contrary to popular belief that subtropical waters are not necessarily marine deserts in terms of their biological production. The large populations of secondary and tertiary consumers (fish, marine mammals, and birds) observed in oligotrophic regions provide evidence in support of this statement.

Why then were the chlorophyll concentrations for this region so low?

One explanation for low surface chlorophyll concentrations observed north of the STF is nitrate limitation of diatom growth despite some available silicate. A similar scenario was observed to the east of our study region by Read et al., (2000a).

The productivity station data (figure.27) may clarify this statement. The integrated silicate value for station NP1 was unbelievably high and considered an outlier, its actual value has therefore not been represented on this graph. However, from Si concentrations at neighbouring stations one can confidently assume that its integrated value is $>90\text{mg-at.m}^{-2}$. Silicate concentrations at all three productivity stations in subtropical waters were high (NP1, NP2, NP3). However, despite high ambient silicate, total nitrogen assimilation remained low at station NP1 and NP2. Silicate was therefore not considered a limiting factor in respect of primary production biomass accumulation in subtropical waters. However, ambient nitrate in the euphotic layer remained low for all subtropical stations, thereby increasing its likelihood as a factor limiting primary production by diatoms within this region.

Microphytoplankton have a fast turnover rate, and the rate of remineralisation of ammonium and urea is not fast enough to support the development of diatom blooms (Malone, 1980; Chisholm, 1992 cited Tremblay et al., 2000). Microphytoplankton therefore have to rely on new sources of nitrogen to allow for increases in their population size or in production passed on to higher trophic levels (Dugdale and Goering, 1967).

The hydrographic characteristics for this region are governed by a shallow surface mixed layer (~75m), below which lies a strong seasonal thermocline (figure.8 and 10b). This permanent thermocline may create a vertical stratification

sufficient to prevent vertical transport of deeper NO_3 rich waters into the euphotic zone through means other than by shear or eddy diffusion.

Subtropical surface water north of the AF is the only water mass region with a $\Delta\text{NO}_3 : \Delta\text{Si}$ regression intercept that infers NO_3 to be more limiting than Si (figure.14a). The intercept lies close to the origin, but gives some evidence that when NO_3 is completely exhausted, there remains a small amount of Si ($\sim 0.33 \text{ mg-at.m}^{-2}$). These data support the contention that low concentrations of NO_3 limit diatom growth, and can account for the almost complete absence of microphytoplankton found in this region. The residual concentrations of silicate are typical of Subtropical Water. The subtropical gyre of the South Indian Ocean is surrounded by water of higher silicate values both to the north in equatorial regions, and to the south across the Antarctic Circumpolar Current (Read et al., 2000a).

The subsurface chlorophyll maximum observed at $\sim 75\text{m}$, was approximately coincident with the base of the surface mixed layer at each station (figure.17a-c). This raises the possibility that organisms living at the boundary between deep and surface water may take advantage of limited NO_3 diffusion across the thermocline. Albeit at a low level, the diffusive nutrient transport may be sufficient to sustain some primary productivity at this depth. Evidence in support of this suggestion is provided in the $\Delta\text{NO}_3 : \Delta\text{Si}$ ratio (figure.14a) and in the f-ratio profiles (figure.15a-c). The relative contribution of NO_3 to total nitrogen uptake is expressed by the f-ratio. In subtropical water, the f-ratio profiles were positively related (quantitatively) to those of ambient NO_3 and generally increased with depth (figure.15a-c). Thus, in deeper water in close proximity to the base of the thermocline, NO_3 uptake by phytoplankton gave a greater contribution to total uptake. The $\Delta\text{NO}_3 : \Delta\text{Si}$ ratio also suggest that nitrate is being taken up to a greater extent than silicate. This implies that most of the nitrate uptake is by phytoplankton not utilising silicate, which probably excludes diatoms. The $\Delta\text{NO}_3 : \Delta\text{Si}$ ratio therefore supports the proposed utilisation of limited nitrate diffusion

across the pycnocline by smaller nano- and picophytoplankton not requiring silicate.

Having attempted to justify the scarcity of microphytoplankton in subtropical surface water. The arguments presented still beg the question: why north of the STF the biomass of pico-and nanophytoplankton remains low, despite apparent nitrate utilisation and the highest concentrations of regenerated nutrients?

A possible explanation may be microzooplankton grazing control of biomass (Froneman and Perissinotto, 1996a).

Compared to microphytoplankton, the smaller nano- and picophytoplankton, have slower growth rates which can probably be met by the rate of nitrogen regeneration processes in surface waters. Their surface area to volume ratio also makes them more efficient (per unit chlorophyll) at nitrogen uptake than microphytoplankton, giving them an advantage in low nutrient subtropical conditions (Holm-Hansen, 1985; Probyn and Painting, 1985; Koike et al., 1986). Although small size confers competitive advantages to assimilate nutrients at low diffusion-limited ambient concentrations, it also increases susceptibility to grazing by microzooplankton (Raven, 1986). At saturating prey abundance, microzooplankton growth rates can greatly exceed those of their picophytoplankton prey (Banse, 1982), which are characterised by an intrinsically lower resource unlimited growth rate than diatoms (Martin and Fitzwater, 1988). One consequence of such grazing pressure must be significant recycling of NH_4 , and the inhibitory effects of NH_4 on NO_3 utilisation would further limit new production (Dortch, 1990).

The low f-ratios (≤ 0.1) for this region confirm that production is based primarily on nutrients recycled in the surface waters (figure.15a-c). If the turnover rate of the nano- and picophytoplankton is closely coupled to the rate of grazing by zooplankton, then predation and limited nitrate concentrations can be considered

as primary factors controlling phytoplankton biomass build up in the subtropical region north of the STF (Froneman and Perissinotto, 1996a,b; Bathmann et al., 2000).

In a subtropical marine environment such as the one considered as part of this study, where a sizeable fraction of the production has shown to be achieved through recycling, and where nano- and picophytoplankton dominate the community. The phytoplankton may be too small to be easily consumed by mesozooplankton and may therefore enter the "microbial loop". This is characterised by many steps in the food chain and inefficient energy transfer (Gifford and Dagg, 1988, 1991 cited Froneman and Perissinotto, 1996 Gifford, 1991; Michaels and Silver, 1988). In such cases, respiratory CO₂ losses are great, and only a small fraction of the organic matter is exported into the deep water (Tremblay et al., 2000).

Chlorophyll distribution south of the STF

Crossing the STF into subantarctic surface water, total chlorophyll concentrations increased and the community structure began to shift in favour of the larger microphytoplankton cells (figure.12b). Nanophytoplankton typically dominate subantarctic waters (90%) with microphytoplankton dominating only under bloom conditions (Weber and El Sayed, 1987 cited Tremblay et al., 2000). This study was in agreement in that the nano- and picophytoplankton size classes dominated south of the STF except at the SAF and over the Prince Edward Island (PEI) plateau bloom region where microphytoplankton dominated the water column community to attain the highest integrated biomass recorded (~35mg.m⁻²) for this size-fraction.

The hydrographic characteristics describing this region can be briefly stated as follows. South of the STF, the depth of the surface mixed layer gradually increased with latitude to a depth of ~110m (figure.8a). Contrasting to the

subtropical waters, the subantarctic waters show no indication of a strong thermocline below the surface mixed layer. The absence of a strong thermocline reduces vertical stability and allows deeper water to be mixed into the surface layer. South of 43°S the potential temperature and salinity sections (figures.8 and 9b) show considerable structure in a sequence from north to south, of cold, fresh and warm, salt features. These features are also apparent in the NO₃ and to a lesser extent in the Si sections (figure.13a and b), with corresponding sequences of high and low nutrient concentrations. These structures may be the result of small shear-edge eddies. Eddies shed from the Agulhas retroflection are typically comprised of warmer Agulhas Return Water and are known to move southwards, sometimes crossing the STF (Lutjeharms and van Ballegooyen, 1988). These anticyclonic eddies are approximately 200-300kms in diameter and have a deep isothermal core. Substantial heat loss and convective overturning may drive the vertical motions responsible for the entrainment of these nutrients into the surface (Dower and Lucas, 1993).

Since the supply of nutrients into the photic zone is maintained by turbulent mixing and large-scale upwelling from deeper nutrient rich waters. Nitrate availability can be ruled out as a limiting factor to phytoplankton growth south of the STF (El Sayed, 1984 cited Probyn and Painting, 1985). However, despite the dominance of the nitrogen pool by NO₃, primary production in this region is still based on regenerated nutrients as can be seen by the low f-ratios (<0.5) (figure.21), and is dominated by the smaller pico- and nanophytoplankton cells (table.2). This scenario in Southern Ocean waters represents the now well known high nutrient low chlorophyll (HNLC) paradox. Implicit in the f-ratio is a measure of that fraction of primary production, which is available for export to the deep ocean or to higher trophic levels (Probyn and Painting, 1985). The low f-ratios mean that CO₂ draw down is lower than one would expect from the potentially large NO₃ pool in this area. This has profound implications for the effectiveness of the biological pump and the global CO₂ budget, in which diatoms play a pivotal role (Smetacek, 1998).

The mechanisms responsible for maintaining phytoplankton biomass at levels of only a few percent of growth potential of this water are thought to involve a combination of physical and biological processes.

Stratification and light limitation

One such mechanism involves light limitation as a function of deep mixing and stability relationships. Subantarctic waters south of the STF show no indication of a strong thermocline and thus offer very little resistance to an increase in the thickness of the surface mixed layer, which in this region deepened to ~90m (figure.17d-f). The mixing depth was deeper than the euphotic depth (which for this region averaged at around 72m) and may have resulted in the phytoplankton experiencing an unfavourable light environment for a time sufficient to limit their productive potential (Dower and Lucas, 1993).

Nitrate uptake has previously been demonstrated to have a high light dependence in differing regions (Morel, 1991; Morel, 1991; Probyn et al., 1996), such that significant nitrate dependent growth at depth is likely to be restricted. This is reflected quantitatively in the f-ratio profiles for the subantarctic (figure.15c and d), where f-ratios decrease with depth, indicating a shift from nitrate uptake in surface waters to reduced nitrogen uptake at depth. This preferential uptake of reduced over oxidised forms of organic nitrogen in low light environments can be explained in terms of the energy expenditure associated with intracellular reduction of nitrate, and is expressed in the relative preference index (RPI) values. The active uptake of NO_3 is energetically expensive and is therefore discriminated against with respect to NH_4 and urea, which are the preferred nutrients and can be considered as energy saving. At depth, in low light intensities, regenerated nutrient assimilation is thus generally favoured over nitrate.

In summary, it can be said that light limitation will contribute to low f-ratios and low rates of new and export production. Limited microphytoplankton abundance would be expected under these circumstances. By contrast, where regenerated production prevails, the assemblage is dominated by small pico- and nanophytoplankton cells, with low or negligible sinking rates. In such light limited environments one would expect weak biological CO₂ draw-down or there may be a net CO₂ source to the atmosphere.

Preference and inhibition

It has been argued that when NH₄ is available to phytoplankton, the active transport of NO₃ into the cell is impaired. This together with a low light environment may set upper limits to new production in nutrient rich grazing balanced environments (Wheeler and Kokkinakis, 1990, Dortch, 1990). These conditions were present in this study and are made manifest by the integrated values of the f-ratios (figure.22), which were typically lower than might be expected on the basis of ambient NO₃ concentrations. The interaction between the uptake of nitrate and ammonium has been separated into two distinct processes: an indirect preference for ammonium and a direct inhibition of nitrate uptake (Dortch, 1990). The indirect preference for NH₄ is expressed in the RPI results (figure.25), which confirms the typical hierarchy of preference for NH₄ > urea > NO₃. Preference for reduced over oxidised forms of nitrogen is hypothesised to be maximal under low light and nutrient deficiency, whereas inhibition will be maximal under conditions of low light and nutrient sufficiency (Dortch, 1990). The relationship between regenerated nutrient concentration and both NO₃ uptake and the f-ratio found in this region (Garside, 1981; Smith and Harrison, 1991) suggests that high regenerated nutrient concentrations (~3mg-at.m⁻³) are able to inhibit NO₃ uptake and reduce the f-ratio (figure.26).

Silicate limitation

Another possible macronutrient, responsible for setting upper limits in new production within the Southern Ocean is silicate (Si), which may be present in

concentrations below the threshold for phytoplankton growth (Allanson et al., 1981; Jacques, 1989; Verlencar et al., 1990 cited Laubscher et al., 1993). Dugdale and Wilkerson (1998) note that nitrate uptake appears to cease when silica concentrations are less than 2mg-at.m^{-3} . For subantarctic surface waters south of the STF this proved to be the case for all Si concentrations (with one exception) and lends credence to the possibility of Si limitation of phytoplankton biomass.

In open ocean waters, Redfield et al. (1963) and Dugdale and Wilkerson (1998) have demonstrated that the nutrients nitrate, silicate and phosphate are typically released in constant atomic proportions $\Delta\text{N} : \Delta\text{Si} : \Delta\text{P}$ of 16 : 16 : 1. Since Antarctic diatoms have high cellular ratios Si:C and Si:N, they require high silicate concentrations to achieve their optimal growth (Jacques, 1989). The $\Delta\text{NO}_3 : \Delta\text{Si}$ ratio in particular significantly effects the driving of the diatom/non-diatom community succession, with implications for food chains and CO_2 sequestration. The $\Delta\text{NO}_3 : \Delta\text{Si}$ regression slope for the subantarctic surface water is ~ 3.5 (figure.14c). This is much greater than Redfield's predicted slope and clearly implies an excess of silicate uptake relative to nitrate uptake. The intercept of the regression line at $\sim 6\text{mg-at.m}^{-3}$ NO_3 , means that Si will be exhausted well before NO_3 , and provides strong evidence for the support of silicate limitation of diatom growth south of the STF.

Further evidence is provided in that despite an increase in ambient nitrate from STF (NP4) to the SAF (NP5), the total uptake rate actually decreased, which confirms that ambient nitrate concentrations are not a factor limiting primary production in subantarctic waters (figure.27). It is only over the Prince Edward Island plateau (NP6) where silicate concentrations show such a significant increase, that primary production increases and subsequent blooms of microphytoplankton can occur.

Fe limitation

The oceanic regions of the Southern Ocean are among the most iron impoverished in the world because of the absence of land masses, which contribute iron through run-off and airborne dust (Martin and Fitzwater, 1988; Martin, 1990; Martin et al., 1990). Evidence suggests that Antarctic phytoplankton may have iron deficiencies, which inhibit nitrate uptake and reduction within the diatom cells. This prevents them from blooming and using up the potential supply of nutrients present in Southern Ocean waters (Martin and Fitzwater, 1988, Martin et al. 1989,1990). Such iron limited nitrate assimilation by diatoms cannot be excluded as a viable mechanism for explaining their relative paucity south of the STF. However, we have no data for this region to further explore this issue.

Enhanced Biomass and Productivity at Ocean Fronts

Elevations of surface chlorophyll concentrations were correlated with the frontal regions on both the Northbound and Southbound transects (figure.7 and 12). The distribution of integrated chlorophyll during the southbound leg showed a significant peak just south of the STF, whereas peaks of lesser magnitude are associated with the SAF and the AF (figure.12b).

This gives an indication of the importance of frontal features, not only as physical boundaries, but also as specific areas of enhanced biological activity.

It is, however, possible that the enhanced chlorophyll concentrations at the fronts are the result of a decrease in loss rates, via reduced mortality or horizontal convergence, which is believed to concentrate buoyant, non-motile organisms at fronts, and is not due to enhanced primary productivity (Ainley and Jacobs, 1981; Olson and Backus, 1985 cited Allanson and Parker, 1983; Heywood and Priddle, 1987; Franks, 1992).

Such mechanisms would lead to a decaying population at the fronts; however, Laubscher et al. (1993) found blooms at three oceanic fronts (STF, SAF and APF) that were strongly dominated by specific size classes and species. This suggests that the increase in biomass was probably the result of enhanced *in situ* production by selected components of the phytoplankton assemblage, rather than by accumulation of cells through hydrographic forces (Laubscher et al., 1993). One may conclude that phytoplankton populations at fronts are probably thriving for specific environmental reasons, and have not been accumulated there as part of the average advection patterns of the sea surface (Allanson and Parker, 1983; Dower and Lucas, 1993; Laubscher et al., 1993; Bracher et al., 2000; Tremblay et al., 2001). The combination of strong horizontal temperature gradients, nutrient gradients, current velocities and sharp but shallow pycnocline boundaries tend to create the dynamical conditions most favourable to stimulate phytoplankton growth (Read et al., 2000a).

Biological activity at fronts has furthermore been shown not to be restricted to lower trophic levels. Atkinson and Targett (1983) have demonstrated a relationship between fish distribution and upwelling along a front, and Ainley and Jacobs (1981) have reported affinities between seabirds and certain fronts in the Southern Ocean. Fronts also seem to be preferred areas of spawning for krill, the main Antarctic macro-zooplankton (Tranter, 1982).

The Agulhas Front

The AF (NP3) was marked by a doubling in chlorophyll biomass (figure.16) and a 3-fold increase in water column productivity, (figure.21) (relative to stations NP1 and NP2). Little change is seen in the community structure, which is consistent with surrounding subtropical waters and dominated by picophytoplankton (~80%) with fewer nanophytoplankton and almost no microphytoplankton (figure.16).

It has already been established that subtropical surface waters are thermally stable and stratified to an extent, which prevents the advection of nutrients into

the surface waters. However, two mechanisms are potential candidates for the introduction of NO_3 into the surface mixed layer at the AF. This may account for the increase in integrated NO_3 concentration from $\sim 19\text{mg-at.m}^{-2}$ at the previous station (NP2) to $\sim 32\text{mg-at.m}^{-2}$ at the AF (NP3), and ultimately for the biological enhancement observed in this region.

The Agulhas Current is known to form part of a shelf current exhibiting meanders on various scales (Grundlingh, 1979; Lutjeharms et al., 1981). The presence of upwelling in the lee of such meanders may cause a flux of nutrients into the euphotic zone, potentially resulting in significant increases in phytoplankton production.

The second mechanism takes into consideration the kinematic nature of the Agulhas Current. Lutjeharms et al. (1985) stated that organisms living in the border-mixing area of a fast flowing current would experience a continuous but low level of nutrient replenishment. This might be sufficient to sustain a higher primary productivity in areas of strong horizontal shear.

What prevents the chlorophyll biomass at the AF from reaching concentrations as high as those at the STF and SAF?

Primary production in subtropical waters is limited by the supply of NO_3 and therefore relies on regenerated nutrients, which constrains the phytoplankton population to small cells. Microzooplankton growth rates can greatly exceed those of their picophytoplankton prey (Banse, 1982; Raven, 1986; Froneman and Perissinotto, 1996). They are thus capable of cropping the phytoplankton population at a rate that can equal or exceed cell division rates (Frost, 1991; Banse, 1992), thereby preventing an increase in phytoplankton biomass, but at the same time, contributing to potential phytoplankton ammonium excretion (Glibert et al. 1992). An increase in phytoplankton population size would require

larger and faster growing microphytoplankton capable of escaping from significant zooplankton grazing pressure (e.g. Dubischar and Bathmann, 1997).

However, why does the increase in NO_3 at the AF fail to encourage any change in the phytoplankton community structure, which continues to be dominated by small picophytoplankton cells?

It is suggested that the replenishment of NO_3 is taking place at a slow rate and at depth. Small cells are better adapted to low light environments, and their surface area to volume ratio makes them more efficient than microphytoplankton at nitrogen uptake. Picophytoplankton thus out-compete the larger cells in low nutrient conditions and remain the dominant size class at frontal regions within subtropical waters despite an increase in new production (Dower and Lucas, 1993; Tremblay et al., 2000)

Why are uptake rates at the AF faster than those at the STF and SAF where chlorophyll biomass is much higher?

Low ambient nitrate may limit the development of microphytoplankton and the size of the population at the AF front. However, the nitrogen requirements of the slow growing picophytoplankton, which dominate here, are satisfied by the preferred, energy saving assimilation of regenerated nutrients.

These phytoplankton cells are photosynthesising efficiently in a high light, Si and regenerated nutrient environment. Some evidence is given in the integrated chlorophyll-a normalised N uptake rates (figure.23), which provide some basis for a photophysiological link to photosynthetic efficiency. Station NP3 at the AF has the highest chl-a normalised photosynthetic rate of all the productivity stations, which may explain the higher nutrient uptake rates found there. On the contrary, phytoplankton new production at the STF and SAF (NP4 and NP5) is limited by light as a function of deep mixing, high NH_4 concentrations, low Si and possibly

low Fe concentrations. Their chlorophyll-a normalised N uptake rates are the lowest of all the productivity stations. This confirms that despite the high biomass found at these fronts, the phytoplankton are probably not photosynthesising at maximum efficiency relative to those at the AF. However, without appropriate P vs. E experimental data, the light dependent physiological response of phytoplankton to the ambient underwater light regime remains rather speculative.

The Subtropical Front

Previous cruises studying the distribution of chlorophyll across frontal boundaries have shown the STF to have consistently high rates of biological activity (e.g. Barange et al., 1998). CZCS composite data have also shown that phytoplankton pigment concentrations for this region are high all year round (Weeks and Shillington, 1994). Enhanced productivity has been recorded most often at the northern boundary between subtropical and subantarctic waters (Plancke, 1977 cited Allanson and Parker, 1983; Lutjeharms et al., 1985; Laubscher et al., 1993) however this study shows a peak in chlorophyll concentration to the south of the STF (figure.12b). Total pigment concentrations are dominated by pico- and nanophytoplankton, while microphytoplankton are largely absent. A community such as this (NP4) is based on regenerated nutrients, utilising urea (56.5%) and NH_4 (37.6%) rather than NO_3 (5.9%) (figure.21). These observations imply little particle export and biological draw-down of CO_2 at the STF for this study at least.

Three possible mechanisms explaining the biological enhancement at convergent fronts such as the STF have been put forward. The first, being due to advective processes only, is considered the least likely explanation. The latter two refer to cross-frontal mixing.

The mixing of nutrient-rich Sub-Antarctic Surface Water northwards across the STF may have biologically significant consequences in transporting nutrients from the well-mixed side of the frontal boundary to the more stratified side. This increase in supply of nutrients would favour primary production and perhaps

explains the major chlorophyll increases found to the north of the STF in various other studies (Plancke, 1977; Allanson et al., 1981; Lutjeharms, 1985).

Similarly, conditions favourable to increased primary production may also be created by the mixing of warm, nutrient poor water southwards across the STF causing an increase in density stratification in the upper layers. Read et al. (2000a) have suggested that the combination of warm but nutrient depleted subtropical water and the cooler but nutrient replete subantarctic water meeting at the STF positively influences mixed layer depth, thermal stratification and the nutrient environment. Flooding from the north could be aided by the meandering nature of the STF and consequent northward movement of the front, but is restricted to the near surface layers. This enhancement in vertical stability causes retention of phytoplankton in the euphotic zone and subsequent biomass accumulation associated with or just south of the STF and its' meandering. Meandering, or meridional displacement of water, appears to occur at irregular localities along the STF creating patches of high biomass (Weeks and Shillington, 1994).

This particular mechanism of biological enhancement could explain the peak in chlorophyll pigments found to the south of the STF on the southbound leg of this cruise (figure.12b). It has been shown that the frontal systems in the Southern Ocean are subject to major changes, and the STF south of Africa has been described as one of dramatic variability (Lutjeharms et al., 1985). During the northbound leg, the STF was situated at 43°30'S (figure.6), whereas on the southbound leg (figure.8a), 10 days later, the STF had shifted northwards to 42° 30' S. This northward movement of the front by 1 degree may enhance the input of warm water from the north, thereby promoting vertical stability and enhanced biomass south of the front.

If elevated pigment concentrations associated with ocean fronts are the result of favourable dynamical conditions, then enhanced primary productivity rates would

indicate a thriving population. This was not the case at 43°S (NP4) within the chlorophyll bloom south of the STF, where the productivity results show very low nutrient assimilation rates (figure.21). Furthermore, the temperature profile for this station shows no indication of enhanced vertical stability and the mixed layer depth is well below the 0.1% light depth (figure.17). The very low integrated chlorophyll-a normalised N uptake rate for this station (figure.23) implies that the population is not photosynthesising as efficiently as it might be. The results suggest that cross-frontal mixing of subtropical water southwards across the STF was not the appropriate mechanism responsible for this particular peak in chlorophyll pigments found south of the STF on the southbound leg of this cruise.

