Phytoplankton associated with mesoscale eddies in the Mozambique Channel

By

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Abstract

The study undertaken was an attempt to provide information on the effect that oceanographic features common in the Mozambique Channel have on primary production. Oligotrophic conditions dominated the Mozambique Channel at the time of sampling and the introduction of nutrients into the euphotic zone by upwelling processes were identified as cyclonic eddies. Differences in physico-chemical variables between surface and *F*-max across all sites proved to be stronger than the physico-chemical variables between 4 grouped oceanographic features. This was revealed by stronger variations in phytoplankton community structure and chlorophyll *a* concentration between surface and *F*-max compared to oceanographic features sampled.

One of the hypotheses presented for the study was that diatoms would dominate phytoplankton communities within a cyclonic eddy. This was not the case as the coccolithophorid, *Emiliania huxleyi* Lohmann (Hay and Mohler 1967) dominated *F*-max and surface water in the cyclonic eddies and most other sites. Phytoplankton community structure did not differ significantly between the oceanographic features sampled which contradicted another one of hypotheses presented in the study. Chlorophyll *a* concentration in surface water of the cyclonic eddies was significantly higher than in surface waters within the anti-cyclonic eddy. *F*-max was not significantly different in phytoplankton biomass between these two system types. The cyclonic eddies and anti-cyclone had similar phytoplankton diversity which did not verify the hypothesis that there would be less phytoplankton species diversity within cyclonic eddies compared to the anti-cyclonic eddy. Phytoplankton community structure differed between *F*-max (depth at which maximum chlorophyll *a* is found) and the surface. This phytoplankton community difference was linked to differences in physico-chemical variables between the two depths.

The diatoms *Thalassionema nitzschioides, Pseudo-nitzschia* sp.A, *Pseudo-nitzschia* sp.B, *Thalassiosira* sp.C*, Thalassiosira sp.E, Bacteriastrum furcatum, Guinardia cylindrus, Nitzschia closterium, Hemiaulus hauckii,* and *Nitzschia braarudii* revealed the only discernible ecological similarity amongst phytoplankton species across all sites and depths. This is important as it revealed that these species were regularly found occupying similar depths and potentially similar physico-chemical ranges in the water column which suggest these diatom species responded to a dominant source of variation. Distribution patterns of species and of ecologically defined groups support the hypothesis that diatom species and assemblages are good indicators of the changing character of an upwelling system. These statements lead to the assumption that the diatom grouping found in this study indicates

areas of upwelling where water temperatures are reduced and nutrients are more readily available. One must keep in mind that ordination techniques are only descriptive and no significance is tested.

The coccolithophorid *D. anthos* and the dinoflagellate *Phalacroma* spp. were noted as being most dissimilar to all other phytoplankton species with regards to their position in the water column and their response to physico-chemical variables.

Finally, the dominance of *E. huxleyi* in the Mozambique Channel during November/December of 2009 reveals the potential vulnerability of phytoplankton in the channel to ocean acidification.

Keywords: Mozambique Channel, mesoscale, phytoplankton, upwelling, nutrients

Table of Contents

Table of Figures

List of Tables

List of Acronyms

AC	Agulhas Current
ACEP	African Coelacanth Ecosystem Programme
ASCLME	Agulhas Somali Current Large Marine Ecosystem
CA	Canonical Analyses
CC	Cold Core
CCA	Canonical Correspondence Analyses
CTD	Conductivity Temperature Depth
EACC	East African Coastal Current
ENSO	El Nino/Southern Oscillation
MCE	Mozambique Channel Eddies
MODIS	Moderate Resolution Imaging Spectroradiometer
NEMC	Northeast Madagascar Currents
NSP	North-South Profile
SEC	South Equatorial Current
SEMC	South East Madagascar Currents
SRP	Soluble Reactive Phosphorus
SST	Sea surface Temperature
SWSIG	South West Subtropical Indian Gyre
SCZ	Subtropical Convergence Zone
WC	Warm Core
XBT	Expendable Bathythermographs

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Student Declaration

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1. General Introduction

Sustainable management of the earth's natural resources is of great importance. The Agulhas Somali Current Large Marine Ecosystem (ASCLME) project is an effort to better manage the fisheries within the western Indian Ocean. South Africa is one of nine east African countries participating in the ASCLME project which is implemented by the United Nations Development Programme as well as the Global Environmental Facility and focuses on building and collating information on oceanographic aspects, coastal livelihoods, persistent organic pollutants, fish spawning as well as nursery areas (Vousden et al., 2008).

Primary production in the pelagic environment is dominated by phytoplankton. Marine phytoplankton is the most abundant and widely distributed form of life on earth (Zeitzschel 1974). Marine phytoplankton is responsible for more than 45% of the earth's annual net primary production but represents less than 1% of the earth's photosynthetic biomass (Field et al., 1998). The importance of phytoplankton can therefore not be underestimated when attempting to understand any marine ecosystem. The primary production of phytoplankton and the distribution of phytoplankton in the world's oceans are generally governed by physical processes (Zeitzschel 1974), which provides fundamental information about, and insight into, physical and biological processes in aquatic systems (Steele 1989).

The western Indian Ocean is one of the least explored and least understood of all ocean regions, particularly the south-west Indian Ocean (Lutjeharms 2006a). The research cruises of the Agulhas and Somali Current Large Marine Ecosystems (ASCLME) Project aimed at filling crucial knowledge gaps, particularly in relation to the effects of ocean currents on the productivity and natural resource sustainability within the Large Marine Ecosystem (Vousden et al., 2008). The present study focuses on leg four (Cruise MC08A) of the ASCLME project which endeavoured to sample biological and physico-chemical parameters within oceanographic features (with particular focus on mesoscale eddies) which occurred within the Mozambique Channel during late November and early December of 2008. According to Barlow et al. (2008) with the exception of the African Coelacanth Ecosystem Programme (ACEP) and the ASCLME there has been very few investigations into phytoplankton biomass and primary production within the Mozambique Channel in the last two decades.

A large proportion of the Mozambique Channel consists of continental shelf area. Within the existing described marine phytoplankton taxa, the diatoms (one of the major lineages within the stramenopiles) and the haptophytes appear to dominate phytoplankton communities on continental shelves (Simon et al., 2009). They are generally the main marine planktonic

primary producers within the nano- and microphytoplanktonic size classes (respectively 2-20 µm and 20 – 200 µm) (Simon et al., 2009).

1.1 Study Site and its Oceanography

The Mozambique Channel lies between Madagascar and Mozambique on the east coast of Africa and is roughly 1500 kilometres long with the narrowest part of the channel estimated to be 450 kilometres wide at 17ºS (Stammer 1997).

The main currents and flow patterns shown in Figure 1.1 include the South Equatorial Current (SEC), the Northeast and Southeast Madagascar Currents (NEMS and SEMC), the East African Coastal Current (EACC), the Agulhas Current (AC), Mozambique Channel Eddies (MCE) and the Mozambique Current (MC). The connection between the SEMC and the AC is not well understood. Flow through the Mozambique Channel is dominated by mesoscale eddies a few hundred kilometres wide and ultimately water moves from north to south through the channel (Stammer 1997). An illustration of the basic flow patterns thought to influence the Mozambique Channel is represented in Figure 1.1. The focus of this research is to look at physical and biological parameters of the mesoscale oceanographic features present in the Mozambique Channel.

1.2 Aims and Hypothesis

The present study aims to contribute to the current knowledge and understanding of phytoplankton and primary production in the Mozambique Channel, off the east coast of Africa.

The hypotheses tested in the study were:

1. There is greater biomass and less diversity of phytoplankton species within the cyclonic eddies relative to that of the anti-cyclonic eddies due to upwelling.
2. Diatoms will dominate the phytoplankton community in the cyclonic eddy.
3. Community structure of phytoplankton will differ between mesoscale features.
4. Community structure of phytoplankton will differ between *F*-max (depth at which maximum chlorophyll *a* is found) and the surface.

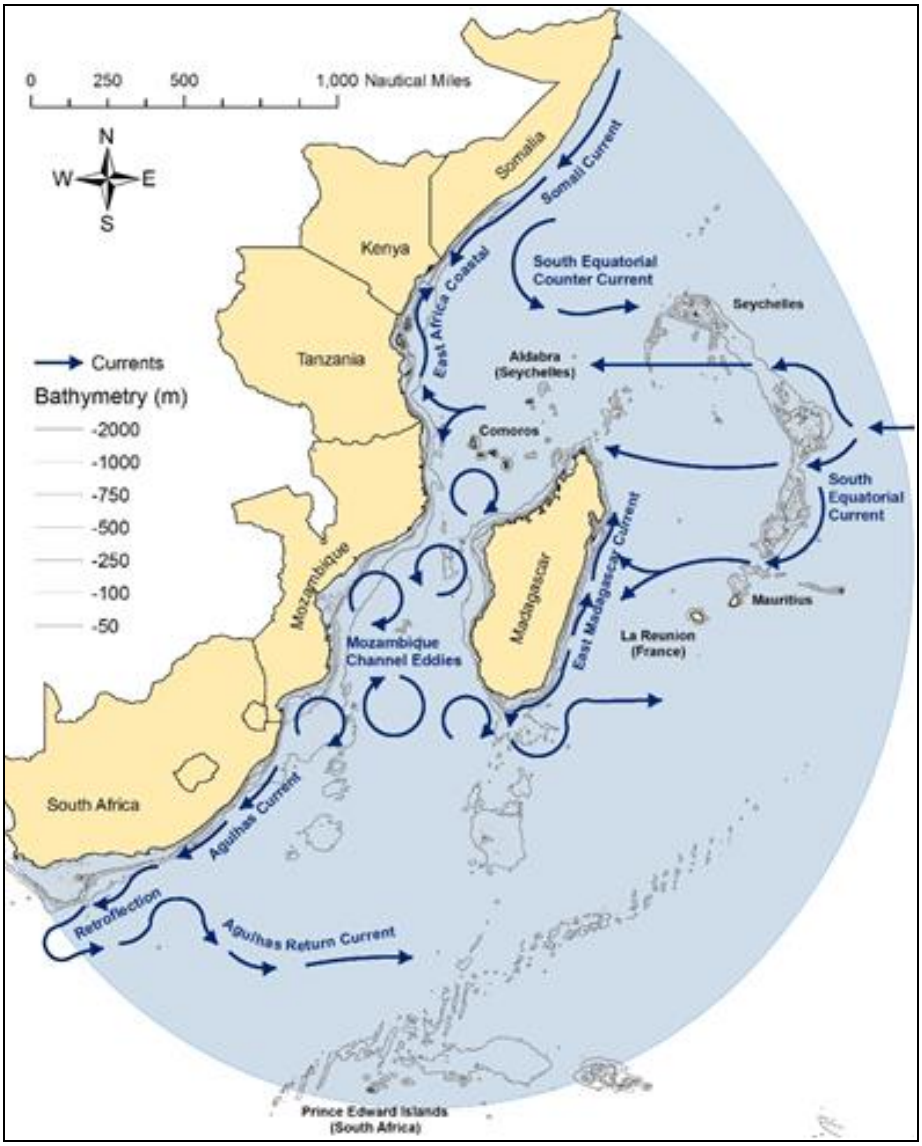

Figure 1.1. Basic flow patterns within the South West Indian Ocean.

This thesis is preceded by a general introduction followed by three related focal chapters, and ends with a general synthesis and conclusion. In the first data chapter (Chapter 2) we introduce the study area within the context of selected transects, profiling the features present in these regions. More specifically, profiles of certain oceanographic features, and combinations of others are displayed, the details of which are outlined in the chapter. The data chapter that follows assesses each mesoscale feature and compares the physico-chemical and biological characteristics therein in greater detail, with Chapter 3 focusing on chlorophyll *a* as an indicator of phytoplankton biomass and Chapter 4 on the phytoplankton community structure.

2 Literature review

2.1 Oceanography of the south-west Indian Ocean

Ocean circulation is considered to be influenced by mesoscale (100km`s in diameter) oceanic features such as the cyclonic and anti-cyclonic eddies (Klein and Lapeyre 2009). The westward flowing South Equatorial Current (SEC) splits as it collides with the east African coast at around 11ºS and water moves northward up the coast to become the EACC and southward into the Mozambique Channel (Figure 1.1). This southward moving water mass passing through the Mozambique Channel ultimately becomes part of the Agulhas Current, which flows southward along the east and south coast of South Africa. At the narrowest part of the Mozambique Channel (around 17ºS) cyclonic and anti-cyclonic eddies are formed and move southward through the channel (Tew-Kai and Marsac 2009). Eddies become more frequent in the central portion of the channel (Schouten et al., 2003). On exiting the channel, these eddies merge with others moving from the southern tip of Madagascar and become part of the southern flowing Agulhas Current (Tew-Kai and Marsac 2009). It is thought that equatorial wind variability plays an important role in the formation of mesoscale eddies in the Mozambique Channel (Schouten et al., 2003). Satellite altimetry observations reveal that eddy kinetic energy within the Mozambique Channel is substantial and that eddies are often present, moving southward through the channel (Stammer 1997). This lack of continuity of flow within the Mozambique Channel indicates that a single southward flowing 'Mozambique Current' is not an accurate description of the flow through the channel (De Ruijter et al., 2002). Because of the complexity of flow within the Mozambique Channel, it is argued that a southern flowing Mozambique Current does not exist. In a study carried out by De Ruijter et al. (2002) to investigate the existence of a Mozambique Current, eight hydrographic sections were placed to intersect the currents between Mozambique and Madagascar where a number of pole-ward moving anti-cyclonic eddies passed through the study site but no consistent southern flowing western boundary current was found.

Mozambique eddies have diameters of 300 kilometres or greater and may extend to the ocean floor where their azimuthal speeds are around 10cm/s whereas at midway depths azimuthal speeds are roughly double the speeds recorded at the ocean floor (Lutjeharms 2006a). The sheer size of eddies in the Mozambique Channel suggest they would have a marked influence on channel waters physically and biologically. Mesoscale eddies within the Mozambique Channel are said to move pole-ward at an average speed of around 4.5km per day whereas the speeds of pole-ward moving mesoscale eddies are faster between 12ºS

and 27ºS (6 kilometres a day) than between 18ºS and 21ºS where the net pole-ward movement is 3 to 4 kilometres per day (Schouten et al., 2003). Eddies follow a constricted path in the western portion of the Mozambique Channel and it is this characteristic which makes it possible for these eddies to combine and become a part of the Agulhas Current (De Ruijter et al., 2002).

As part of the Agulhas Current Sources Experiment, Ridderinkhof and de Ruijter (2003) showed, using moored current observations in the Mozambique Channel at around 17ºS, that during the time an anti-cyclonic eddy passes southward through the Mozambique Channel, low-frequency currents were dominated in duration and magnitude by 'strong current events'. Also, when the southward transport through the mooring section was strongest, an anti-cyclonic eddy was formed. As a conclusion to the study it was argued that it may be possible for Mozambique Channel eddies to exert some type of control on the inter-basin exchange between the Indian and Atlantic Oceans since net surface southward flow of surface currents and northward flowing undercurrents form an important part of the global overturning ocean circulation (Ridderinkhof and de Ruijter 2003). Circulation patterns within the Mozambique Channel are thought to be seasonal with the summer season being dominated by anti-cyclonic eddies whereas winter eddies are not as frequent (Schouten et al., 2003).

In a study carried out by Schouten et al. (2003) eddy paths were found to be relatively uniform and followed the African coastal bathymetry, strengthening due to latitudinal displacement between 12ºS and 20ºS. It was also suggested that south of 20ºS there is a reduction in the frequency of eddies. Eddies merging into larger oceanographic structures is thought to be the cause of this reduction but is not proven by statistical method (Schouten et al., 2003).

Flow characteristics on the western side of the Mozambique Channel are thought to be different to those on the eastern side (Lujteharms 2006b). The western side of the channel is said to have more frequent eddy occurrences than the eastern portion and these flow patterns can have a substantial effect on the adjacent shelf and slope regions (Lujteharms 2006b). According to variable data sets collected over the years concerning property distributions, transport estimates and direct current measurements, it is thought that the Mozambique Channel has a complex and inconstant system of currents which interact at several depths (DiMarco et al., 2002).

2.2 Nutrients

Nutrients commonly measured to assess phytoplankton biomass and primary productivity are nitrate, phosphate and silicate. A basic explanation of the relationship between phytoplankton and nutrients is explained in von Liebig`s 'Law of the Minimum' where phytoplankton growth is limited by those elements or element which are least available (Rosenzweig 1973). Although phosphorus and iron are said to be limiting in certain circumstances, adequate levels of these nutrients can be achieved within cells so that reasonable growth rates may be sustained for a few generations in cases where the nutrient becomes depleted (Flynn 2003).

Phosphorus is biologically available as orthophosphoric acid, OP $(OH)_3$ and is a weak tribasic acid that is water soluble (Reynolds 2006). Silicate is important to diatoms for growth due to the fact that it cannot be redistributed, as uptake of silicate is needed for each cell division in diatoms (Martin-Jezequel et al., 2000). As such, silicate concentrations have been found to be negatively correlated with both abundance and diversity of coccolithophorid assemblages (Mohan et al., 2008). According to Reynolds (2006) nitrogen is an element whose relative shortage affects upon the ecology of phytoplankton. High nitrate concentrations often corresponded with a high abundance of mono-specific assemblages of *E. huxleyi* at high latitudes in a study carried out by Mohan et al. (2008).

Introduction of nutrients into the euphotic zone in the pelagic environment is thought to be largely through cyclonic eddies which are able to transport deep, cold, nutrient rich waters towards upper euphotic surface layers in the centre of the eddy, thus influencing local primary production (Bakun 2006). In the Mozambique Channel land based freshwater input is also thought to be a major source of nutrients into the marine environment (Tew-Kai and Marsac 2009). The Mozambican land mass is known to release nutrient rich freshwater into the Mozambique Channel during episodic events generated by atmospheric tropical cyclones (Lutjeharms 2006b).

Sewage is not treated in Mozambique but discharged directly into the sea. Industrial and agricultural residue reaches the sea through river effluent (Chemane 1997). The influence of untreated sewage on primary production within the Mozambique Channel should not be underestimated.

In the Natal Bight, the influence of the Tugela River on nutrient distributions in the bight is noticeable and a recurrent lee eddy situated off the southern end of the Natal Bight is thought to introduce nutrients to the centre of the bight (Meyer et al., 2002). According to Paula et al. (1998) at Inhaca Island in southern Mozambique, nitrates, silicates and total phosphorus all showed an increase during the warmest months which were said to be

coupled with the maximum values of precipitation in the hydro-graphic basins of the rivers which discharge into Maputo Bay.

In a study carried out by Lourey et al. (2006) on the Leeuwin current along the west coast of Australia, a cross-shelf seasonal gradient in chlorophyll *a* coincided with increased winter flow of the Leeuwin current southward along the coast which suggested that the origin of nutrients in the region may have been terrestrial.

Mesoscale eddies are able to entrain nutrient rich coastal waters which generally results in higher chlorophyll concentrations inside the eddy (Lutjeharms 2006b; Omata et al., 2009). Entrained chlorophyll travels with eddies in a pole-ward direction through the Mozambique Channel (Omata et al*.,* 2009). The largest shelf areas in the Mozambique Channel are found along the Madagascan coast, thus one would expect greater chlorophyll values on the eastern side of the channel but this is generally not the case. The entrained nutrients which travel down the eastern side of the Mozambique Channel generally results in higher chlorophyll a concentrations than those found over the shelf areas on the western side of the Mozambique Channel (Tew-Kai and Marsac 2009).

In a study carried out by DiMarco et al. (2002) on the Leeuwin Current in Western Australia, chlorophyll *a* concentrations were highest (up to 1 µg l^{-1}) inshore directly adjacent to the coast. These chlorophyll concentrations exceeded those found on the outer shelf region (0.5 µg l^{-1}) of the study area and still higher than concentrations found within the Leeuwin Current further offshore (0-0.25 µg l^{-1}). This suggests that nutrients from terrestrial input played a role in maintaining phytoplankton biomass in the area.

2.3 Sea Surface Temperature

Sea surface temperature (SST) is a valuable tool used to understand the physical and biological systems at work in the ocean. According to Tew-Kai and Marsac (2009) seasonal variability in SST within the northern (10ºS - 16ºS) and southern (24ºS - 30ºS) sections of the Mozambique Channel is evident, whereas seasonal variability in the central section (16ºS - 24ºS) is not as obvious due to mesoscale eddy activity. Sea surface chlorophyll concentration and SST are closely related to one another due to the fact that chlorophyll production is often reliant on cold nutrient rich waters reaching the upper layers of the ocean. In a study carried out by Bouman et al. (2003; 2005) it was found that as an environmental influence, temperature played a pivotal role in productivity of phytoplankton communities.

In a study carried out by Konda et al. (2002) a regional analysis of the SST and heat content in the mixed layer revealed a marked difference in the mechanisms which controlled SST between the central and western basins of the Indian Ocean and those found in the east.

Shinoda et al. (2004) inspected surface and subsurface temperature variability in the Indian Ocean and its relation to El Nino/Southern Oscillation (ENSO). It was found that the leading cause of temperature variability in the equatorial Indian Ocean is due to a dipole character, with modest temperature loadings at surface waters compared to those at the thermocline. These findings are of interest as the majority of water entering the Mozambique Channel originates from the SEC. Temperature dipole differences are said to be common from September to November at surface waters in the Mozambique Channel which can be correlated with ENSO, but occur year round in subsurface waters which were found to be mostly independent of ENSO (Shinoda et al., 2004).

2.4 Chlorophyll *a*

Over an entire seasonal cycle in 2003 the Mozambique Channel displayed highest surface chlorophyll concentrations in winter and its lowest readings in summer, with very low chlorophyll values of up to 0.2 µg l^{-1} through most of the central Mozambique Channel in spring (Omata et al., 2009). Machu and Garcon (2001) have shown that areas in the South West Indian Ocean exhibit inconstant phytoplankton production rates and that the Subtropical Convergence Zone (SCZ) displayed higher chlorophyll *a* concentrations in summer whereas the South West Subtropical Indian Gyre (SWSIG) production rates were highest in winter.

Measuring chlorophyll *a* in situ is time consuming and a convenient and popular method of measuring chlorophyll *a* concentrations are by satellite imagery. Kyewalyanga et al. (2007) revealed good agreement between field-measured and satellite-derived chlorophyll *a* concentrations in data obtained in the Delagoa Bight. However, it has been argued that one cannot directly correlate surface chlorophyll concentrations measured by satellites to phytoplankton biomass (Zhang et al., 1998). The reason for this is the simple fact that chlorophyll is not biomass and the ratio between chlorophyll and phytoplankton biomass is not constant (Lorenzen 1967). Phytoplankton species have specific chlorophyll to biomass ratios which also increases variability in satellite derived results (Zhang et al., 1998).

In a study carried out by Sathyendranath and Platt (1989) the depth profile of chlorophyll concentrations were evaluated by using a spectral model of reflectance on a generalized pigment profile. The study revealed that the assumption of a vertically constant chlorophyll distribution can lead to sizeable errors in the estimation from satellite data of photic depth and total pigment content in surface waters. In addition, chlorophyll maxima are said to often be found within the thermocline or near the base of the euphotic zone (Lorenzen 1967). Backscattering in satellite images is also highlighted by many researchers as something

which produces data which is not consistent. Air bubbles, carbonate shells and size distribution of suspended particles are listed as some of the most important influences resulting in backscattering in satellite images (Ulloa et al., 1994; Zhang et al., 1998; Balch et al., 2005). Most of the primary production in the ocean is close to the base of the surface mixed layer which makes it difficult to observe when using satellite images alone (Crawford, et al., 2007).

Research vessels are not capable of sampling vast areas in a short time but the measurements recorded from research vessels are potentially more accurate. The great advantage of satellite imagery is that they can capture fast and/or far reaching changes in chlorophyll concentrations over very large areas (Kyewalyanga et al., 2007). Satellite images of chlorophyll *a* concentrations are capable of detecting eddies as they pass the continental shelf edge off the African coast in the Mozambique Channel (Quartly and Srokosz 2004).

2.5 Phytoplankton distribution and composition

Biochemical composition, physiology and community composition of phytoplankton populations are indicators which can be used to determine rates of vertical mixing and the vertical distribution of phytoplankton within mesoscale eddies (Dusenberry 2000). Direct environmental factors which influence phytoplankton include sunlight which provides energy to allow for growth, survival of cells and reproduction. Temperature acts indirectly and influences respiration, growth, photosynthesis and motility (Reynolds 2006). In a study carried out by Thompson et al. (2007) in the south-eastern Indian Ocean it was found that diatoms and coccolithophorids dominated a warm core eddy while dinoflagellates and cryptophytes dominated a cold core eddy. In contrast, Barlow et al. (2008) found diatoms dominating the colder (<22°C) waters in the Delagoa Bight (approximately 25°S, 35°E) as well as in colder (<22°C) waters southwest of the Natal Bight and stated that the eutrophication of the two cold patches was made possible by eddy-driven upwelling processes at work in the Mozambique Channel.