An alternative explanation of the chlorophyll peak situated one degree south of the STF could be that it represents a senescent phytoplankton population. The zone of peak production associated with the front having migrated one degree further north.

The temperature section for the Northbound transect located the STF at 43°30' S 10 days previously. A decrease in surface temperature across the front from 17.22°C at 43° 15' S to 13.85°C at 43° 45' S coincides with a two fold increase in the surface total chlorophyll from 0.18-0.36mg.m⁻³ (figure.7a). One may infer that the physico-chemical characteristics associated with the STF at this time favoured enhanced productivity and can account for the increase in surface chlorophyll across the front. Shallow surface mixed layer depths (~30m), and increased vertical stability (figure.6) supports mixing of subtropical water southwards across the front, as the mechanism responsible for creating the conditions favourable for increased production and subsequent biomass south of the STF on the Northbound transect.

However, with the migration of the STF further north, the favourable conditions associated with the front, which are responsible for initialising and essential in maintaining enhanced productivity and biomass are no longer present at this

location (43°30' S). Apart from light limitation through deep mixed layer depths, phytoplankton growth at this station is also limited by low Si concentrations. The integrated Si concentration (figure.27) for the euphotic layer of station NP4 confirms low silicate concentrations, which most likely limits diatom growth and the uptake of available nitrate (apparent in low integrated f-ratio in figure.22). The low assimilation rates and poor photosynthetic efficiency (figure.23) within the chlorophyll bloom at 43°S (NP4) supports this theory, which suggest that since conditions are no longer favourable, production has become limited and the population is in a state of decay.

The Subantarctic Front

A peak in chlorophyll concentration coincides with the position of the SAF at 45°S (figure.12b). Total biomass is only slightly higher than at the AF and STF, however the community structure is significantly different (figure.19). Once south of the chlorophyll peak associated with the STF, microphytoplankton biomass begins to increase together with their percentage contribution to total pigments. The chlorophyll peak at the SAF is the first population in which microphytoplankton are the dominant size class (>58%).

Microphytoplankton frequently rely on new sources of nitrogen to support increases in their population size (Dugdale and Goering, 1967). The upward sloping isopycnals for NO_3 at the SAF (figure.19a) indicates an advection of nutrient (NO_3 and Si) rich deep water into the surface layer. This would stimulate new production and cause an increase in diatom biomass, if zooplankton grazing is ineffective; a scenario the results from this study support. A study by Laubscher et al. (1993) also concluded that a microphytoplankton bloom associated with the SAF probably occurred as a result of cross frontal mixing of silicate into the surface layer. The SAF is therefore a potentially important open ocean site where subsequent sinking of diatom frustules provides a downward flux of biogenic silica, and probably carbon, into the ocean interior.

Despite the bloom in microphytoplankton (figure.19) and the increase in percentage new production at the SAF, station NP5 shows very low total nitrogen uptake rates (figure.21). What are the factors limiting primary production at the SAF?

Antarctic diatoms have high Si:N ratios and require high silicate concentrations to achieve their optimal growth (Jacques, 1989). Such an increase in new production and diatom biomass (which is associated with the SAF) would have required an increased uptake of silicate. There is some evidence for this in the Si section (figure.19b) where peaks in microphytoplankton at the SAF coincide with the depletion of silicate in the euphotic surface layer.

The uptake of nitrate by diatoms is energetically expensive and requires a high light environment (Probyn et al., 1996 cited Read et al., 2000a). The temperature profile for station NP5 (figure.17) indicates a very well mixed layer greater than 150m, which is nearly 3x the 0.1% light depth (53m). Light limitation as a result of a deep mixed layer, and the depletion of Si, which limits new production, might contribute to the low uptake rates in the diatom bloom at this station.

Enhanced Biomass and Production in the Prince Edward Inter-Island Region

The physico-chemical parameters responsible for enhanced production and phytoplankton biomass associated with the Prince Edward archipelago, compared to the surrounding open ocean, have been thought to be due to an "island mass effect" (Allanson et al., 1985). Similar enhanced productivity associated with South Georgia is well documented and for review, see Atkinson et al. (2001). However, do the inter island results from this study provide any evidence in support of the supposed "island mass effect"?

Chlorophyll concentrations in this region were relatively high, with surface maximum values four times those of its neighbouring region south of the STF. At the productivity station (NP6) in the vicinity of the Prince Edward Island (PEI) shelf, microphytoplankton dominate the community to the extent of 61.4% and attain the highest integrated biomass recorded ($45.3\text{mg}\cdot\text{m}^{-2}$) for this size fraction, followed by pico- and nanophytoplankton in relative abundance (figure.19). Surface and subsurface maximum uptake rates (figure.20f) coincide with maximum chlorophyll concentrations (for all three size classes) (figure.18f), and are 2.5 and 5 times higher than at the STF and SAF. Total integrated nitrogen uptake for this station (NP6) is high (figure.21), second only to the AF (NP3) and dominated by NH_4 assimilation (~70.7%) with the highest rates of uptake for this nutrient of all the productivity stations. Similar observations have been made previously (e.g. Boden, 1988; Perissinotto et al. 2000).

The increase in chlorophyll concentrations and primary production around the Prince Edward Islands confirms the general validity of an "island mass effect" (Boden, 1988). The surface temperature distribution (figure.28a) shows the SAF as a single front, steered by the shallow bottom topography of the region, and deflecting northwards around the islands.

In warmer waters, closer to the shore and between the islands (figure.29), the phytoplankton population was dominated by the smaller pico- (~26%) and nanophytoplankton (~16%) size classes (figure.30c and d). Further offshore but within the islands' domain colder waters were encountered. Although diatoms dominated total surface pigments for the inter-island region as a whole (~58%), their abundance was somewhat restricted to populations further offshore (figure.30b). Microphytoplankton distribution mirrors that of surface temperature (figure.29), bloom concentrations coinciding with colder waters.

Smith (1987 cited Ismail, 1990) stated that due to the high annual rainfall, guano gets dissolved and carried out into sea via run-off, spreading out from the islands and giving rise to enhanced concentrations of reduced nitrogen in near shore areas. The flux of fresh water in the inter-island region decreases the density of the surface mixed layer, with consequential local increase in water column stability (Perissinotto et al., 1990; Duncombe Rae, 1989). Figure.29, revealed a relatively warm body of surface water between the two islands providing evidence of trapped circulation over the inter-island plateau (see also Perissinotto et al., 2000). Whilst being trapped, these waters were thermally enhanced, from the surface allowing an even more stable, stratified water column to develop. A temperature profile from within the nanophytoplankton bloom (figure.31a), provided further evidence in support of enhanced vertical stability, with a well developed surface mixed layer of thermally enhanced ($\sim 8^{\circ}\text{C}$) water to $\sim 60\text{m}$. This enhancement in vertical stability causes retention of phytoplankton in the euphotic zone and subsequent biomass accumulation.

In an environment such as this, high NH_4 concentrations could potentially inhibit the uptake of nitrate and new production in surface waters (Dortsch, 1990). The particulate nitrogen pool becomes more and more based on regenerated nutrients through microzooplankton grazing and bacterial degradation of organic substrates and is reflected in the highest rates of uptake for NH_4 . Unlike microphytoplankton, production within the nano- and picophytoplankton size class is satisfied by the assimilation of regenerated nutrients without resorting to nitrate. Their surface area to volume ratio also makes them more efficient at nutrient uptake than diatoms, allowing them to out compete the larger cells, which explains their dominance in waters nearer the shore and between the islands (Koike et al., 1981,1986; Holm-Hansen, 1985; Probyn and Painting, 1985).

Further offshore, microphytoplankton dominate total chlorophyll (figure.30a), with bloom conditions occurring in the shelf region to the east of Marion Island, as has

been recorded previously (e.g. Boden, 1988). The temperature profile for a station within the diatom bloom shows slightly cooler surface temperatures of 7.5°C, and a shallower surface mixed layer of (~30m). The upward sloping isopycnals over the P.E.I plateau (figure.19a) indicates an advection of cold, nutrient (NO₃ and Si) rich (Antarctic Intermediate Water) into the surface layer. This would stimulate new production and cause an increase in diatom biomass. A shallow surface mixed layer above the 0.1% light depth allows the phytoplankton population to grow in a relatively high irradiance environment. With the high light and nutrient (NO₃, Si) requirements of nitrate assimilation being met, faster growing microphytoplankton can out compete the smaller cells thereby increasing the size of their population or production passed on to higher trophic levels (Malone, 1980; Chisholm, 1992 cited Tremblay et al., 2000). Thus the presence of diatom blooms and their ability to dominate phytoplankton populations offshore from the islands can be accounted for.

The last productivity station of the Southbound transect NP6 was in the shelf region just north of the Prince Edward Islands. The f-ratio profile for this station is rather anomalous for a subantarctic station in that the f-ratio increases with depth. From low f-ratios in surface waters (~0.09), where regenerated production dominates, to a maximum value (~0.49) at the 0.1% light depth (96m). This apparent paradox may be explained in the close proximity of this station to the Prince Edward Islands. The flux of fresh water run-off, spreading out from the islands gives rise to enhanced concentrations of reduced nitrogen in surface waters. It is generally believed that NH₄ recycling and high ambient NH₄ concentrations can inhibit or repress nitrate uptake by phytoplankton (Dortch, 1990). A possible explanation for the low surface f-ratios observed at this station may be direct inhibition of nitrate uptake by ammonium, which is hypothesised to be maximal under conditions of low light and nitrogen sufficiency (Dortch, 1990). The temperature and nutrient sections (figure.13a and b) show corresponding, sloping isopycnals over the P.E.Island plateau, depicting the advection of cold nutrient rich bottom water towards the surface. In deeper waters of station NP6

an increase in the supply of nitrate and silicate will favour new production and diatom growth and can thus account for the higher f-ratios at depth.

Diatom dominated communities such as these are likely to result in a short food chain, with efficient energy transfer to higher trophic levels and minimum respiratory CO₂ losses. This cycle is based principally on new production, where a large fraction of the organic matter is exported into deep water through the rapid sinking of large diatom cells (Jacques, 1989). Having the highest integrated f-ratio verifies the importance of nitrate in primary production for the inter-island region. The ability of the Prince Edward Island Seas to provide and sustain diatom dominated communities, significantly affects the avifauna and benthic community as well as the “biological pump” by strengthening the CO₂ “sink” of the region.

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CONCLUSIONS

An analysis of the data from this survey revealed two regions of contrasting characteristics. The most conspicuous changes in chemical, physical and biological variables occurred at the STF, which separated the two regions. To the north, a warm, salty, highly stratified water column with low nitrate concentrations distinguished the region of the South Atlantic subtropical gyre, while the region south of the STF was characterised by cold nutrient-rich Subantarctic Surface Waters of the Southern Ocean. The third component of this study was the Prince Edward Inter-Island region, whose waters are influenced by the "island mass effect" causing enhancement of water column stability and increased levels of reduced nitrogen in surface waters surrounding the islands.

Subtropical waters were characterised by low concentrations of small phytoplankton cells and very low f-ratios, indicating productivity based almost entirely on recycled ammonium and urea. It is thought that the strong seasonal thermocline present in this region may create a vertical stratification sufficient to prevent vertical transport of deeper nitrate into the euphotic zone, thereby limiting diatom growth. The potential to accumulate biomass was however, thought to be controlled by microzooplankton grazing. In subtropical marine environments such as these, energy transport within the food chain is inefficient, this together with the low sedimentation rates of smaller flagellated algae means that export production and CO₂ draw down is minimal.

Crossing the STF into subantarctic surface water, total chlorophyll concentrations increased and the community structure began to shift in favour of the larger microphytoplankton cells. Nano- and picophytoplankton however, still typically dominate subantarctic waters with diatoms dominating only under bloom conditions. South of the STF, the supply of nutrients is maintained by turbulent mixing and large-scale upwelling. However, despite the dominance of the nitrogen pool by nitrate, primary production in this region is still based on

regenerated nutrients as can be seen by the low f-ratios. This scenario in Southern Ocean waters represents the high nutrient low chlorophyll (HNLC) paradox. The results from this study favour the possibility of silicate limitation of new production, and light limitation resulting from the combination of shallow euphotic depths and deep surface mixed layers as the two mechanisms which exert the most control on primary production in subantarctic waters. However, since information on macrozooplankton biomass and iron concentration for this study was not available, these hypotheses can only be considered as possible explanations. The low f-ratios mean that CO₂ draw down is lower than one would expect from the potentially large NO₃ pool in this area. This has profound implications for the effectiveness of the biological pump and the global CO₂ budget, in which diatoms play a pivotal role (Smetacek, 1998).

It is important to note that at a given point in time and space a phytoplankton bloom may eventually succumb for just one reason, e.g. a shortage of either, nitrate, a trace element, light, or intense grazing pressure. However for the many and various ecosystems integrated over time and space, control by just one single factor would appear most unlikely (de Baar et al., 1990).

Increased concentrations of microphytoplankton cells and rates of new production did however occur at oceanic frontal regions, and at bloom conditions in the Prince Edward Island region. In this study, the most likely factors favouring increases in phytoplankton biomass and production are thought to be the hydrographical conditions of water column stabilization in the upper layers, and an increase in dissolved nutrients (NO₃, Si) into surface waters, which probably stimulate phytoplankton growth rates especially diatoms. Open ocean regions such as these provide important areas for the export of carbon into the deep sea (biological pump) and associated draw down of CO₂ from the atmosphere.

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FIGURES

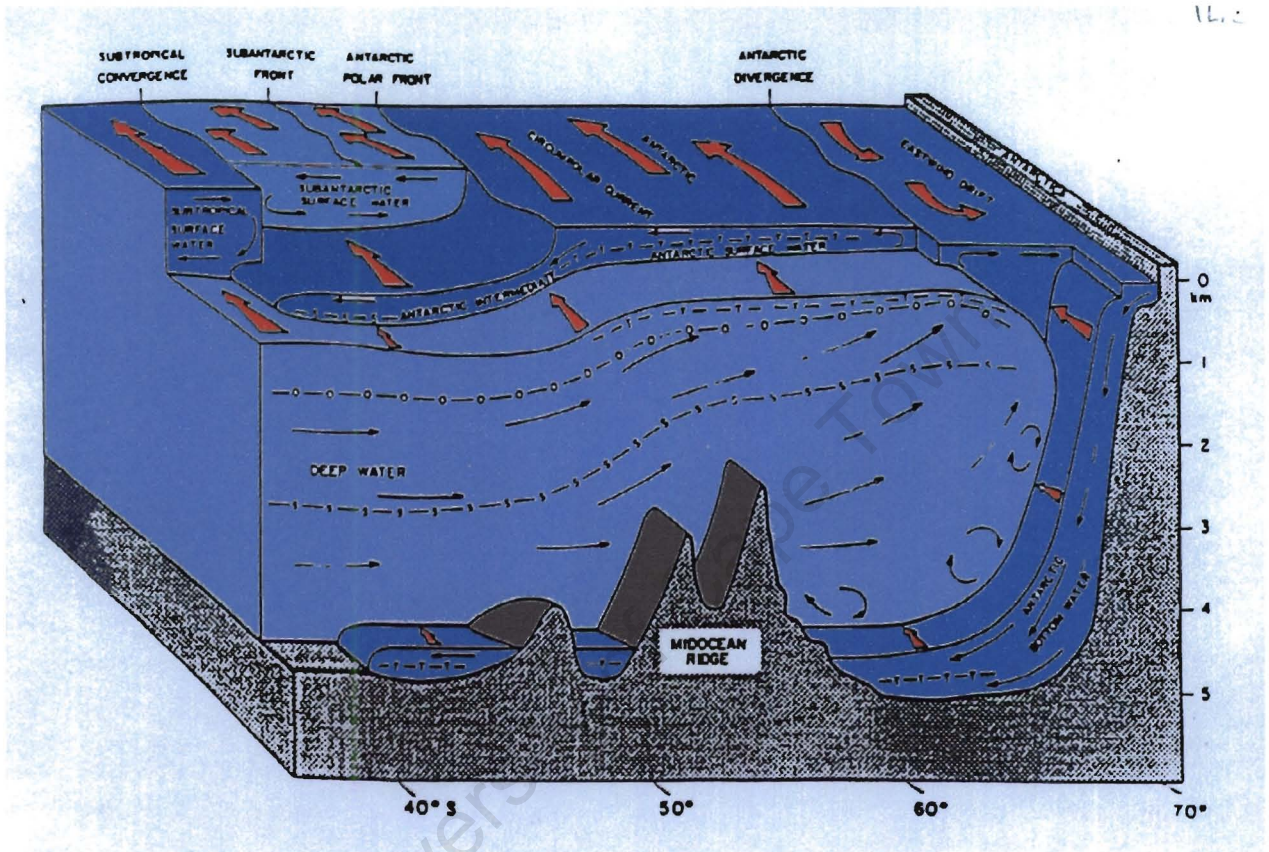


Figure. 1. Schematic presentation of water types and their movements, frontal zones and hydrographic variable maxima and minima in the Southern Ocean sector south of Africa. Red arrows indicate lateral movement while black line arrows inferred vertical movement. (Lutjeharms et al., 1985).

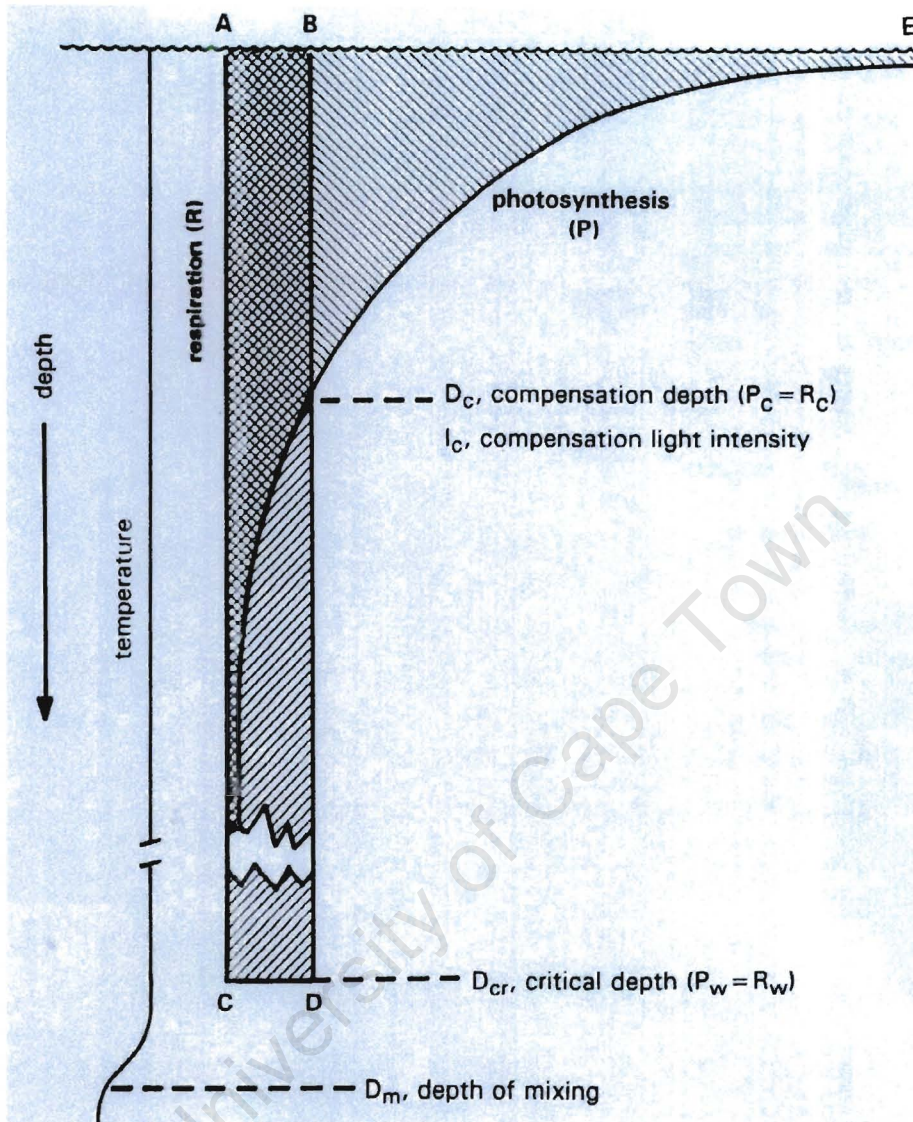


Figure. 2. An illustration of the relationships between the compensation light depth (D_c), the critical depth (D_{cr}), and the depth of mixing (D_m). The area bounded by points A, B, C and D represents phytoplankton respiration, and the area bounded by points A, C and E represents photosynthesis; these two areas are equal at the critical depth. When the critical depth is less than the depth of mixing (as illustrated in this figure), no net production takes place because photosynthesis throughout the water column is less than respiration. (Sverdrup, 1953).

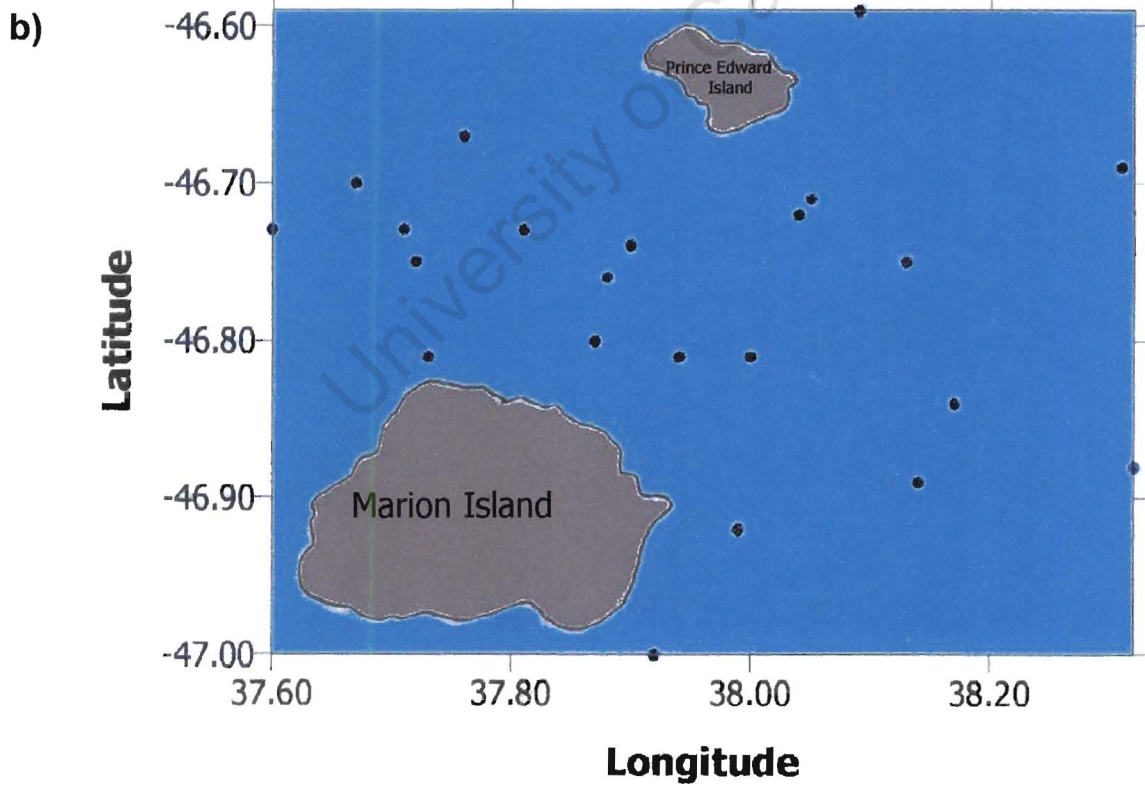
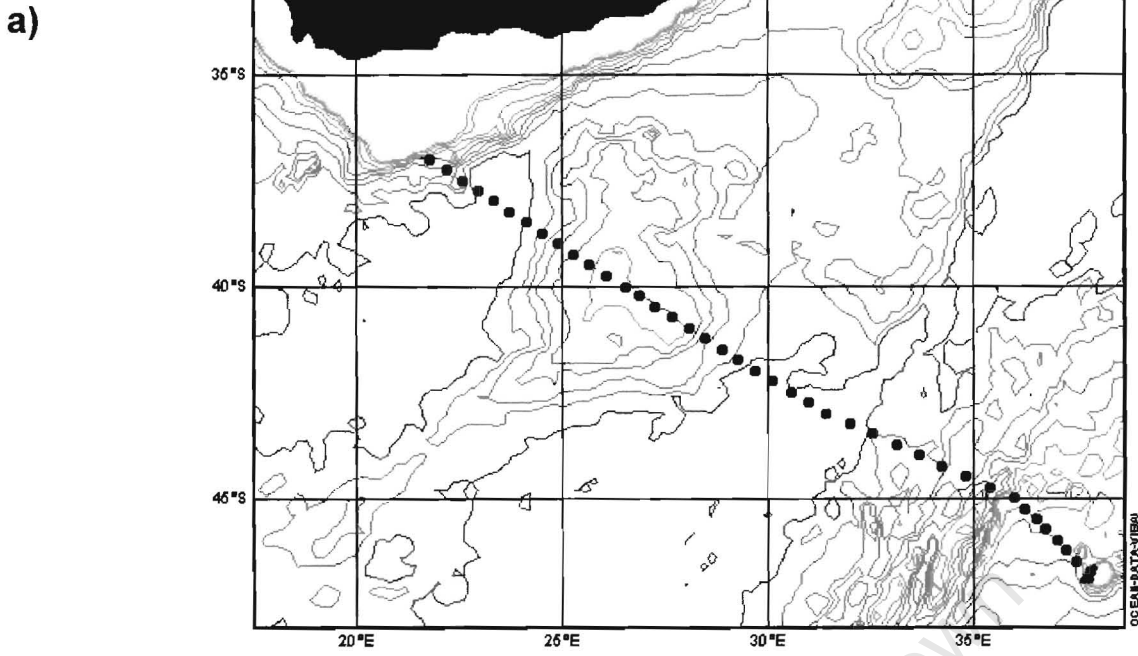


Figure. 3a) Cruise track and XBT station positions for the Marion Underway transect from Cape Town to the Prince Edward Islands and **b)** the positions of sampling stations for the Prince Edward Inter-Island region.

c)

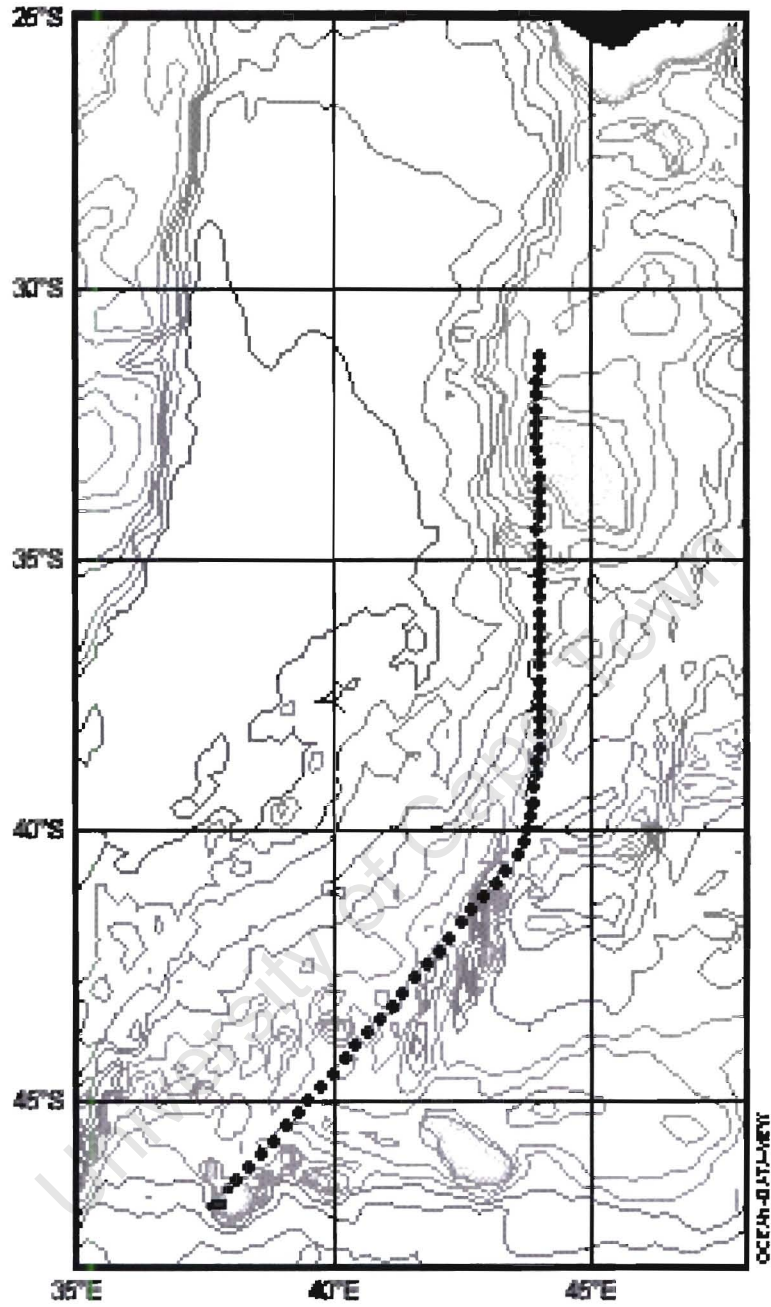


Figure. 3c) Cruise track and XBT station positions for the Northbound leg of the Northern Transect from the Prince Edward Islands to 31°S.

d)

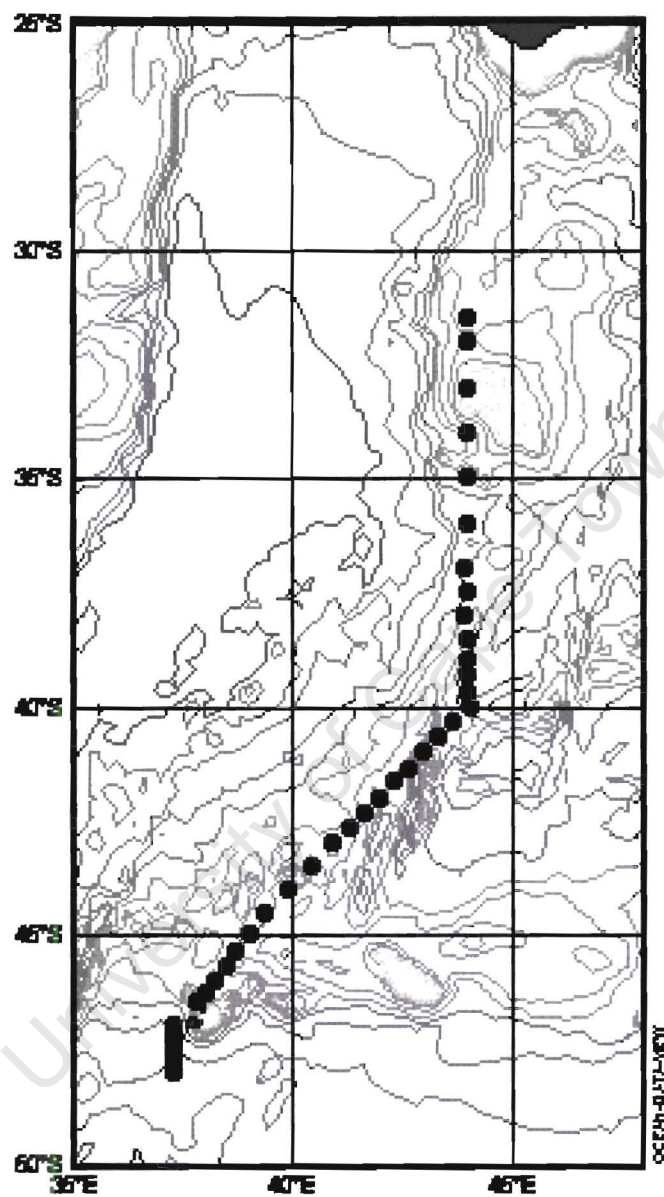


Figure. 3d) Cruise track and CTD station positions occupied on the Southbound transect from 31°S to the Prince Edward Islands.

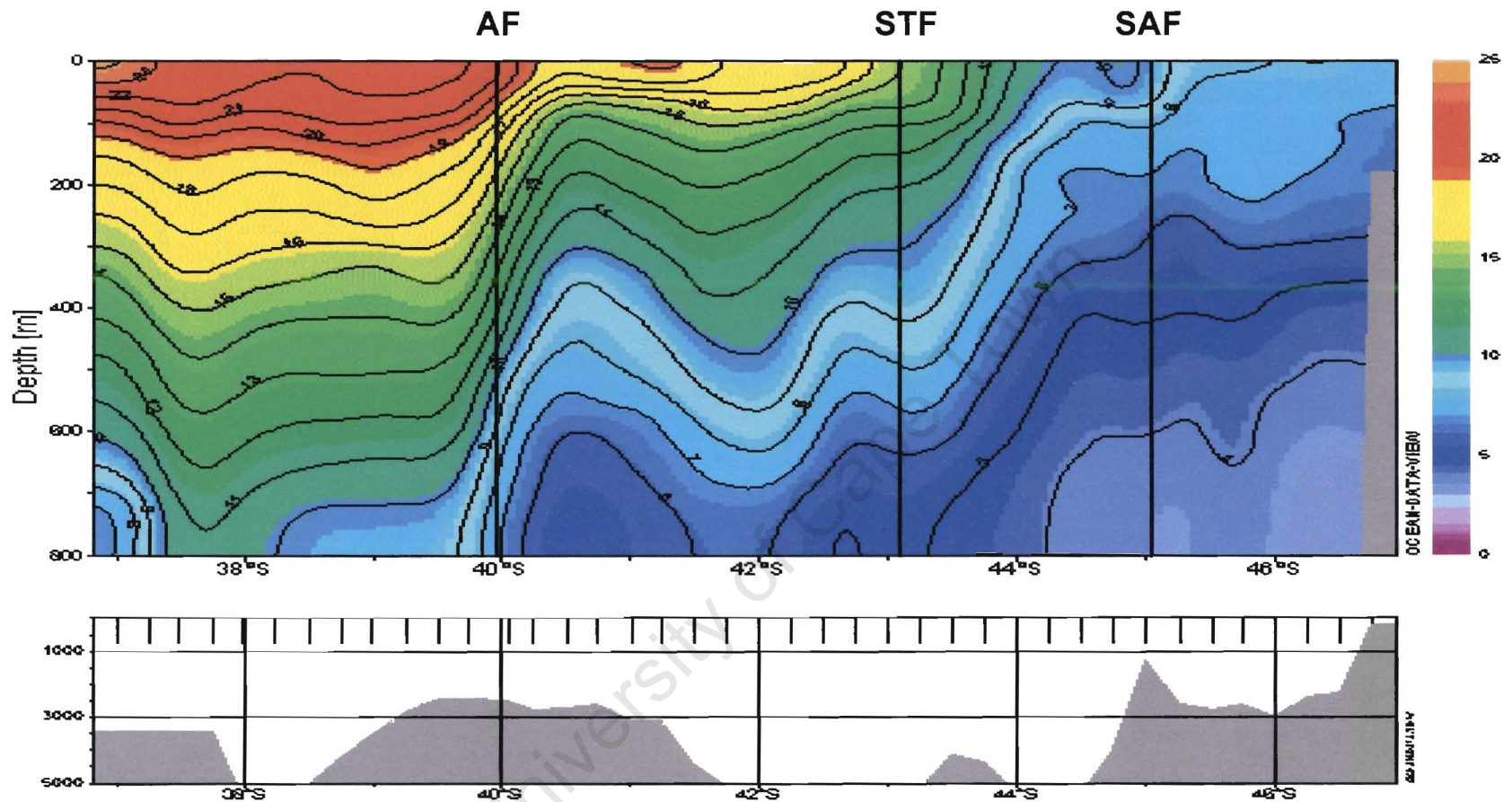


Figure 4. Temperature ($^{\circ}\text{C}$) section obtained during the Underway transect from Cape Town to the Prince Edward Islands. Topography section shows the position and depth of each XBT station.

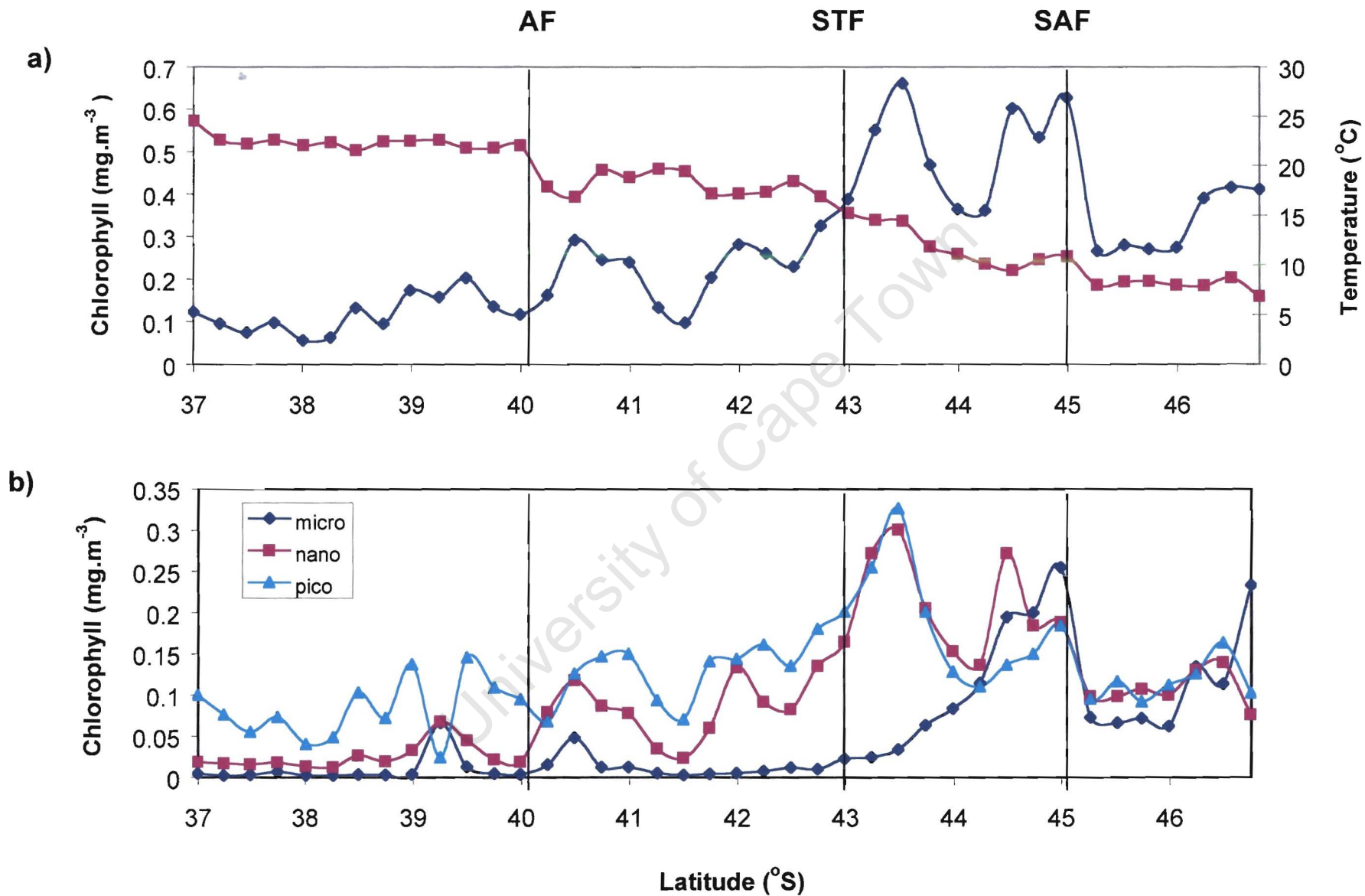


Figure 5. Distribution of a) total chlorophyll ($\text{mg}\cdot\text{m}^{-3}$) and temperature ($^{\circ}\text{C}$) at the sea surface and b) variability of the size structure and biomass of surface phytoplankton along the Marion Underway transect.

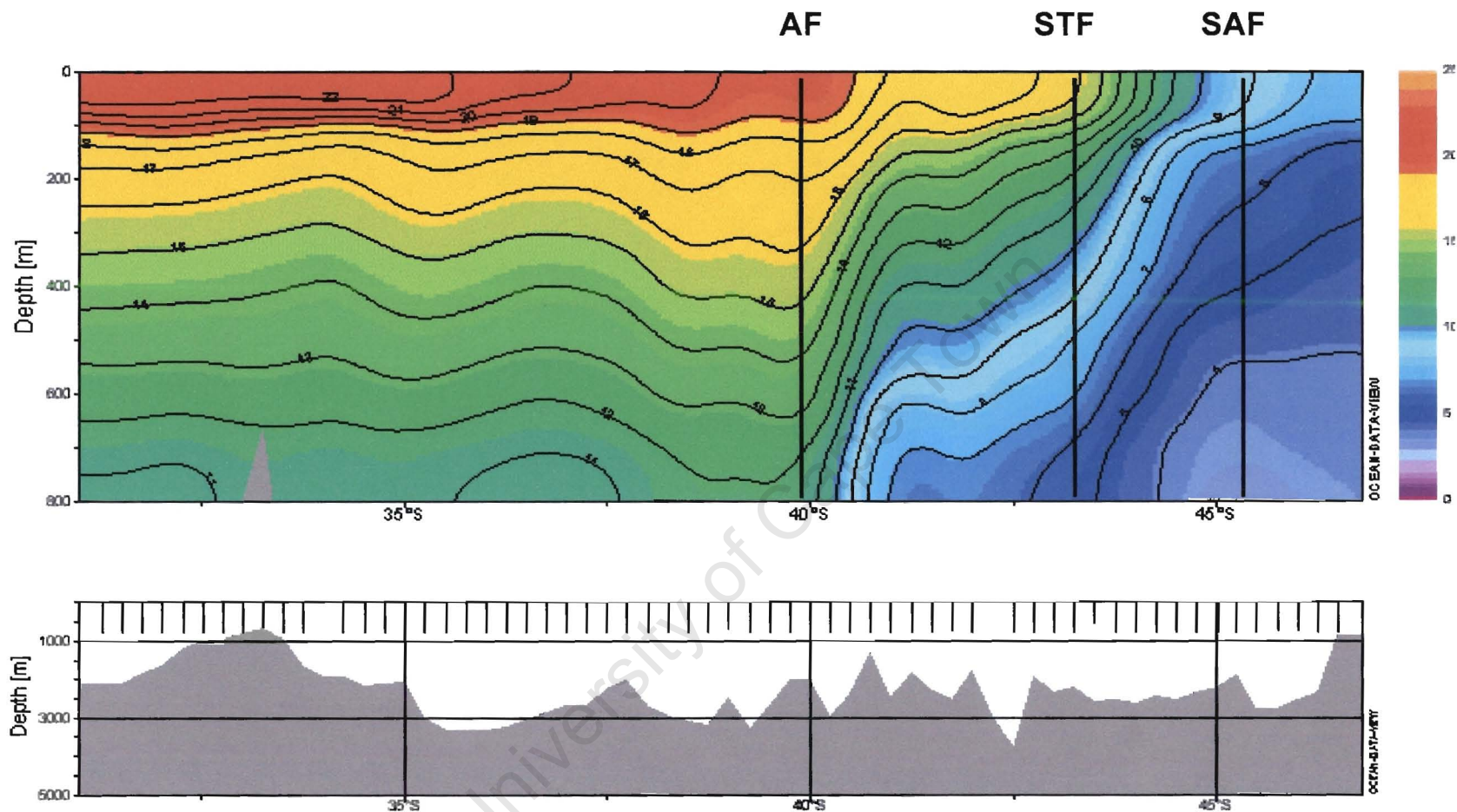


Figure 6. XBT temperature ($^{\circ}\text{C}$) section obtained during the Northbound leg of the Northern Transect between the Prince Edward Islands and 31°S . Topography section shows the position and depth of each XBT station.

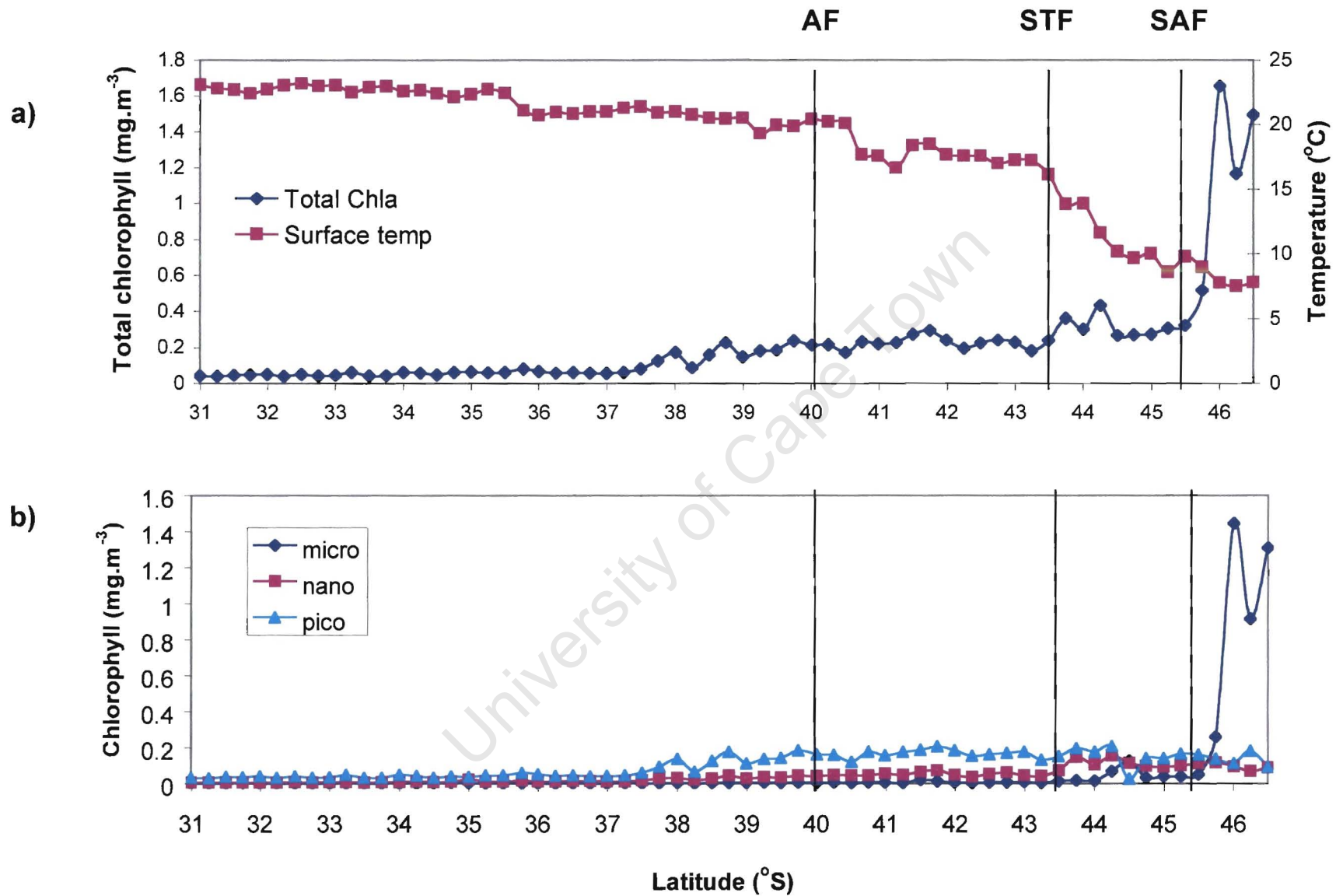


Figure. 7 a) Surface chlorophyll (mg.m⁻³) and sea surface temperature (°C) distribution, and b) size fractionated distribution (mg.m⁻³) of the surface phytoplankton population along the Northbound leg of the Northern Transect

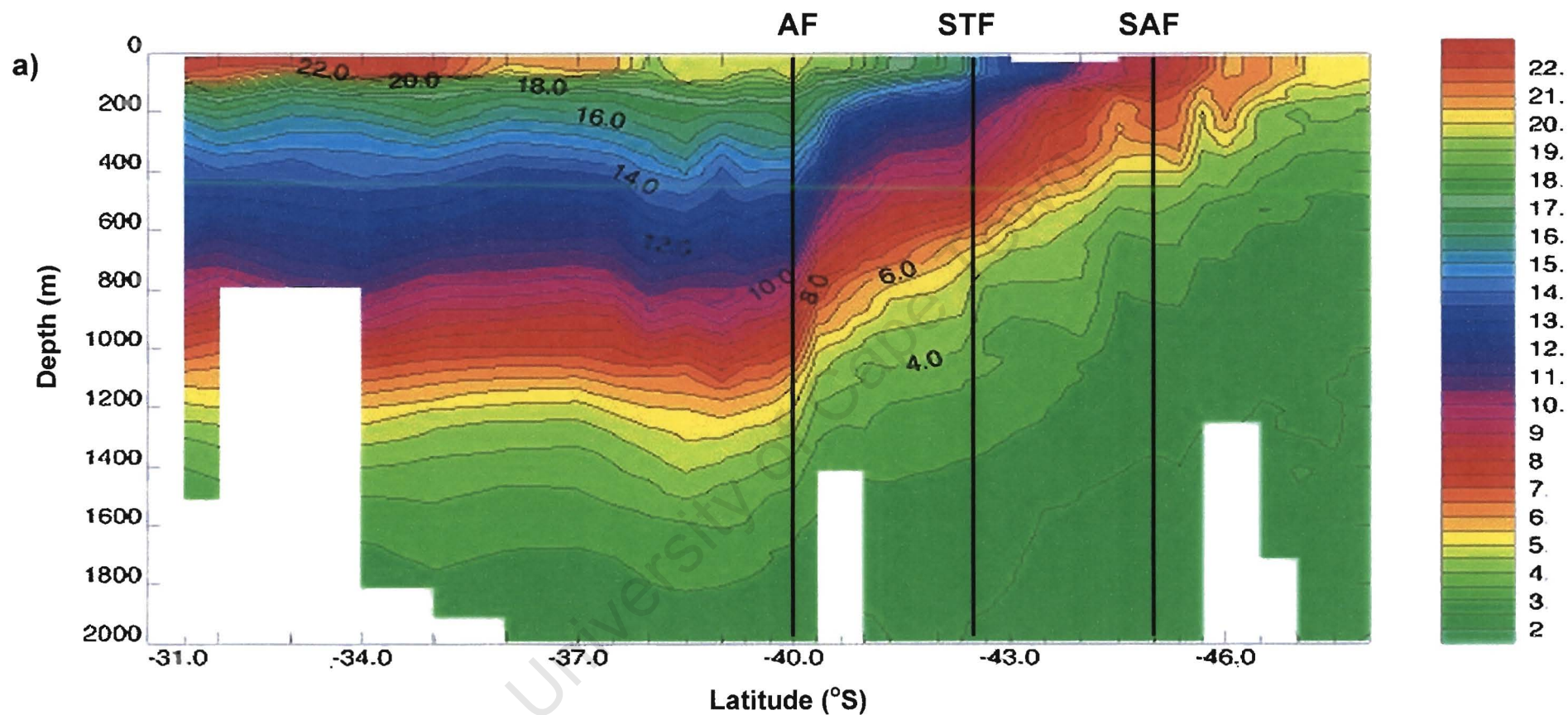


Figure. 8 a) CTD potential temperature (°C) section to 2000m for the Southbound leg of the Northern transect between 31°S and the Prince Edward Islands.