Gomi et al. (2010) compared diatom species composition between the warm surface layer, the intermediate mixed layer and cool subsurface chlorophyll maximum in the Indian division of the Southern Ocean during the summers of 2002 and 2003. Species composition of the diatom assemblages were found to be similar in the subsurface chlorophyll maximum and mixed layer at most stations. Furthermore, the study revealed that the subsurface chlorophyll maximum diatom assemblages had inter-annual variability in species composition.

2.6 Phytoplankton ecology

The marine environment has complex processes which to a large extent control the distribution of phytoplankton vertically and horizontally (Reynolds 2006). One of the processes is known as upwelling, which is primarily a seasonal occurrence. This process is initiated in oceanic environments by strong winds or currents that force colder, nutrient rich water to the surface resulting in a mixture of nutrient rich water, which combined with sufficient light in the photic zone, promotes the growth of phytoplankton (Lee 1980). Dispersion through physical features such as fronts, upwelling, river plumes and eddies play an important role in the characteristics and functioning of regional ecosystems (Martin et al., 2001).

Mesoscale eddy features of the world's oceans are areas of increased biological activity (Weimerskirch et al., 2004). Mesoscale eddies can be the dominant physical feature influencing the distribution of phytoplankton in both subtropical and tropical oceans (Thorpe 1998). Eddies are known to play an important role in the biological developments of pelagic ecosystems by converting physical energy into trophic energy (Bakun 2006). Growth in phytoplankton biomass occurs when mesoscale (tens to hundreds of kilometres) features raise the concentrations of growth-limiting nutrients (Vaillancourt et al., 2003). Eddies in particular are common and often long-lived features of ocean circulation with demonstrable, though highly variable impacts on phytoplankton production, biomass and community structure (Landry et al., 2008). The greater Agulhas Current system has several components with high mesoscale turbulence and the phytoplankton distribution in the southwest Indian Ocean reflects this activity (Machu et al., 2005). In cyclonic cold core (CC) eddies, horizontal distribution of phytoplankton occurs via a range of processes from the physical concentration of phytoplankton to the introduction of dissolved inorganic nitrogen into the euphotic zone that may increase net primary production and growth in chlorophyll *a* (McGillicuddy et al., 1998). Anti-cyclonic warm core (WC) eddies are generally expected to have reduced rates of primary production as a result of isolation of the phytoplankton community from outlying nutrient sources (Thompson et al., 2007). However anti-cyclonic eddies have been observed generating an upward movement of rich waters, but only located around their edges where phytoplankton enrichment has also been observed (Quartly and Srokosz 2004).

However, a study carried out by Vaillancourt et al. (2003) on the impact of a cyclonic eddy (warm core, downwelling in the northern hemisphere) on phytoplankton community structure and photosynthetic capability in the subtropical North Pacific Ocean showed that stations nearest the eddy's centre had higher concentrations of most plant pigments than did those outside and nearer the eddy's margin. Total chlorophyll *a* values inside the eddy were 20 mg/m^2 versus total chlorophyll *a* values of 16 mg/m^2 outside the eddy. Previous observations

therefore suggest that mesoscale eddies will play an important role in the horizontal as well as vertical distribution of phytoplankton in the present study.

2.7 Species composition

The coccolithophorid composition of 11 plankton depth stations from the South Atlantic Subtropical Gyre to the Sub Antarctic Zone was examined by Boeckel and Baumann (2008). Results showed that within the upper 50 metres of the euphotic zone in the Subtropical Gyre the coccolithophorid community comprised mostly of *Umbellosphaera irregularis* (Paasche 1955); *Umbellosphaera tenuis* (Kamptner) Paasche in Markali and Paasche 1955; *Discosphaera tubifera* (Murray and Blackman) Ostenfeld, 1900*; Rhabdosphaera clavigera* (Murray and Blackman 1898) and *E. huxleyi*, which are said to be well suited for warm oligotrophic environments. Coccolithophorids found in the deeper photic zone profiting from higher nutrient concentrations closer to the nutricline were *Florisphaera profunda* (Okada and Honjo 1973), *Gephyrocapsa ericsonii* (McIntyre and Bé) and *Oolithotus* spp. (Reinhardt 1968) and a distinct Subtropical Frontal Zone dominated by *E. huxleyi.*

In a study carried out by Guptha et al. (2005) on the living coccolithophorids during the northeast monsoon from the Equatorial Indian Ocean, it was found that the most abundant coccolithophorid species were *U. irregularis* followed by *U. sibogae* (Weber-van Bosse, 1901) Gaarder, 1970, *Gephyrocapsa oceanica* (Kamptner 1943) and *E. huxleyi.* The consistency of *U. irregularis* floral assemblage in the upper mixed layer (50 metres depth) during the northeast monsoon suggested oligotrophic conditions (Guptha et al., 2005).

Work carried out by Takahashi and Okada in 2000 regarding the environmental control on the biogeography of modern coccolithophorids in the south-eastern Indian Ocean offshore of Western Australia revealed that at shallow depths in the tropics *U. irregularis* dominated whereas *D. tubifera, R. clavigera* and *U. tenuis* dominated coccolithophorid communities in shallow subtropical waters. *E. huxleyi, G. ericasonii* and *Umbilicosphaera hulburtiana* (Gaarder, 1970) are said to be coccolithophorid species which are commonly found in subtropical waters (Takahashi and Okada 2000). Coccolithophorid species which are said to dominate the deeper waters of the euphotic zone in the southeast Indian Ocean are *F. profunda, Oolithotus antillarum* (Cohen 1964)*, Gladiolithus flabellatus* (Halldal and Markali 1955*)* and *Algirosphaera oryza* (Takahashi and Okada 2000).

In a study carried out by Cortés et al. (2001) on coccolithophorid ecology around Hawaii, a highly seasonal community structure was apparent. Five species (*E. huxleyi*, *U. irregularis*, *U. tenuis*, *F. profunda* and *G. ericasonii*) out of a total of 125 constituted on average more

than 30% of the total community composition. Cell densities of all dominant taxa within the study were highly correlated to temperature variability.

Haidar and Thierstein (2001) found a noticeable seasonal variability in coccolithophorid population structures near Bermuda after a 3 year plankton study. One species, *E. huxleyi* dominated the upper euphotic zone in spring, while *F. profunda* dominated the same depth during autumn. The study found that a seasonal sequence seemed to roughly follow oceanographic parameters, with changes in abiotic parameters explaining at least one-third of the variability of individual taxa.

Broerse et al. (2000) found *F. profunda* and *G. fabellatus* (diatom spp.) dominating the deep-photic zone in the early SW Monsoon when coastal up-welled water carried by a large gyre passed over their sampling station in the northwest Indian Ocean. During the peak of the SW Monsoon *E. huxleyi* and *G. oceanica* and demonstrated maximum fluxes towards the end of the upwelling period in September.

Koning et al. (2001) placed an array of sediment traps on the Somali slope directly below one of the main upwelling gyres in the region and placed a second set in the Somali Basin away from direct coastal upwelling influence. Diatoms represented over 90% of the total micro-organisms at both sites. Results also reveal a distinct seasonal diatom species succession at both sites which were categorised as ‘pre-upwellers’, ‘upwellers’ and oceanic species. More than 75% of the deposition for each of the species *Thalassionema nitzschioides* (Grunow) Mereschkowsky, 1902 and of *Chaetoceros* spp. occurred during the upwelling period.

A previous study carried out by Brown et al. (2008) in the subtropical North Pacific on a cold core cyclonic eddy on the lee of the Hawaiian Islands revealed that the majority of the phytoplankton biomass in the eddy was composed of diatoms, which represented 85% of the living biomass in the core region (Brown et al., 2008). Two large centric diatom genera, *Rhizosolenia* spp. (Brightwell, 1858) and *Chaetoceros* spp. dominated the eddy bloom, accounting for 35-45% of the diatom biomass. The remaining diatoms consisted of a variety of pennate and chain forming centric species. The diatom populations in surface waters comprised largely *Mastogloia* spp. (Thwaites ex W.Smith 1856) complexes, more typical of oligotrophic waters (Brown et al., 2008). In Brown’s explanation on the effects physical forcing had on the diatom population she states that the doming dense water brought deep water containing light limited phytoplankton and abundant nutrients into the well-lit euphotic zone, creating an environment conducive to rapid growth and biomass accumulation. Besides stimulating the subsurface diatom bloom, nutrients from the uplifted nutricline also affected phytoplankton dynamics in the upper mixed layer of Cyclone *Opal* and although not

as dramatic as at depth Brown et al. (2008). These studies all indicate the importance of physico-chemical variables on phytoplankton community structure.

2.8 Phytoplankton taxonomy

Diatoms

Approximately 40% of all described marine phytoplankton are diatoms and are of great importance from an ecological and biochemical point of view (Falkowski et al., 2004). Diatoms can be planktonic, benthic, epiphytic, epizoic and endophytic (Hasle and Syvertsen 1997). Diatom morphology, like all phytoplankton morphology is complex and very demanding with regards to identification. The following paragraph is a brief and simplified description of diatom morphology as the subject is immense and a full description of diatom morphology would take decades to complete.

Diatom cells are encased within a cell wall made of silica, called the frustule (Simon et al., 2009). It is this feature that forces most diatom cells to directly absorb silicate from the water column in order to maintain their frustules (Hasle and Syvertsen 1997). The diatom wall is multipartite, always consisting of two large, finely sculptured units called valves (Round et al., 1990). Diatoms often form chains or colonies that extend and create radical structures, such as in the case of the surf diatom *Anaulus australis* (G.Drebes and D.Schulz). Morphologically diatoms consist of an epitheca overlapping a hypotheca and these valves are usually joined by pectinaceous bands or small teeth-like structures within the inner edge of one girdle (Boney 1989). Diatoms are traditionally divided into two groups, Biddulphiales (centric) and Bacillariales (pennate). The centric diatoms have valve striae (rows of pores) arranged basically with central symmetry, and may be unipolar (radial centrics) or multipolar (Simon et al., 2009). Pennate diatoms have valve striae arranged more or less in a line. The frustules of raphid pennate diatoms have a slit called a raphe (Kooistra et al., 2007).

Coccolithophorids

Coccolithophorids are unicellular pelagic algae that secrete calcified scales called coccoliths (Ziveri and Thunell 2000, Reynolds 2006). Coccolithophorids are biflagellate or coccoid unicells, which rarely exceed 30µm in size and are usually smaller than 10µm and may be ovoid to oval, elongated cylinders, spherical, or spindle-shaped cells that taper gradually towards one or both ends (Heimdal 1997). The coccolithophorids are exclusively marine and are common in oceanic waters across the globe. Unlike the diatoms which have frustules made of silica, coccoliths which encase coccolithophorids are made of calcium carbonate.

Coccolith morphology is unique to each species, for this reason identification and classification of coccolithophorids is greatly dependent on the morphology of the coccoliths which make up the outer covering of the organisms (Heimdal 1997). The species shows impressive variation in the ratio of cellular biomass to calcite due to the inconstant number of coccoliths generated by an individual cell as well as the open structure of the coccoliths, which promotes variation of individual coccoliths (Paasche 2002). The most commonly studied coccolithophorid genus is *Emiliania* which can be found in almost every ocean on the planet. Coccolithophorids are sensitive to changing environmental conditions and therefore play an important role in understanding any marine ecosystem.

In a modelling study undertaken by Gregg and Casey (2007) it was found that distributions of coccolithophorids were dependent upon exchanges and competition with the other phytoplankton groups. The model suggested that coccolithophorids had a greater ability to utilise nutrients and light at low levels thus creating an advantage over diatoms in these conditions. When light and nutrients were abundant, the model suggested that the sinking rates of the coccolithophorids became a disadvantage.

Research carried out in Guaymas Bay in the Gulf of California by Ziveri and Thunell (2000) revealed that oligotrophic conditions during spring and summer of 1992 resulted in greater numbers of coccolithophorids. These oligotrophic conditions coincided with an intensification of ENSO, which reduced the strength of spring upwelling in the Gulf of California and increased SST. Reductions in diatom fluxes were observed during the intensified ENSO conditions suggesting diatom growth is promoted by upwelling in the region. Coccolithophorid species which dominated during strong ENSO periods were *E. huxleyi*, and *F. profunda*. A tropical/subtropical species associated with high nutrient conditions (*G. oceanica*) was present in the Gulf throughout the study period. Oligotrophic conditions suiting the production of coccolithophorid communities is an important insight to this study as the pelagic environment in the Mozambique Channel is known to be oligotrophic.

However, Andruleit (2007) sampled coccolithophorid communities around Indonesia during the oligotrophic phase of the monsoon cycle. A total of 98 taxa were identified in the study, with only ten coccolithophorid species reaching significant cell numbers. Low abundance coccolithophorid communities were found with surface assemblages either dominated by *G. oceanica* or *U. irregularis* or a varied mixture of the two previously mentioned coccolithphores plus *Palusphaera vandelii, Ophiaster hydroideus, Syracosphaera* spp. and *Calciosolenia* spp.

Dinoflagellates

The dinoflagellates are a large group of unicellular eukaryotic microbes which can be either heterotrophic, autotrophic, parasitic, mixotrophic or symbiotic (Soyer-Gobillard 2009). To date just over 2000 species have been identified. A typical dinoflagellate cell displays 2 flagella, one in an equatorial groove, the cingulum, and the other projecting toward the posterior of the cell, often in a groove known as the sulcus (Simon et al., 2009). Dinoflagellates can possess thick cellulose plates located in alveoli under the plasmalema and forming a rigid theca (armoured dinoflagellates) (Simon et al., 2009). Less than half of all dinoflagellate species are photosynthetic and the majority have peridinin as their main accessory pigment (Gomez 2005).

According to Smayda and Reynolds (2003) the adaptive strategies and ecological traits that dinoflagellates have acquired over thousands of years, and how they are able to continually exploit global coastal waters is not well understood. The study states that pelagic microalgae including dinoflagellates must grow and survive under adverse conditions (physical disturbance, intense light and nutrient limitation) in order to achieve a planktonic life mode.

3 The Photic Zone in the Mozambique Channel

3.1 Introduction

This chapter describes physico-chemical and biological characteristics of select oceanographic features sampled during the MC08A cruise. Two different size class oceanographic features were sampled in the study, namely mesoscale size range (tens to hundreds of km in diameter) and a sub-mesoscale size range (less than 10 km). The presence of sub-mesoscale (10 km in diameter) oceanic features between larger eddies can be identified using satellite imagery (Klein and Lapeyre 2009). Two of the four oceanographic features sampled were mesoscale in size (anti-cyclones and cyclones) and the two remaining features were sub-mesoscale in size (frontal and coastal zones). For the purposes of this study, the two different size class features (mesoscale and sub-mesoscale) will be compared to one another.

One of the main objectives of the study was to track oceanographic features using satellite imagery and to sample *in situ* physico-chemical, nutrients, chlorophyll *a* and phytoplankton variables in these mesoscale and sub-mesoscale features. In this way, we attempt to better understand the biological and physical dynamics of these oceanographic features in the Mozambique Channel. The Mozambique Channel is thought to be dominated by anti-cyclonic eddies in summer (Saetre and Jorge da Silva 1984; Schouten et al., 2002). Indeed, during our sampling period (November/December 2008), a large anti-cyclonic eddy dominated the central region (the narrows) of the Mozambique Channel, before propagating southward through the channel.

It is only natural that the importance of bottom-up effects is highlighted as an important process that assists in making energy available for other trophic groups through photosynthesis (Whittaker 1975). In order to understand phytoplankton production, the physical processes which generate that production must be understood (Machu et al., 2005). Biological oceanographers tend to consider planktonic communities as being controlled by nutrients and light (bottom – up controlled) despite the range of zoological predation which occurs on these communities which would indicate top-down control (Danovaro et al., 2001). A close link between primary productivity and physical processes in the sea are said to be the reason for this bottom-up theory (Danovaro et al., 2001). Thus nutrients, temperature and vertical mixing play the most important roles in controlling phytoplankton physiology, biomass and primary production on a whole (Kyewalyanga et al., 2007). The introduction of nutrients into the euphotic zone by upwelling generated by a cold core eddy (cyclonic in the southern hemisphere) may produce a localised increase in chlorophyll *a* concentrations,

which would have an effect on phytoplankton populations in the euphotic zone (McGillicuddy et al., 1998).

In order to explore the role that eddies play in the distribution of nutrients and the structuring of phytoplankton communities, nutrients in the form of nitrogen (total dissolved inorganic nitrogen); total soluble reactive phosphorus (SRP) and silicate (Si) were recorded. Physical parameters included temperature (degrees Celcius), salinity as practical salinity units (PSU) and dissolved oxygen (milliliters per litre). The species composition of the phytoplankton populations present was also examined.

The first section sampled in the present study was through three mesoscale features comprising a large anti-cyclonic eddy wedged between two smaller cyclonic eddies. The second section sampled covered a frontal zone situated relatively close to the Mozambican coast between an anti-cyclonic eddy and a cyclonic eddy at around 17.5^{o}S. A second frontal zone situated on the edge of the large central cyclonic eddy was also sampled and included in the data used in Chapter 3 and 4. It was not included in this chapter however, as representation of both frontal zones in a single Ocean Data View (Schlitzer 2010) map would not be possible. The third and final section sampled was through a coastal stretch close to the Mozambican coastline, henceforth defined (for the purposes of this study), as an oceanographic feature. The reason for sampling the latter was due to the notion that the Mozambique Channel is said to be influenced by freshwater input from rivers. Freshwater is then entrained into the pelagic environment as mesoscale eddies pass over the continental shelf (Tew-Kai and Marsac 2009). For these reasons, the coastal region was therefore predicted to exhibit different biological features and was, as such, sampled.

By sampling phytoplankton and environmental parameters in defined oceanographic features in the Mozambique Channel it may be possible to determine whether these oceanographic features provide a unique environment for phytoplankton communities.

3.2 Materials and methods

3.2.1 Study site

A dipole eddy consisting of a large downwelling anti-cyclonic eddy (17°S) wedged between two smaller upwelling cyclonic eddies, a frontal zone situated between a cyclonic and anti-cyclonic eddy, and finally a coastal zone were sampled during the November/December 2008 ASCLME cruise (Cruise MC08A). Geostrophic currents within the Mozambique Channel at the time of sampling are represented in Figure 3.1.

Sampling began within a weak cyclonic eddy situated in the north (14.5°S) of the channel at A in Figure 3.1. The *RV Dr Fridtjof Nansen* then steamed southwards to the centre of the anti-cyclonic eddy at approximately 17°S (B) before concluding the section at approximately 19°S at C. This section was named the North-South Profile (NSP). Once sampling of the NSP was complete, a frontal zone (D) situated between a cyclonic eddy present at the time of sampling (but not illustrated here) and an anti-cyclonic (B) eddy at around 17.5°S was sampled. Finally, an area close to the Mozambique coast was sampled at approximately 23°S (See coastal in Figure 3.2).

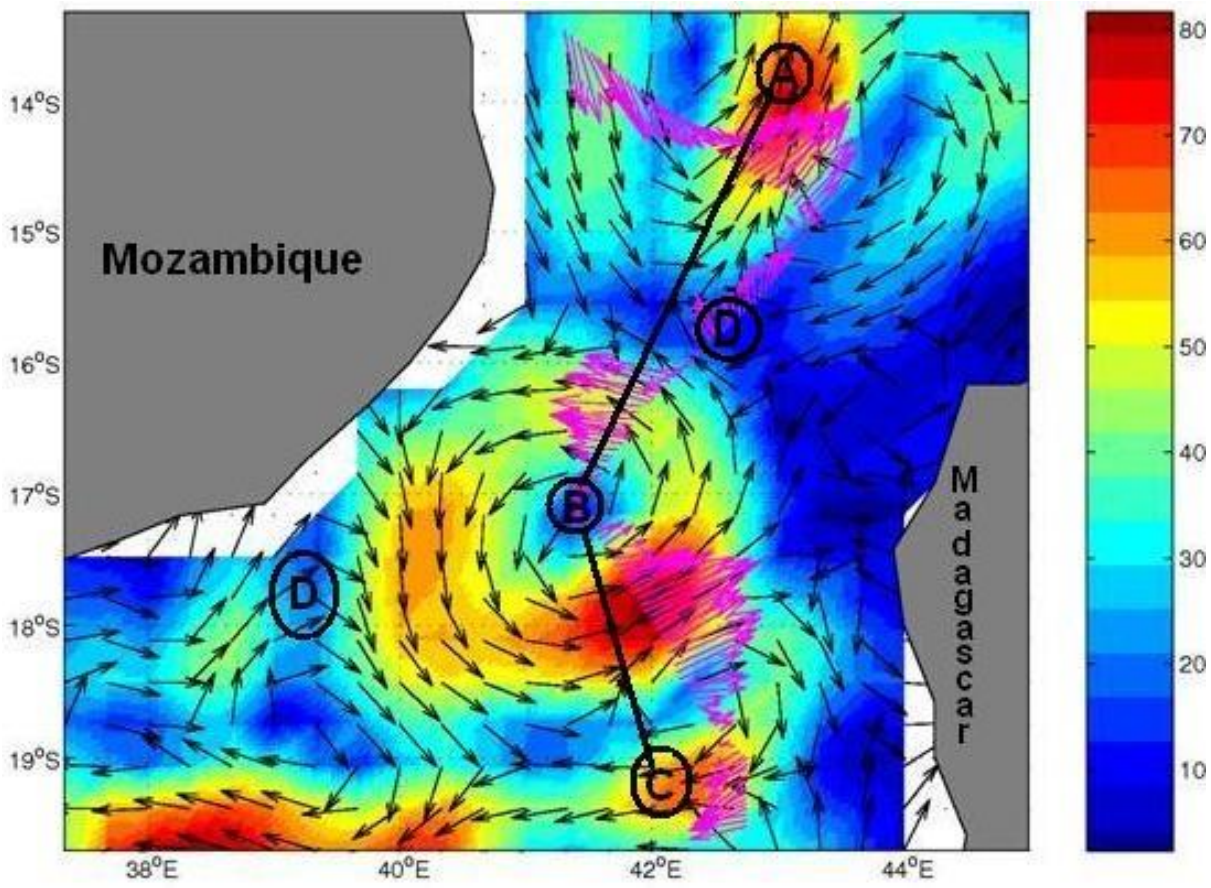

Figure 3.1. Geostrophic currents derived from satellite altimeter sea level measurements on December 1st 2008 and the Acoustic Doppler Current Profiler current vectors from 16 metres depth). The purple arrows indicate current strength. A = Cyclone; B = Anti-cyclone; C = Cyclone and D = Frontal (Kaehler et al., 2008).

Mesoscale features were identified from satellite sea-surface height anomalies and current velocities. Height anomalies, velocities and bathymetry (ECOTOP1) were extracted for each station and subjected to discriminant function analysis to allocate the stations into the four categories. In situ temperature data at 100 metres depth was also used as a check on the classification of stations within a hydro-graphic context. Details of satellite data extraction,

mesoscale feature identification, statistical analysis and station categorization are presented in Lamont et al. (2012).

3.2.2 Station categorisation

Stations were categorised according to whether they were located in anti-cyclonic or cyclonic eddies; within frontal zones situated between mesoscale eddies or whether they occurred in coastal waters. Methods used in determining mesoscale features are described in the next paragraph. A total of 51 stations were sampled during the MC08A cruise. Of the 51 stations sampled, 12 were situated within anti-cyclonic mesoscale features, 20 more in three separate smaller cyclonic systems, 14 in frontal areas and a further 5 stations sampled in coastal waters. The locations for all stations sampled during the MC08A (not just for this study) cruise as well as the general locations of the oceanographic features are illustrated in Figure 3.2.

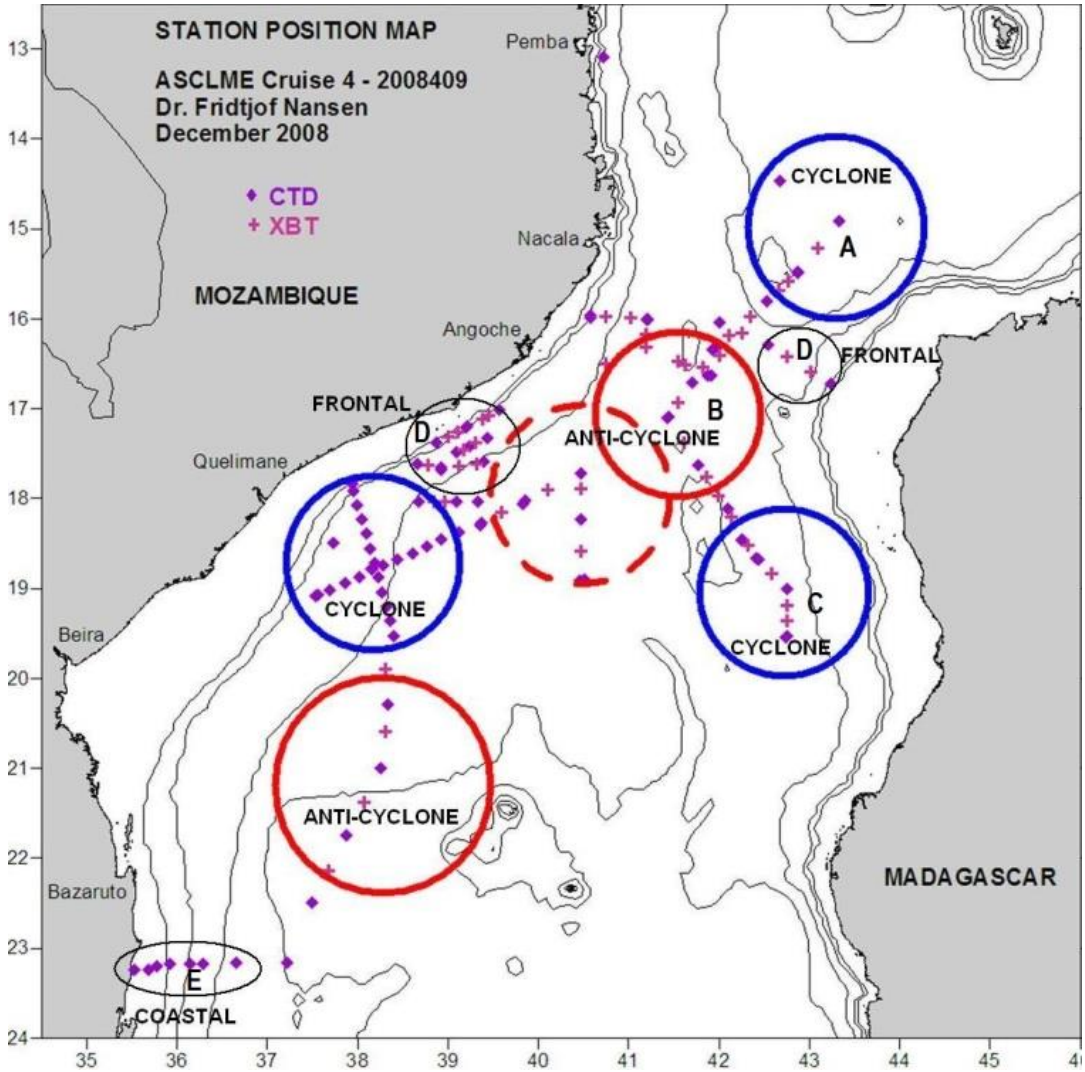

Figure 3.2. Oceanographic features identified within the Mozambique Channel: Anti-cyclone, Cyclone, Frontal and a Coastal region. Diamonds represent CTD stations. Crosses represent expendable bathythermographs (XBT) deployed.

More specifically, the locations of the stations used for this study are provided in Figure 3.3. The stations are colour coded per oceanographic feature.

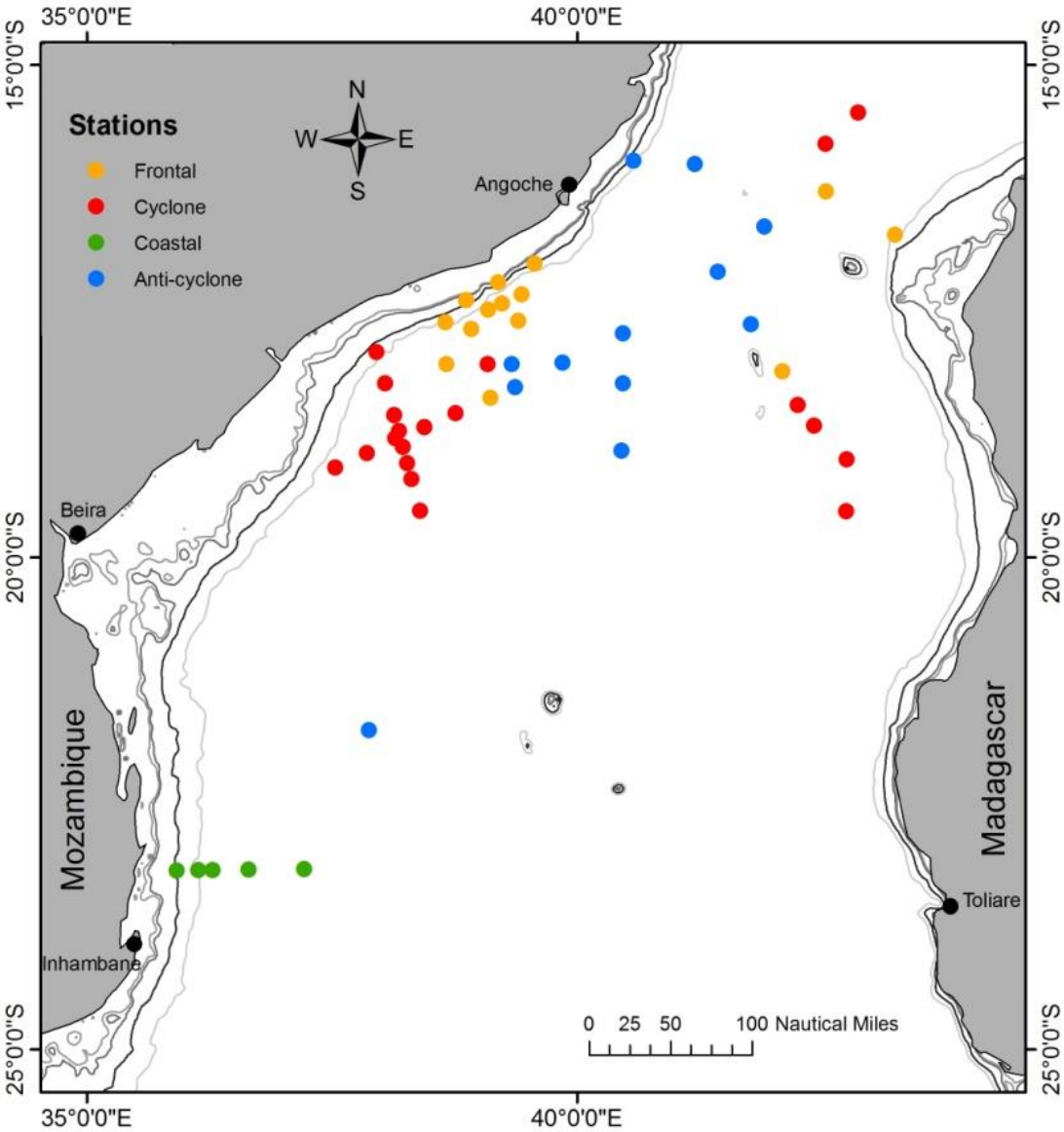

Figure 3.3. Positions of stations sampled during the MC08A cruise for this study.

Satellite altimetry provides unique opportunities for identifying mesoscale features (Chelton et al., 2007). The classification of each individual station was managed using three variables (sea level anomaly, geostrophic speed and bathymetry) and a discriminant function estimated from an extra training dataset (Lamont et al., 2012). Ocean bathymetry information was gathered from ETOPO1 Global Topography (data access: http://www.ngdc.noaa.gov/mgg/global/global.html). Sea level anomaly and the matching geostrophic speed were extracted from AVISO products “DT - MSLA Ref” (Delayed Time, DT; Reference, “Ref”) with 0.33° × 0.33° spatial resolution on a Mercator grid. The

predictions from the linear discriminate analysis were estimated for each station using the values taken by the three explanatory variables at the corresponding temporal and spatial positions.

Satellite images of sea surface temperature (SST) and surface chlorophyll *a* concentrations reveal relatively high SST in the Mozambique Channel coupled with relatively low surface chlorophyll concentrations during the time of sampling (Figure 3.4). This is typical of the oceanography of the Mozambique Channel during the summer months (October – March) which is dominated by anti-cyclonic eddies (Saetre and Jorge da Silva 1984). Please note the filaments of chlorophyll *a* in the frontal zones between the mesoscale features (Fig 3.4) and the apparent lack of chlorophyll *a* within them.

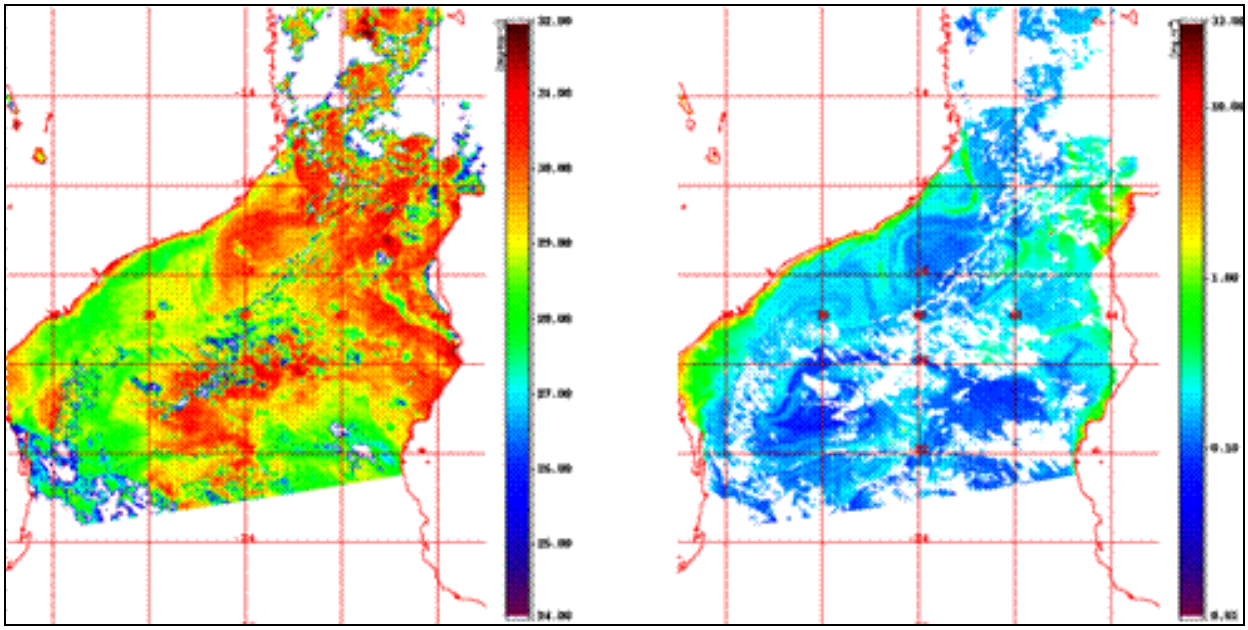

Figure 3.4. Sea surface temperature (left) and surface chlorophyll concentrations (right) in the Mozambique Channel at time of sampling (December 2008).

3.2.3 Environmental data

All environmental data were collected *in situ* from the R/V *Dr Fridjtof Nansen* during ruise MC08A in 2008. Physical parameters measured included temperature (°C), salinity (PSU) and dissolved oxygen (ml l^{-1}). Five different depths were sampled at each of the stations except in areas where the depth of the ocean floor did not allow (too shallow). Two depths above fluorescence maximum (*F*-max) were sampled and two depths below *F*-max. Vertical profiles of temperature, salinity and oxygen were obtained by using a Seabird 911 Plus

Conductivity/Temperature/Depth (CTD) analyser. Plotting and logging (real time) was undertaken using the Seabird Seasave software installed on a PC. The following CTD sensor calibrations were used for the survey:

1) The conductivity cell was calibrated by comparing samples analysed on a Guildline Portasal System with the derived salinity obtained from the CTD.
2) No corrections were undertaken on the raw data obtained for dissolved oxygen as the sensor proved to be very stable. The Winkler Titration on a manual 725 Dosimat System was used for calibration.

In addition, a Chelsea Mk III Aquatracker Fluorometer was attached to the CTD. The instrument measures chlorophyll *a* concentrations in micrograms per litre with an uncertainty of 3%. Offset and factory slope remained constant at 0.02 and 0.921.

Two salinity samples were taken at most stations where 5 depths were sampled for calibration purposes. This had to be stopped however as the Guildline Portasal had to be serviced. Sample bottles were washed three times with seawater from the Niskin bottle before being filled completely for analyses. The samples were stored next to the Portasal and analysed once they reached room temperature.

Two dissolved oxygen samples, usually from the bottom and from oxygen minima of a hydro-graphic station were tapped from the Niskin bottle using a PVC pipe placed over the Niskin bottle tap. Without entrapping any air bubbles, water was allowed to flow into the glass sample bottle for 20 seconds before the pipe was removed. Two reagents, Manganese chloride and Potassium Iodide (1 ml each) were then added to the sample bottles. The sample bottles were then shaken in order to capture all of the dissolved oxygen from the seawater. The precipitant obtained from this procedure was then mixed in 2 ml of concentrated hydrochloric acid and titrated against Sodium thiosulphate. The titrated volume was then used to calculate dissolved oxygen using the Winkler titration method (Winkler 1888).

3.2.4 Nutrients

Samples were collected at the same depths sampled for total chlorophyll *a* and size fractionated chlorophyll *a* (*F*-max, two depths below, two depths above) using Niskin bottles. The test tubes used for nutrients on the cruise were cleaned in a laboratory in Cape Town before they were loaded onto the R/V *Dr Fridjtof Nansen*. Test tubes were rinsed three times with seawater from the Niskin bottle to be sampled and filled ¾ to allow enough space for expansion during freezing. Test tubes were marked by station number and depth and once the samples had frozen, trays of samples were placed in plastic bags in the freezer. Silicate,

DIN and SRP concentrations were determined according to Strickland and Parsons (1972) modified for use with a Technicon Auto Analyser II (Mostert 1983).

3.2.5 Biomass data

For the purposes of this study, chlorophyll *a* concentrations were used as an indicator of phytoplankton biomass. Five samples were taken at each station. One sample was taken at *F*-max, one near the surface, two samples between the surface and *F*-max and one sample below *F*-max.

For each depth, 500 ml of seawater was collected and filtered through a serial filtration tower. The tower set comprised 20 µm Nylon Net Millipore filter positioned at the top, a 2 µm Macherey-Nagel filter in the middle and a 0.7 µm GF/F Whatman filter at the bottom. Once the 500 ml of seawater had passed through the entire tower, the filters were removed using tweezers and placed in plastic tubes with 10 ml of acetone. To prevent exposure to light, trays with plastic tubes were covered with aluminium foil. Samples were cooled in a fridge for 24 hours before determining chlorophyll a concentrations using a Turner Designs fluorometer. All procedures were performed in subdued light.

Fluorescence readings were converted with the following formula:

Chlorophyll *a* ($mg.m^{-3}/\mu g.l^{-1}$) = FD * (T/T-1)*(RB-RA)*(v/V)

Where:

v = volume of acetone used for extraction (10 ml)
V = volume of seawater filtered (500 ml)
RB = fluorescence reading prior to adding acid
RA = fluorescence reading after adding acid
Acid ratio T = RB/RA
T = 2.19
T/T-1 = 1.84
FD was a calibration factor determined prior to the cruise, dependent on the sensitivity of the fluorometer:
1x sensitivity on Min and 3.16 settings: 25.792
1x sensitivity on 20 and 31.6 settings: 2.7948
100x sensitivity on Min and 3.16 settings: 0.2876
100x sensitivity on 10 and 31.6 settings: could not be determined

3.2.6 Data analysis

All physico-chemical data as well as phytoplankton biomass data was used for the profiling of the North-South Profile A-B-C. Similarly, profiles were created for sections through the frontal and coastal zones sampled. The cross sectional graphs were created using a data-interpolarity variational analysis in Ocean Data View Version 4.3.7 (Schlitzer 2010).

3.3 Results

3.3.1 North-South Profile

The NSP was dominated by a mesoscale anti-cyclonic eddy which was flanked to the north by a weak cyclonic eddy and a stronger cyclonic system to the south. This type of oceanographic system or occurrence is known as a dipole eddy. Sampling via CTD began in the weak northern cyclonic eddy at approximately 15ºS, moving southward into the large anti-cyclonic eddy and coming to an end in a cyclonic eddy to the south of the large anti-cyclone at around 19ºS (Fig 3.5).

The physico-chemical parameters presented below are cross-sections along the NSP. The general location of the NSP section is highlighted in red (Fig. 3.5) through the narrows of the Mozambique Channel. The NSP began in the north (red star) and ended closer to the centre of the channel in the south. Blue dots situated outside the red line represent sampling stations for other oceanographic features (frontal and coastal) which are examined later on in this chapter.

Physico-chemical

Figure 3.6a exhibits reduced salinity values at depth in the central region of the NSP whereas the northern and southern sections were associated with increased levels of salinity. Decreased oxygen levels were found at depth in the northern and southern region, while relatively high oxygen levels were found throughout the euphotic zone (Fig. 3.6b). High surface water temperatures were evident across the entire NSP while cold water was being upwelled from the bottom of the euphotic zone in the northern and southern end of the profile (cyclonic eddies) (Fig. 3.6c).

Nutrients

Total Dissolved Inorganic Nitrogen (DIN) concentrations were elevated in the cyclonic eddies (Figure 3.7a). Increased concentrations of Soluble Reactive Phosphorus (SRP) were associated with the cyclonic eddies at the bottom of the euphotic zone (Fig. 3.7b). Increased silicate (Si) concentrations were evident at depth in the cyclonic eddies (Figure. 3.7c).

Chlorophyll a

The highest chlorophyll *a* concentrations within the NSP were found at around 50 metres depth in both the southern and northern extents (cyclonic eddies) of the section (Fig. 3.8a). A low concentration of microphytoplankton (20µm) (as chlorophyll *a*) was evident across the entire section (Figure. 3.8b). A slight increase in nanophytoplankton (2µm) chlorophyll *a* concentration is evident (Figure 3.8c), while the majority of the phytoplankton biomass was made up of picophytoplankton (0.7µm) (Figure 3.8d).

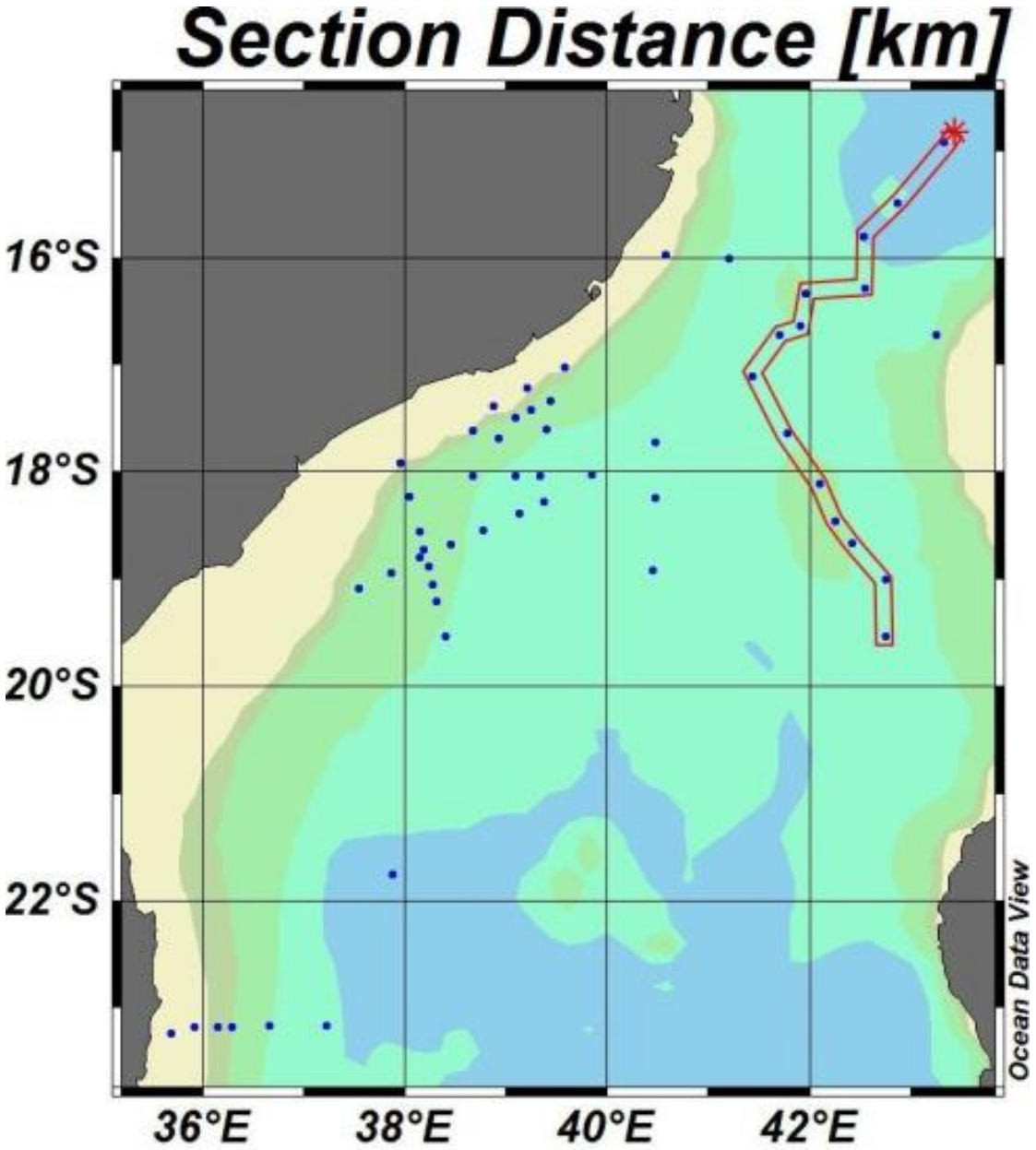

Figure 3.5. Location of the North South Profile.

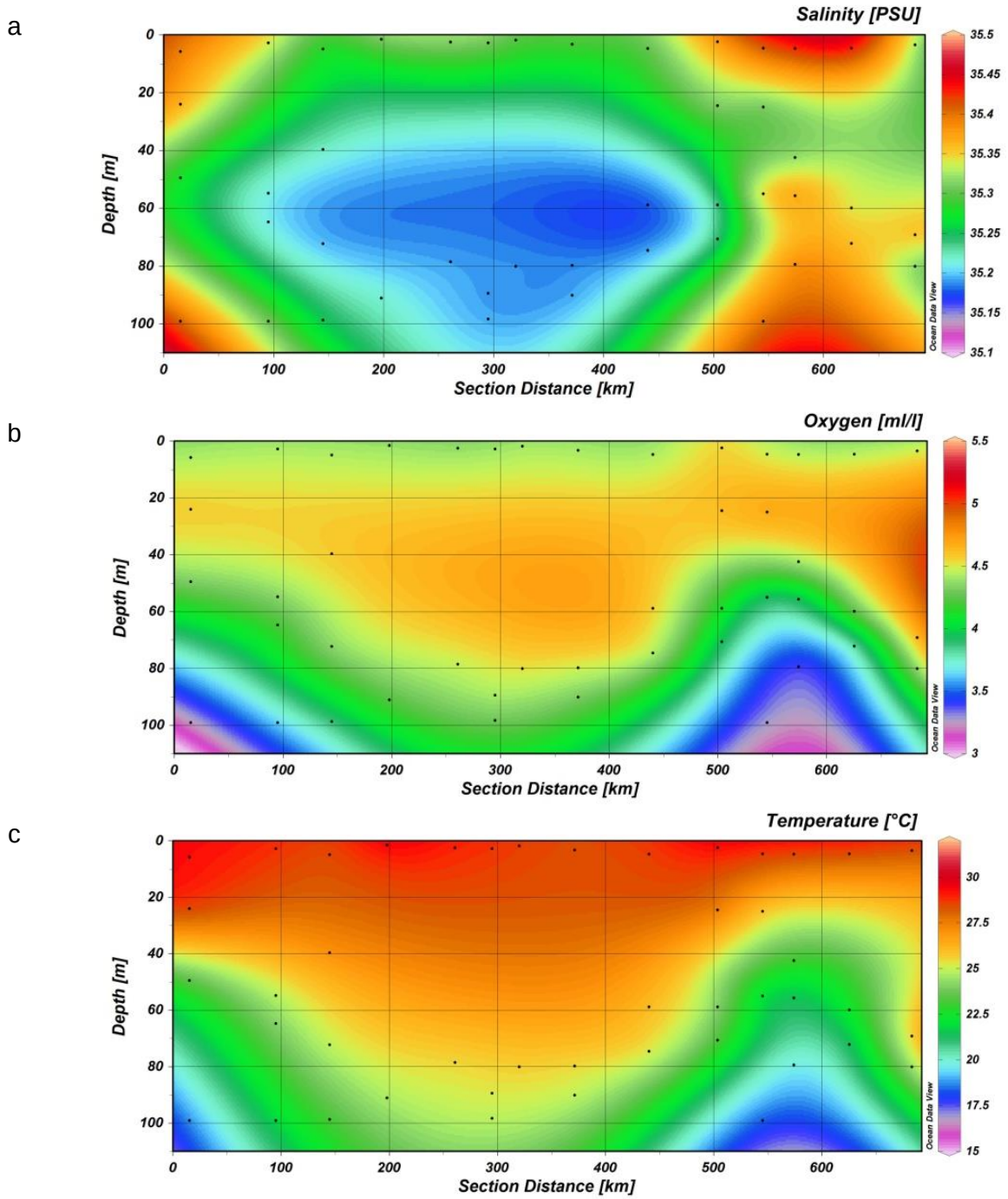

Figure 3.6. Cross-section of salinity, oxygen and temperature along the NSP from north (left) to south (right). a = Salinity in Practical Salinity Units (PSU); b= Dissolved Oxygen in milliliters per litre; c = Temperature in degrees Celsius. Black dots indicate sampling positions in the water column.