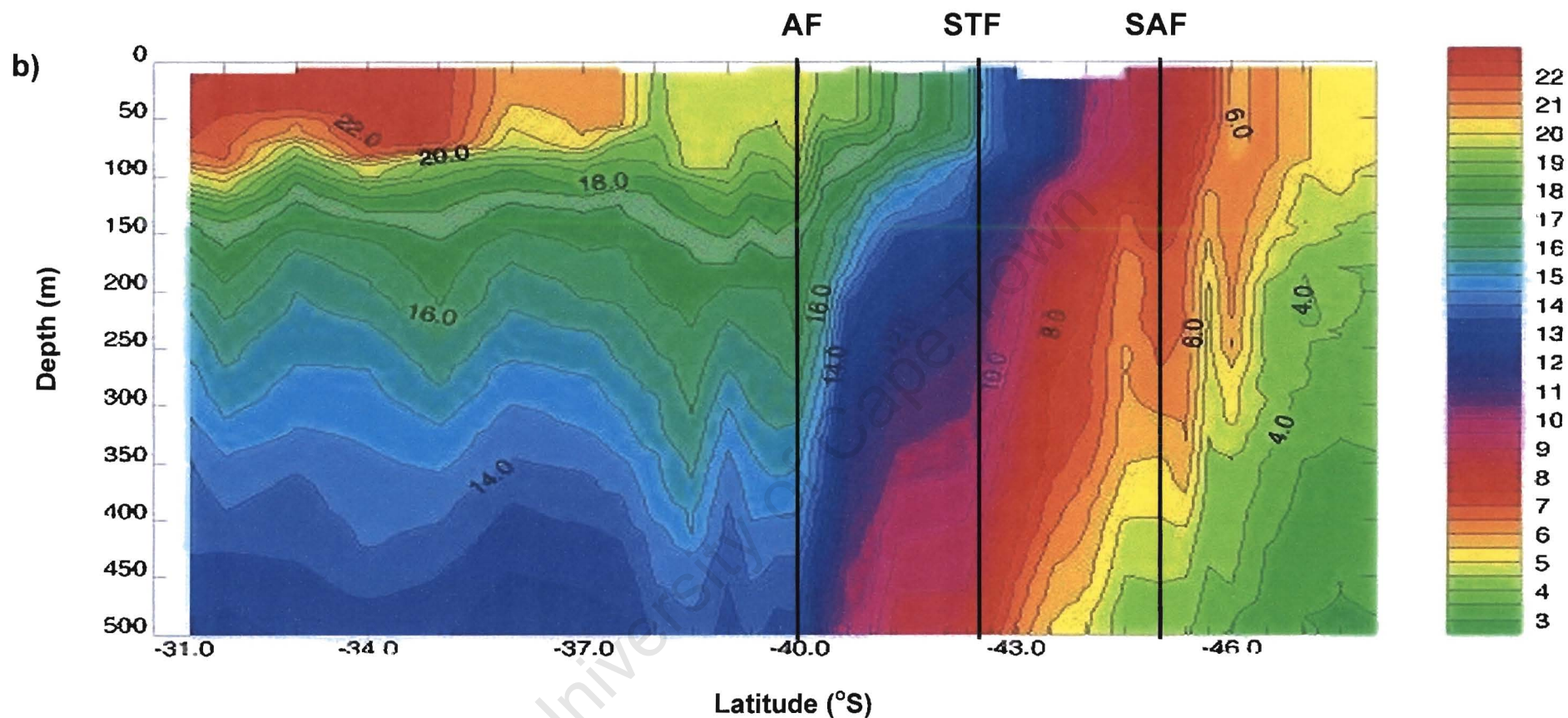


Figure. 8 b) CTD potential temperature ($^{\circ}$ C) section to 500m for the Southbound leg of the Northern transect between 31° S and the Prince Edward Islands.

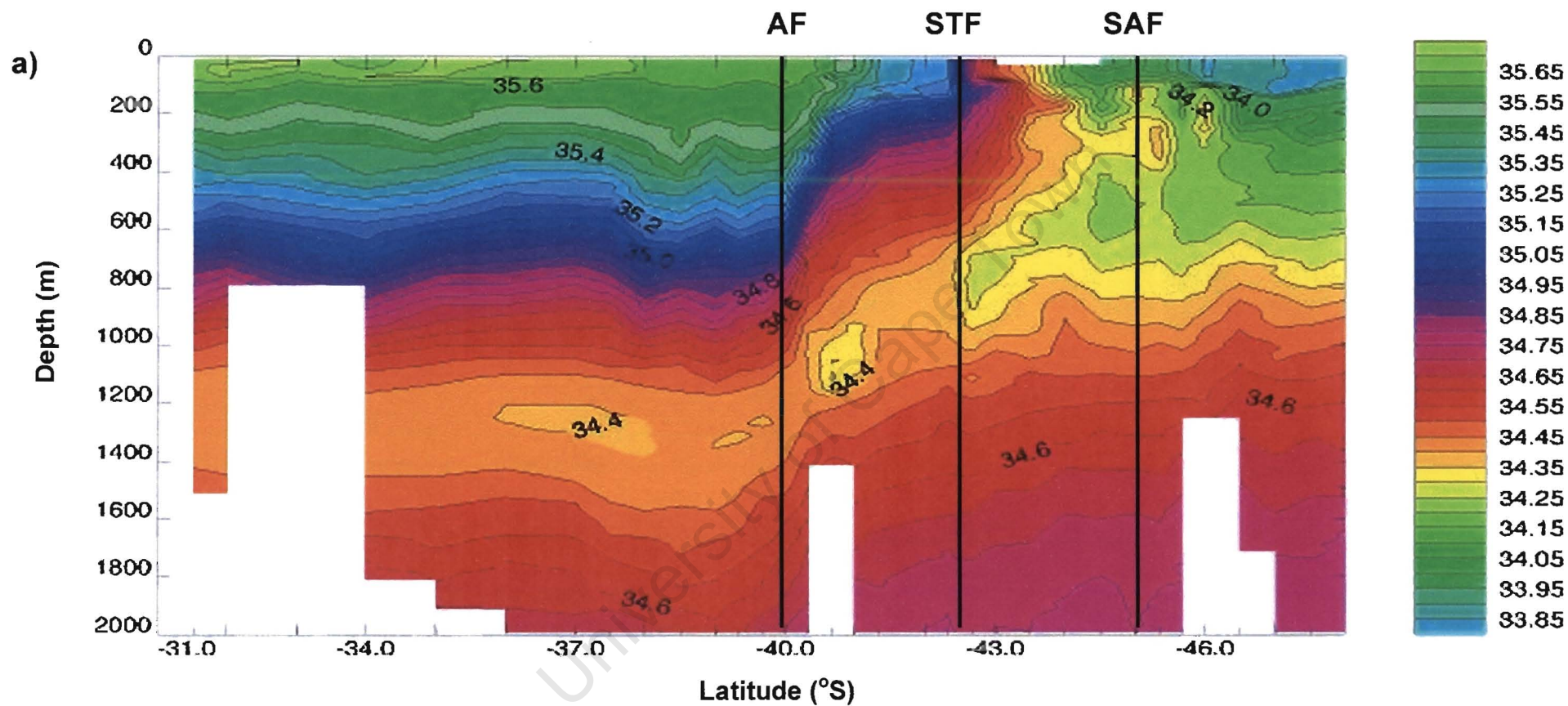


Figure. 9 a) CTD salinity (‰) section to 2000m for the Southbound leg of the Northern transect between 31° S and the Prince Edward Islands.

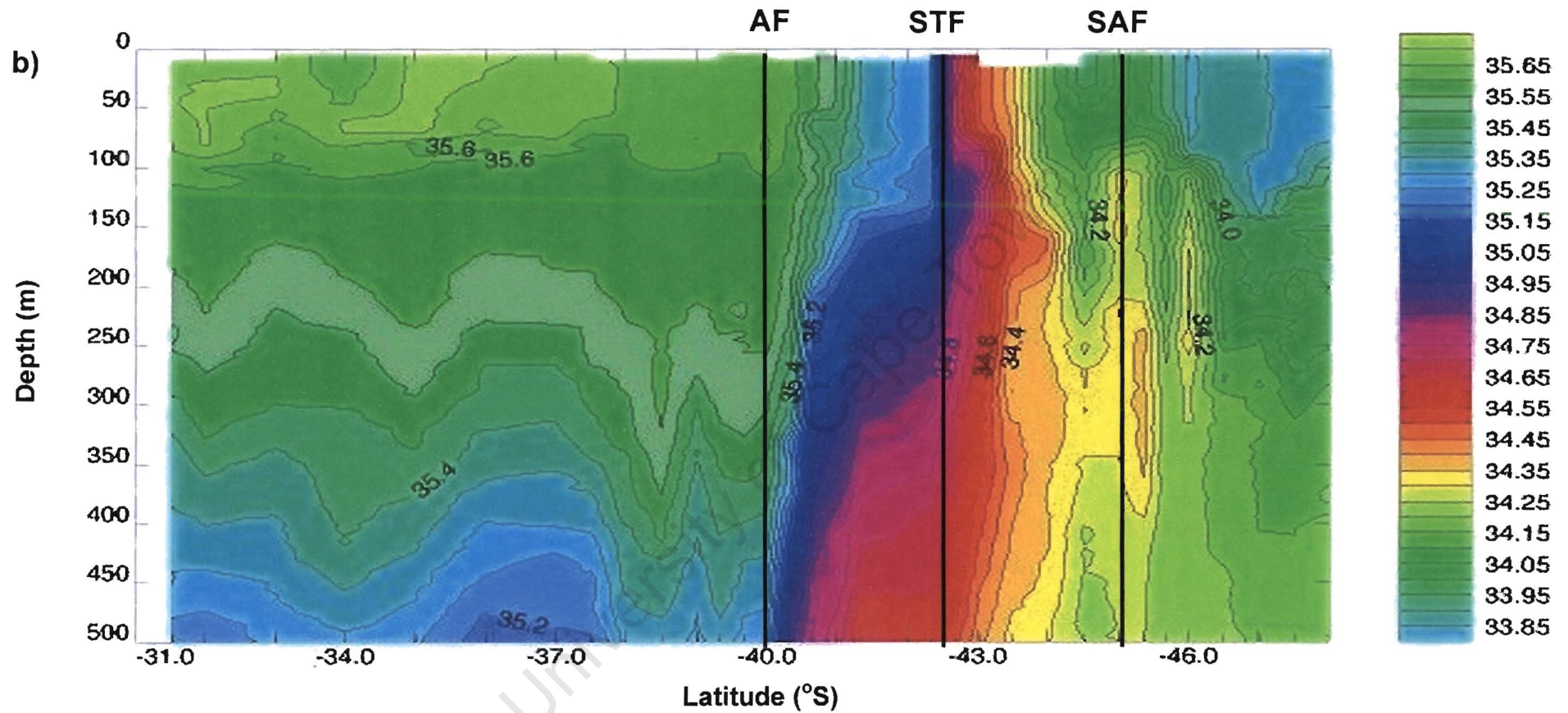


Figure. 9 b) CTD salinity (‰) section to 500m for the Southbound leg of the Northern transect between 31°S and the Prince Edward Islands.

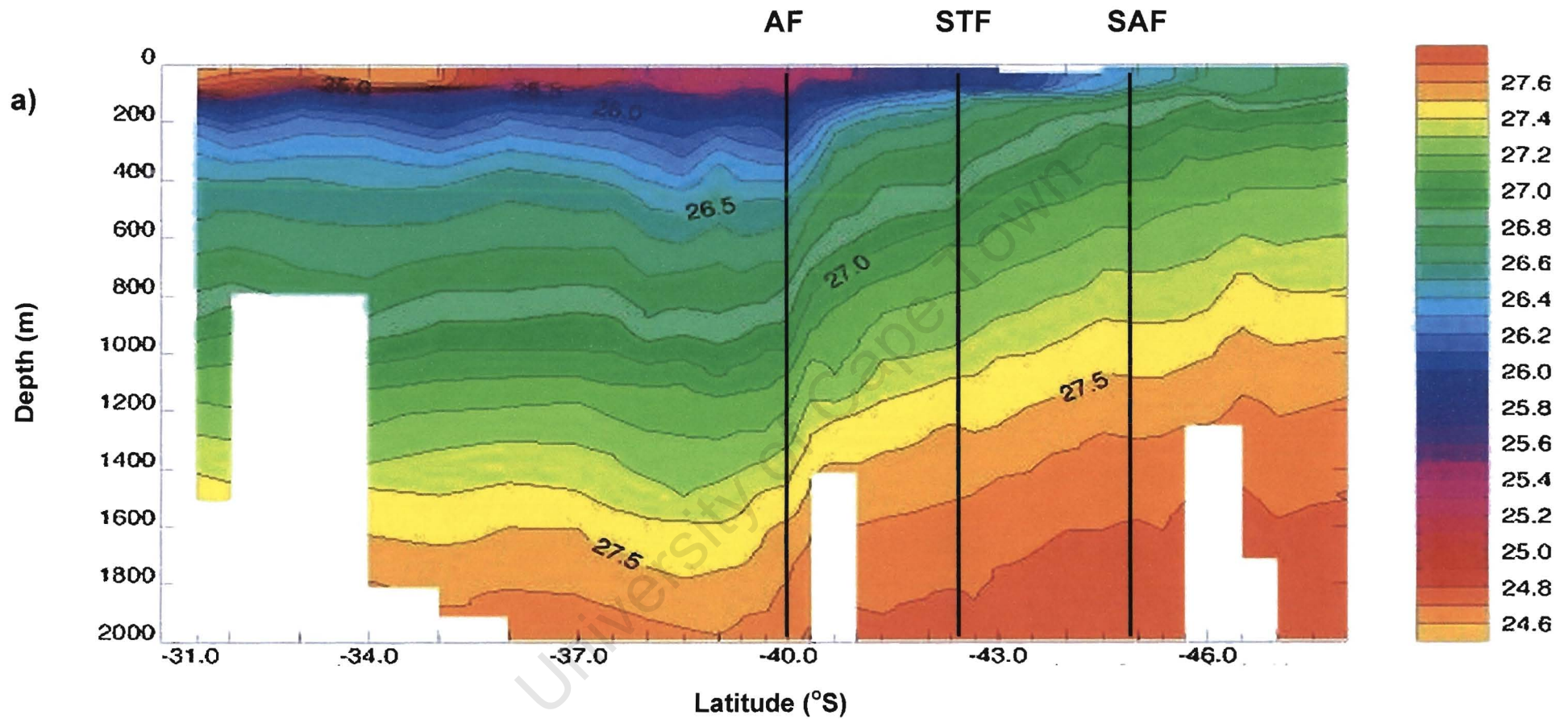


Figure. 10 a) CTD density (kg.m^{-3}) section to 2000m for the Southbound leg of the Northern transect between 31°S and the Prince Edward Islands.

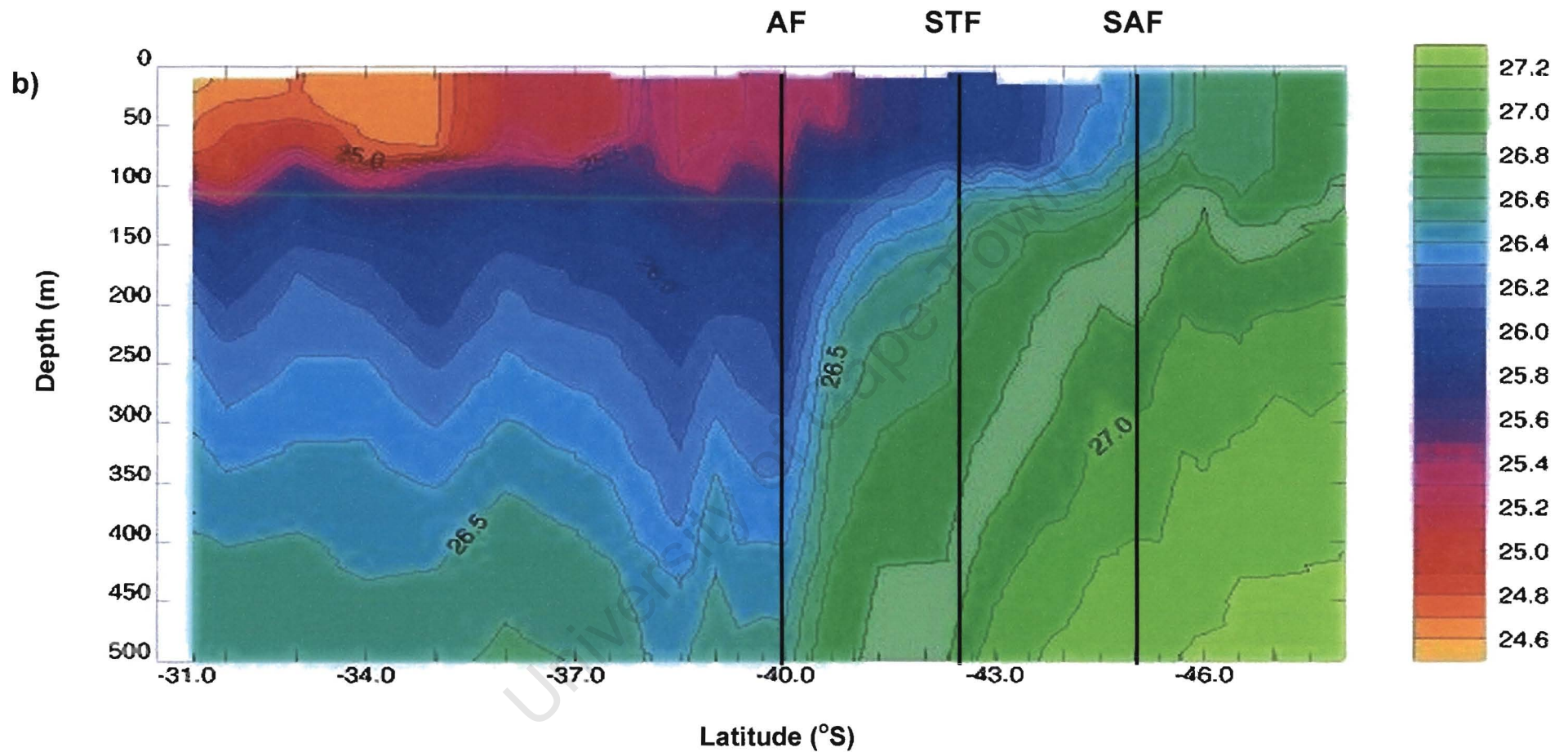


Figure. 10 b) CTD density ($\text{kg}\cdot\text{m}^{-3}$) section to 500m for the Southbound leg of the Northern transect between 31°S and the Prince Edward Islands.

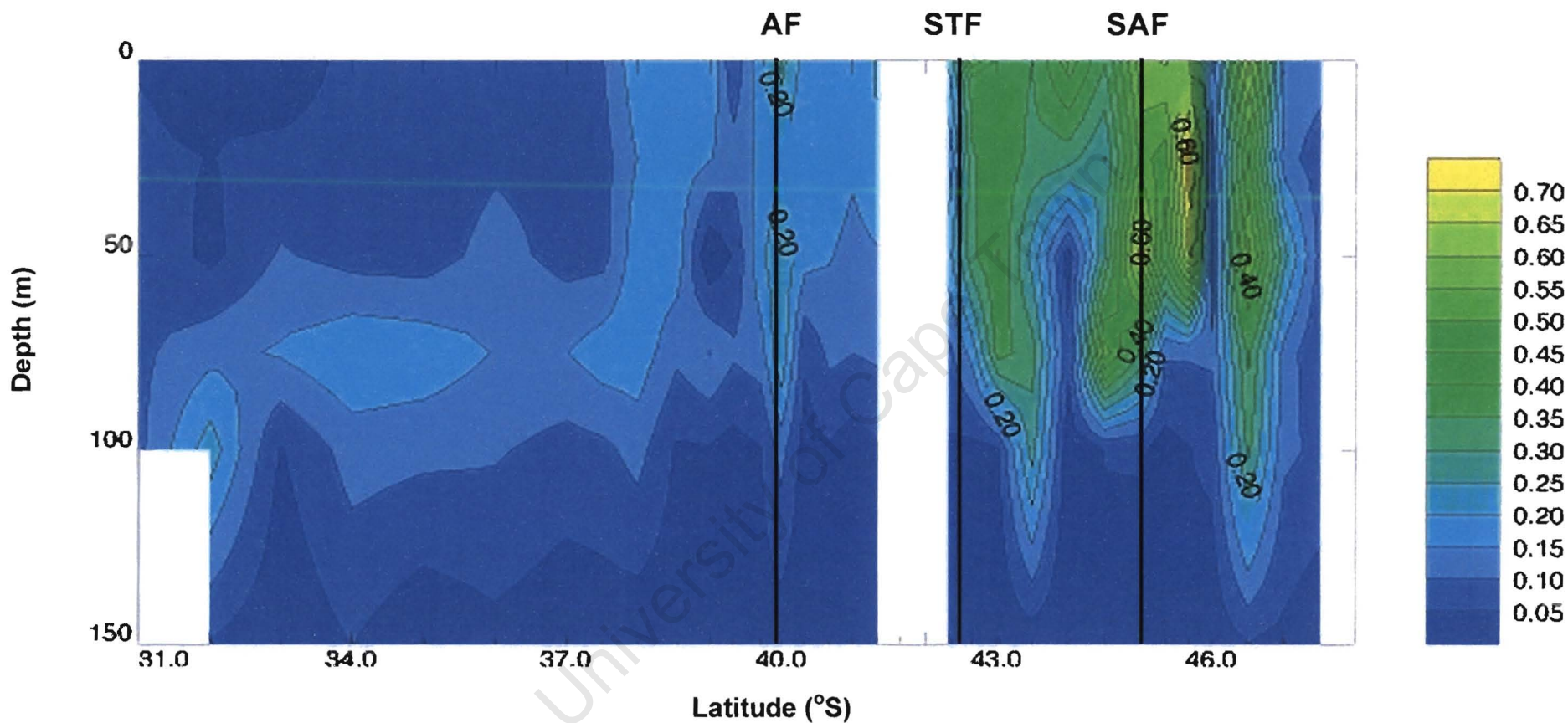


Figure. 11. CTD total chlorophyll ($\text{mg}\cdot\text{m}^{-3}$) section to 150m for the Southbound leg of the Northern transect between 31°S and the Prince Edward Islands.