a

b

c

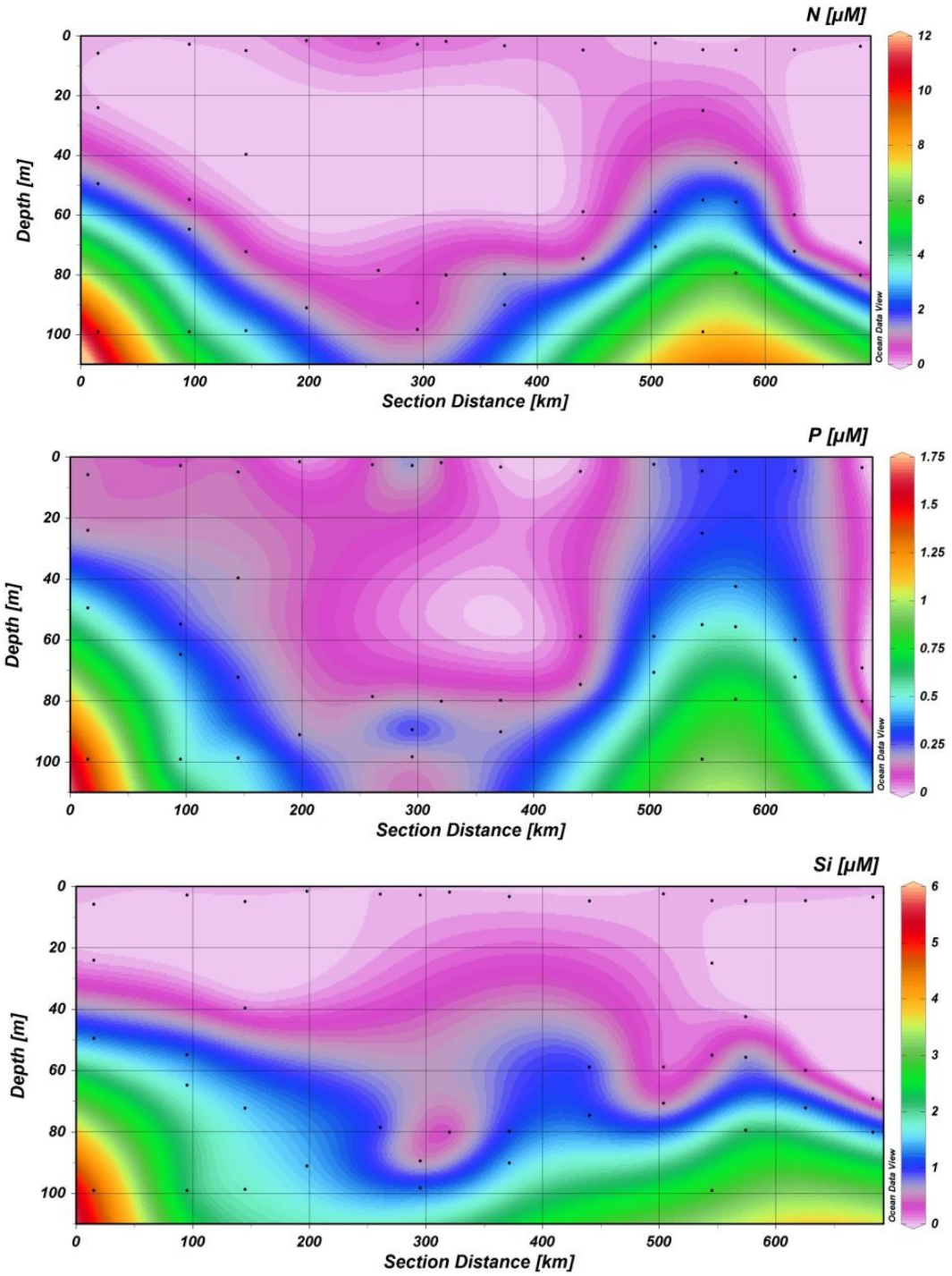

Figure 3.7. Cross-section of nutrient concentrations in µM along the NSP from north (left) to south (right). a = Total Nitrogen (Total Dissolved Inorganic Nitrogen); b = Soluble Reactive Phosphorus; c = Silicate. Distance along the x-axis is in kilometres and depth along the y-axis is in metres. Black dots indicate sampling positions.

a

b

c

d

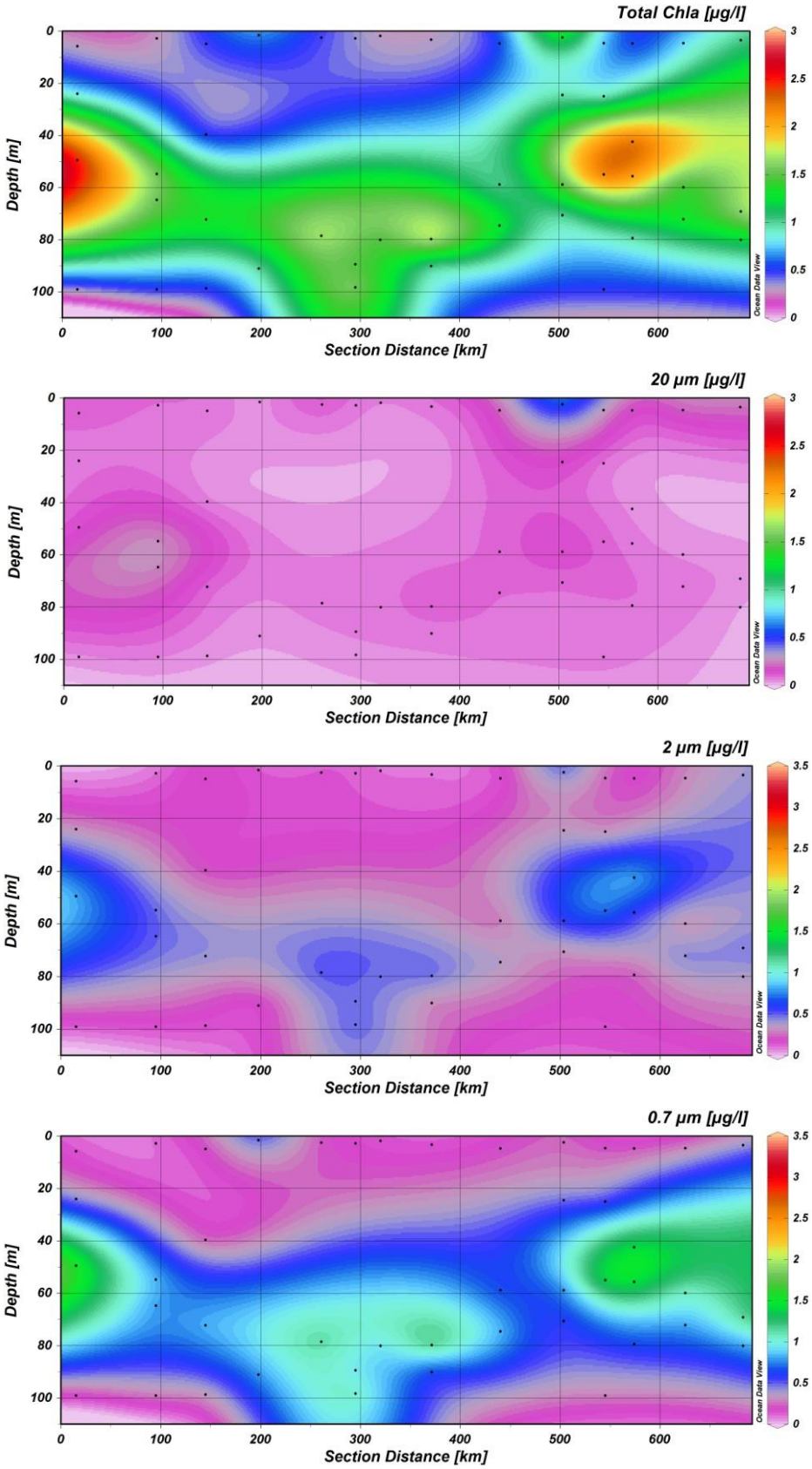

Figure 3.8. Cross-section of phytoplankton biomass as indicated by chlorophyll *a* concentrations (µg l^{-1}) along the NSP from north (left) to south (right). a = Total Chl-*a* concentration; b = 20 µm size fraction; c = 2 µm size fraction and d = 0.7 µm size fraction. Distance along the x-axis is in kilometres and depth along the y-axis is in metres. Black dots indicate sampling positions in the water column.

3.3.2 Frontal zone

Physico-chemical

The general locality of the section undertaken through a frontal zone situated between a cyclonic and anti-cyclonic eddy at around 17.5ºS is highlighted in red (Fig. 3.9). The profile starts in the south (red star) and ends in the north. Slightly reduced salinity concentrations are evident in the surface waters at the northern end of the profile (Fig 3.10a). Oxygen concentrations are relatively stratified and reduced at depth (Figure 3.10b). Water column temperatures also show a typical pattern with surface temperatures higher than temperatures found at depth (Fig. 3.10c).

Nutrients

Increased concentrations of DIN and Si were evident at depth in Figures 3.11a and 3.11c respectively. Both these nutrients were reduced throughout the NSP in the surface waters (Figures 3.11a and 3.11c). No discernible pattern in SRP concentrations were evident (Fig. 3.11b), although all three nutrient concentrations were elevated and the nutricline was raised in the south compared to the north.

Chlorophyll a

The highest chlorophyll *a* concentrations (4.97 ± 0.89 µg l^{-1}) were located off the Mozambican coast within the frontal zone between the southern cyclonic eddy and the central anti-cyclonic eddy (Figure 3.12a). Microphytoplankton dominated chlorophyll *a* in the frontal zone (Fig. 3.12b). Nano- and picophytoplankton chlorophyll *a* concentrations were lower than the larger size phytoplankton size class (microphytoplankton), evident in Figures 3.12c and 3.12d respectively, but followed a similar pattern.

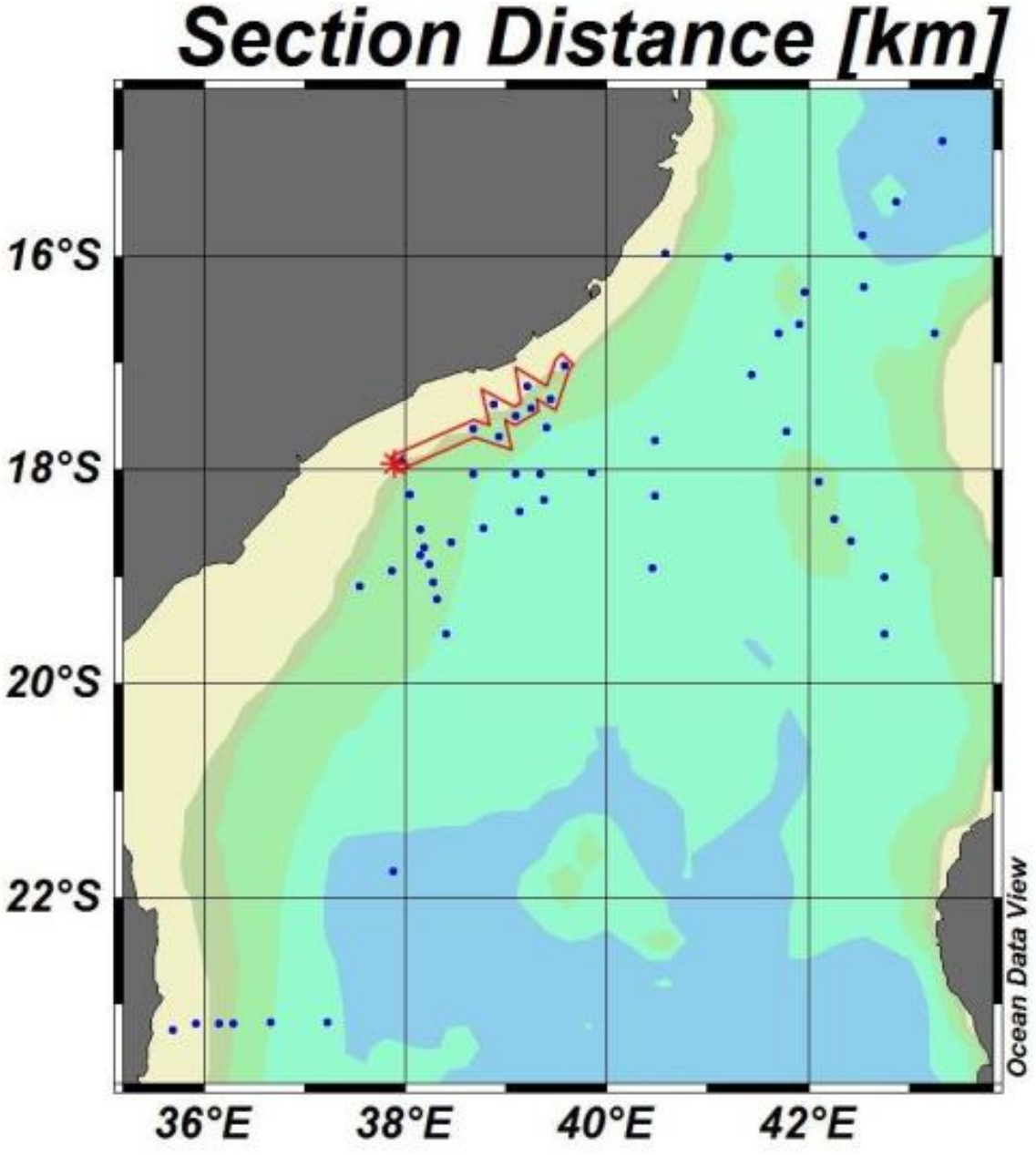

Figure 3.9. Location of frontal zone.

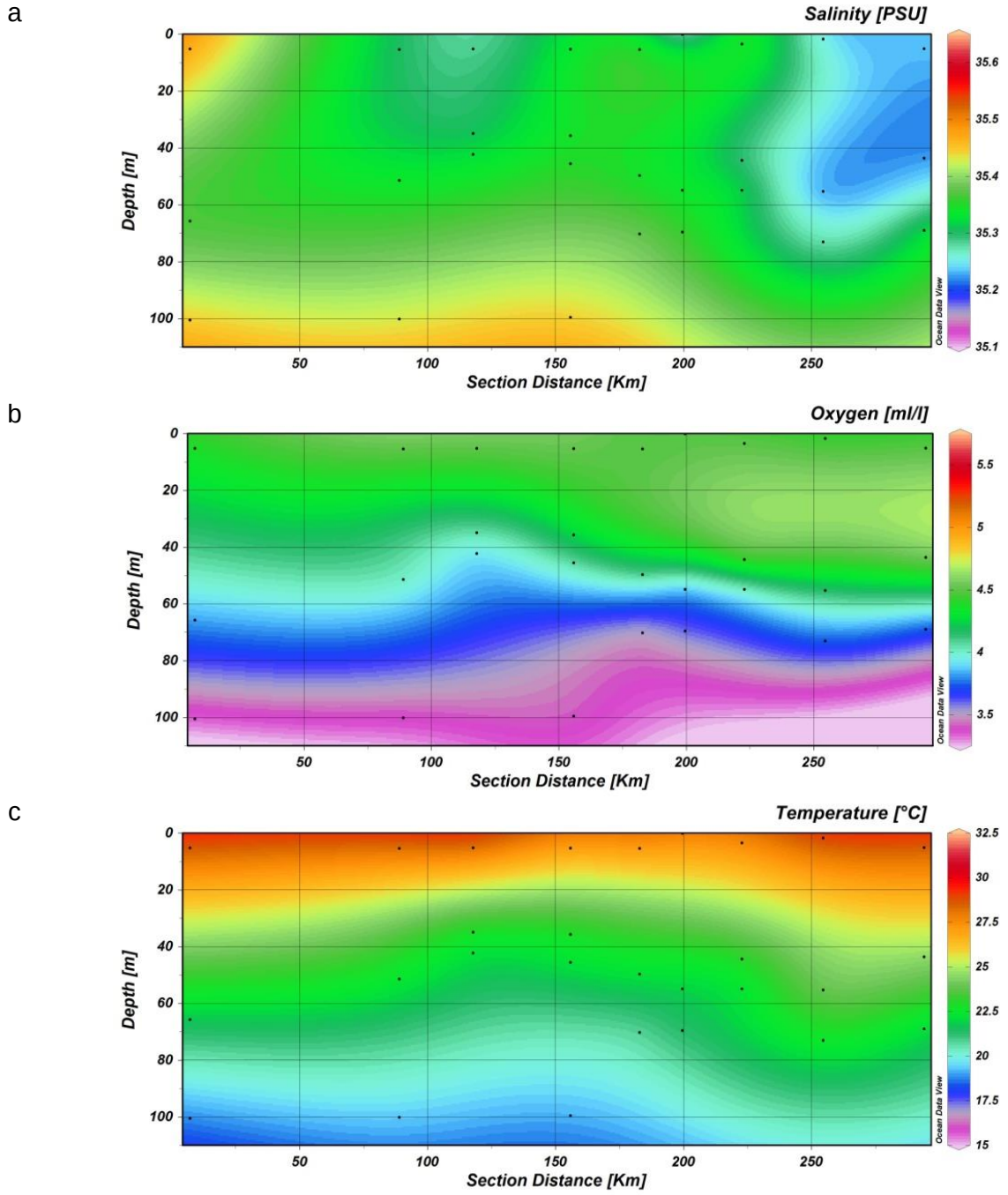

Figure 3.10. Cross-section of salinity, oxygen and temperature along the frontal zone from south (left) to north (right). a = Salinity in Practical Salinity Units (PSU); b = Dissolved Oxygen in milliliters per litre; c = Temperature in degrees Celsius. Distance along the x-axis is in kilometres and depth along the y-axis is in metres. Black dots indicate sampling positions in the water column.

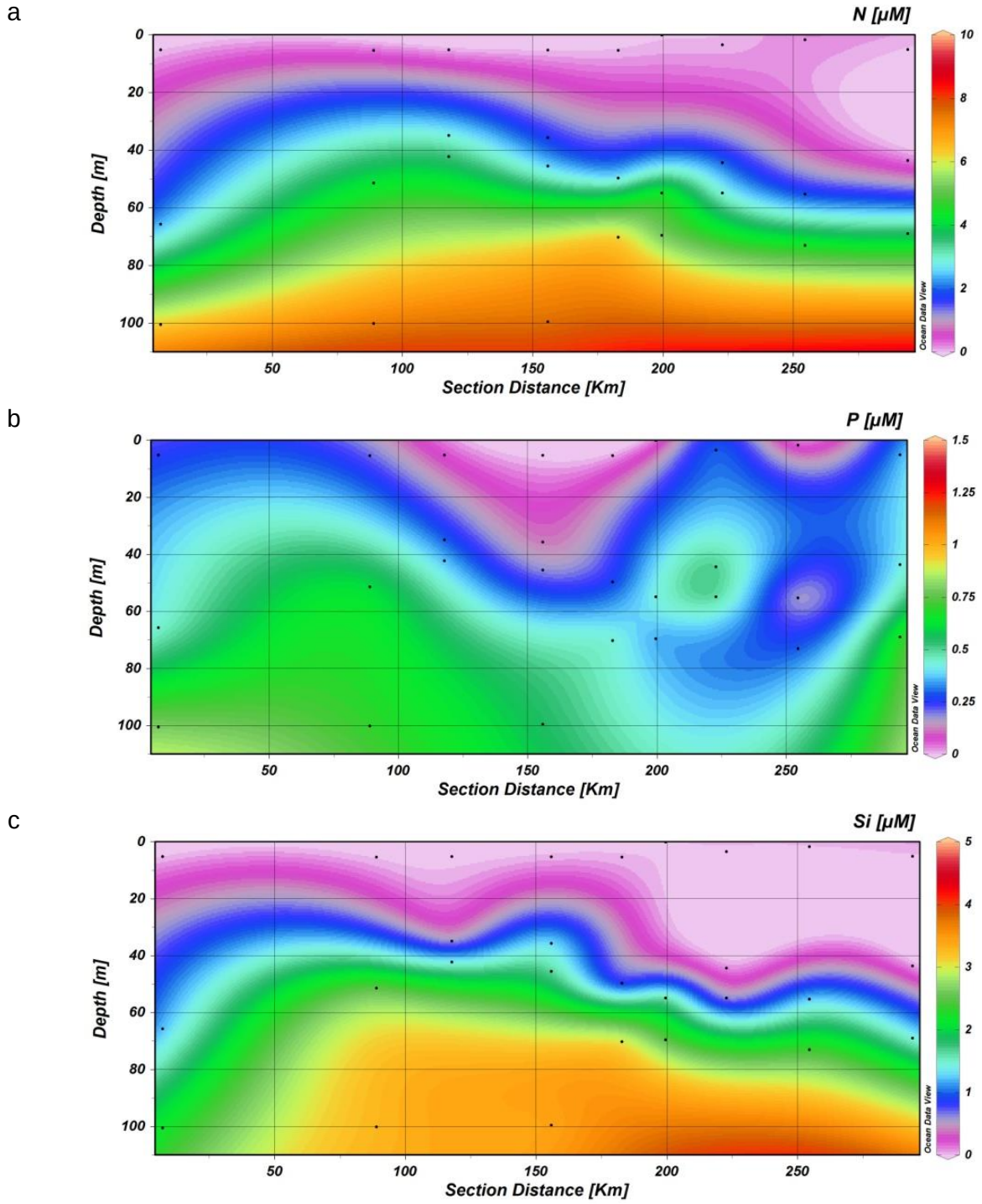

Figure 3.11. Cross section of nutrient concentrations in µM the frontal zone from south (left) to north (right). a = Total Nitrogen (Total Dissolved Inorganic Nitrogen in µM), b = Soluble Reactive Phosphorus and c = Silicate. Distance along the x-axis is in kilometres and depth along the y-axis is in metres. Black dots indicate sampling positions in the water column.

a

b

c

d

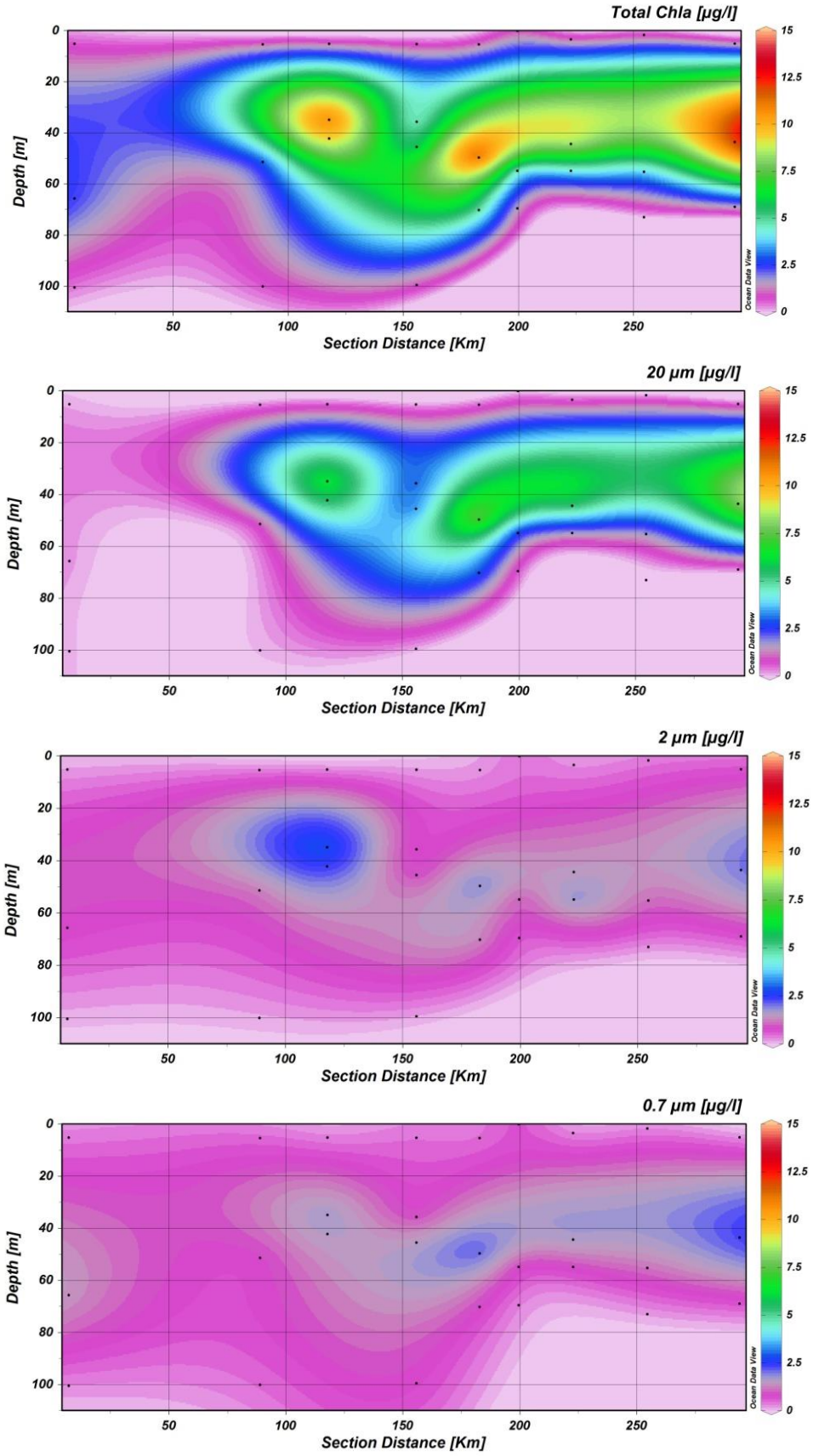

Figure 3.12. Cross-section of phytoplankton biomass as indicated by chlorophyll *a* concentrations (µg l^{-1}). a = Total Chl-*a* concentration; b = 20 µm size fraction; c = 2 µm size fraction; and d = 0.7 µm size fraction. Distance along the x-axis is in kilometres and depth along the y-axis is in metres. Black dots indicate sampling positions in the water column.

3.3.3 Coastal Zone

Physico-chemical

The general locality of the section undertaken through the coastal zone close to Inhambane is highlighted in red (Fig. 3.13). The profile starts offshore (red star) and ends inshore. Salinity concentrations observed between 40 to 80 metres depth for the entire length of the section sampled within the coastal zone was lower than concentrations observed in the frontal zone (Fig. 3.14a). Oxygen concentrations and temperature revealed stratification between 100 and 50 metres depth (Figure 3.14b and 3.14c respectively).

Nutrients

Elevated concentrations of all three nutrients (N, P and Si) sampled appear to be present at depth within the coastal zone (Fig. 3.15a, 3.15b, 3.15c). The nutricline is raised higher in the coastal zone than it was in the other areas sampled.

Chlorophyll a

The highest concentrations of total chlorophyll *a* were found at approximately 50 metres depth within the coastal zone (Figure 3.16a). Chlorophyll *a* concentrations indicated a moderate presence of the larger microphytoplankton (Fig. 3.16b) and the lowest abundance by the nanophytoplankton size class (Fig. 3.16c). Chlorophyll *a* concentrations also indicated that the smaller picophytoplankton size class to be the most abundant of the three size classes in the coastal zone (Fig. 3.16d). Two separate cells of elevated chlorophyll *a* are evident.

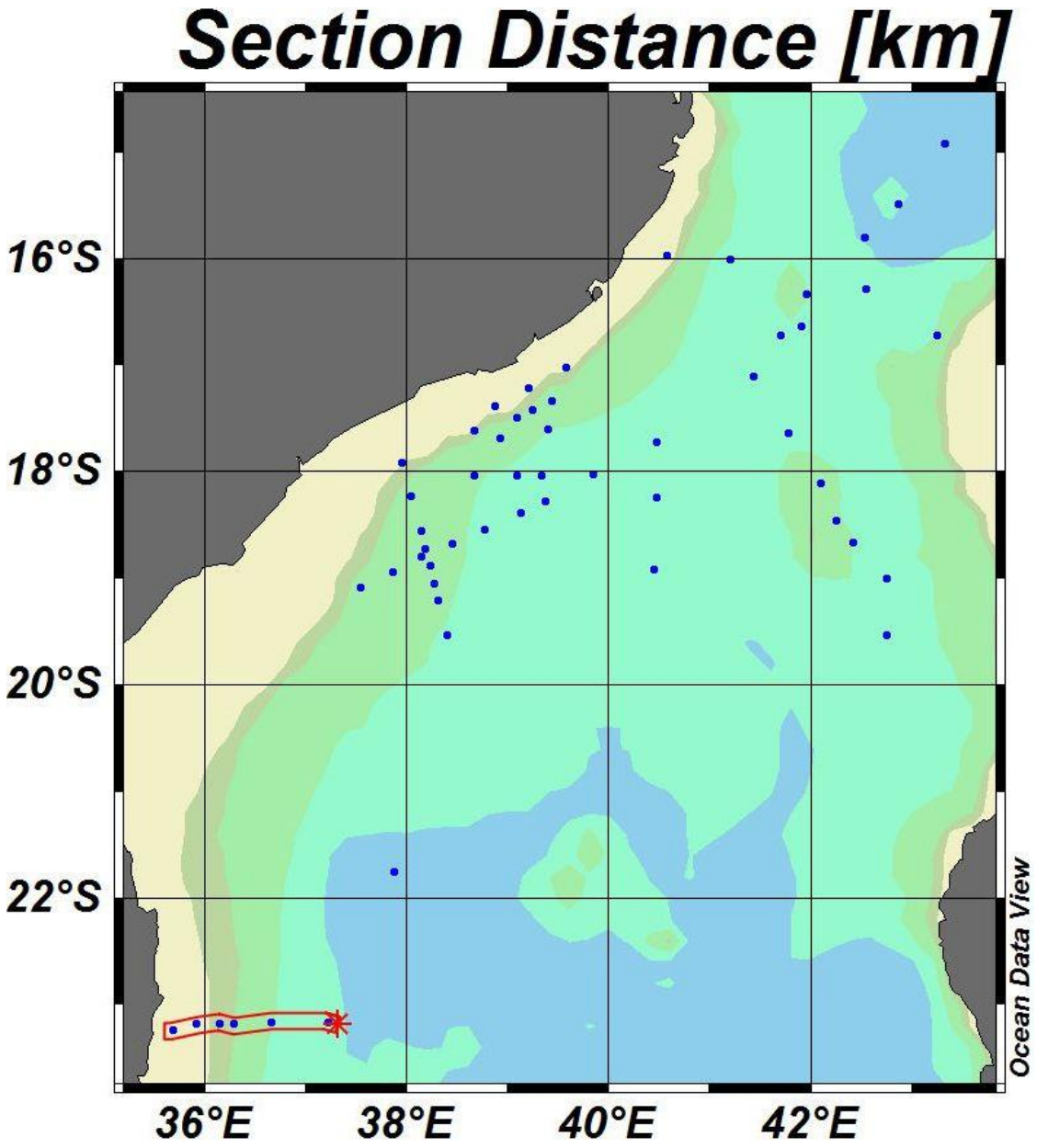

Figure 3.13. Locality of the coastal zone transect.

a

b

c

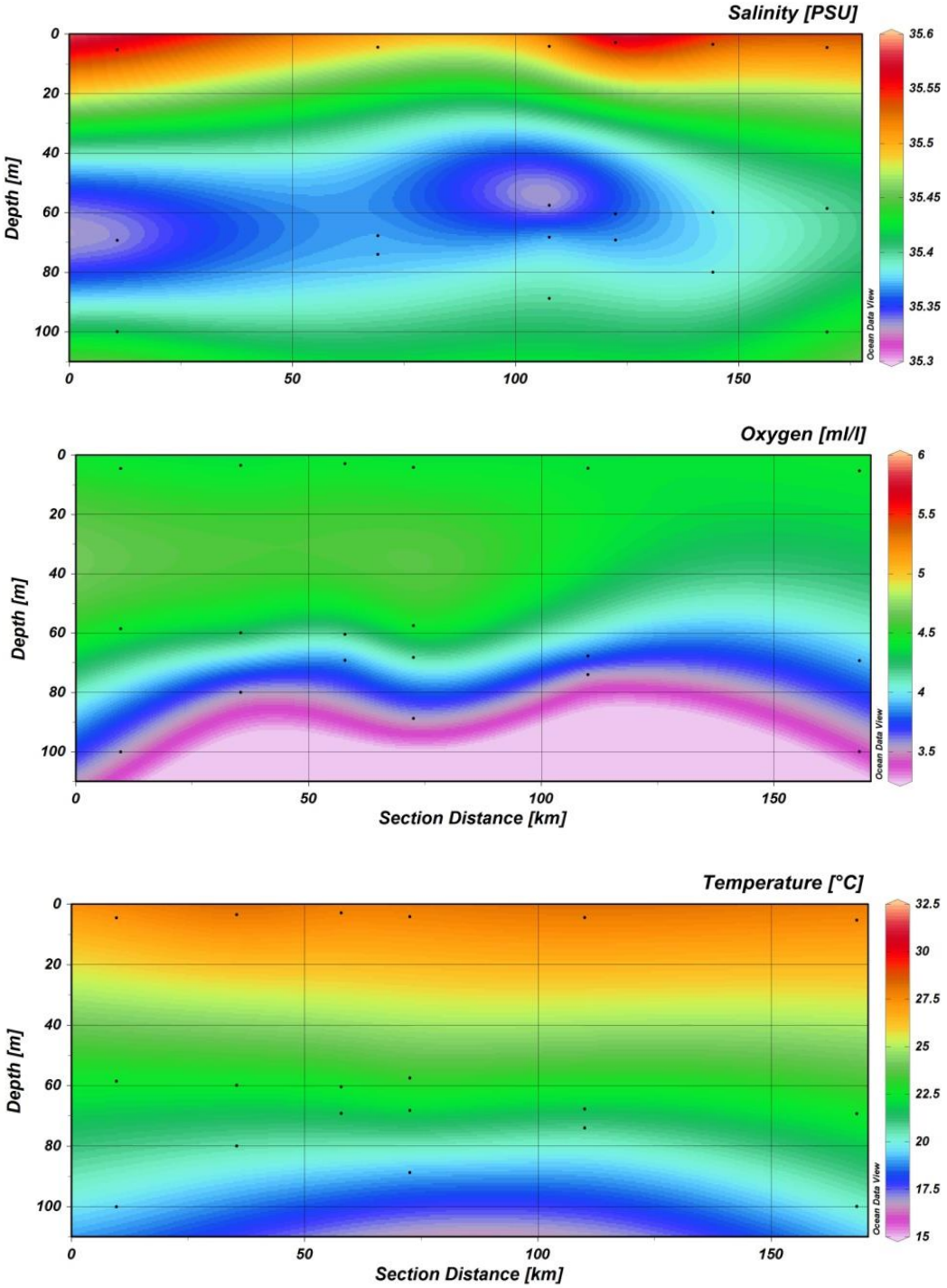

Figure 3.14. Cross-section of salinity, oxygen and temperature along the coastal zone from east (left) to west (right). a = Salinity in Practical Salinity Units (PSU); b = Dissolved Oxygen in milliliters per litre; c = Temperature in degrees Celsius. Distance along the x-axis is in kilometres and depth along the y-axis is in metres. Black dots indicate sampling positions in the water column.

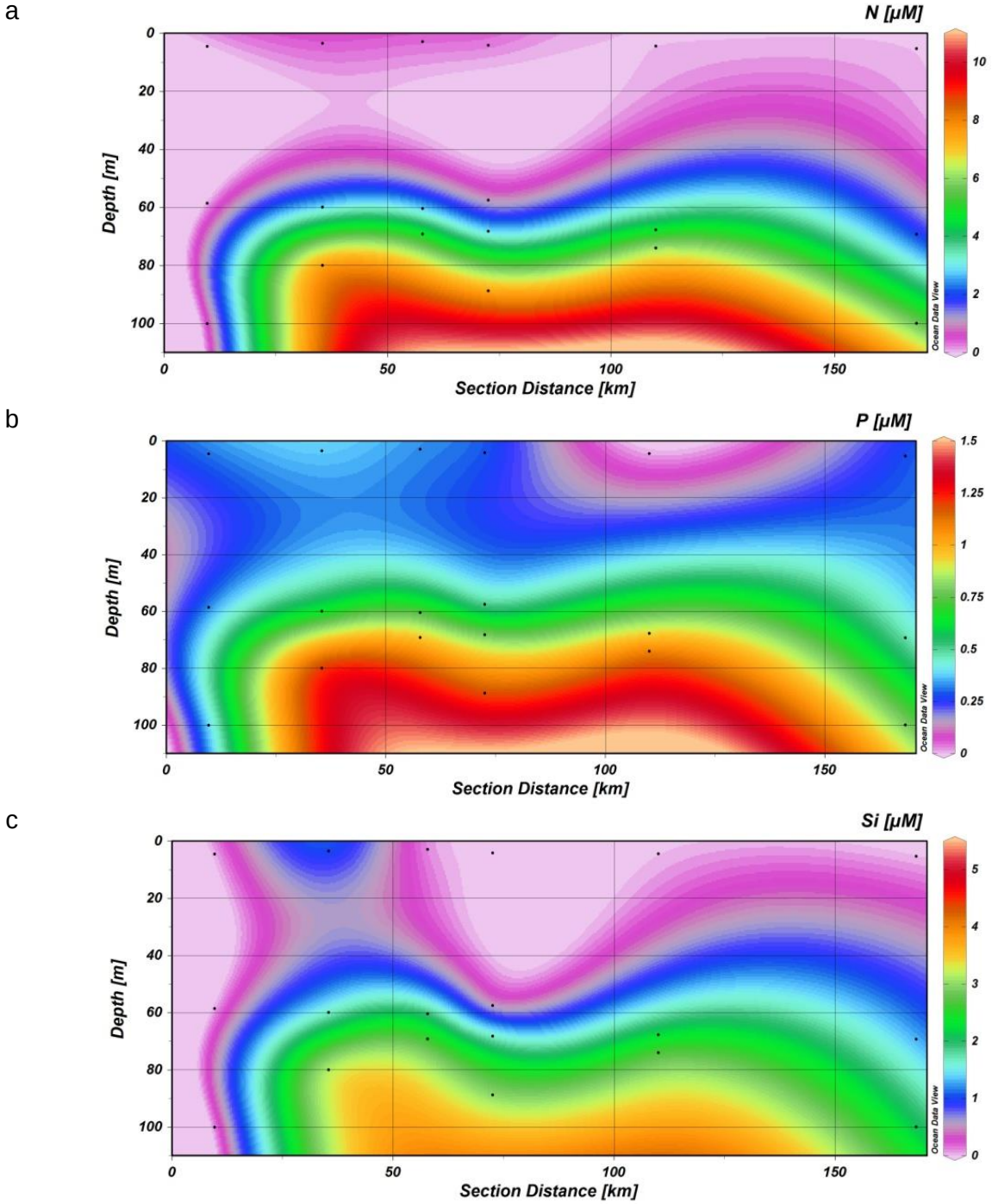

Figure 3.15. Cross section of nutrient concentrations in µM along the coastal zone from east (left) to west (right). a = Total Nitrogen (Total Dissolved Inorganic Nitrogen), b = Soluble Reactive Phosphorus and c = Silicate. Distance along the x-axis is in kilometres and depth along the y-axis is in metres. Black dots indicate sampling positions in the water column.

a

b

c

d

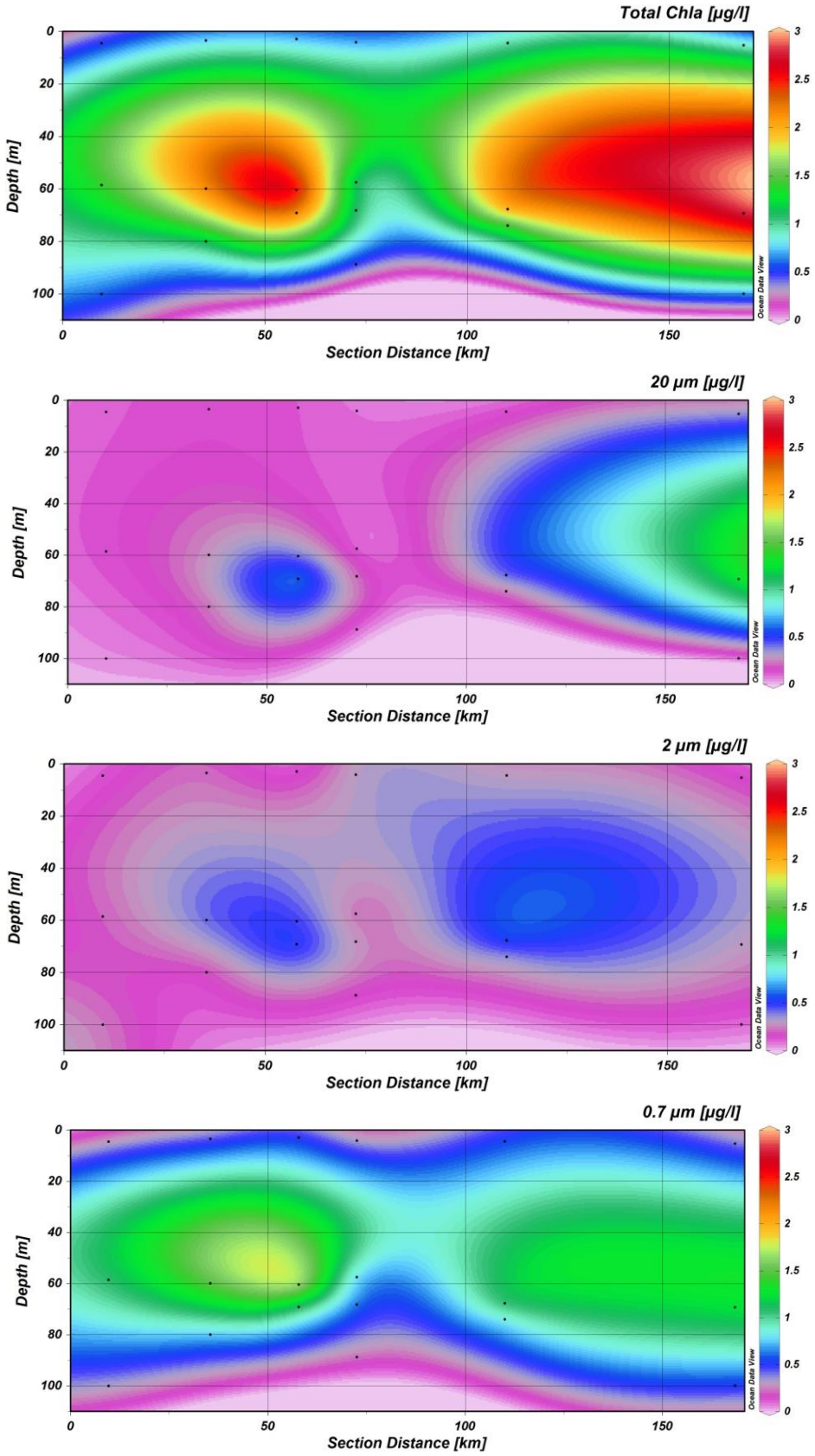

Figure 3.16. Cross-section of phytoplankton biomass as indicated by chlorophyll concentrations along the coastal zone from east (left) to west (right). a = Total Chl-*a* biomass; b = 20 µm size fraction; c = 2 µm size fraction and d = 0.7 µm size fraction. Distance along the x-axis is in kilometres and depth along the y-axis is in metres. Black dots indicate sampling positions in the water column.

3.4 Discussion

3.4.1 North-South Profile

Pelagic waters in the Mozambique Channel are dominated by oligotrophic conditions that are interrupted by mesoscale eddies moving southward through the channel causing vertical mixing in the water column and influencing primary production (Quartly and Srokosz 2004). In oligotrophic (low-nutrient) environments mesoscale eddies perform an important function by introducing nutrients into the euphotic zone (Gruber et al., 2011). Biological production in the ocean is influenced by mesoscale eddies (Godø et al., 2012). The rate of primary production in offshore oligotrophic oceans is primarily linked to the vertical nutrient transport associated with mesoscale eddies (McGillicuddy et al., 1998). A productive pelagic environment in the generally oligotrophic Mozambique Channel would not be possible without the influence of some sort of vertical mixing feature.

Reduced salinity concentrations at depths of below 100 metres between 200 and 400 kilometres south of the northern starting point of the NSP coupled with increased temperature and oxygen values in the same portion of the water column reveals evidence of typically oligotrophic pelagic surface waters. Towards the south, increased salinity values paired with depleted oxygen levels closer to the surface indicated upwelling in the region. ‘Doming’ of cold, deep oxygen depleted water at depth is evident in the northern and southern region of the NSP. These results suggest that a large anti-cyclonic eddy was wedged in-between two cyclonic eddies to the north and south. The doming of physico-chemical variables at depth in the extreme north is not as obvious as the doming present in the south of the section. The lack of nutrients at depth evident in the central region of the NSP is characteristic of an anti-cyclonic down-welling system forcing warm nutrient poor water into the depths of the water column. Increased nutrient concentrations at around 100 metres depth in the southern region of the NSP are typical of cyclonic upwelling systems which draw deep, cold nutrient rich waters into the euphotic zone (Saji et al., 1999; Quartly and Srokosz 2004). The effects of physical and biogeochemical processes on phytoplankton communities in upwelling zones is difficult to separate as there is a close relationship between the two processes (Tiltstone et al., 2000). Eddies provide sporadic pulses of nutrients to oligotrophic surface waters of the mid-latitudes which supports phytoplankton growth in those areas (Williams 2011). This ‘doming’ is a signature characteristic of a cyclonic upwelling system. Vaillancourt et al. (2003) found surface concentrations of inorganic nitrate, phosphate and silicate to be enhanced within the centre of a cyclonic eddy. In a study carried out by Landry et al. (2008), input of new nutrients into the euphotic zone had a significant effect on plankton biomass, productivity and community composition.

The underlying seasonal cycle of the Mozambique Channel (productive winters, unproductive summers) is said to be interrupted regularly by mesoscale eddies which pass through the channel (Saetre and Jorge da Silva 1984; Ridderinkhof and de Ruijter 2003; Tew-Kai and Marsac 2009). Mesoscale eddies influence basic seasonal primary productivity patterns by mixing the water column and introducing nutrient rich waters from the deep in the case of the upwelling cyclonic eddies or by forcing warm nutrient poor surface waters down the water column in the case of the anti-cyclonic eddies. The availability of nitrogenous nutrients limits phytoplankton production for most of the year in oligotrophic waters of the open ocean (Martin and Richards 2001).

The circulation within the Mozambique Channel is dominated by large anti-cyclonic eddies (Schouten et al., 2003). Primary production associated with warm core eddies (anti-cyclonic in the southern hemisphere) are expected to have reduced chlorophyll *a* concentrations due to the isolation of the phytoplankton community from an outside nutrient source (Thompson et al., 2007). Results observed by Tew-Kai and Marsac (2009) stressed the importance played by cyclonic eddies on phytoplankton enhancements in the Mozambique Channel. The `doming` of physico-chemical variables and nutrients caused by the cyclonic eddies to the north and south (more apparent in the south) of the central anti-cyclonic eddy brought deep nutrient rich (2.23 ± 0.83 µM N) water into the euphotic zone. One third of all new nitrate entering the euphotic zone in the subtropics and mid-latitudes is due to mesoscale eddy activity (Oschlies and Garçon 1998).

The phytoplankton assemblages present in the NSP were dominated by the picophytoplankton size range. These assemblages were slightly more concentrated towards the southern end of the NSP. The results suggest sufficient amounts of nutrients were being introduced into the euphotic zone by the cyclonic eddy to enhance phytoplankton growth. Picophytoplankton (0.7-2 µm) dominates both photosynthetic biomass and production in the open oceans (Worden et al., 2004). Close associations between nitrate concentrations, chlorophyll *a* and temperature suggest that environmental factors play an important role in determining the average size of phytoplankton cells (Chen and Liu 2010).

3.4.2 Frontal Zone

Cold dense water situated at depth in the frontal zone did not penetrate surface waters to any great extent and the relatively stratified temperature gradient suggest that no significant vertical mixing occurred within the frontal zone at the time of sampling. Increased concentrations of DIN, SRP and Si were recorded at depth and were found in lower concentrations within the top 50 metres of the water column across the entire section.

Lamont et al. (In Press) found that due to the interaction of the mesoscale eddies with the continental slope on the western side of the Mozambique Channel during the MC08A cruise, phytoplankton biomass tended to be higher in the sub-mesoscale oceanographic features (frontal zones in this study). Lamont et al. (In Press) also found minimal variation in chlorophyll *a* between mesoscale and sub-mesoscale oceanographic features and the deep chlorophyll maximum (*F*-max) was often located at the bottom of the euphotic zone.

In periods of diatom growth, natural waters show a decline in silicate content (Boney 1989). Microphytoplankton (>20µm), made up mostly of diatoms, was the dominant group within the frontal zone. Nutrient rich (relative to the study (DIN, SRP and Si)) coastal water (2.06 ± 0.39 µM) was drawn offshore in a north-easterly direction by the cyclonic eddy creating favourable conditions for phytoplankton growth further off-shore towards the pelagic environment. The presence of a cyclonic eddy in close proximity to the frontal zone may have assisted in drawing water off the shelf. High resolution numerical studies point to the fact that vertical interactions of nutrients and physico-chemical variables in the upper oceanic layers often occur within sub-mesoscale eddies located adjacent to larger mesoscale eddies (Lévy et al., 2009). This statement is relevant to the present study as a sub-mesoscale frontal system was situated adjacent to both mesoscale cyclonic and anti-cyclonic oceanographic features.