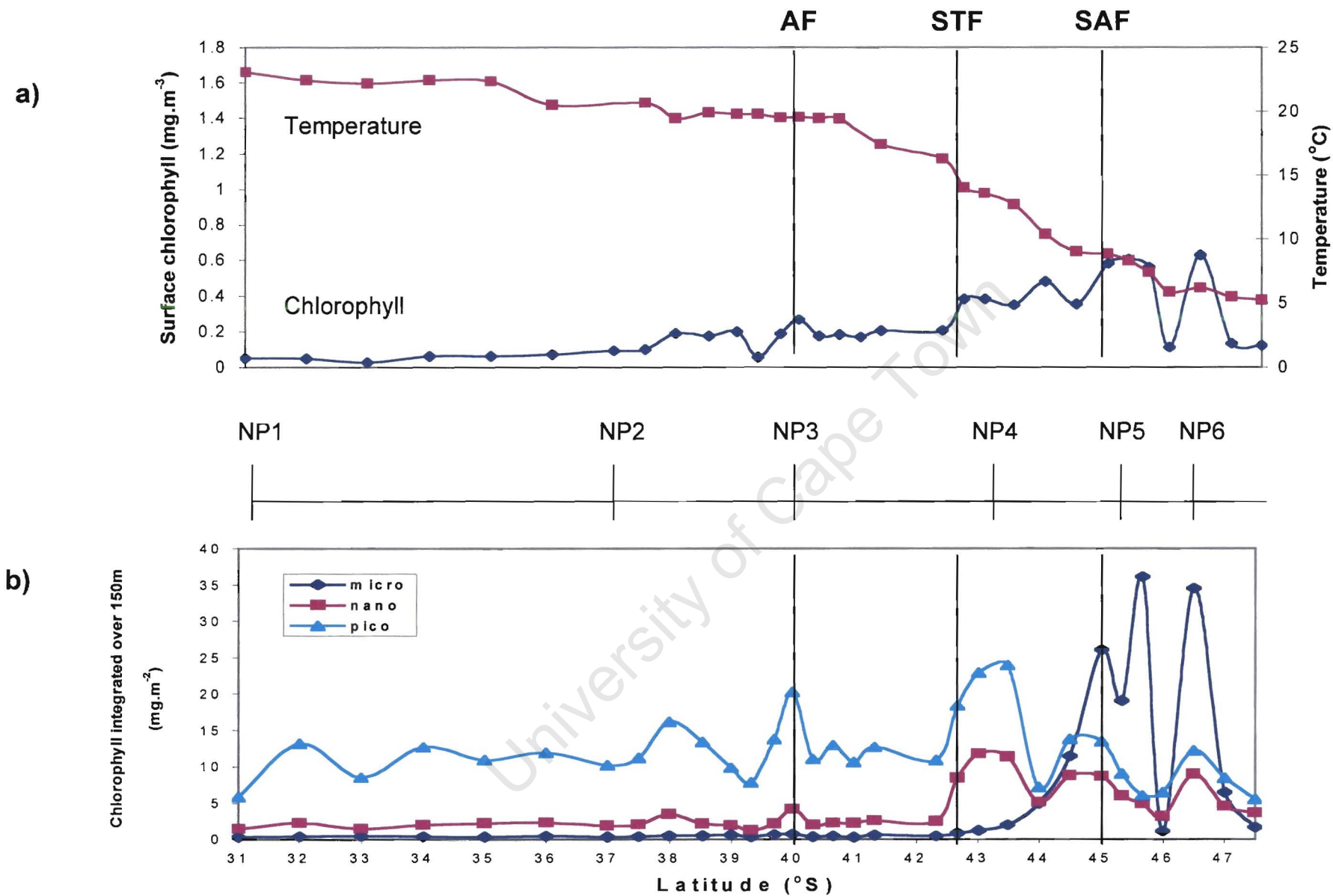


Figure. 12 a) Sea surface temperature ($^{\circ}\text{C}$) and total chlorophyll distribution ($\text{mg}\cdot\text{m}^{-3}$), and b) size fractionated chlorophyll distribution ($\text{mg}\cdot\text{m}^{-2}$) integrated over the top 150m for the Southbound leg of the Northern Transect.

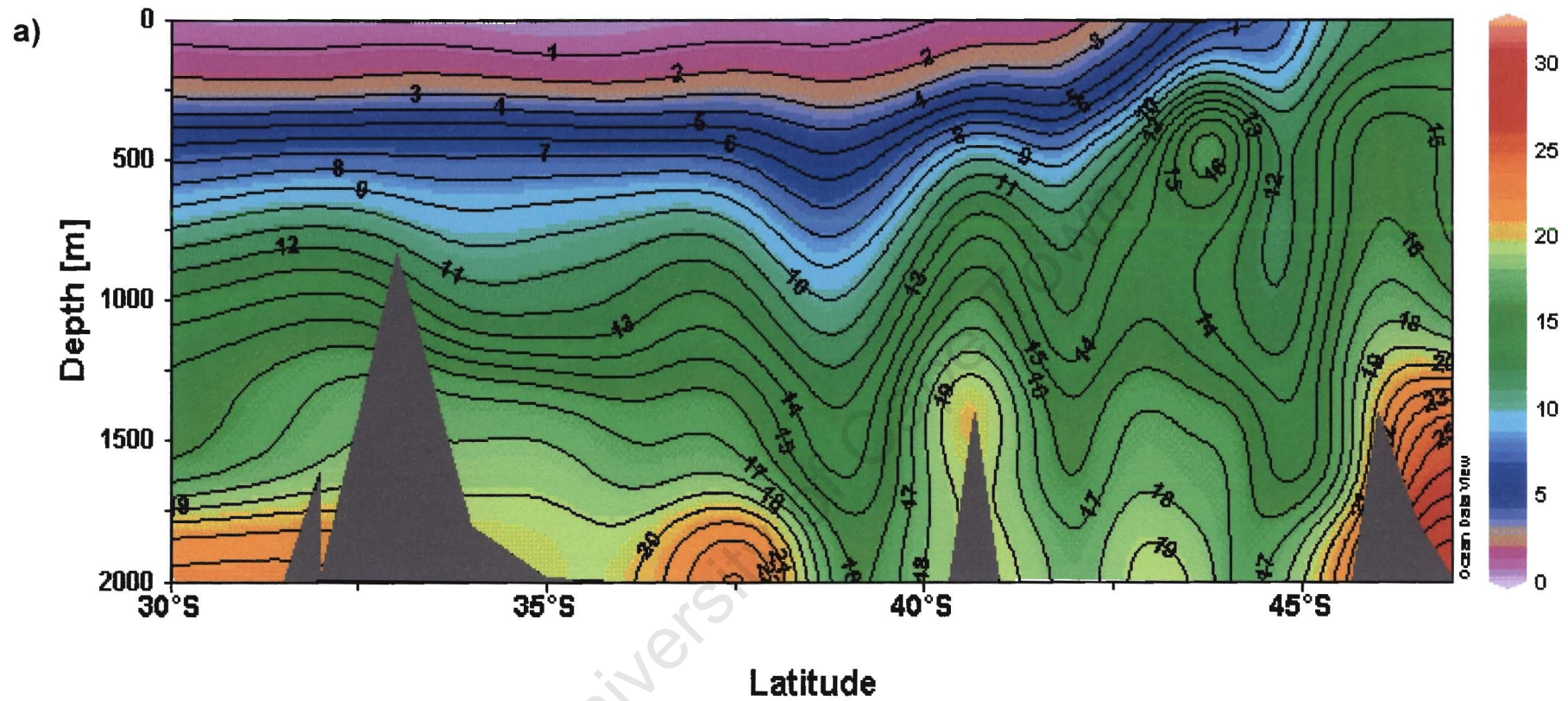


Figure. 13 a) Nitrate (mg-at.m^{-3}) section to 2000m for the Southbound transect from 31°S to the Prince Edward Islands.

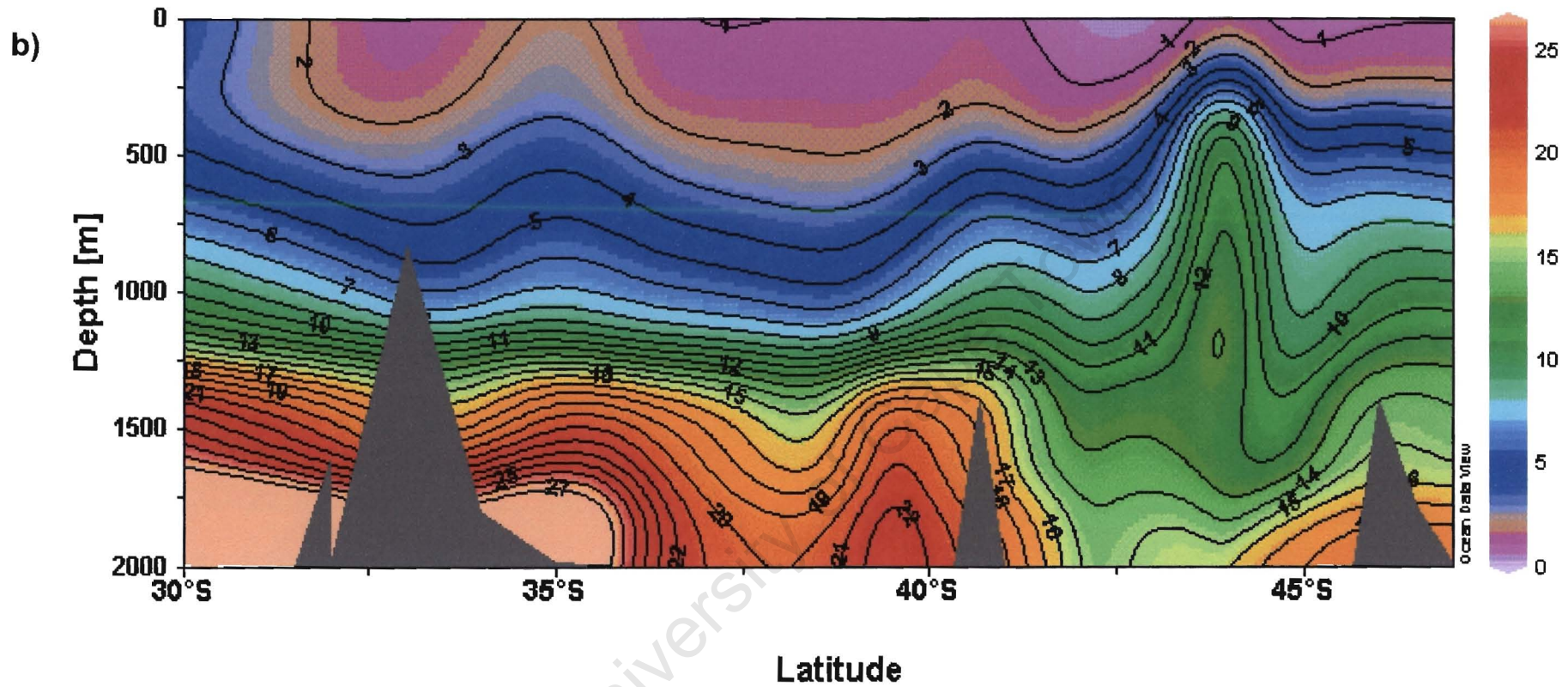


Figure. 13 b) Silicate (mg-at.m^{-3}) section to 2000m for the Southbound Transect from 31°S to the Prince Edward Islands.

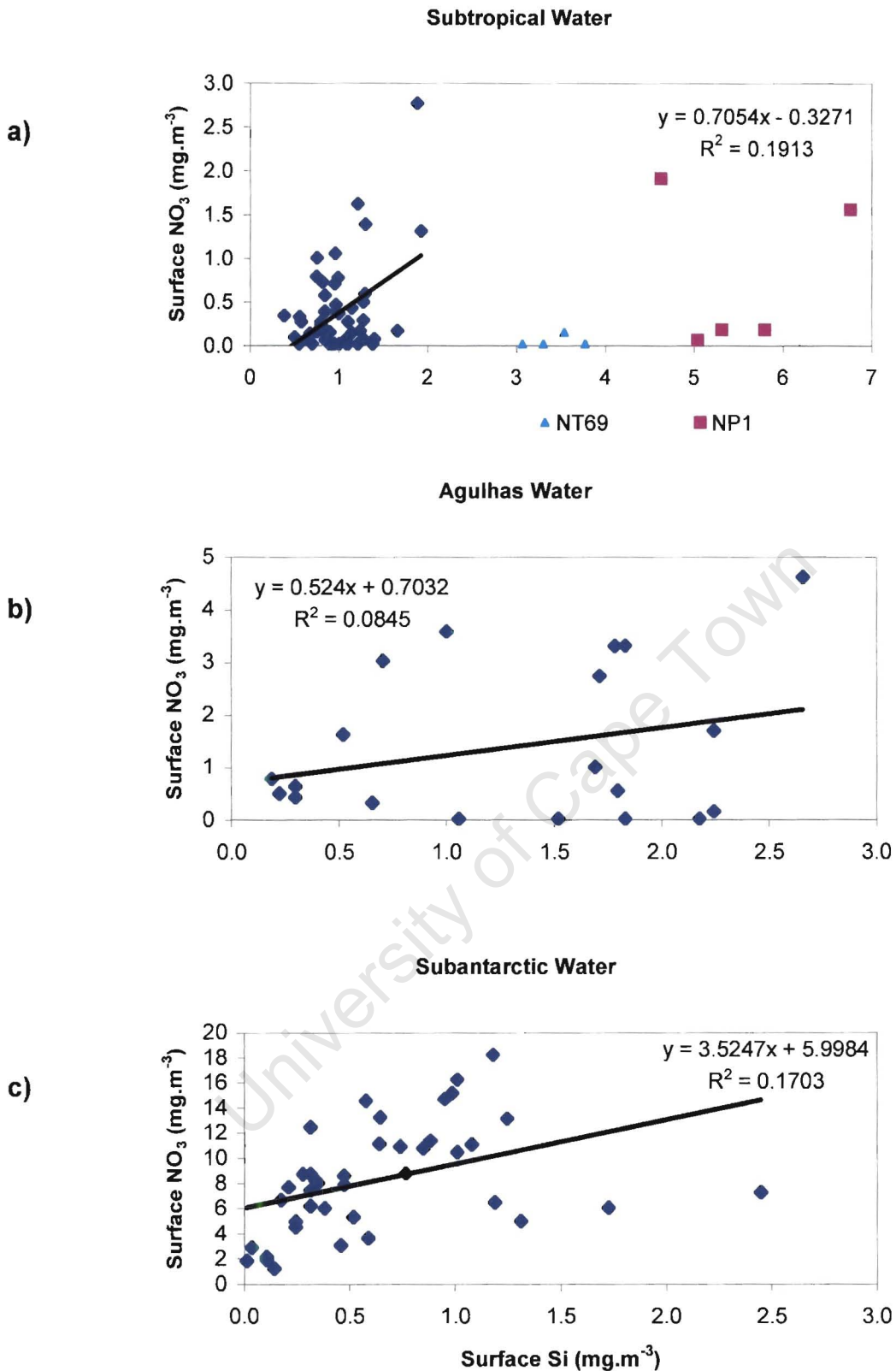


Figure. 14. Inter nutrient relationships for nitrate and silicate ($\text{mg}\cdot\text{at}\cdot\text{m}^{-3}$) in the surface waters of the Southbound transect, showing patterns of utilisation and limitation. In figure. 14 a) Stations NT69 and NP1 have abnormally high Si and low surface NO_3 concentrations. These two stations are considered to be outliers and their data has not been included in the regression analysis.

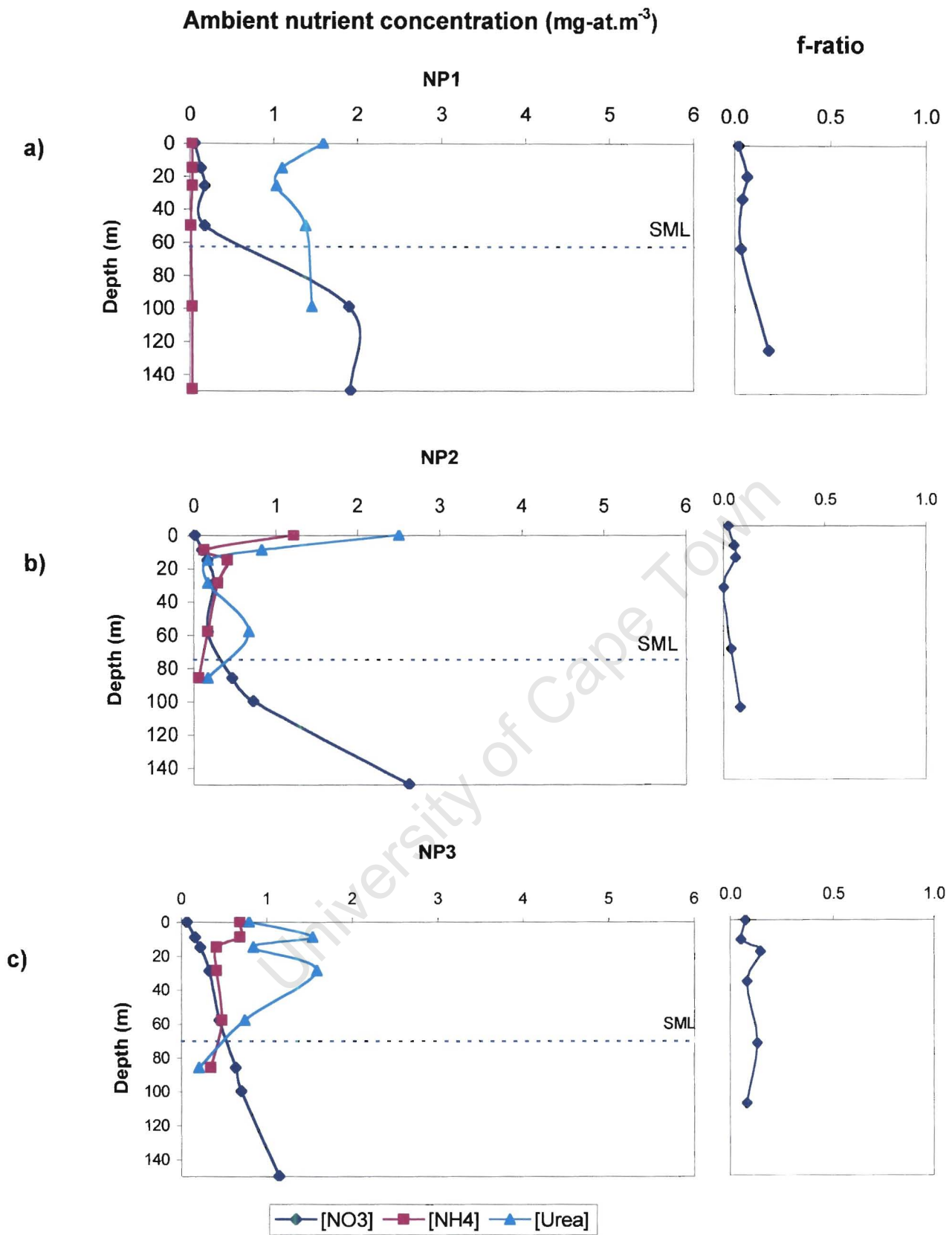


Figure. 15. Vertical profiles of nitrate, ammonium and urea concentrations (mg-at.m^{-3}) for subtropical stations NP1(a) to NP3 (c) together with vertical f-ratio profiles for each productivity station.

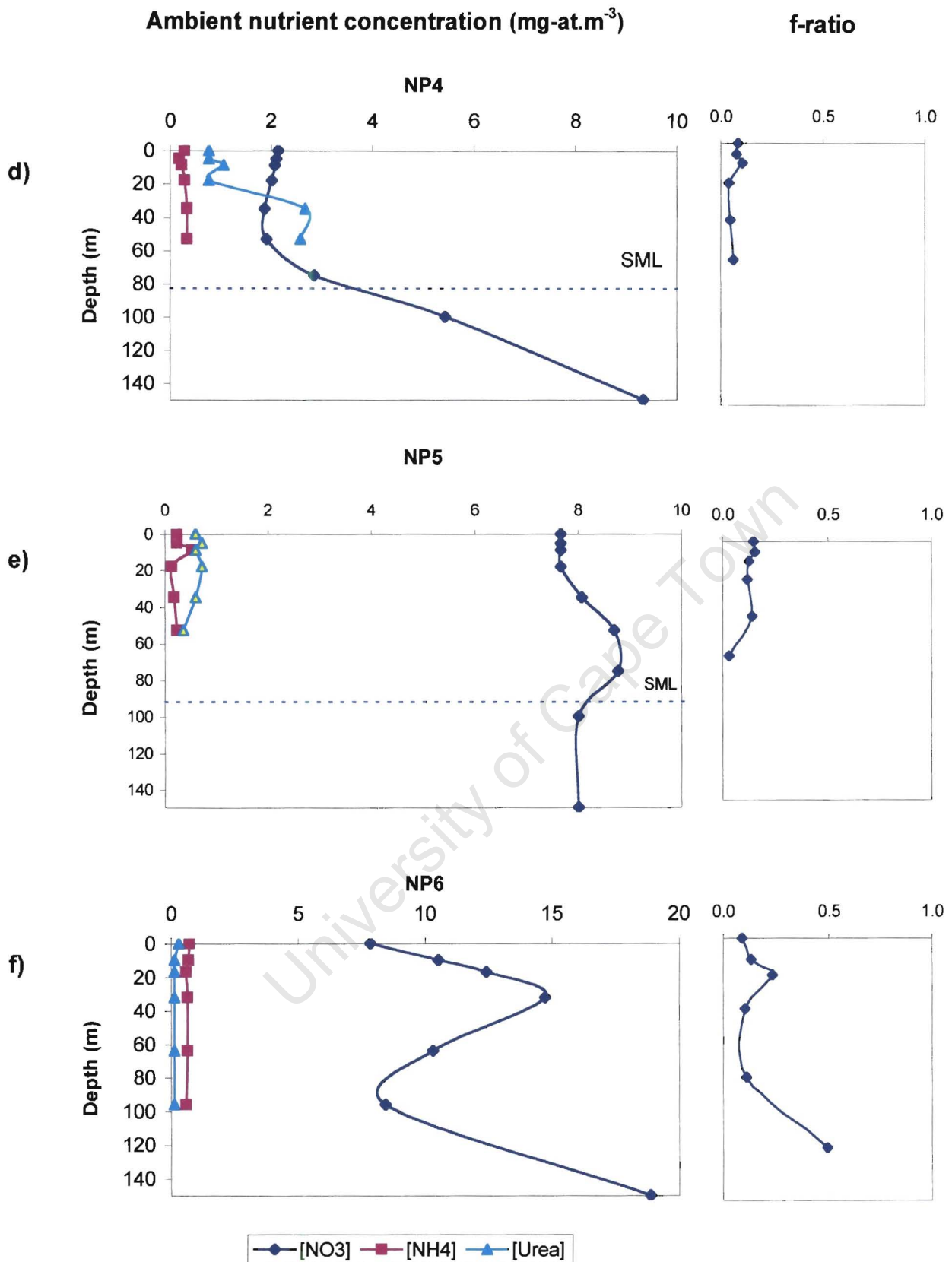


Figure 15. Vertical profiles of nitrate, ammonium and urea concentrations (mg-at.m⁻³) for subantarctic stations NP4 d) to NP6 f) together with vertical f-ratio profiles for each productivity station.

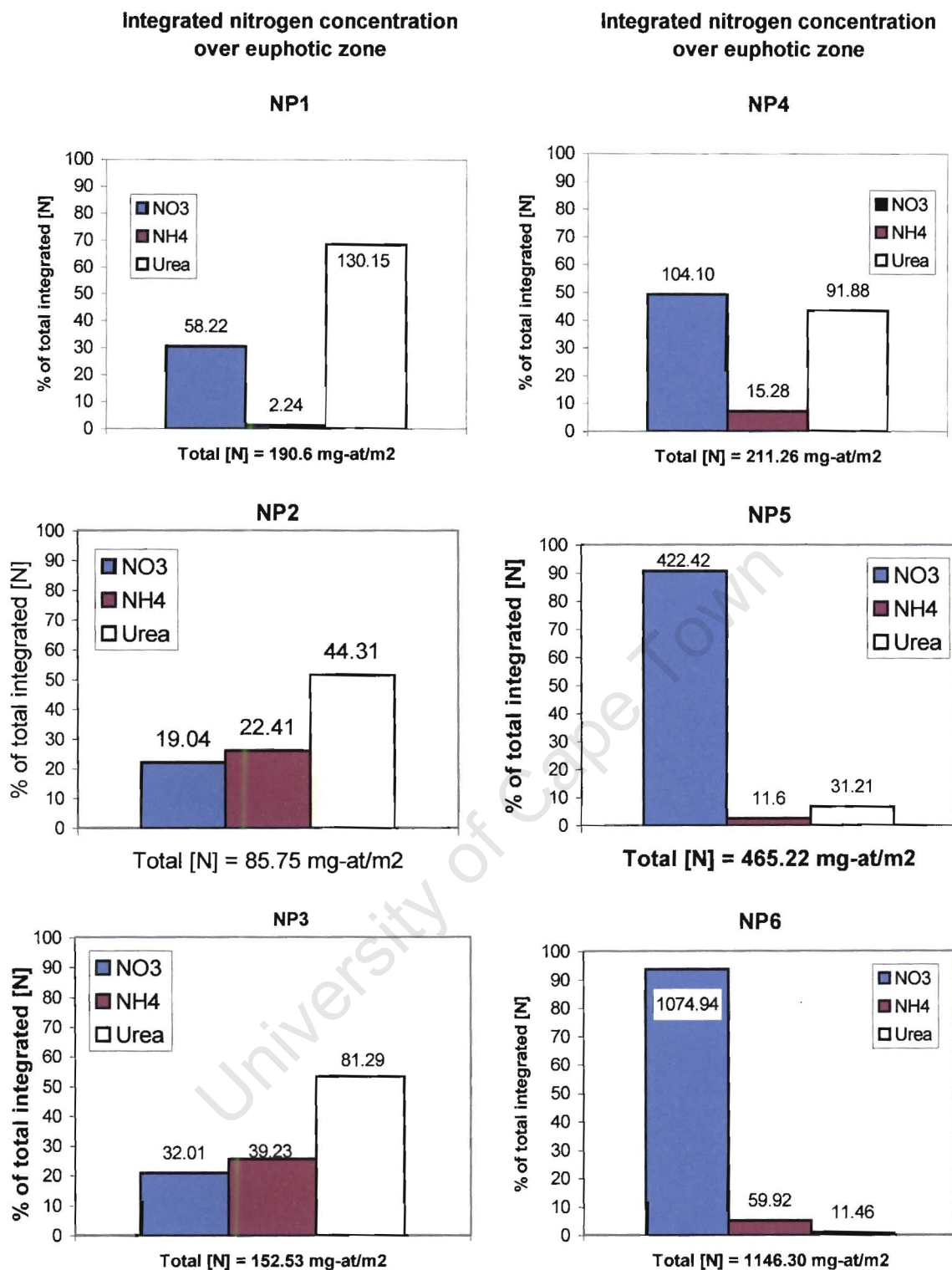


Figure. 16. Integrated (to the 0.1% light depth) measurements of nitrate, ammonium and urea (mg-at.m⁻²) concentrations represented as a percentage of the total ambient nitrogen, for each of the six productivity stations.

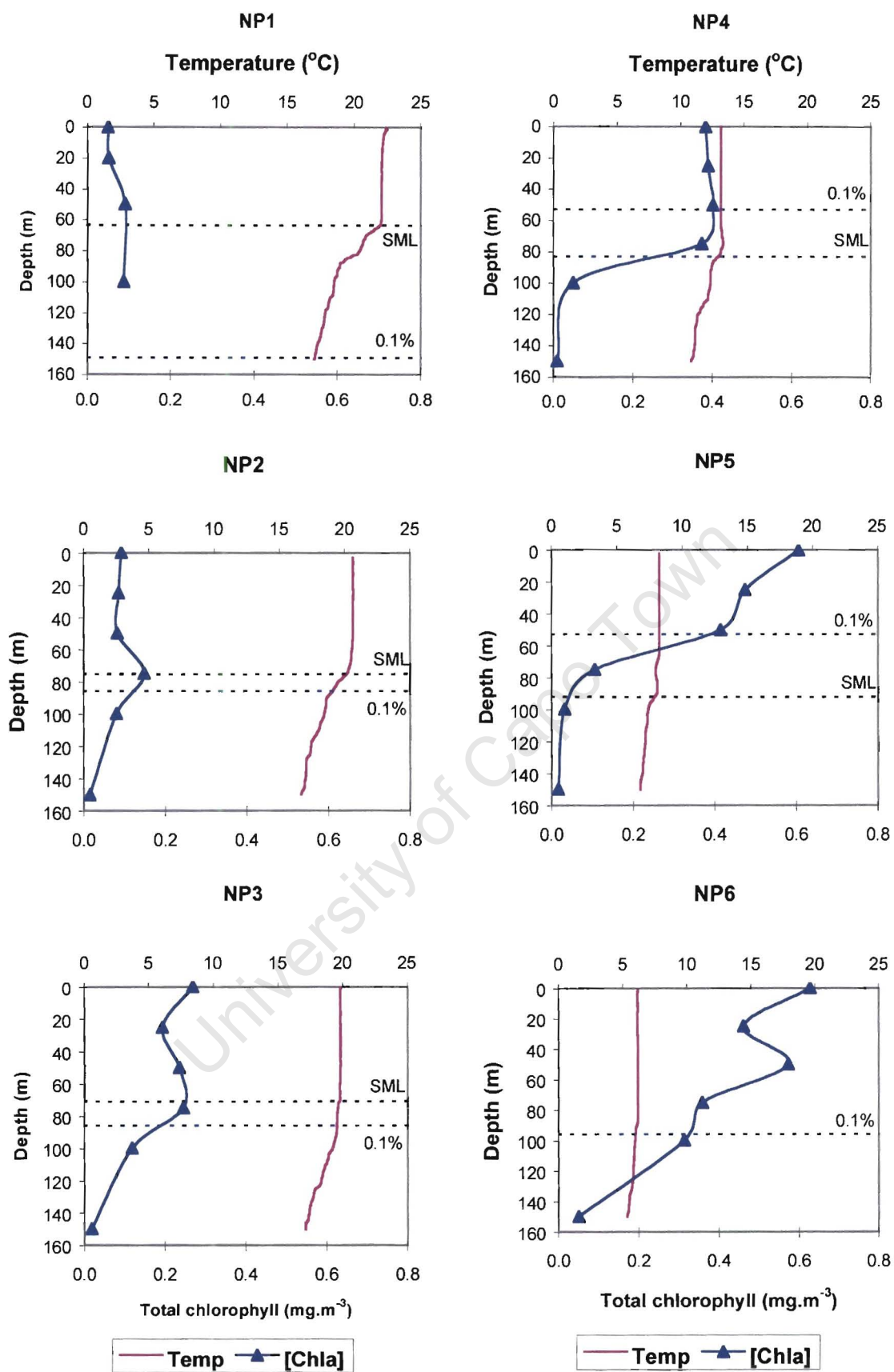


Figure 17. Vertical profiles of temperature (°C) and total chlorophyll (mg.m⁻³) for the top 150m of each productivity station on the Southbound transect. Together with surface mixed layer and euphotic (0.1% light) depths.

Ambient chlorophyll (mg.m-3)

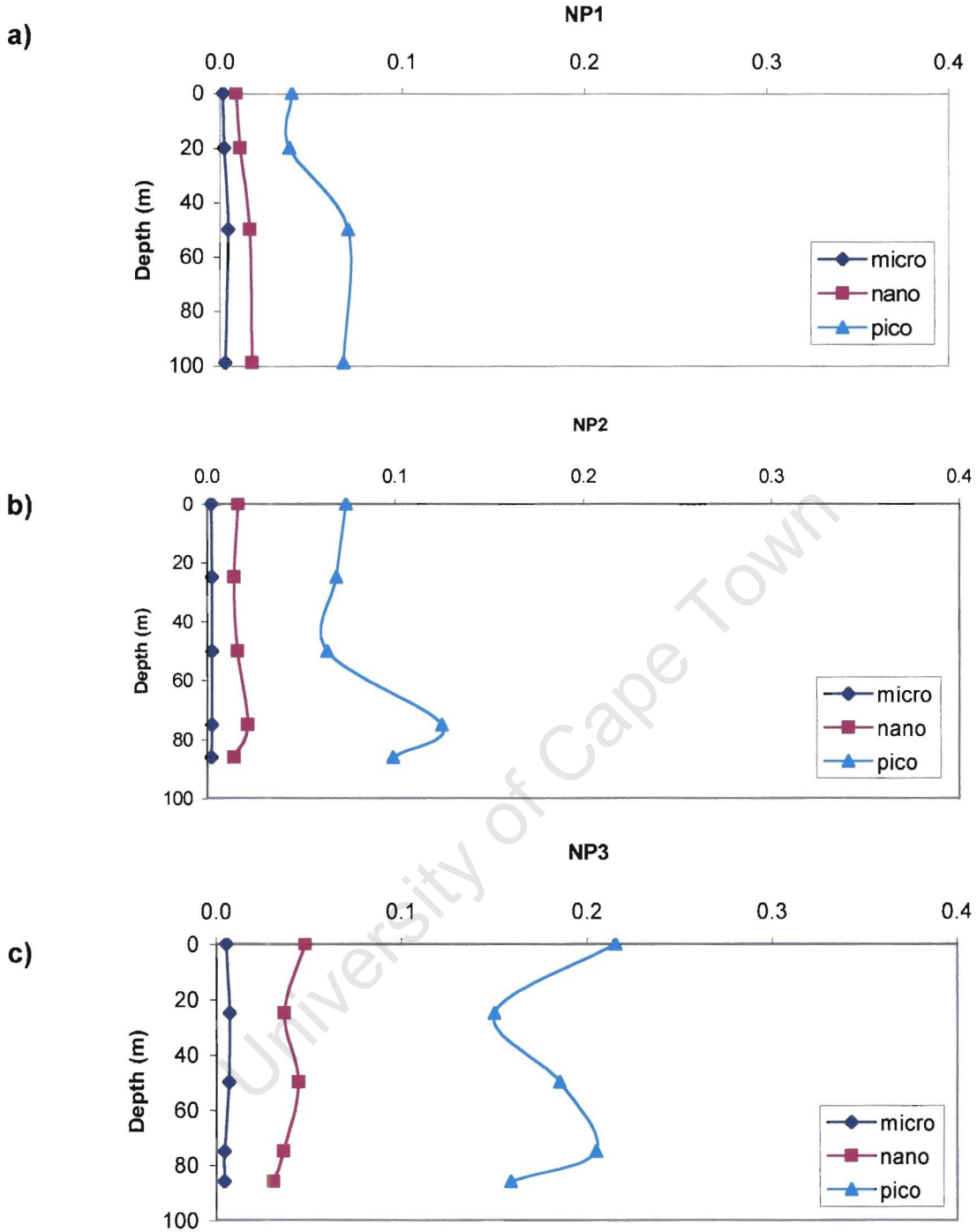


Figure 18. Vertical profiles of size-fractionated chlorophyll-a concentration (mg.m⁻³) in subtropical waters from a) station NP1 to c) the Agulhas Front at station NP3.

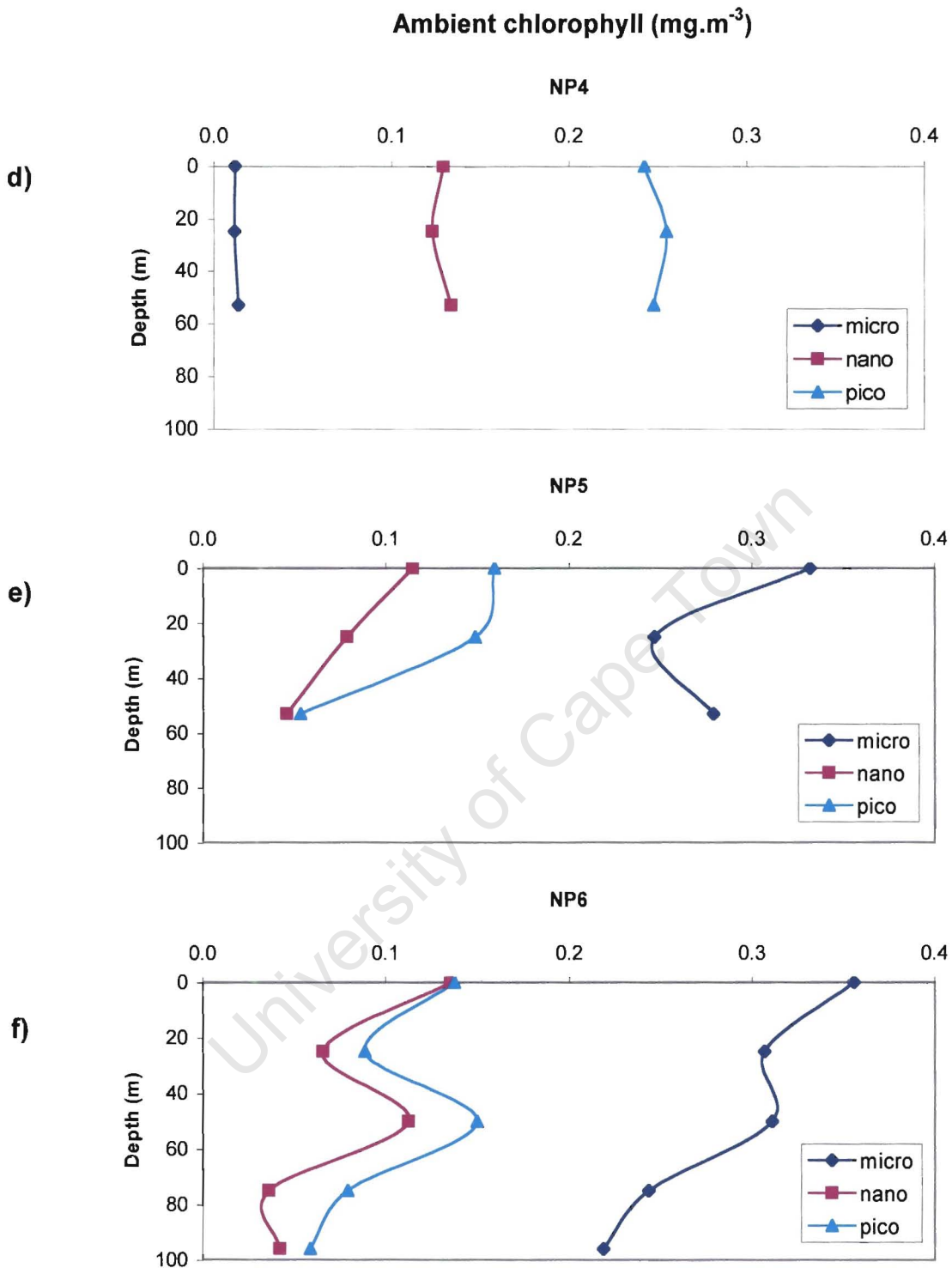


Figure 18. Vertical profiles of size-fractionated chlorophyll-a concentration ($\text{mg}\cdot\text{m}^{-3}$) for d) the STF region station NP4, e) the SAF region station NP5 and f) the region of the Prince Edward Island plateau station NP6.

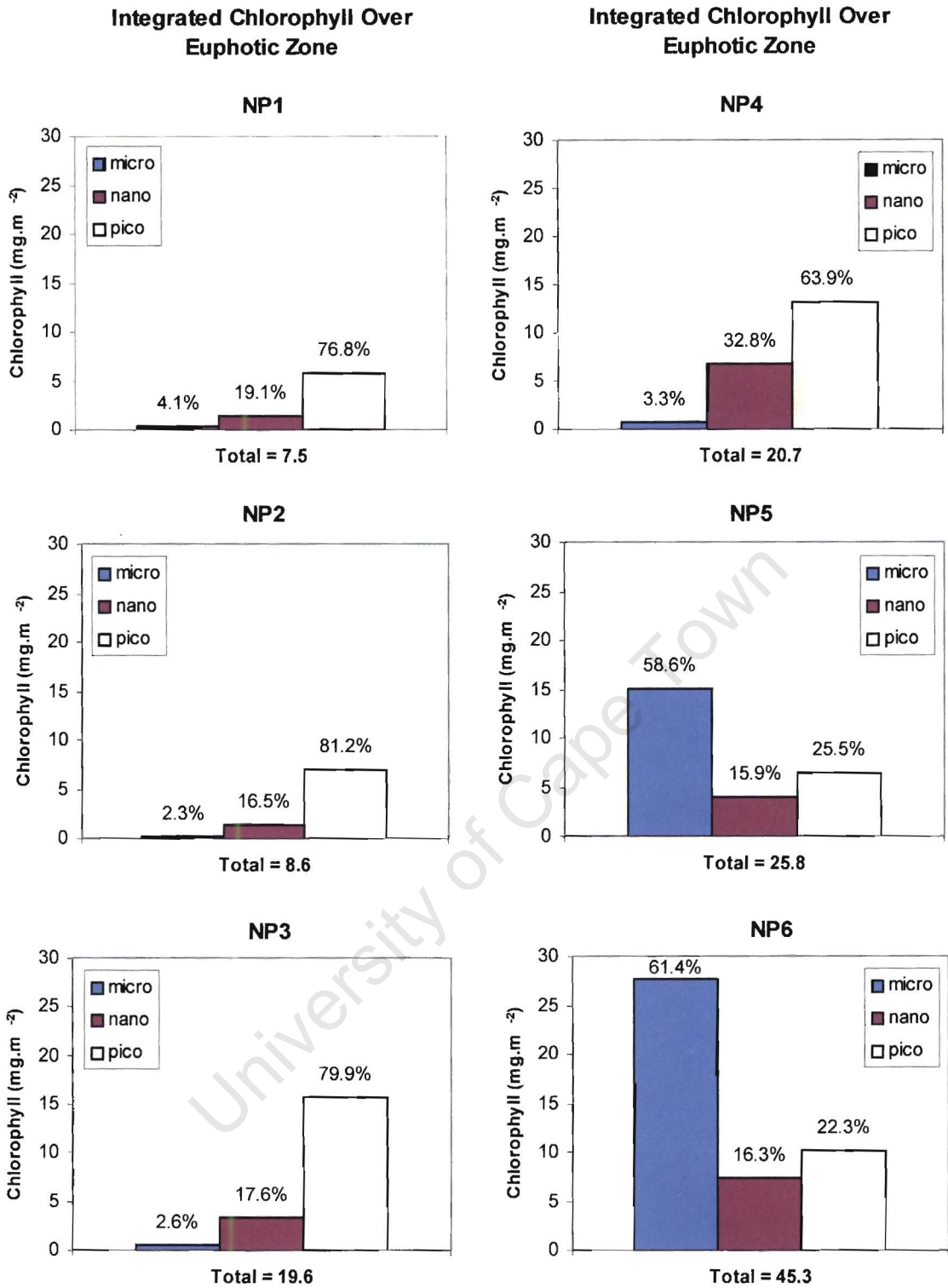


Figure. 19. Euphotic zone integrated measurements of size-fractionated chlorophyll concentration (mg.m⁻²) for the six productivity stations on the Southbound transect.

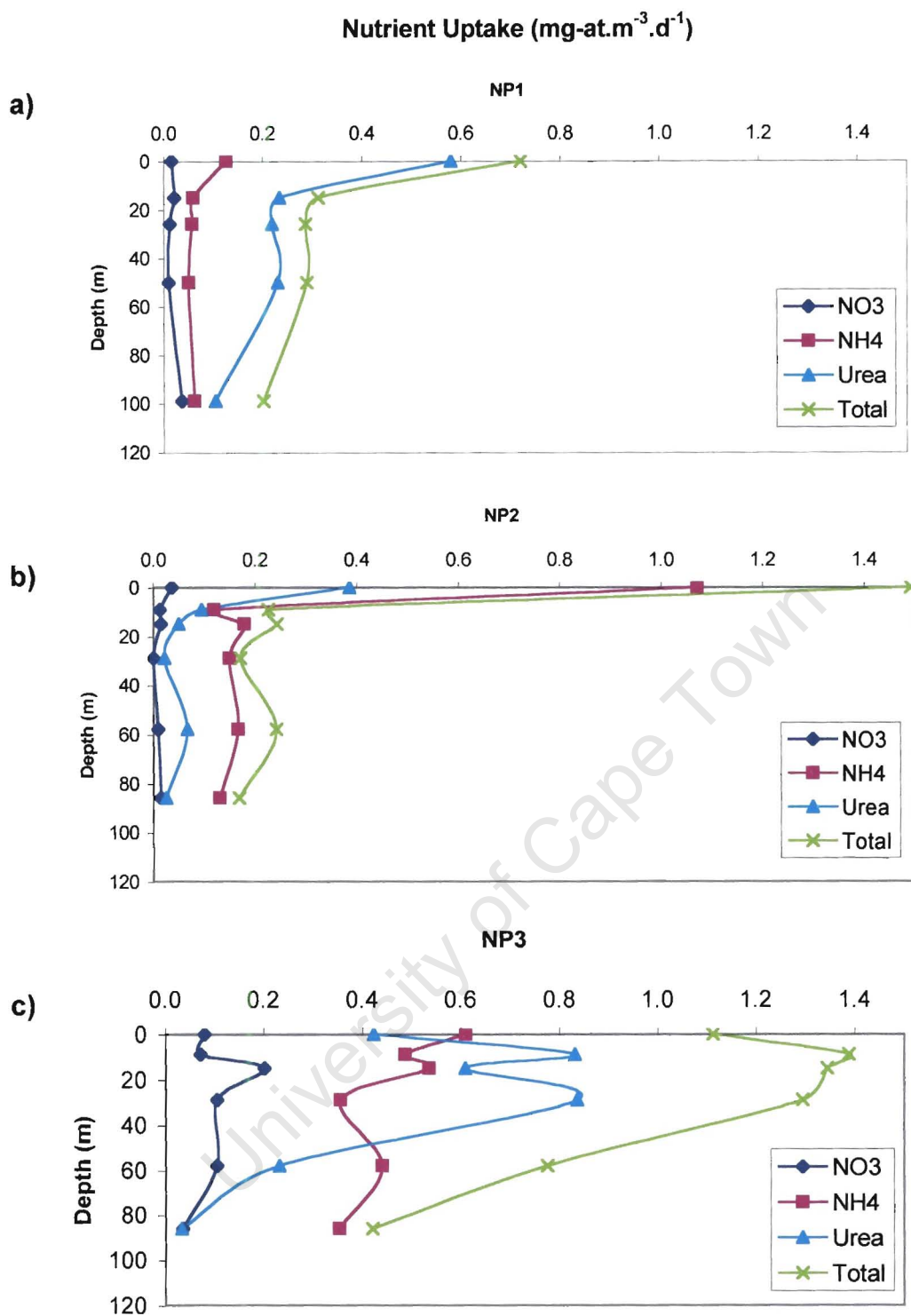


Figure. 20. Vertical profiles of $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, urea-N and total-N uptake ($\text{mg-at.m}^{-3}.\text{d}^{-1}$) for the euphotic zone of subtropical stations NP1 a), NP2 b) and NP3 c).