Slightly decreased concentrations of salinity may suggest coastal water influence in the area. The proximity of the stations to the mainland and specifically to Angoche, which is known to be an area of freshwater enrichment (Tew-Kai and Marsac 2009) advances this possibility. As mentioned previously, due to the samples being dominated by microphytoplankton (probably diatoms), the reduced DIN and Si concentrations may be due to direct absorption by diatoms for growth. Most diatom species are able to store phosphorus and therefore not influence SRP in the water column as severely (Flynn 2003). In a study carried out by Braga et al. (2008) terrestrial influence on shelf waters was demonstrated less intensively by phosphates compared to the silicates due to the range and flocculation processes associated with phosphates.

Increased chlorophyll *a* concentrations above the Mozambican continental slope in the frontal zone are thought to be induced by nutrient rich freshwater from the African continent (Tew-Kai and Marsac 2009). On the Mozambican coast close to Angoche there is a significant offset in the continental shelf edge and although there is a lack of evidence to support the theory, passing Mozambique eddies may generate intense lee eddies in the immediate area (Nehring et al., 1987). The relevance of this statement refers to the importance of entrainment of nutrient rich waters from the shelf regions into the pelagic environment. Freshwater input from the African continent has been regarded by many

researchers to have a significant influence on the primary production of coastal and shelf waters (Lee 1980; Martin et al., 2001; Quartly and Srokosz 2004; Reynolds 2006; Kyewalyanga et al., 2007). The Sofala Banks and Delagoa Bight are coastal regions that are thought to be heavily influenced by nutrient rich freshwater (Lutjeharms 2006a; Kyewalyanga et al., 2007; Barlow et al., 2008). Coastal and shelf regions are known to be more productive than pelagic regions because of land originated nutrient inputs and tidal mixing (Tew-Kai and Marsac 2009).

In a study carried out by Braga et al. (2008) in South America, low salinity values associated with high nutrient concentrations revealed the influence of freshwater inputs onto the continental shelf. Lourey et al. (2006) stated that during their study on the Leewin Current on the west coast of Australia, a cross-shelf (inshore to offshore) gradient in chlorophyll *a* concentration suggested that nutrients delivered from the mainland played an key role in sustaining phytoplankton production on the shelf. Clearly terrestrial inputs of nutrients are of great importance to primary production in regions where freshwater input is common.

Tew-Kai and Marsac (2009) state that even though the eastern side of the Mozambique Channel boasts large shelf areas, primary production is substantially higher on the western side. Tew-Kai and Marsac (2009) found an increase in chlorophyll *a* concentration along the western continental shelf of Madagascar, the explanation for this increase in chlorophyll *a* was that the northern regions of Madagascar experience significant precipitation during the warm season, highlighting the importance of riverine input onto shelf regions and primary production. Mozambican coastal waters are enriched by rivers flowing into the channel and mesoscale eddies entrain this nutrient rich water from the continental shelf into the pelagic environment (Tew-Kai and Marsac 2009). Entrainment of surface chlorophyll into the pelagic environment is almost always observed through satellite imagery but the three-dimensional dynamics of shelf entrained chlorophyll into the pelagic environment cannot be confidently verified using this method as only surface chlorophyll concentrations are recorded. The majority of chlorophyll *a* sampled in the water column is generally situated at around 50 - 100 metres depth, and not in surface waters. The three dimensional dynamics of basic physico-chemical and biological relationships revealed in this study would have not been possible using satellite imagery alone.

According to Machu and Garcon (2001) the Mozambique Channel exhibits a seasonal variation in chlorophyll *a* with a peak in austral winter and a minimum in austral summer. With no winter chlorophyll *a* values to compare with the summer data set collected on the MC08A cruise one cannot be certain of a seasonal variation for this specific study. It is unknown whether the seasonal variation in chlorophyll *a* within the Mozambique Channel is

due to wider, less intense eddies tracking south through the channel in summer compared to those in winter or induced by other factors not accounted for (Omata et al., 2009).

The total chlorophyll *a* values measured in this study within the cyclonic eddies (1.16 ± 0.23 µg l^{-1}) and the anti-cyclonic eddy (0.9 ± 0.24 µg l^{-1}) are higher than those described by Omata et al. (2009) who measured annual mean chlorophyll levels (0.3 µg l^{-1}) with a summer average of around 0.15 µg l^{-1} within the Mozambique Channel. Chlorophyll values of up to 0.2 µg l^{-1} characterised most of the central Mozambique Channel in spring (Omata et al., 2009). In a study carried out by Lujteharms (2006b) chlorophyll *a* values were found to be relatively low over most of the Mozambican shelf waters. The highest value of 98 µg l^{-1} found at the shelf edge far exceed those found within the frontal zone sampled during this particular study which revealed the variable nature of primary production within the Mozambique Channel.

3.4.3 Coastal zone

Seasonal and main pycnoclines are often `domed` within cyclonic oceanographic features, whereas anti-cyclones reduce both density interfaces (McGillicuddy et al., 2007). The apparent ‘doming‘ of nutrients in the coastal zone could indicated upwelling in the area. However, the relatively stratified vertical temperature gradient through the Coastal zone suggests alternative influences at work here. The dominance of picophytoplankton in the coastal zone confirms the theory that in warmer waters (>22°C) picophytoplankton tended to dominate the phytoplankton community (Bouman et al., 2003; 2005).

Other than the picophytoplankton dominance, no additional discernible patterns regarding physico-chemical or biological variables were evident within the coastal zone. This may have been due to the variable nature of the results for this specific area.

3.5 Synthesis

The entrainment of nutrient rich coastal waters into the pelagic environment is a common occurrence in the Mozambique Channel especially on the Mozambican coastline (Martin et al., 2001) and can clearly be seen in the satellite image (Figure 3.17) below. Also, the proximity of the frontal zone to Angoche (ca. 70 kilometres offshore) and the additional entrainment of the freshwater by eddies may have influenced the salinity characteristics of the Frontal zone. In stating this it must be recognized that in general salinity values were relatively constant throughout all stations.

In Mozambique, the wet season (summer) extends on average from November to April (Schouwennars 1987). A seasonal variation in chlorophyll *a* (low summer; higher winter) is evident in the Mozambique Channel (Machu and Garcon 2001; Omata et al., 2009). The seasonal variation suggests that freshwater riverine input into the Mozambique Channel is not as important as it is thought to be (Schouten et al., 2003).

The Mozambique Channel is said to be dominated by large anti-cyclonic eddies in summer (Saetre and Jorge da Silva 1984) with an average of four per year (De Ruijter et al., 2002). Chlorophyll variability in the north (10ºS-16ºS) and south (24ºS-30ºS) of the Mozambique Channel is mostly forced by seasonal oceanographic features whereas the central region of the channel (16ºS-24ºS) the seasonality signal has less of an influence due possibly to well-developed eddies dominating the central region of the channel and thus imposing a non-seasonal regime to the region (Tew-Kai and Marsac 2009).

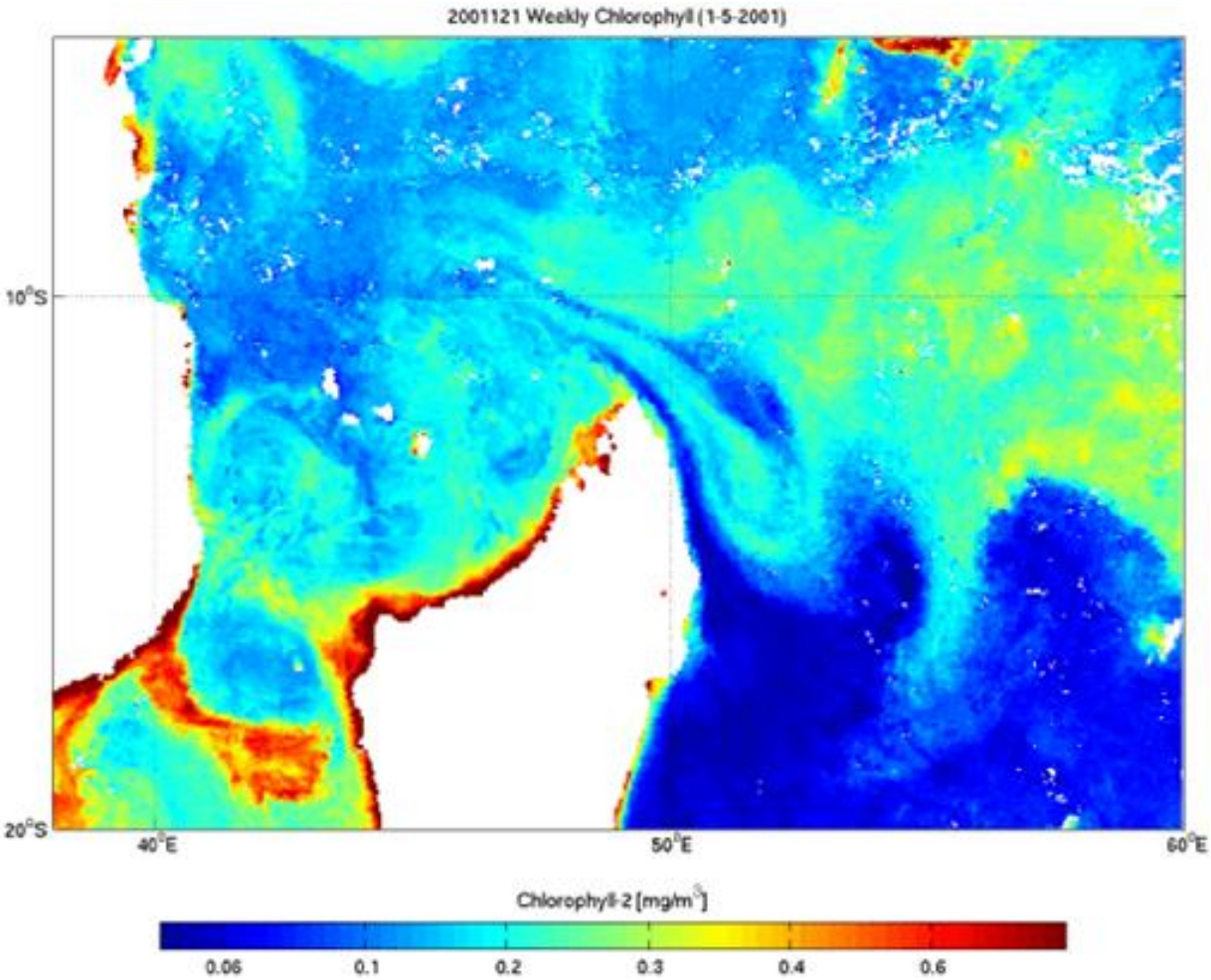

Figure 3.17. Weekly Chlorophyll composite (MODIS) at the end of April 2001, clearly showing the increased productivity on the continental shelves of Mozambique and Madagascar as well as the entrainment of chlorophyll offshore from the shelves by the anti-cyclonic eddies in the Mozambique Channel.

Seasonal variability of SST in the Indian Ocean has previously been described as being wind-induced through entrainment and lateral Ekman transport (Loschnigg and Webster 2000). Malauene et al. (In Press) found no direct correlation between the presence of eddies and upwelling events during 2008 and 2009 in the Mozambique Channel. The warm core downwelling anti-cyclonic eddies which dominate the Mozambique Channel during the summer months seem to have an overriding influence on primary production in the channel. During a seven year study from 1998 to 2005, Tew-Kai and Marsac (2009) found that anti-cyclonic eddies and low chlorophyll concentrations (0.15 µg l^{-1}) dominated the Mozambique Channel from 1998 to 2000, and from 2001 to the end of 2004 cyclonic eddies coupled with higher chlorophyll concentrations (1.0 µg l^{-1}) were dominant in the Mozambique Channel. The study excluded shelf areas in an attempt to rule out high and local values from the regional analysis. The exclusion of the shelf areas by Tew-Kai and Marsac (2009) was an attempt to provide a more accurate description of primary production in the pelagic Mozambique Channel due to the sporadic influence that riverine nutrient input is said to have on shelf regions (Braga et al., 2008). It must be kept in mind that entrained nutrient rich shelf waters are said, and is clearly evident in Figure 3.13, to influence primary production in oligotrophic pelagic environments (Lee 1980; Martin et al., 2001; Quartly and Srokosz 2004; Reynolds 2006; Kyewalyanga et al., 2007). The findings of Tew-Kai and Marsac (2009) suggest that eddy seasonality within the Mozambique Channel exists on a broader time scale than simply winter-summer seasonality and that eddy seasonality plays a significant role on chlorophyll seasonality within the Mozambique Channel. Their results also highlight the important role eddies have on phytoplankton enhancements within the channel.

A study carried out by Zinke et al. (2004) on the oxygen isotope records within the coral reefs of Ifaty, off southwestern Madagascar, revealed changes in SST on seasonal to multi-decadal time scales. Strong Indian Ocean subtropical dipole events which occur during austral summers were revealed in the Ifaty coral record (Zinke et al., 2004). The austral summer oxygen isotope record within the coral reef at Ifaty was coherent and in phase with El Nino/Southern Oscillation (ENSO) indices on inter-annual time scales (2-4 years). These results also revealed the influence of ENSO on southwest Indian Ocean SST and atmospheric circulation. ENSO cycles have changed in the region (Mozambique Channel) significantly since 1970 related to a warming of the southwest Indian Ocean surface waters changing the regional signature of ENSO (Zinke et al., 2004). These findings have relevance to the present study as long term changes (ENSO cycles) influence on seasonal patterns in the Mozambique Channel which would also influence primary production. Work carried out by Loschnigg and Webster (2000) revealed an unusual relationship between the heat

content anomaly and the climatic variables in the Indian Ocean which suggested that a varied wind field associated with ENSO may alter the relative importance between the surface thermal forcing and wind-driven heat transfer. The importance of long term studies (5 years or more) with regards to the consistency of mesoscale eddies (cyclonic or anti-cyclonic) travelling through the channel is clearly evident.

3.6 Conclusion

Phytoplankton species profiles, CTD and nutrients are often used to identify the main hydrographic and biochemical characteristics of a region. However, these hydrographic and biochemical characteristics are restricted to static descriptions (Tiltstone et al., 2000).

A theory suggested regarding the reduced phytoplankton biomass in both cyclonic and anti-cyclonic eddies during the MCO8A cruise is that grazing from the high zooplankton biomass recorded within the cyclonic eddies had a negative effect on phytoplankton biomass (Huggett In Press).

The ODV profiles of physical (temperature, salinity and oxygen) and chemical (nutrients) environmental variables showed a strong relationship, which in turn had an impact on the phytoplankton (total, micro-, nano- and picophytoplankton) distribution through the water column.

‘Snap shot’ studies such as the study undertaken here may provide modest insights into the direct features influencing primary production in the Mozambique Channel but will not reveal long term changes and influences of primary production within the Mozambique Channel as a whole. Long term data sets consisting of studies such as the one undertaken here may reveal a relationship between primary production and mesoscale eddies within long term ENSO cycles. The challenge with understanding phytoplankton ecology is the fact that samples are almost always random ‘snap shots’ of living communities. A large number of samples are needed in order to provide sufficient information on patterns of phytoplankton biomass dynamics.

4 Phytoplankton Biomass

4.1 Introduction

Generally, there are two methods used to determine phytoplankton biomass in the ocean. The first and most commonly used method is that of satellite imagery in which total surface chlorophyll *a* is quantified and interpreted as phytoplankton biomass. An obvious advantage of this method is that large areas of ocean can be 'sampled' in a short amount of time. One of the primary disadvantages of this method is the two-dimensional (surface only) nature of the results obtained. The second method used to determine phytoplankton biomass is by sampling *in situ* and using laboratory methods (see Materials and Methods section in Chapter 2) to extract chlorophyll *a* from water samples. The key advantage of this method is the three-dimensional nature of the results achieved (i.e. chlorophyll concentrations at different depths). This allows for a potentially broader understanding of the phytoplankton biomass within the specific water column. Both methods however, assume a direct relationship between chlorophyll concentration and phytoplankton biomass. A direct relationship is not necessarily an accurate portrayal of phytoplankton biomass as the two themes are related, but not precisely (Ulloa et al., 1994). It has been argued that one cannot directly correlate surface chlorophyll concentrations measured by satellites to phytoplankton biomass (Zhang et al., 1998) as phytoplankton biomass (and thus chlorophyll *a* concentrations) will vary with depth.

This chapter focuses on the concentrations of chlorophyll *a* as an indicator of phytoplankton biomass at the surface and *F*-max (fluorescence maximum) across all sampled sites. In particular, sites are categorised within the context of oceanographic features (Cyclonic, Anti-cyclonic, Frontal and Coastal), and comparisons between these regions are assessed. Depth related differences in chlorophyll concentrations are well documented (Anderson 1969; Saijo et al., 1969; Hobson and Lorenzen 1972; Jamart et al., 1977; Takahashi and Hori 1984; Magazzu and Hull 1985; O`Reilly and Zetlin 1998; Leala et al., 2009) and concentrations are highly variable, both temporally and spatially. Rarely, with the exception of intense water column mixing, are vertical profiles of chlorophyll *a* homogeneous (Takahashi et al., 1972). The depth of chlorophyll *a* concentration-maximum (*F*-max) is also highly variable and can occur somewhere close to the distal end of the euphotic zone or somewhere near surface waters (Steele and Yentsch 1960). According to Cullen (1982) the majority of chlorophyll *a* vertical distribution patterns can be described by the interaction between hydrography and growth, physical adaption or behaviour of phytoplankton, with no special consideration for grazing by herbivores. Furthermore, he concludes that the

mechanisms, facilitating maintenance and formation of deep chlorophyll maximum, vary greatly across regions of the world's oceans.

This chapter attempts to explain phytoplankton biomass features related to physico-chemical parameters within the various oceanographic features sampled as well as to identify any differences/ similarities in phytoplankton biomass between surface and *F*-max waters within and between the oceanographic features sampled (Cyclonic, Anti-cyclonic, Coastal and Frontal).

The following hypothesis will be tested in this chapter: Phytoplankton biomass and size class structure is determined by the physico-chemical characteristics of the different oceanographic features and as a result the different mesoscale and sub-mesoscale features will be significantly different.

4.2 Materials and Methods

4.2.1 Field work and laboratory analysis

Fifty-one stations were sampled, comprising 12 stations within anti-cyclonic features, 20 stations within cyclonic features, 14 stations in frontal features and the remaining 5 stations sampled at coastal locations (Figure 3.2). All data were collected from the R/V *Dr Fridtjoff Nansen* during the November/December cruise of 2008 (Figure 3.1). Conductivity, salinity and dissolved oxygen were measured from each of the 51 Mozambique Channel study sites at both surface and *F*-max. Similarly, soluble reactive phosphorus (SRP), total dissolved inorganic nitrogen (DIN) and silicate concentrations were determined from the same locations (details described in Chapter 2). Nutrients were sampled in order to identify any relationships present between chlorophyll *a* concentrations and phosphorous, nitrogen and silicate. Chlorophyll *a* measurements from surface and *F*-max were extracted as described in Chapter 2 and included as total chlorophyll *a* and size fractionated (20 µm, 2 µm and 0.7 µm) chlorophyll *a* measurements.

4.2.2 Data analyses

Assumptions for normality and homogeneity of variance were not met by physico-chemical or biological data and as such, non-parametric tests were used to analyse the data. Physical and chemical variables within each of the oceanographic features and chlorophyll *a* variables measured were tested for differences between surface and *F*-max as well as between mesoscale features sampled, using the Mann-Whitney U test. Spearman rank correlations were used to investigate significant relationships between physico-chemical

variables and chlorophyll *a* (total and fractionated). All statistical analyses were conducted using STATISTICA 10 (StatSoft 2011).

The phytoplankton functional groups, species and environmental data were analysed using CANOCO for Windows (version 4.52, 2003). Canonical Correspondence Analysis (CCA) was used to obtain an ordination of total size fractionated chlorophyll *a* as an indication of biomass as constrained by environmental variables. Monte Carlo permutation tests (999 permutations) were performed to assess the significance of the canonical axis showing the relationship between the groups and the selected environmental variables. The result of the CA and the CCA was plotted as a two-dimensional graph using CanoDraw for Windows (version 4.12, 2003). The environmental variables were plotted as arrows originating from the centre of the graph. The origin represents the mean value of each separate variable and the direction of the arrow line represents an increase in the value of that particular variable.

4.3 Results

4.3.1 Environmental variability

Salinity, oxygen and temperature averages and ranges of the four mesoscale features sampled (Cyclone, Anti-cyclone, Frontal and Coastal) are represented in Table 4.1. *F*-max stations within the coastal zone showed slightly cooler water temperatures than any of the other stations. The *F*-max stations within the cyclone grouping revealed lowest oxygen levels on average.

The coastal zone *F*-max samples had on average the highest dissolved inorganic nitrogen, silicate and phosphorus concentrations, represented in Table 4.2. The lowest levels of nitrogen were found within the frontal surface stations. The lowest concentrations of silicate were found within the cyclonic surface waters. The surface waters sampled within the anti-cyclones revealed the lowest concentrations of phosphorus. Nutrient concentrations found at *F*-max were higher than concentrations found at surface waters in all stations and oceanic features.

Physico-chemical differences between mesoscale features were more prominent in *F*-max samples than they were for surface water (Table 4.3), however no significant differences in physical variables were found between coastal and cyclone *F*-max samples. The anti-cyclone vs. coastal and anti-cyclone vs. cyclone *F*-max samples revealed significant differences in all physical variables measured (Table 4.3). No significant difference was found between surface water values for any of the measured nutrient parameters.

All nutrients at *F*-max in the coastal zone were significantly higher than nutrients found at *F*-max in the anti-cyclone (Table 4.4). This was the only example of a specific depth having a significant difference in all nutrients between oceanographic features.

Table 4.1. Mean (range) for salinity, oxygen and temperature within the four different mesoscale features sampled in the Mozambique Channel. Salinity = PSU; Oxygen = ml l^{-1}; Temperature = °C.

	Cyclone		Anti-cyclone		Frontal		Coastal	
	Surface	*F*-max	Surface	*F*-max	Surface	*F*-max	Surface	*F*-max
Salinity	35.4 (35.26 - 35.49)	35.33 (35.19 -35.39)	35.29 (35.14 - 35.46)	35.21 (35.18 - 35.3)	35.31 (35.19 - 35.43)	35.27 (35.19 - 35.35)	35.53 (35.48 - 35.57)	35.37 (35.33 - 35.39)
Oxygen	4.39 (4.31 - 4.48)	4.03 (3.49 - 4.65)	4.43 (4.37 - 4.74)	4.32 (4.12 - 4.52)	4.47 (4.38 - 4.6)	4.18 (3.75 - 4.55)	4.39 (4.38 - 4.42)	4.08 (3.9 - 4.33)
Temp	28.41 (27.78 - 28.85)	22.46 (20.92 - 25.88)	28.43 (27.32 - 28.81)	24.65 (22.57 - 25.49)	28.41 (26.9 - 29.52)	23.49 (21.85 - 24.98)	27.72 (27.52 - 27.96)	22.28 (21.87 - 22.50)

Table 4.2. Mean (range) for nitrogen, silicate and phosphorus concentrations within the various mesoscale features sampled in the Mozambique Channel. Phosphorus = Soluble Reactive Phosphorus; Nitrogen = Total Dissolved Inorganic Nitrogen. 0 = not detectable. Nutrient concentrations = (µM).

	Cyclone		Anti-cyclone		Frontal		Coastal	
	Surface	*F*-max	Surface	*F*-max	Surface	*F*-max	Surface	*F*-max
Nitrogen	0.13 (0 - 1.32)	1.9 (0 - 6.38)	0.14 (0 - 0.78)	0.89 (0.27 - 1.85)	0.09 (0 - 0.46)	2.03 (0.18 - 5.66)	0.21 (0 - 0.41)	2.77 (1.95 - 4.24)
Silicate	<0.01 (<0.01)	1.34 (0 - 3.36)	0.19 (0 - 1.78)	0.88 (0 - 1.72)	0.08 (0 - 1.21)	1.05 (0 - 2.66)	0.22 (0 - 1.1)	1.78 (1.29 - 2.2)
Phosphorus	0.18 (0 - 0.4)	0.40 (0 - 0.6)	0.17 (0 - 0.39)	0.26 (0.07 - 0.54)	0.14 (0 - 0.37)	0.31 (0 - 0.63)	0.26 (0 - 0.38)	0.70 (0.47 - 0.89)

Table 4.3. Results of Mann-Whitney U test for physical variables in mesoscale features at the surface and at *F*-max in the Mozambique Channel. Salinity = PSU; Oxygen = ml l^{-1}; Temperature = °C.

	F-max		Surface	
	p	U	p	U
Anti-cyclone vs. coastal				
Salinity	**0.002**	< 0.001	**0.002**	< 0.001
Oxygen	**0.013**	5.0	0.874	28.0
Temperature	**0.002**	< 0.001	**0.013**	6.0
Anti-cyclone vs. cyclone				
Salinity	**< 0.001**	8.0	**0.001**	36.0
Oxygen	**0.024**	55.0	0.425	99.0
Temperature	**0.001**	31.0	0.302	93.0
Anti-cyclone vs. frontal				
Salinity	**0.009**	29.0	0.487	70.0
Oxygen	0.198	53.0	**0.019**	38.0
Temperature	**0.040**	39.0	0.777	78.0
Coastal vs. cyclone				
Salinity	0.096	25.0	**< 0.001**	0.0
Oxygen	0.812	46.0	0.973	50.0
Temperature	0.973	49.0	**0.002**	3.0
Coastal vs. frontal				
Salinity	**0.011**	7.0	**0.001**	< 0.001
Oxygen	0.151	19.0	**0.023**	10.0
Temperature	**0.023**	10.0	0.105	17.0
Cyclone vs. frontal				
Salinity	**0.011**	67.0	**0.003**	53.0
Oxygen	0.119	95.0	**0.002**	52.0
Temperature	**0.022**	74.0	0.637	126.0

Table 4.4. Results of Mann-Whitney U test for nutrient concentrations at *F*-max between mesoscale features (no significant differences in surface water values) sampled in the Mozambique Channel. P = soluble reactive phosphorus; Si = silicate; N = total dissolved inorganic nitrogen. Nutrient concentrations = (µM).