Nutrient Uptake ($\text{mg-at.m}^{-3}.\text{d}^{-1}$)

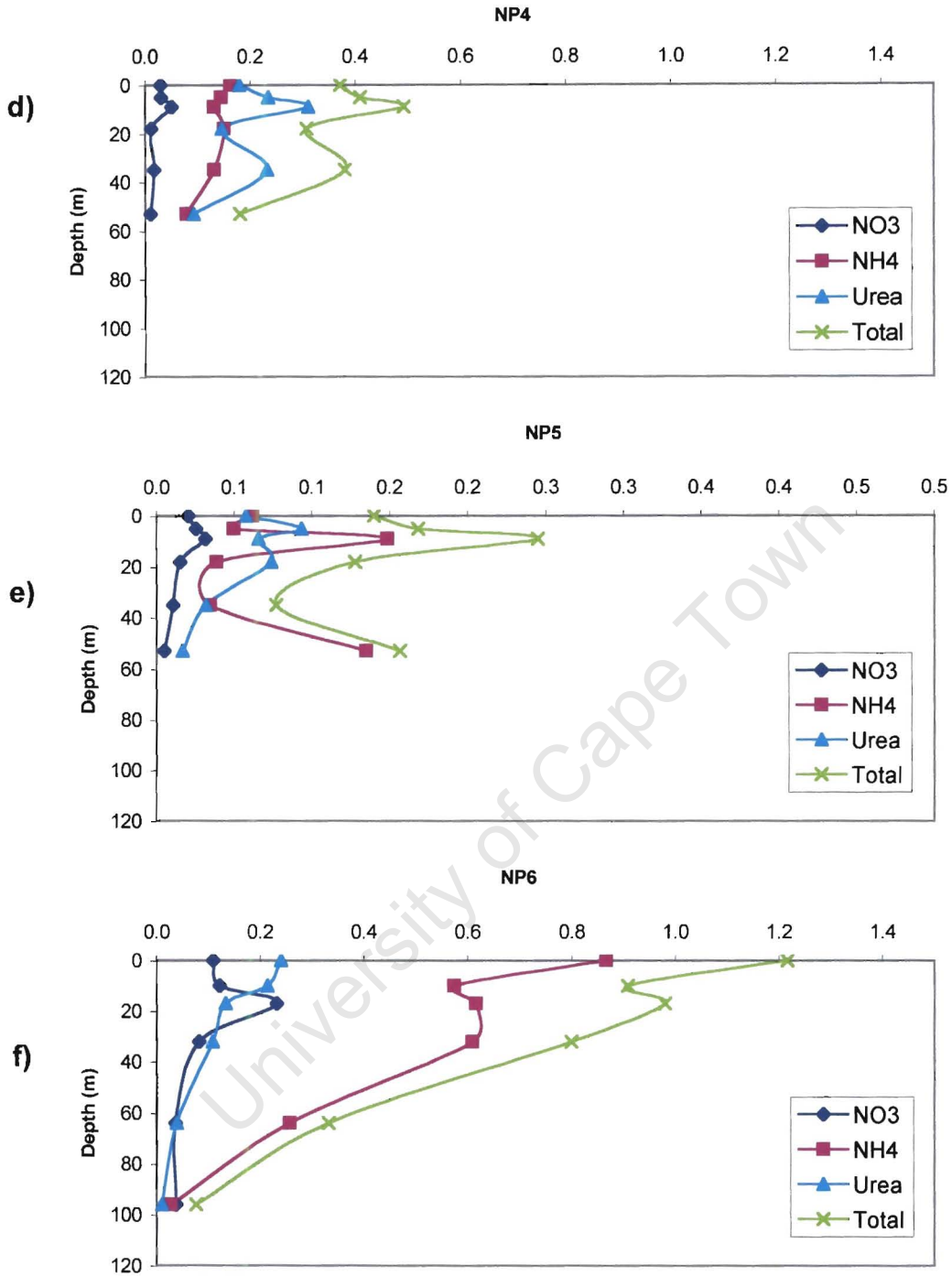


Figure. 20. Vertical profiles of $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, urea-N and total-N uptake ($\text{mg-at.m}^{-3}.\text{d}^{-1}$) for the euphotic zone of subantarctic stations NP4 d), NP5 e) and NP6 f).

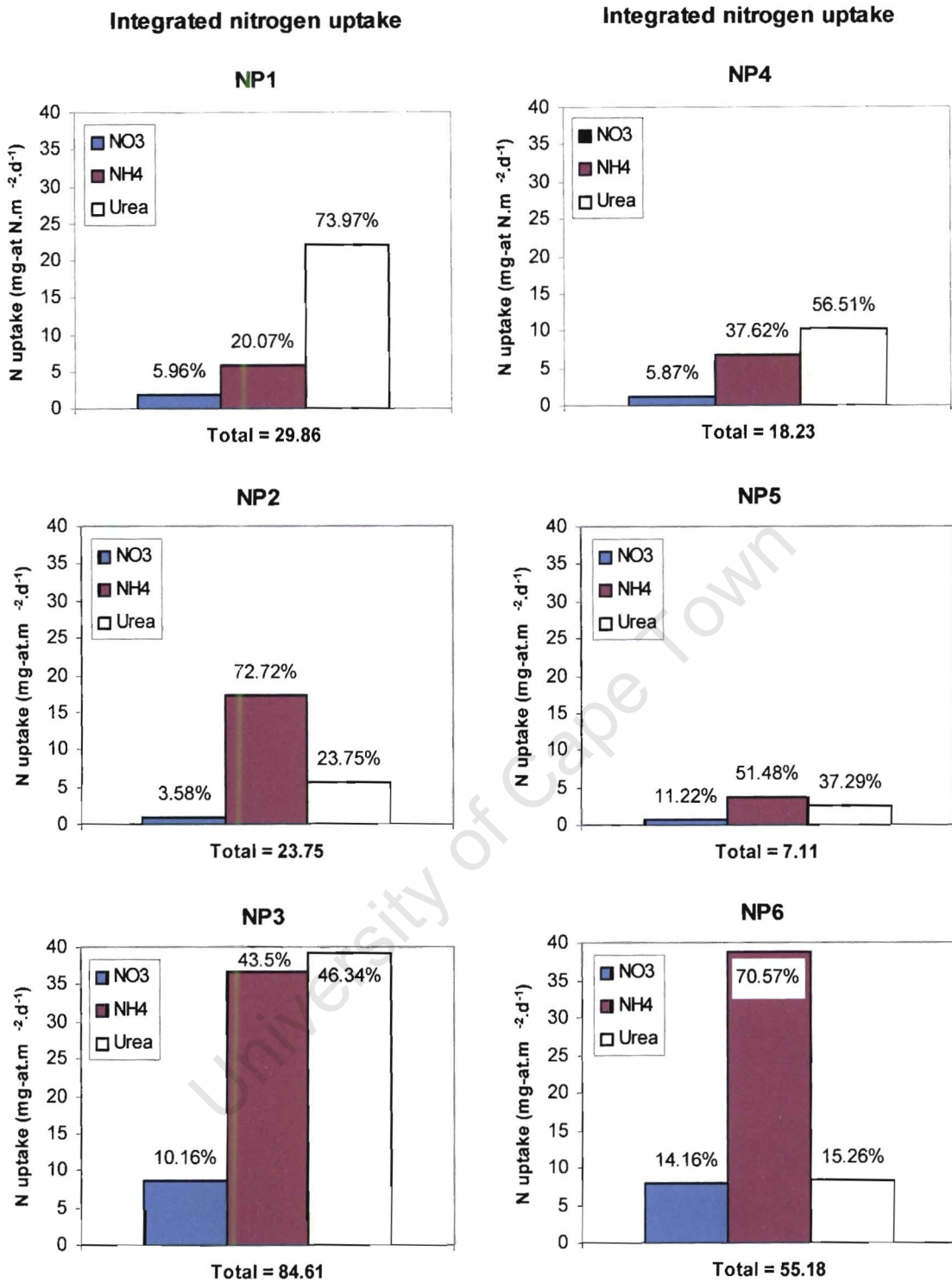


Figure. 21. Euphotic zone integrated measurements of nitrate, ammonium and urea uptake (mg-at.m⁻².d⁻¹) for all productivity stations NP1-NP6.

Integrated f-ratio's

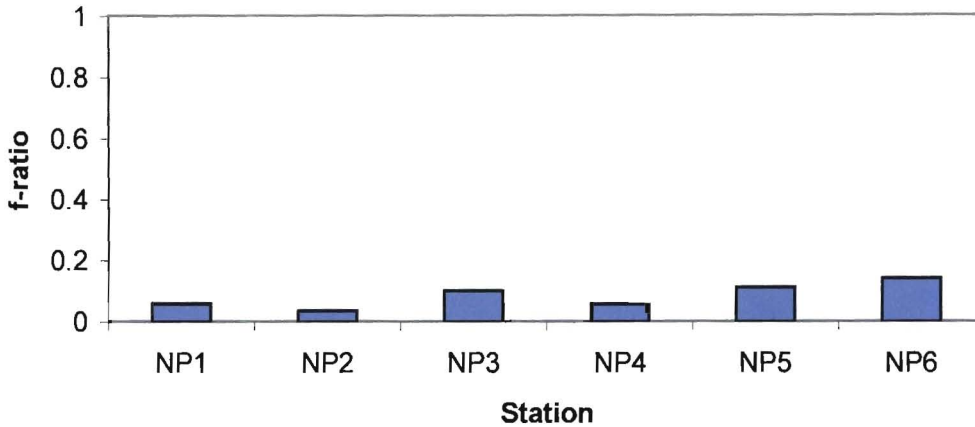


Figure. 22. f-ratio's integrated over the euphotic zone for the six productivity stations of the Southbound transect.

Integrated chlorophyll-a normalised N uptake

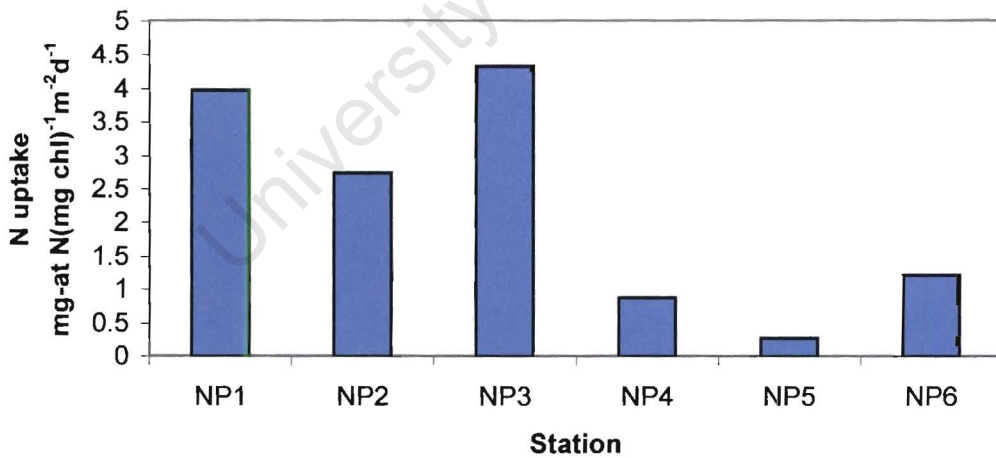


Figure. 23. Euphotic zone integrated chlorophyll-a normalized nitrogen uptake (mg-at N(mg chl)⁻¹.m⁻².d⁻¹) for the six productivity stations of the Southbound transect.

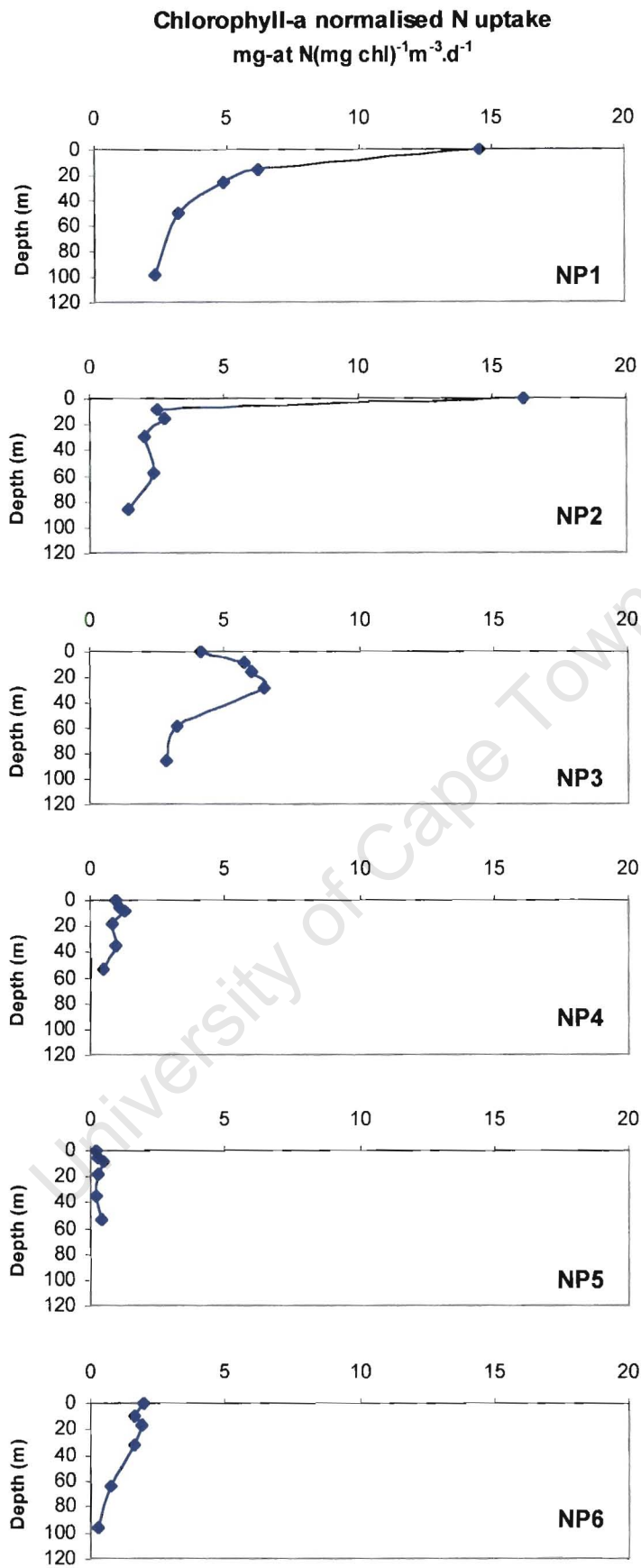


Figure 24. Profiles for productivity stations NP1 to NP6 of chlorophyll-a normalized nitrogen uptake ($\text{mg-at N}(\text{mg chl})^{-1}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$), provides a photophysiological link to photosynthetic efficiency.

Relative Preference Index

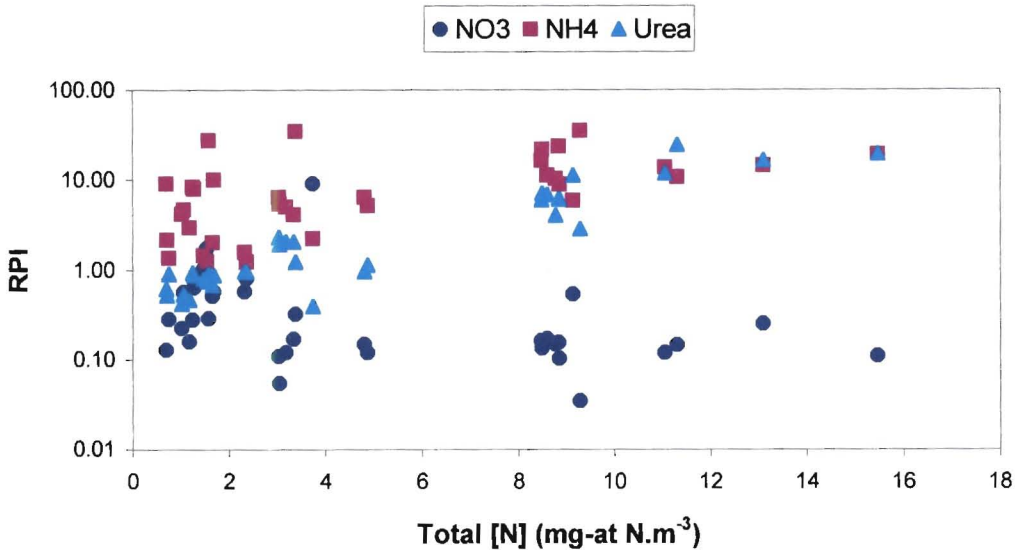


Figure 25. Relative Preference Index (RPI) plotted against total nitrogen concentration (mg-at.m³) for the six productivity stations and depth.

Preference and Inhibition NP4-NP6

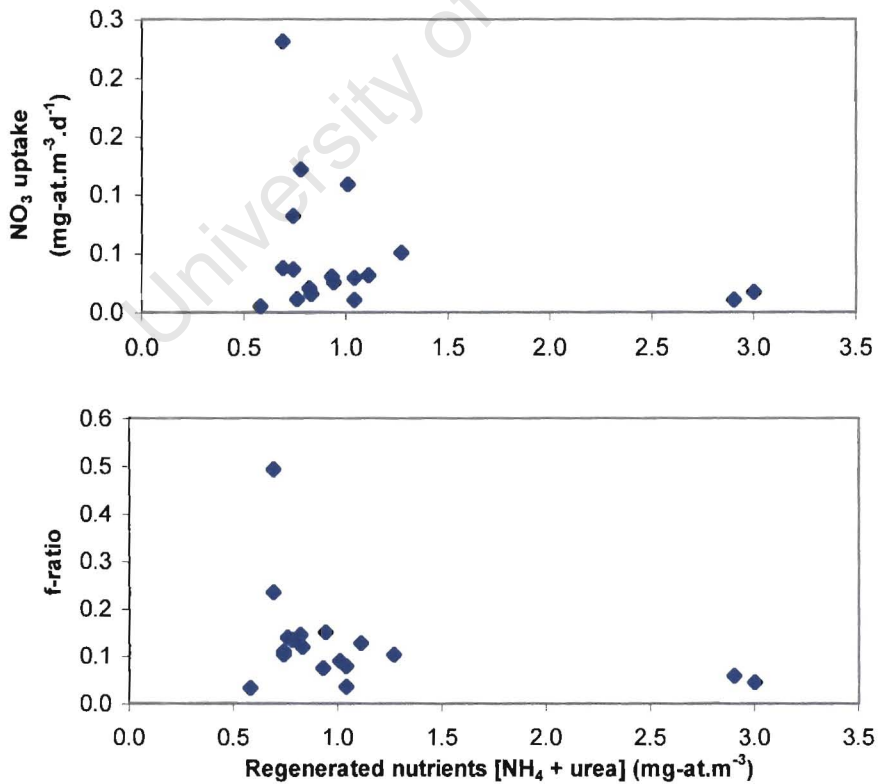


Figure 26. Relationship between new production (f ratio and NO₃ uptake (mg-at.m⁻³.d⁻¹) and ambient regenerated nutrient concentration (mg-at.m⁻³) for subantarctic stations NP4, NP5 and NP6.

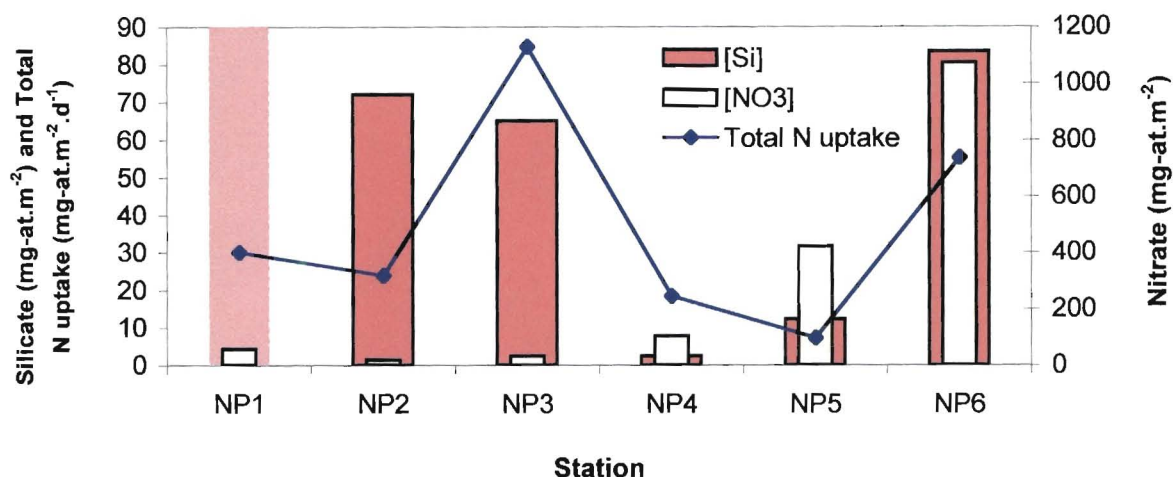


Figure. 27. Relationship between total nitrogen uptake ($\text{mg-at.m}^{-2}.\text{d}^{-1}$) and integrated nitrate and silicate concentrations (mg-at.m^{-2}), from station NP1 at 31°S to NP6 in the region of the Prince Edward Islands.

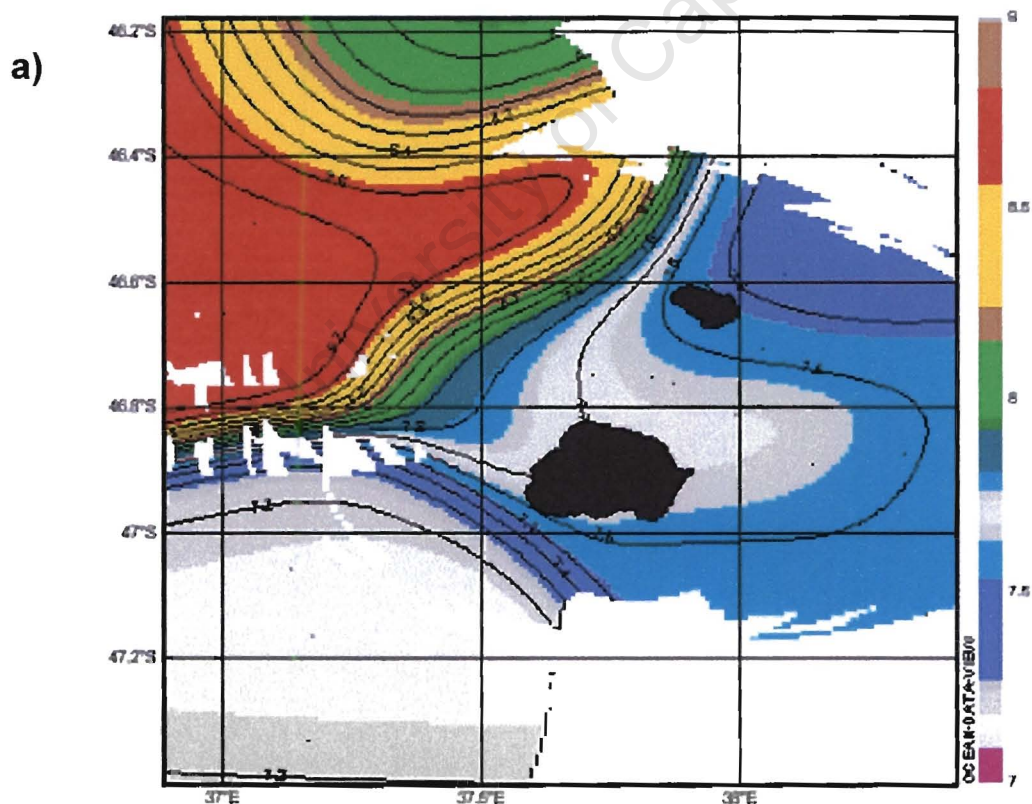


Figure. 28 a) Interpolated surface temperature ($^{\circ}\text{C}$) distribution for the Prince Edward Islands and surrounding ocean.

b)

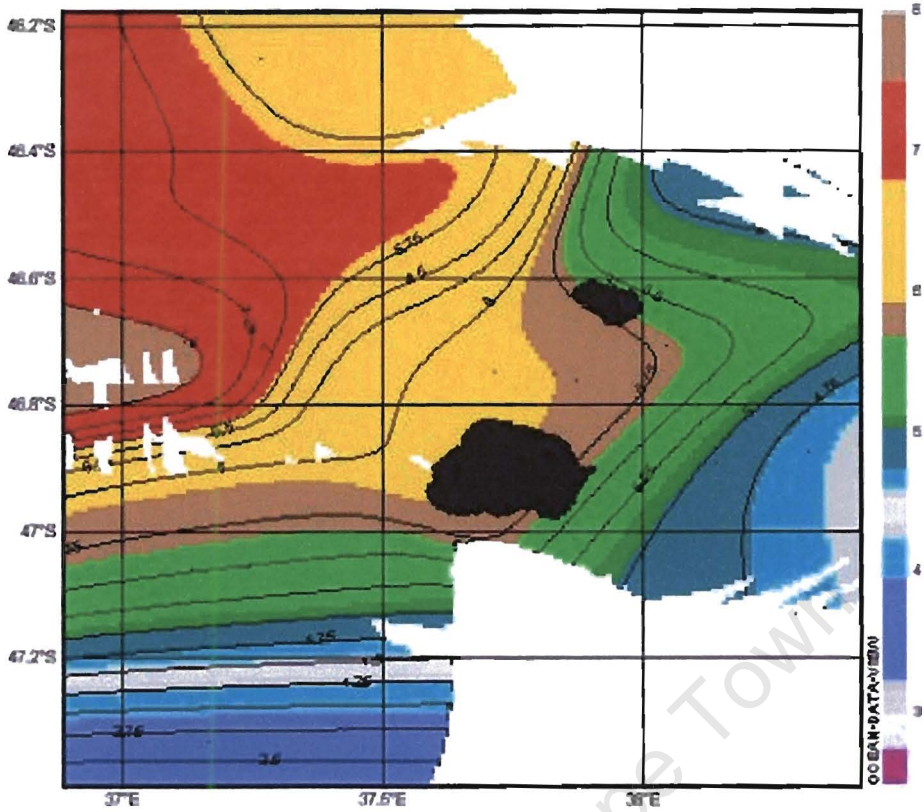


Figure. 28 b) Interpolated temperature ($^{\circ}\text{C}$) distribution at 200m for the Prince Edward Islands and surrounding ocean.