	F-max		Surface	
	p	U	p	U
Anti-cyclone vs. coastal				
Phosphorus	**0.004**	1.5	0.49	23.0
Silicate	**0.031**	8.0	0.792	27.0
Nitrogen	**0.002**	< 0.001	0.493	23.0
Anti-cyclone vs. cyclone				
Phosphorus	0.073	66.0	0.969	118.5
Silicate	0.650	98.5	0.712	110.0
Nitrogen	0.592	96.5	0.321	94.0
Anti-cyclone vs. frontal				
Phosphorus	0.722	70.0	0.425	68.0
Silicate	0.913	74.5	0.959	82.5
Nitrogen	0.352	59.5	0.589	73.0
Coastal vs. cyclone				
Phosphorus	**0.004**	7.0	0.110	26.0
Silicate	0.077	23.5	0.519	40.0
Nitrogen	0.062	22.0	0.234	32.0
Coastal vs. frontal				
Phosphorus	**0.005**	4.0	0.105	17.0
Silicate	0.087	16.0	0.746	31.0
Nitrogen	0.058	14.0	0.247	22.0
Cyclone vs. frontal				
Phosphorus	0.077	89.0	0.184	101.5
Silicate	0.637	126.0	0.740	130.0
Nitrogen	0.740	130.0	0.944	137.5

Upon closer investigation, differences in physico-chemical variables between surface and *F*-max physical features within each mesoscale type varied, with only temperature showing consistent differences between these depths in each system (Table 4.5). The coastal and cyclonic mesoscale systems showed significant differences in salinity, oxygen and temperature between *F*-max and surface waters. In a similar way nutrient characteristics between surface and *F*-max varied across mesoscale features (Table 4.6). The coastal and cyclonic systems showed significant differences in phosphorus, nitrogen and silicate concentrations between *F*-max and surface waters. The anti-cyclonic systems showed only a significant difference in phosphorus concentrations between *F*-max and surface waters (Table 4.6).

Table 4.5. Comparisons in physical environmental variables between *F*-max and surface samples within mesoscale features. Salinity = PSU; Oxygen = ml l^{-1}; Temperature = °C.

	Anti-cyclone		Coastal		Cyclone		Frontal	
	p	U	p	U	p	U	p	U
Salinity	**0.004**	21.0	**0.012**	< 0.001	**0.016**	110.5	0.206	70.0
Oxygen	0.141	46.0	**0.012**	< 0.001	**0.004**	93.5	**0.020**	47.0
Temperature	**< 0.001**	< 0.001	**0.012**	< 0.001	**< 0.001**	8.5	**< 0.001**	16.0

Table 4.6. Comparisons between *F*-max and surface, within mesoscale features for nutrients. P = soluble reactive phosphorus; Si = silicate; N = total dissolved inorganic nitrogen. Nutrient concentrations = (µM).

	Anti-cyclone		Coastal		Cyclone		Frontal	
	p	U	p	U	p	U	p	U
P	0.157	47.0	**0.012**	< 0.001	**< 0.001**	63.0	0.098	61.5
Si	0.057	38.5	**0.010**	< 0.001	**< 0.001**	60.0	**0.043**	53.5
N	**< 0.001**	14.0	**0.011**	< 0.001	**< 0.001**	67.0	**< 0.001**	25.0

4.3.2 Size fractionated Chlorophyll *a* biomass

Total chlorophyll *a* concentrations were on average highest in the frontal submesoscale features at both *F*-max (6.18 µg l^{-1}) and the surface (1.26 µg l^{-1}) within the frontal mesoscale features (Table 4.7). The frontal systems also revealed the highest maximum chlorophyll *a* concentrations for each size fractionated phytoplankton classes at *F*-max (Table 4.7).

Generally there was little biomass difference between mesoscale features for both depths sampled (Table 4.8). No differences were found for any of the total or size fractionated *F*-max chlorophyll *a* concentrations between mesoscale features. Surface water biomass in the anti-cyclone however showed significant differences to all other mesoscale features at some level (Table 4.8).

Aside from the 2 – 20 µm in all oceanographic features and the coastal 0.7 to 2 µm phytoplankton size fraction, all other chlorophyll *a* concentrations differed significantly between surface and *F*-max (Table 4.9). Both anti-cyclonic and cyclonic systems showed the greatest degree of depth differences in chlorophyll *a*.

Table 4.7. Mean (range) for total, 20 µm, 2 µm and 0.7 µm size fractionated chlorophyll *a* concentrations (µg l^{-1}) within the mesoscale features.

	Cyclone		Anti-cyclone		Frontal		Coastal	
Chl *a*	Surface	*F*-max	Surface	*F*-max	Surface	*F*-max	Surface	*F*-max
Total	0.77 (0.25-1.84)	3.13 (1.18-24.96)	0.96 (0.20-6.76)	3.61 (0.60-12.9)	1.26 (0.45-6.88)	6.18 (0.85-17.08)	0.79 (0.69-0.94)	2.26 (0.98-2.94)
20 µm	0.17 (0.00-0.71)	1.27 (0.00-19.93)	0.52 (0.03-5.12)	1.73 (0.01-10.25)	0.51 (0.02-4.27)	3.71 (0.03-14.52)	0.15 (0.08-0.34)	0.51 (0.16-1.27)
2 µm	0.21 (0.05-0.99)	0.74 (0.17-3.65)	0.18 (0.06-0.99)	0.64 (0.07-1.70)	0.37 (0.05-1.80)	1.08 (0.06-1.08)	0.21 (0.08-0.32)	0.41 (0.24-0.66)
0.7 µm	0.39 (0.10-1.51)	1.10 (0.05-1.75)	0.24 (0.06-0.64)	1.25 (0.30-2.37)	0.38 (0.12-0.80)	1.38 (0.28-2.84)	0.42 (0.28-0.54)	1.32 (0.56-2.13)

Table 4.8. Comparisons between mesoscale features for *F*-max and surface water chlorophyll *a* concentrations (µg l^{-1}).

	F-max		Surface	
	p	U	p	U
Anti-cyclone vs. Coastal				
Total Chl *a*	1.000	27.0	**0.023**	8.0
20 µm	0.365	19.0	0.225	18.0
2 µm	0.571	22.0	0.102	14.0
0.7 µm	0.910	26.0	**0.031**	9.0
Anti-cyclone vs. Cyclone				
Total Chl *a*	0.549	95.0	**0.015**	57.0
20 µm	0.332	86.0	0.251	90.0
2 µm	0.409	89.5	0.139	81.5
0.7 µm	0.433	90.5	0.052	69.5
Anti-cyclone vs. Frontal				
Total Chl *a*	0.427	62.0	**0.005**	29.0
20 µm	0.239	55.0	0.068	48.0
2 µm	0.412	61.5	**0.022**	39.0
0.7 µm	0.763	71.0	0.105	52.0
Coastal vs. Cyclone				
Total Chl *a*	0.435	38.0	0.435	38.0
20 µm	0.083	24.0	0.973	50.0
2 µm	0.174	29.5	0.497	39.5
0.7 µm	0.709	44.0	0.262	33.0
Coastal vs. Frontal				
Total Chl *a*	0.611	29.0	0.963	35.0
20 µm	0.677	30.0	0.405	25.5
2 µm	0.247	22.0	0.611	29.0
0.7 µm	0.963	34.0	0.287	23.0
Cyclone vs. Frontal				
Total Chl *a*	0.255	107.0	0.319	111.0
20 µm	**0.029**	77.0	0.178	101.0
2 µm	0.517	121.0	0.119	95.0
0.7 µm	0.336	112.0	0.847	134.0

Table 4.9. Comparisons in chlorophyll *a* biomass (µg l^{-1}) between *F*-max and surface within mesoscale features.

	Anti-cyclone		Coastal		Cyclone		Frontal	
	p	U	p	U	p	U	p	U
Total Chl *a*	**< 0.001**	12.0	**0.012**	< 0.001	**< 0.001**	11.5	**< 0.001**	16.0
20 µm	0.525	60.5	0.060	3.0	0.402	168.5	0.135	65.0
2 µm	**0.002**	18.5	0.060	3.0	**< 0.001**	38.0	**0.012**	43.0
0.7 µm	**< 0.001**	6.0	**0.012**	< 0.001	**< 0.001**	62.0	**< 0.001**	13.0

4.3.3 Physico-chemical / Biological relationships

Total, nano- and picophytoplankton chlorophyll *a* concentrations across all samples revealed significant relationships with all three nutrients sampled (Table 4.10). The higher the nutrient concentrations the higher the total, pico and nanophytoplankton biomass. The correlation between microphytoplankton and nutrients were not significant (Table 4.10). Similarly, total, nano and picophytoplankton reveal inverse relationships with all three physical variables sampled. Microphytoplankton on the other hand showed no significant relationships to the physico-chemical parameters sampled.

Table 4.10. Spearman rank correlations between chlorophyll *a* (µg l^{-1}) and physico-chemical parameters. Salinity = PSU; Oxygen = ml l^{-1}; Temp = Temperature (°C). P = soluble reactive phosphorus; Si = silicate; N = total dissolved inorganic nitrogen. Nutrient concentrations = (µM). Significant correlations are presented in bold.

	Total Chl *a*	20µm Chl *a*	2µm Chl *a*	0.7µm Chl *a*	P	Si	N	Salinity	Oxygen	Temp
Total Chl *a*	1.000									
20µm Chl *a*	**0.505**	1.000								
2µm Chl *a*	**0.820**	**0.385**	1.000							
0.7µm Chl *a*	**0.840**	**0.232**	**0.507**	1.000						
P	**0.367**	0.189	**0.295**	**0.328**	1.000					
Si	**0.376**	-0.047	**0.244**	**0.424**	**0.446**	1.000				
N	**0.505**	0.056	**0.381**	**0.556**	**0.443**	**0.705**	1.000			
Salinity	**-0.250**	-0.082	-0.136	**-0.266**	0.144	-0.127	-0.130	1.000		
Oxygen	**-0.322**	0.062	**-0.263**	**-0.345**	**-0.401**	**-0.560**	**-0.648**	-0.138	1.000	
Temp	**-0.695**	-0.151	**-0.550**	**-0.691**	**-0.574**	**-0.627**	**-0.701**	0.083	**0.565**	1.000

In Figure 4.1 the first canonical axis described 88.5 % of the species – environment relation (Table 4.11). This axis was positively correlated to Si and salinity (Table 4.12). The second canonical axis described 100% of the variation and was negatively correlated to Si, DIN and salinity (Table 4.11 and 4.12). The strongest correlations were between the second canonical axis and DIN (-0.55) and salinity (-0.50) (Table 4.12).

Nanophytoplankton revealed environmental inclination for elevated nutrient and salinity concentrations and reduced dissolved oxygen levels (Figure 4.1).

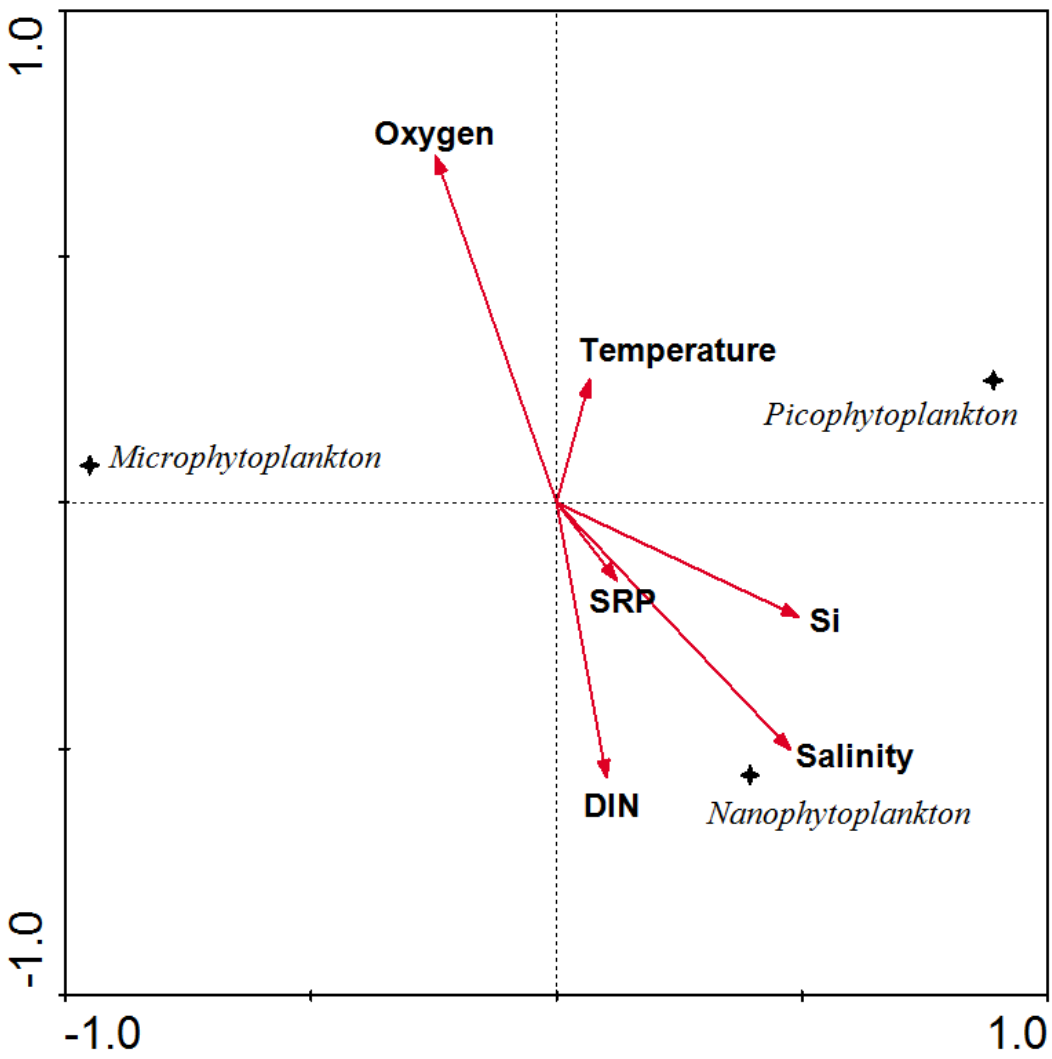

Figure 4.1. Ordination diagram with environmental variables and phytoplankton size classes across all sites and depths. The distance between each size class identifies the dissimilarity of those groups. DIN = Total dissolved inorganic nitrogen; SRP = Soluble reactive phosphorus; Si = Silicate.

Table 4.11. Summary of CCA of biomass (micro, nano and picophytoplankton) and environmental data (p = 0.001)

	Axes	
Axes	1	2
Eigenvalues	0.081	0.011
Species-environment correlation	0.462	0.349
Cumulative percentage variance of species data	17.3	19.6
Cumulative percentage of species environment relation	88.4	100.0
Sum of all unconstrained eigenvalues	0.467	
Sum of all canonical values	0.092	

Table 4.12. Spearman rank correlations of environmental variables with the first and second canonical axes of the CCA. Significant correlations are presented in bold.

	Species Axis1	Species Axis 2	Environmental Axis 1	Environmental Axis 2
SRP	0.0568	-0.055	0.123	-0.1575
Si	**0.2282**	**-0.0807**	**0.4941**	**-0.2313**
DIN	0.0473	**-0.1946**	0.1024	**-0.5576**
Salinity	**0.2206**	**-0.175**	**0.4777**	**-0.5016**
Oxygen	-0.1136	0.2458	-0.2459	0.7042
Temp	0.0314	0.0872	0.0679	0.2499

4.4 Discussion

4.4.1 Environmental variability

Oxygen content in the world`s oceans is controlled by a number of parameters. Respiration of organic matter by biological activity, mixing of water and the air-sea interface are the main contributors of dissolved oxygen in the ocean (Miyake and Saruhashi 1967). Oxygen produced by photosynthesis in the surface layers of the world`s oceans is removed by the respiration of biological matter in the layer directly below (Joost et al., 1998). The slightly increased dissolved oxygen concentrations in surface waters across all mesoscale features suggests that the oxygen being dissolved at the air-surface interface exceeded the amount of oxygen being produced by phytoplankton at *F*-max. Another theory may be that there were fewer zooplankton in surface waters compared to *F*-max. The relatively low overall chlorophyll *a* concentration values recorded during the MC08A cruise may also have had a part to play as low primary production rates are common in oligotrophic waters. The replenishment of nutrients to surface layers depends largely on the recycling process of mineralisation in the deeper waters (Boney 1989). The warmer surface temperatures across all mesoscale systems were expected due to variations in ocean temperature created by the heating of surface waters by the sun. In regions where upwelling is strong, the thermocline becomes well mixed and water temperatures become relatively uniform up to a certain depth. Mean surface water temperatures compared to the deeper *F*-max water temperatures across all systems suggest that vertical mixing was not particularly strong in the Mozambique Channel during the time of sampling.

Salinity is generally influenced by terrestrial freshwater runoff, evaporation and large scale eddies upwelling dense saline water to the surface (Garrett 1979). The relatively consistent vertical salinity values across all mesoscale features also suggest, like temperature, that vertical mixing was not particularly strong at the time of sampling.

Nitrogen, phosphorus and silicon are the most important macronutrients controlling phytoplankton growth rate and community composition (Malone et al., 1996; Mallin et al., 1999). The slightly increased concentrations of nitrogen, silicate and phosphorus concentrations found within *F*-max waters in the coastal zone suggest an alternate nutrient source, e.g. shelf edge upwelling. Freshwater enrichment of the coastal waters is common in regions with moderate to high rainfall patterns (Chemane 1997; Neal et al., 2000). Salinity values were very uniform throughout the study and it is difficult to say whether the small freshwater signature evident in the frontal zone was in fact as a result of terrestrial input or some other factor.

4.4.2 Size fractionated Chlorophyll *a*

The low chlorophyll *a* concentrations recorded in the Mozambique Channel at the time of sampling is a testament to the traditionally oligotrophic nature of the region. Lamont et al. (In Press) also found phytoplankton biomass to be comparatively low and not significantly different in both cyclonic and anti-cyclonic eddies in the Mozambique Channel during the MC08A cruise. One explanation for the relatively higher total chlorophyll *a* concentrations at both *F*-max and surface depths recorded in the frontal systems sampled may be the notion that frontal or sea-surface fronts that have the characteristics of convergence zones (where two systems e.g. cyclone/anti-cyclone meet) with high levels of chlorophyll *a* at certain locations (Lutjeharms et al., 1985). Similarly, Laubscher et al. (1993) found that increased chlorophyll *a* at ocean fronts were dominated by specific size classes and species of phytoplankton. Phytoplankton in the deep chlorophyll maximum layer represented 50 – 82% of the total biomass in the euphotic zone during the MC08A cruise (Lamont et al., In Press). The results also suggest that in terms of chlorophyll *a* concentration, the position of phytoplankton within the water column (*F*-max or surface) was generally more important to primary production rates than between mesoscale oceanographic features. That is to say, the differences between surface and *F*-max environments were greater than the differences between environments within individual mesoscale and sub-mesoscale eddies.

4.4.3 Physico-chemical / Biological relationships

It is widely accepted that nutrient availability influences the diversity of phytoplankton (Choudhury and Pal 2010). The importance of the various factors which influence the growth of phytoplankton communities especially with regards to physico-chemical factors has been researched in many parts of the ocean (Grenz et al., 2000). Emphasis on the importance of physical processes in ecosystem organisation has in principal, been an artifact of the links found between these drivers of ecosystems and primary production (Rosenzweig 1973).

In almost all cases the majority of chlorophyll *a* was found to be within the micro and nanophytoplankton size range. In a study undertaken by Rodríguez et al. (1998) it was discovered that picophytoplankton biomass within the deep chlorophyll maximum (*F*-max) was independent of circulation features whereas nanophytoplankton and microphytoplankton biomass increased within cyclonic upwelling environments. The relationships between total, nano and picophytoplankton and all three nutrients sampled across all sites reveal that the availability of nutrients played an important role in the distribution of phytoplankton in the water column. Similarly, the inverse relationship between total pico and nanophytoplankton and the physical variables sampled supports the notion that cold, deep waters are nutrient rich and when upwelled, assist in the production of phytoplankton in the euphotic zone.

These results also confirm to some level that the surface/*F*-max environment distinction seems to be more pronounced than that of individual oceanographic features as originally hypothesised.

5 Phytoplankton community

5.1 Introduction

Phytoplankton is the most important primary producers in the pelagic environment and therefore a critical component of the ecosystem as a whole. Barnes et al. (2011) suggests that in order to determine food chain lengths, consumer biomass and production for any given ecosystem the accurate description of the size composition of the primary producers in that ecosystem is necessary. Phytoplankton community structure between the cyclonic, anti-cyclonic, frontal and coastal oceanographic features sampled during the MC08A cruise was the focus of this chapter. The oceanographic features sampled were categorised according to the methods explained in Chapter 2 entitled `Station Categorisation`.

The phytoplankton community structure between surface and *F*-max waters across all sites was compared in an attempt to expose any differences/similarities between the two zones. Surface and *F*-max waters within and between the various mesoscale features sampled were also scrutinised so as to determine any variations in phytoplankton community structures. The following community structure characteristics between surface and *F*-max waters as well as between and within the various mesoscale features sampled were examined: Species composition; Spatial trends in species richness and diversity; Functional group spatial trends; Relationships between the functional groups sampled and physico-chemical variables and finally a community analyses was undertaken.

Lavoie et al. (2006) recommended the use of relative abundance when studying the influence of environmental variables on diatom community structures. The results of their study concluded that increasing the weight of large species of diatoms by using a metric that accounts for cell size will offer the same information concerning species-environment relationships as using a relative abundance metric. For this reason, the species composition component of this study was based on relative abundances of phytoplankton species within 100 ml samples of seawater.

Direct linkages between size composition of phytoplankton communities and temperature have been suggested where colder water may be dominated by larger cells due to the varied temperature dependence of heterotrophs and autotrophs (Lopez-Urrutia 2008). In cool regions, heterotrophs may not be able to control the autotrophs due to the slow growth rates associated with heterotrophs in these conditions (Lopez-Urrutia 2008). As the references suggest, temperature is an important factor in determining phytoplankton communities and linkages between the two are examined further in this chapter. Although heterotrophs were

not sampled in this study it is important to consider the grazing effects they might have had on the phytoplankton communities. Phytoplankton community structure is expected to be primarily influenced by nutrient supply where colder waters often correspond to regions with increased nutrients (e.g. upwelling and coastal areas) compared to warm water regions (e.g. oligotrophic subtropical gyres) (Barnes et al., 2011). The process of introduction of nutrients associated with cold water into the photic zone of the generally oligotrophic pelagic environment within the Mozambique Channel was therefore an important aspect of this study. Nutrient concentrations measured at various depths in the water column linked to temperature data helped to understand the processes at work within the Mozambique Channel that could promote primary production. Variations in environmental factors such as nutrient concentrations, light availability and physical environmental conditions significantly regulate the biomass, chlorophyll *a* concentrations and species composition of the phytoplankton community in question (Alejandra-Paredes and Montecino 2011).

In a study carried out by Thompson et al. (2007) on a pair of dipole eddies in the south-eastern Indian Ocean it was found that diatoms and coccolithophorids dominated the anti-cyclonic eddy while dinoflagellates and cryptophytes dominated the cyclonic eddy.

Thorrington-Smith (1969) found diatoms to dominate waters in the Algulhas Current off the coast from the Tugela River where there was relatively high nutrients. The study did not sample nanophytoplankton and thus coccolithophorids were not included in the study.

The following hypothesis was tested: Phytoplankton functional groups (e.g. diatoms, coccolithophorids, etc.) have specific environmental requirements and as a result significant differences in species composition will be found between oceanographic features and within a single oceanographic feature (between the surface and *F*-max).

5.2 Materials and Methods

5.2.1 Study site

The same study sites were sampled for community phytoplankton data as were sampled for chlorophyll *a* concentration, at the same time of collection. Surface and *F*-max water samples were collected at each of the 51 stations in their respective oceanographic feature as determined by the station categorisation explained in Chapter 2.

5.2.2 Field work

Niskin bottles were deployed from the vessel, collecting 500 ml of seawater per sample. These samples were collected from *F*-max and surface waters, preserved with formalin at a 5% final concentration and stored in trunks away from direct sunlight.