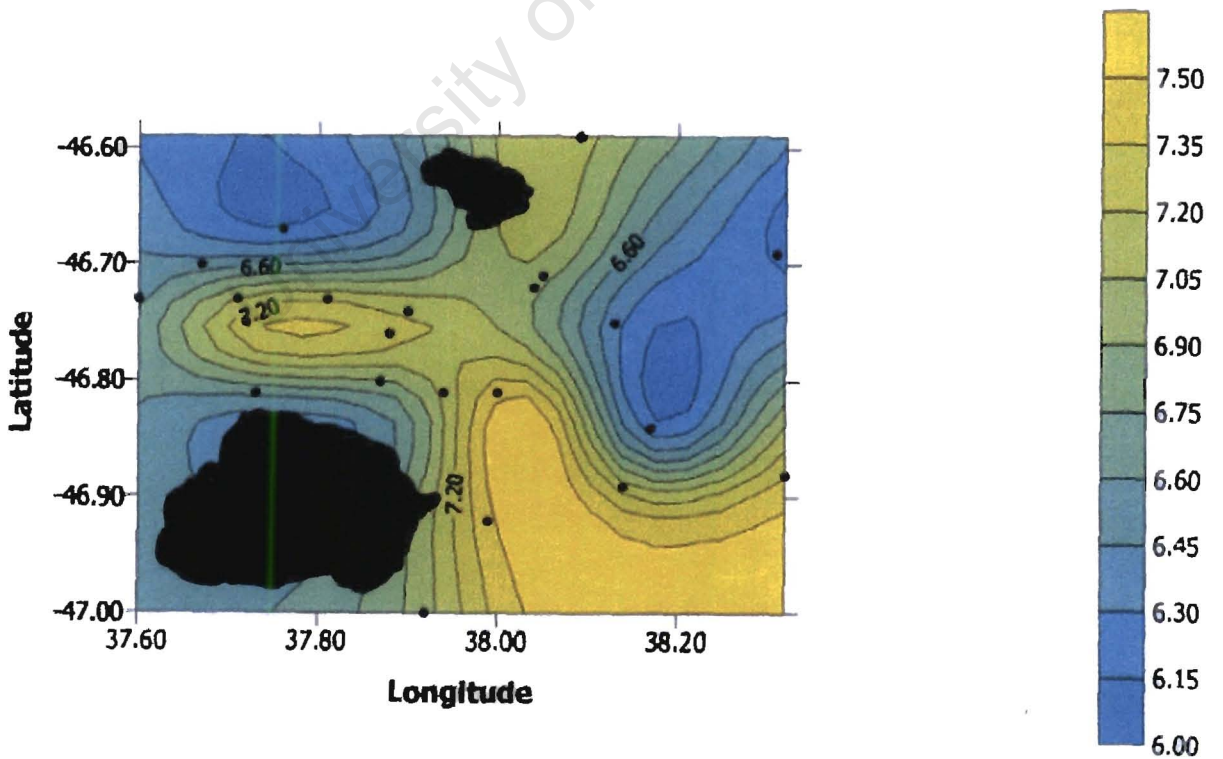


Figure. 29. Sea surface temperature ($^{\circ}\text{C}$) distribution for the Prince Edward Inter-Island region

a)

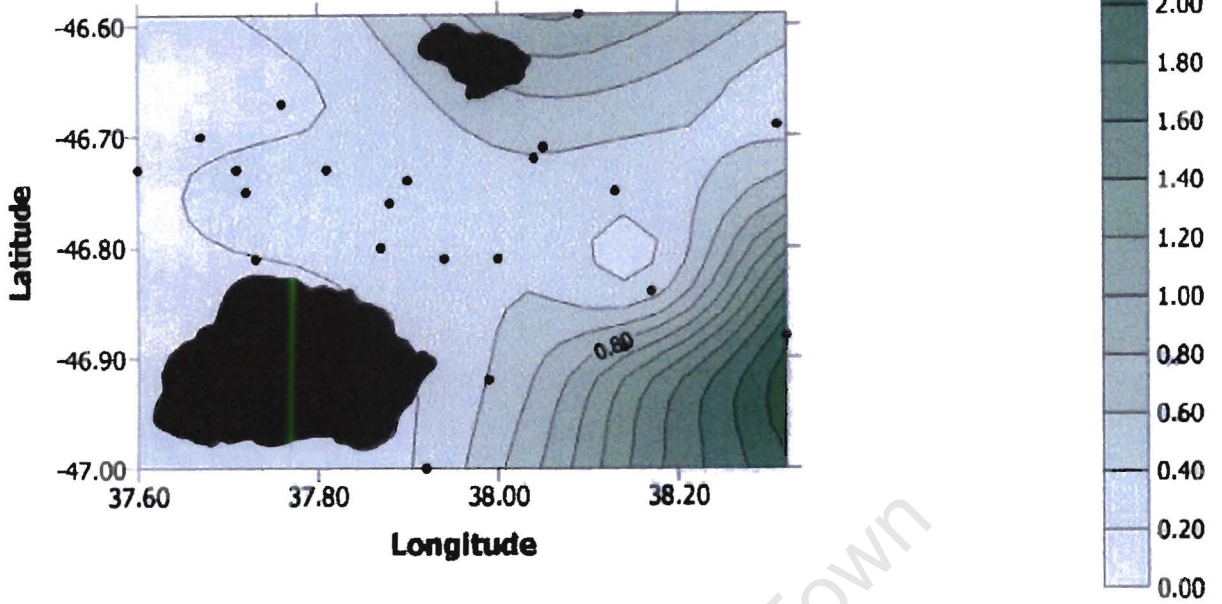


Figure. 30 a) Total surface chlorophyll ($\text{mg}\cdot\text{m}^{-3}$) distribution for Prince Edward Inter-Island region.

b)

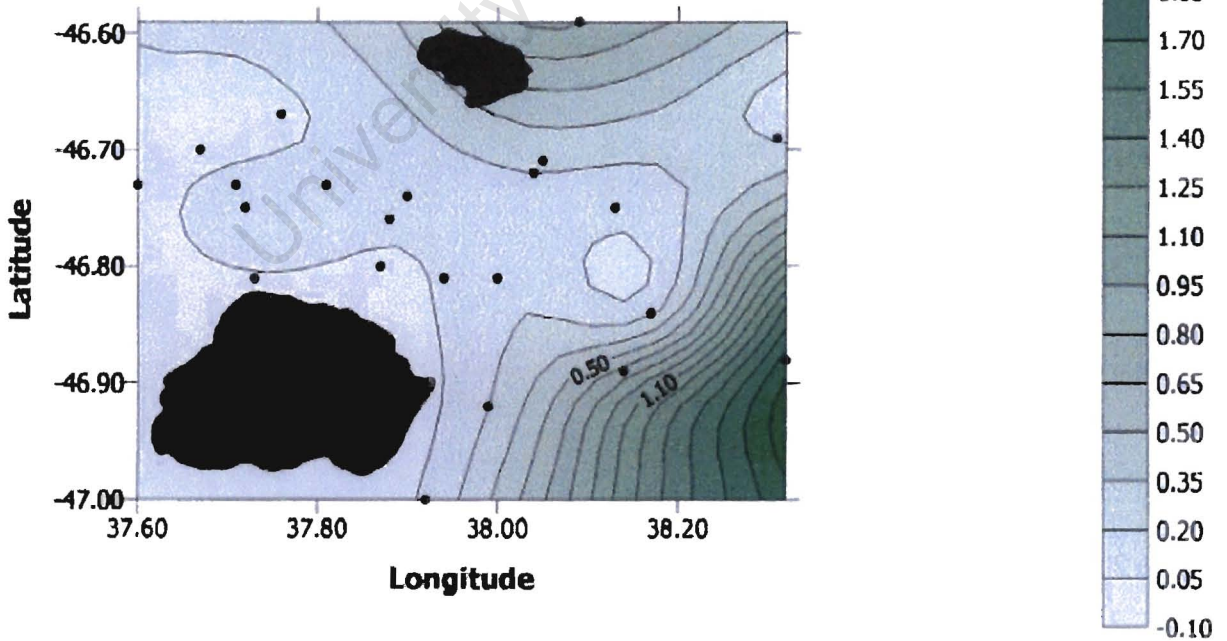


Figure. 30 b) Surface microphytoplankton ($\text{mg}\cdot\text{m}^{-3}$) distribution for the Prince Edward Inter-Island region.

c)

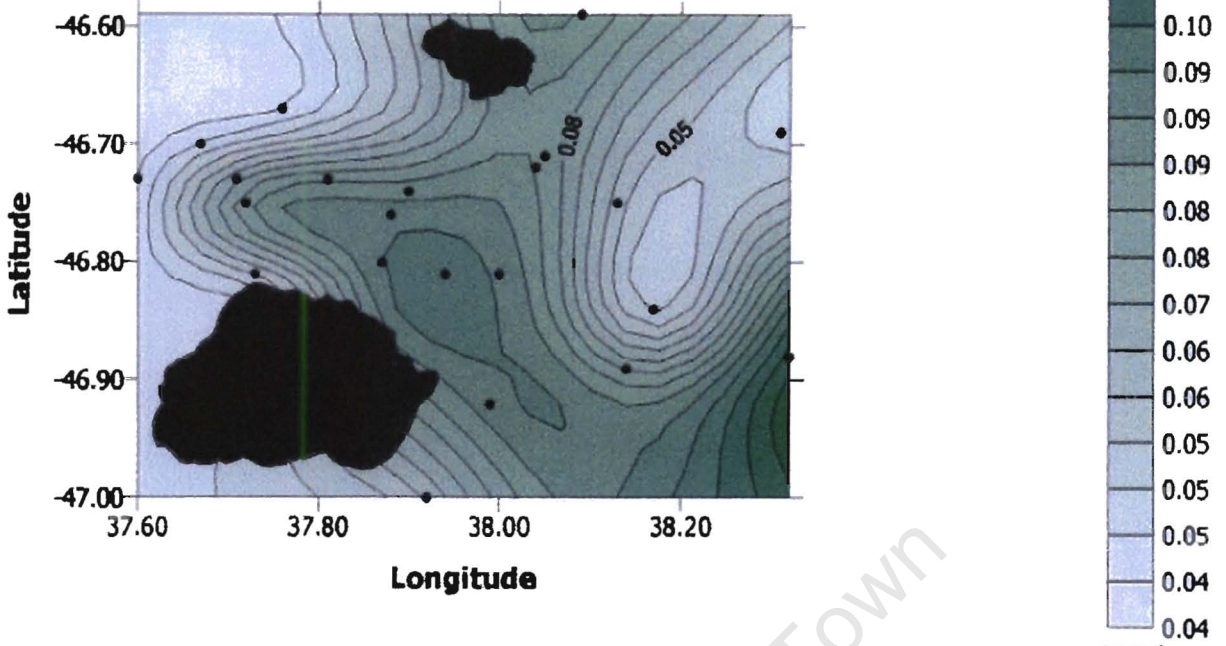


Figure. 30 c) Surface nanophytoplankton ($\text{mg}\cdot\text{m}^{-3}$) distribution for the Prince Edward Inter-Island region.

d)

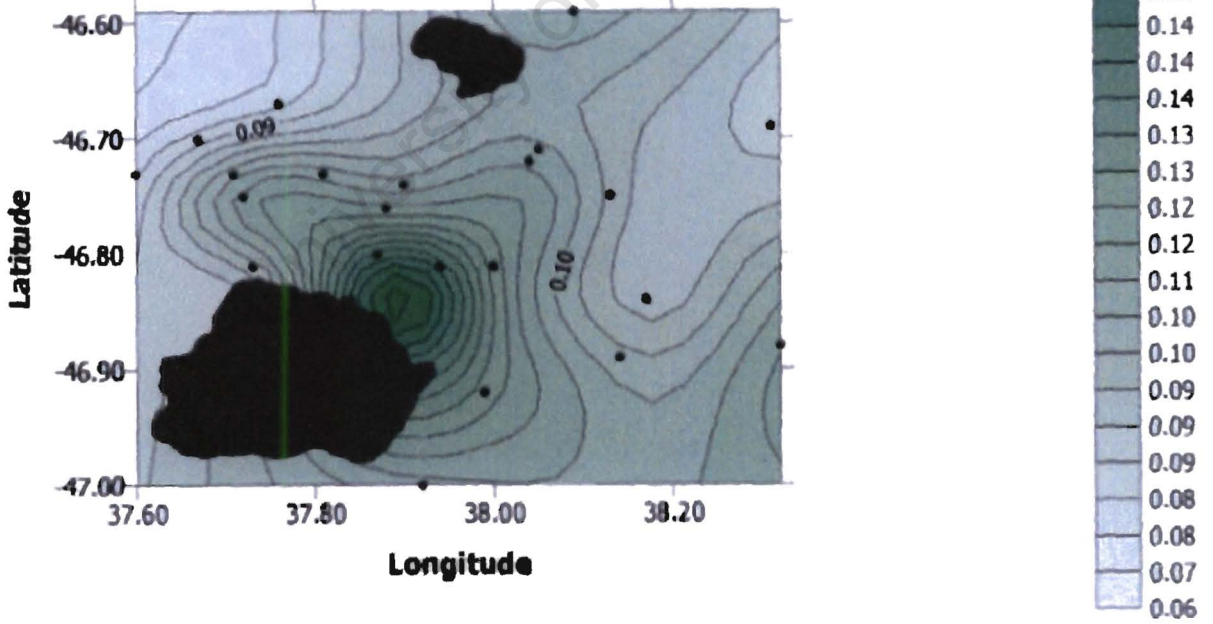


Figure. 30 d) Surface picophytoplankton ($\text{mg}\cdot\text{m}^{-3}$) distribution for the Prince Edward Inter-Island region.

a)

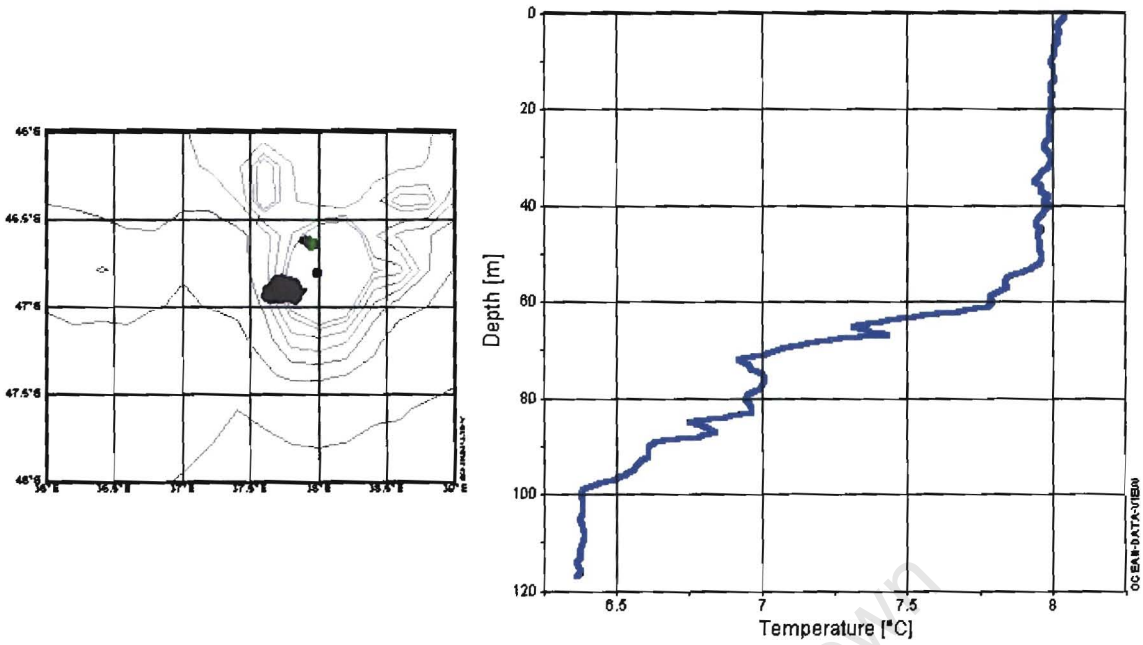


Figure. 31 a) Temperature ($^{\circ}\text{C}$) profile for a station between Prince Edward and Marion Island, within the nanophytoplankton bloom. Notice the well developed surface mixed layer to $\sim 60\text{m}$.

b)

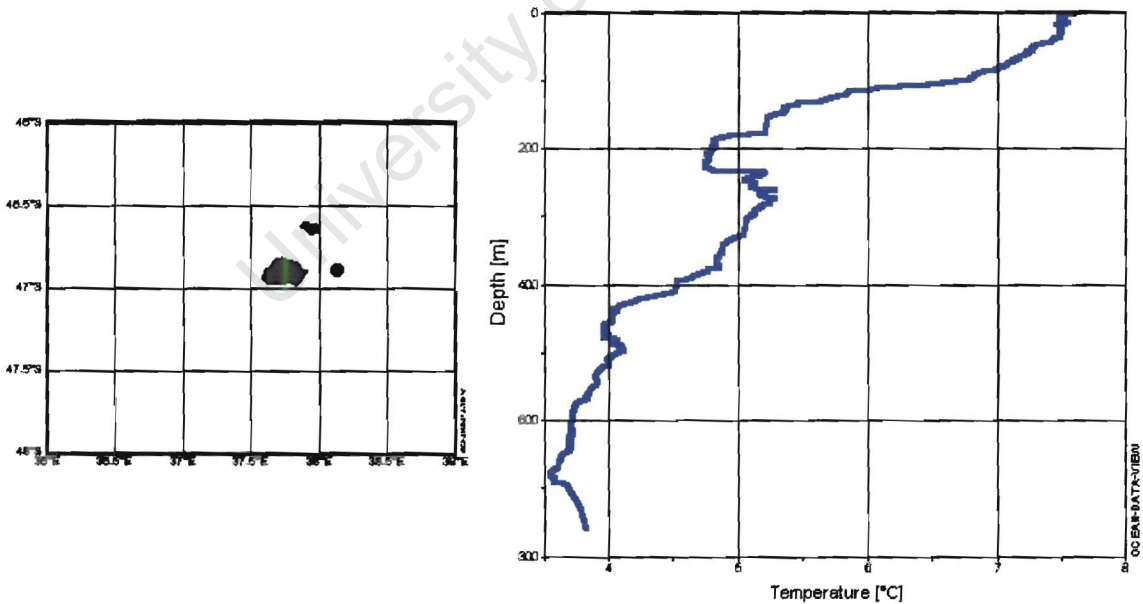


Figure. 31 b) Temperature ($^{\circ}\text{C}$) profile for a station offshore from Marion Island, within the microphytoplankton bloom. Notice the shallower surface mixed layer of $\sim 30\text{m}$.

TABLES

Table 1. Sampling dates and positions of the six, productivity stations along the Southbound transect.

Station	Date	Latitude	Longitude	Region
Number	1999	(Degrees S)	(Degrees E)	
NP1	17/04	31 00.04	43 58.43	N of AF
NP2	19/04	37 00.20	43 58.33	N of AF
NP3	20/04	40 00.43	44 02.27	AF
NP4	23/04	43 01.02	40 57.36	STF
NP5	24/04	45 20.60	38 44.18	SAF
NP6	24/04	46 30.28	37 52.37	PEI plateau

Table 2. Depth of chlorophyll maximum and size fractionated community structure of the different regions along the Southbound transect.

	Chlorophyll	within the	top 150m	(mg/m ³)	
Region	Max	Depth (m)	micro (%)	nano (%)	pico (%)
N of AF	0.23	100	3	15	82
AF - STF	0.27	0	2.5	16.9	80.6
STF - SAF	0.53	75	12.2	31	56.8
S of SAF	0.74	24	52.5	18.5	29

Table 3. Nitrate, ammonium and urea concentration (mg-at.m^{-3}) at the various light depths for the productivity stations of the Southbound transect, together with temperature ($^{\circ}\text{C}$) and total chlorophyll (mg.m^{-3}) concentrations in the top 150m.

Station Number	% Light	Ambient [NO3] (mg-at/m^3)	Ambient [NH4] (mg-at/m^3)	Ambient [Urea] (mg-at/m^3)	Depth (m)	Temperature (Degrees C)	Total Chlorophyll (mg chl/m^3)
NP1	100	0.06	0.03	1.59	0	23.07	0.05
	50	0.13	0.03	1.1	20	22.75	0.05
	25	0.18	0.03	1.03	50	22.73	0.09
	10	0.18	0.01	1.38	100	19.08	0.09
	1	1.89	0.03	1.45			
NP2	100	0.01	1.22	2.5	0	20.63	0.09
	50	0.10	0.12	0.83	25	20.62	0.09
	25	0.16	0.41	0.17	50	20.54	0.08
	10	0.24	0.29	0.17	75	19.87	0.15
	1	0.17	0.17	0.67	100	18.25	0.08
	0.1	0.47	0.06	0.17	150	16.82	0.01
NP3	100	0.06	0.68	0.79	0	19.53	0.27
	50	0.16	0.68	1.53	25	19.55	0.19
	25	0.22	0.41	0.84	50	19.56	0.24
	10	0.33	0.41	1.58	75	19.56	0.25
	1	0.44	0.47	0.74	100	19	0.12
	0.1	0.63	0.34	0.2	150	17.21	0.02
NP4	100	2.13	0.28	0.76	0	13.54	0.38
	50	2.10	0.17	0.76	25	13.52	0.39
	25	2.07	0.22	1.05	50	13.55	0.4
	10	2.01	0.28	0.76	75	13.55	0.37
	1	1.86	0.33	2.67	100	12.23	0.05
	0.1	1.91	0.33	2.57	150	10.53	0.01
NP5	100	7.66	0.23	0.59	0	8.27	0.61
	50	7.66	0.23	0.71	25	8.27	0.47
	25	7.66	0.52	0.59	50	8.25	0.41
	10	7.66	0.12	0.71	75	8.01	0.11
	1	8.07	0.17	0.59	100	7.41	0.03
	0.1	8.69	0.23	0.35	150	6.69	0.02
NP6	100	7.84	0.72	0.29	0	6.17	0.63
	50	10.51	0.67	0.11	25	6.17	0.46
	25	12.39	0.58	0.11	50	6.16	0.57
	10	14.71	0.63	0.11	75	6.2	0.36
	1	10.29	0.63	0.11	100	6.3	0.31
	0.1	8.44	0.58	0.11	150	5.26	0.05