5.2.3 Laboratory analysis

The Utermöhl method was used to count and identify phytoplankton. Samples were gently stirred and a 100 ml sub-sample was carefully poured into a settling chamber and allowed to settle onto a twenty-eight millimetre diameter glass cover slip for 24 hours. All diatom, coccolithophorid and dinoflagellate cells on the slide were then counted using a Leica inverted microscope at 400x magnification (Lund et al., 1958). A Philips Scanning Electron Microscope was used to take micrographs of dominant species as well as to assist in the identification of species present. Plates of dominant species are included in Appendix B.

5.2.4 Data analysis

As with the biomass data, functional group (diatoms, coccolithophorids and dinoflagellates) data was found to be non-parametric. Functional group data were tested for differences between surface and *F*-max as well as between mesoscale features sampled, using the Mann-Whitney U test. Spearman rank correlations were used to investigate significant relationships between physico-chemical variables and phytoplankton functional groups. Canonical correspondence analyses (CCA) were executed in order to assess the associations between environmental variables and phytoplankton species as well as between environmental variables samples (split into *F*-max and surface within each mesoscale feature). Correspondence analyses (CA) were performed to assess the similarity/dissimilarity amongst phytoplankton functional groups across all sites.

Phytoplankton functional groups, species and environmental data were analysed using CANOCO for Windows (version 4.52, 2003). Correspondence Analysis (CA) was used to identify patterns in the distribution of the functional groups in the mesoscale features (Ter Braak 1995). Canonical Correspondence Analysis (CCA) was used to obtain an ordination of functional groups as constrained by environmental variables. Monte Carlo permutation tests (999 permutations) were performed to assess the significance of the canonical axis showing the relationship between the groups and the selected environmental variables. The result of the CA and the CCA was plotted as a two-dimensional graph using CanoDraw for Windows (version 4.12, 2003). The environmental variables were plotted as arrows originating from

the centre of the graph. The origin represents the mean value of each separate variable and the direction of the arrow line represents an increase in the value of that particular variable.

Refer to Appendix A for the comprehensive species list, authorities and classification according to Tomas et al. (1997).

5.3 Results

5.3.1 Species composition

Thirty-nine species (Table 5.1) with a total cell count of 8761 were recorded during the study. Of the 8761 cells counted, 5892 (67.3%) were from *F*-max and 2861 (32.7%) were from the surface waters. The coccolithophorid *Emiliania huxleyi* (Plate 1) was the overall dominant species and accounted for 29.5% of all phytoplankton cells counted across all sites and depths. The diatoms *Thalassionema nitzschioides* (15.5%), *Pseudo-nitzschia* sp. A (12.5%) and *Bacteriastrum furcatum* (7%) followed in order of overall dominance. Combined, the coccolithophorids *Deutschlandia anthos*, *Discosphaera tubifer* and *Gephyrocapsa oceanica* accounted for a further 13.3% of the total number of cells counted. The dominant dinoflagellate, *Ceratium* spp. accounted for 2.3% of the total number of cells counted.

The three cyclonic systems sampled consisted of a total of 2566 cells of which 1874 (73%) were from *F*-max and the remaining 692 (27%) cells were found at the surface. *F*-max waters within the cyclonic features were dominated by *E. huxleyi* (35.3%) followed by the diatoms *T. nitzschioides* (13.1%), *Pseudo-nitzschia* sp. A (12.9%) and *B. furcatum* (5.8%). The coccolithophorid *D. tubifer* represented 5% of the total phytoplankton cells sampled at *F*-max within the three cyclonic oceanographic features. Surface waters within the cyclonic systems were also dominated by *E. huxleyi* (35%). The second and third dominant species were *D. anthos* (7.9%) and *T. nitzschioides* (7.8%). The dinoflagellate *Ceratium* spp. was fourth dominant and represented 6.9% of the cells accounted for in surface waters. Three times more phytoplankton cells were counted in cyclonic *F*-max waters than in the surface waters. A total of 1795 cells were counted within the two anti-cyclonic systems sampled of which 1040 (57.9%) were from *F*-max and 755 (42.1%) from surface waters. *E. huxleyi* dominated waters at *F*-max (32.4%). The diatoms *B. furcatum* (15.5%), *T. nitzschioides* (11%) and *Pseudo-nitzschia* sp. A (9.9%) were the second, third and fourth most dominant species recorded. The coccolithophorids *G. oceanica* and *D. anthos* represented 8.4% and 5.8% of the phytoplankton cells respectively. The coccolithophorids, *E. huxleyi* (28.9%) and *D. anthos* (23%) dominated surface waters followed by the diatoms *B. furcatum* (10.9%) and *T. nitzschioides* (9.4%).

Table 5.1. Presence/Absence of species at *F*-max and surface between mesoscale features. F = *F*-max, S = surface. Species are listed in order of overall dominance across all sites. a = diatom; b = dinoflagellate; c = coccolithophorid. Refer to Appendix A for Authorities according to Tomas et al. (1997).

Species		Anti-cyclone		Cyclone		Coastal		Frontal	
		F	S	F	S	F	S	F	S
Emiliania huxleyi	c	+	+	+	+	+	+	+	+
Thalassionema nitzschioides	a	+	+	+	+	+		+	+
Pseudo-nitzschia sp. A	a	+	+	+	+	+		+	+
Bacteriastrum furcatum	a	+	+	+	+			+	+
Deutschlandia anthos	c	+	+	+	+	+	+	+	+
Discosphaera tubifer	c	+	+	+	+	+		+	+
Gephyrocapsa oceanica	c	+	+	+	+	+		+	+
Nitzschia closterium	a			+	+			+	+
Ceratium spp.	b	+	+	+	+			+	+
Hemiaulus hauckii	a		+	+	+	+		+	+
Guinardia cylindrus	a			+	+			+	+
Umbellosphaera irregularis	c	+	+	+	+			+	+
Thalassiosira sp. A	a	+		+	+			+	+
Oolithotus fragilis	c	+	+	+	+	+	+	+	+
Prorocentrum gracile	b	+	+	+	+		+	+	+
Navicula sp. A	a	+	+	+	+			+	+
Nitzschia sp. A	a	+	+	+	+			+	+
Thalassiosira sp. B	a	+	+	+	+	+		+	+
Nitzschia sp. C	a	+	+	+	+			+	+
Phalacroma rotundatum	b	+	+	+	+	+		+	+
Thalassiosira sp. C	a	+		+				+	
Rhizosolenia spp.	a			+	+	+	+	+	+
Calciosolenia murrayi	c	+		+			+	+	
Navicula sp. B	a	+	+	+	+		+	+	+
Thalassiosira sp. D	a	+		+	+			+	
Nitzschia sp. B	a	+	+	+	+			+	
Rhabdosphaera claviger	c	+	+	+	+			+	+
Fragilaria spp.	a	+		+	+			+	+
Nitzschia braarudii	a				+		+	+	+
Pseudo-nitzschia sp. B	a	+							
Nitzschia sp. D	a		+	+	+			+	
Thalassiosira sp. E	a	+		+				+	
Navicula sp. C	a		+	+	+				+
Halopappus adriaticus	c			+				+	
Syracosphaera histrica	c		+	+	+				+
Nitzschia sp. E	a		+	+	+				+
Phalacroma spp.	b	+	+		+				
Planktoneilla spp.	a	+						+	
Navicula sp. D	a					+			

A total of 4231 cells were counted in the two frontal zones sampled. *F*-max consisted of 2835 (67%) cells and the remaining 1396 (33%) cells were found in surface waters. The diatom *T. nitzschioides* (24%) dominated *F*-max samples within the frontal zones closely followed by the coccolithophorid *E. huxleyi* (23.6%). The diatom *Pseudo-nitzschia* sp. A was third most dominant accounting for 15.1% of the total number of phytoplankton cells counted within the frontal systems at *F*-max. *E. huxleyi* constituted 25.4% of phytoplankton cells counted within frontal zone surface waters. The diatoms *Pseudo-nitzschia* sp. A and *T. nitzschioides* constituted 19% and 13% respectively.

A total number of 169 phytoplankton cells were counted at the coastal zone stations sampled. *F*-max accounted for 145 (85.8%) of the total number of cells with the remaining 24 (14.2%) cells occurring within surface waters. Coccolithophorids dominated the coastal *F*-max samples. *E. huxleyi* accounted for 64.1% of the total number of cells counted followed by *G. oceanica* (7.6%) and *Oolithotus fragilis* (6.2%). Surface waters within the coastal zone were dominated by *E. huxleyi* (37.5%). The dinoflagellate *Prorocentrum gracile* was second most dominant and accounted for 16.6% of the total number of cells counted. The coccolithophorid *D. anthos* was third most dominant representing 12.5% of the total number of phytoplankton cells sampled within coastal zone surface waters.

5.3.2 Spatial trends in Species Richness and Diversity

The cyclonic systems showed on average the highest species richness (4.459) and species diversity (2.446) while the coastal zone revealed on average the lowest species richness (2.924) and species diversity (1.632) (Table 5.2). The frontal and anti-cyclonic systems sampled were similar with regards to both species richness and species diversity. Species richness was generally higher in *F*-max samples whereas species diversity was largely higher in surface waters.

Table 5.2. Margalef`s species richness (d) and Shannon-Weiner diversity (H') for total sampled phytoplankton community numbers as well as for those of *F*-max and surface values within mesoscale features.

	Sample	d	H'
Anti-cyclone	Total	4.271	2.342
	F-max	3.887	2.252
	Surface	3.622	2.211
Cyclone	Total	4.459	2.446
	F-max	4.379	2.304
	Surface	4.74	2.526
Coastal	Total	2.924	1.632
	F-max	2.21	1.425
	Surface	2.203	1.812
Frontal	Total	4.192	2.408
	F-max	4.025	2.298
	Surface	3.729	2.456

5.3.3 Functional group spatial trends

Phytoplankton functional groups found in surface samples within coastal waters differed significantly when compared to all other mesoscale features (Table 5.3). Anti-cyclone and frontal systems however, showed no significant differences between phytoplankton functional groups (surface samples). Similarly, no differences were found between any of the functional groups when comparing *F*-max samples between mesoscale features.

The only significant functional group difference found between *F*-max and surface waters were between coccolithophorids within coastal waters and the dinoflagellates within the cyclonic samples (Table 5.4).

Table 5.3. Comparisons between oceanographic features for *F*-max and surface water phytoplankton functional groups. Significant differences ($p < 0.05$) are shown in bold.

	F-max		Surface	
	p	U	p	U
Anti-cyclone vs. Coastal				
Coccolithophorid	0.141	14.0	**0.002**	0.0
Diatom	0.340	19.5	**0.035**	9.5
Dinoflagellate	0.193	15.5	0.155	16.0
Anti-cyclone vs. Cyclone				
Coccolithophorid	0.112	71.0	**0.018**	58.5
Diatom	0.918	107.0	0.861	115.0
Dinoflagellate	0.804	103.5	0.559	104.5
Anti-cyclone vs. Frontal				
Coccolithophorid	0.622	67.5	0.797	78.5
Diatom	0.147	50.0	0.090	50.5
Dinoflagellate	0.603	67.0	0.341	65.0
Coastal vs. Cyclone				
Coccolithophorid	0.659	43.0	**0.002**	4.0
Diatom	0.325	35.0	**0.042**	19.5
Dinoflagellate	0.221	31.50	**0.035**	18.5
Coastal vs. Frontal				
Coccolithophorid	0.105	17.0	**0.001**	0.0
Diatom	0.052	13.5	**0.006**	5.0
Dinoflagellate	0.058	14.0	0.052	13.5
Cyclone vs. Frontal				
Coccolithophorid	0.093	91.5	**0.002**	53.0
Diatom	0.057	85.0	**0.018**	72.0
Dinoflagellate	0.363	113.5	0.506	120.5

Table 5.4. Comparisons between *F*-max and surface water samples within oceanographic features for phytoplankton functional groups. Significant differences ($p < 0.05$) are shown in bold.

	Anti-cyclone		Coastal		Cyclone		Frontal	
	p	U	p	U	p	U	p	U
Coccolithophorid	0.773	66.5	**0.0121**	0.0	0.137	144.5	0.312	75.5
Diatom	0.908	69.5	0.296	7.0	0.800	190.0	0.872	94.0
Dinoflagellate	0.273	52.5	0.602	9.5	**0.019**	113.0	0.161	67.0

5.3.4 Correlations

The relationship between the functional groups sampled and physico-chemical variables across all sites and samples (surface and *F*-max) is presented in Table 5.5. No significant relationships were found between any of the phytoplankton groups and phosphorus. Coccolithophorids and diatom groups however correlated negatively with salinity. Dinoflagellates however correlated positively with oxygen and temperature, while correlating negatively with the nutrients, silicate and nitrogen.

5.3.5 Community Analyses

Species analysis

Figure 5.1 indicates the similarity/dissimilarity between species sampled during the December 2008 cruise. The coccolithophorid *D. anthos* and the dinoflagellate *Phalacroma* spp. are noted as outliers. The coccolithophorids *Calciosolenia murrayi* and *Umbellosphaera irregularis* also showed dissimilarity to most other species.

Table 5.5. Spearman rank correlations between functional groups numbers and physico-chemical variables. Salinity = PSU; Oxygen = ml l^{-1}; Temperature = Degrees Celcius; P = soluble reactive phosphorus; Si = silicate; N = total dissolved inorganic nitrogen. Nutrient concentrations = (µM). Significant correlations are presented in bold.

	Cocco Total	Diatom Total	Dino Total	P	Si	N	PSU	Oxygen	Temp
Cocco Total	1.000								
Diatom Total	**0.380**	1.000							
Dino Total	**0.365**	**0.301**	1.000						
P	-0.081	-0.047	-0.180	1.000					
Si	-0.011	-0.046	**-0.247**	**0.446**	1.000				
N	-0.015	0.024	**-0.291**	**0.443**	**0.705**	1.000			
Salinity	**-0.395**	**-0.218**	0.021	0.144	-0.127	-0.130	1.000		
Oxygen	0.180	0.148	**0.267**	**-0.401**	**-0.560**	**-0.648**	-0.138	1.000	
Temperature	-0.077	-0.077	**0.271**	**-0.574**	**-0.627**	**-0.701**	0.083	**0.565**	1.000

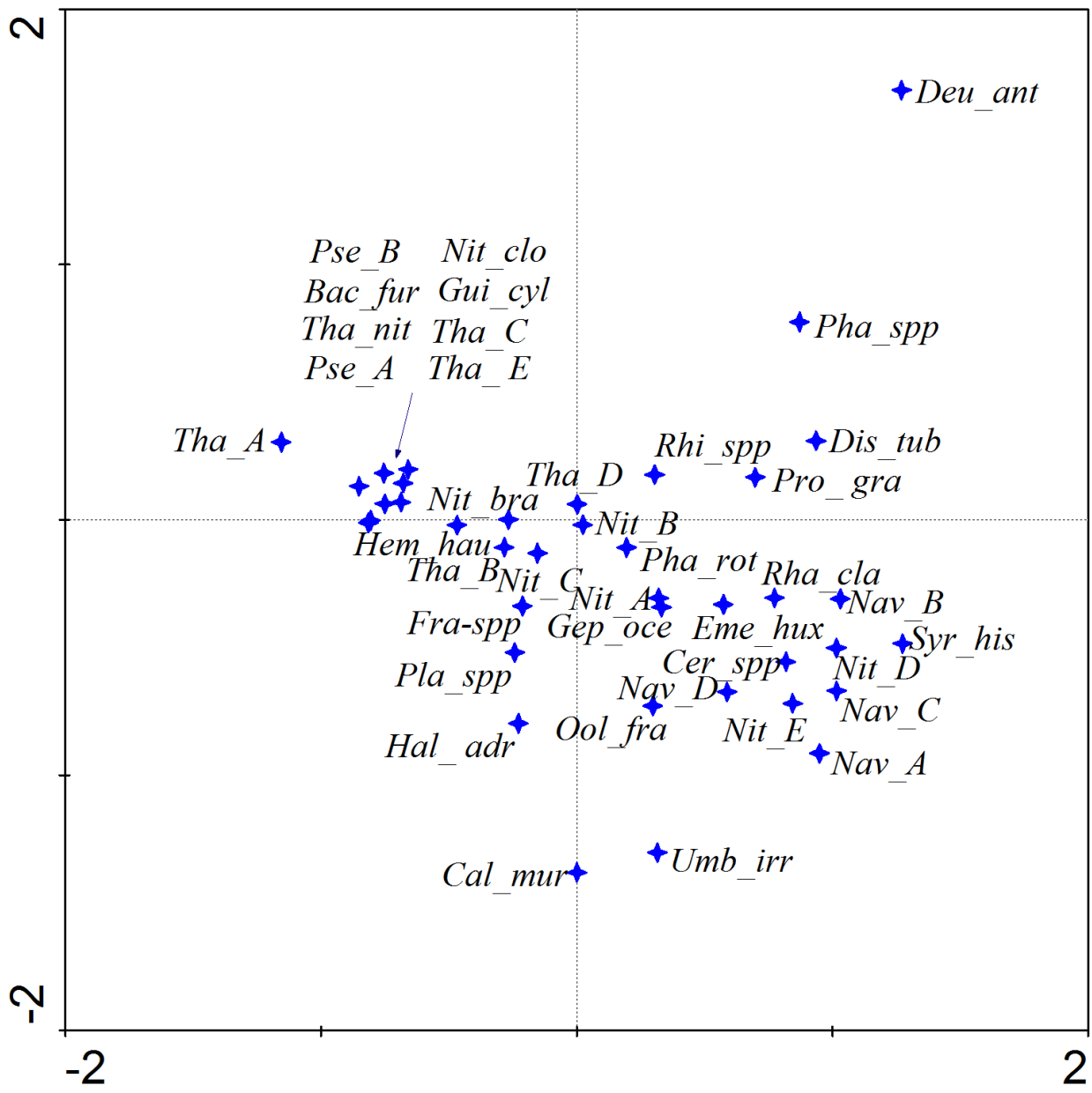

Figure 5.1. Canonical Analyses of phytoplankton species.

A ‘cluster’ of diatom species indicated by the arrow consisting of *T. nitzschioides, Pseudo-nitzschia* sp.A, *Pseudo-nitzschia* sp.B, *Thalassiosira* sp.C, *Thalassiosira sp.E, B. furcatum, Guinardia cylindrus, Nitzschia closterium, Hemiaulus hauckii,* and *Nitzschia braarudii*. Descriptions of all abbreviations are presented in Appendix A.

Table 5.6. Summary of CA between phytoplankton species data (p = 0.001).

Axes	1	2	3	4	Total inertia
Eigenvalues	0.546	0.282	0.220	0.200	3.118
Cumulative percentage variance of species data	17.5	26.5	33.6	40.0	
Sum of all eigenvalues					3.118

Species vs. environmental variables across all sites

Four of the dominant coccolithophorids *O. fragilis*, *E. huxleyi, D. anthos* and *D. tubifer* were found to exist in varied water temperatures and/or nutrient levels (Figure 5.2). The coccolithophorids *Rhabdosphaera claviger* and *Syracosphaera histrica* were found more frequently in warm oxygen rich waters with reduced nutrient levels. The coccolithophorids *Halopappus adriaticus* and *C.murrayi* revealed a preference to slightly cooler, nutrient rich waters more so than any other coccolithophorid species.

The three dominant diatom species *T. nitzschioides, Pseudo-nitschia* sp. A and *B. furcatum* showed no preference to specific water temperature or nutrient levels throughout all sites sampled.

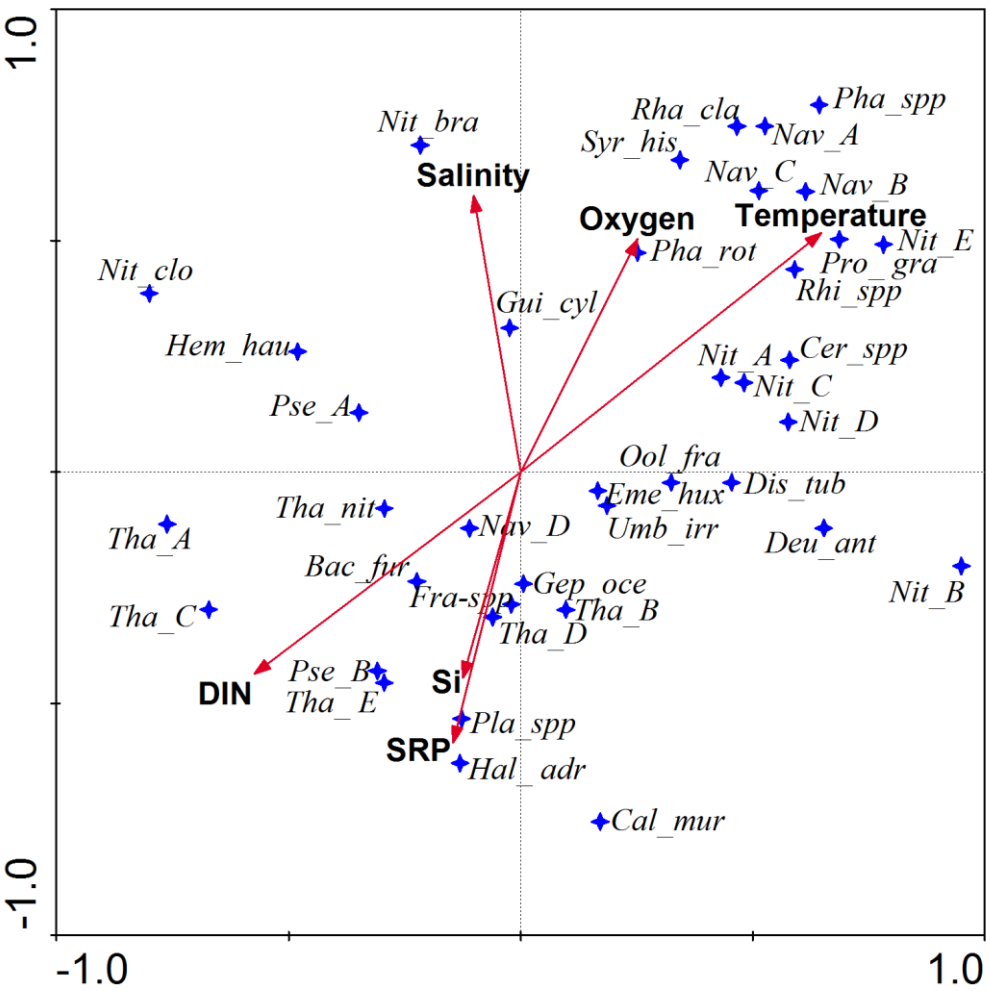

Figure 5.2. Canonical Correspondence Analyses displaying species as constrained by physico-chemical variables across all stations.

Table 5.7. Summary of CCA between phytoplankton species and environmental data (p = 0.001)

Axes	1	2	3	4	Total inertia
Eigenvalues	0.254	0.073	0.051	0.036	3.118
Species-environment correlations	0.729	0.655	0.490	0.559	
Cumulative percentage variance of species data	8.1	10.5	12.1	13.3	
Cumulative percentage variance of species-environment relation	55.2	71.1	82.2	90.0	
Sum of all eigenvalues					3.118
Sum of all canonical eigenvalues					0.460

In Figure 5.2 and Figure 5.3 the first canonical axis described 55.2 % of the species – environment relation (Table 5.7). This axis was positively correlated to temperature (Table 5.8.). The second canonical axis described 71.1% of the variation and was negatively correlated to Si, DIN and SRP and positively correlated to salinity, oxygen and temperature (Table 5.7 and 5.8).

Table 5.8. Spearman rank correlations of environmental variables with the species and environmental axes of the CCA (Significant correlations are in bold). Significant correlations are presented in bold.

	CCA Species Axes				CCA Environmental Axes			
Axis	1	2	3	4	1	2	3	4
SRP	-0.1058	-0.3833	0.0274	-0.0775	-0.145	**-0.5847**	0.0561	-0.1387
Si	-0.0909	-0.2911	0.1888	0.3892	-0.1246	**-0.4441**	0.3856	**0.6963**
N	-0.4182	-0.2856	-0.052	0.3456	-0.5733	**-0.4358**	-0.1063	**0.6182**
Salinity	-0.0738	0.3917	0.0777	0.2078	-0.1011	**0.5975**	0.1587	0.3717
Oxygen	0.1841	0.3299	-0.0713	-0.3671	0.2524	**0.5033**	-0.1457	**-0.6567**
Temp	**0.4726**	0.3391	-0.1838	-0.0758	**0.6479**	**0.5173**	-0.3754	-0.1357

Surface and F-max samples vs. physico-chemical variables

A CCA of the samples constrained by environmental variables is illustrated in Figure 5.3. Circles represent all *F*-max stations and the diamonds represent the samples taken near the surface water (5m). With the exception of the outliers (Station 1191 and 1197) there is a clear difference in samples taken at *F*-max and those taken at the surface (circles vs. diamonds) and these are constrained by different sets of environmental variables (Figure 5.3).

No discernible difference between the various *F*-max groupings (cyclone, anti-cyclone, frontal and coastal) is evident. Surface samples on the other hand showed a slight separation between groupings with cyclone and coastal samples marginally separating out from anti-cyclone and frontal zones.

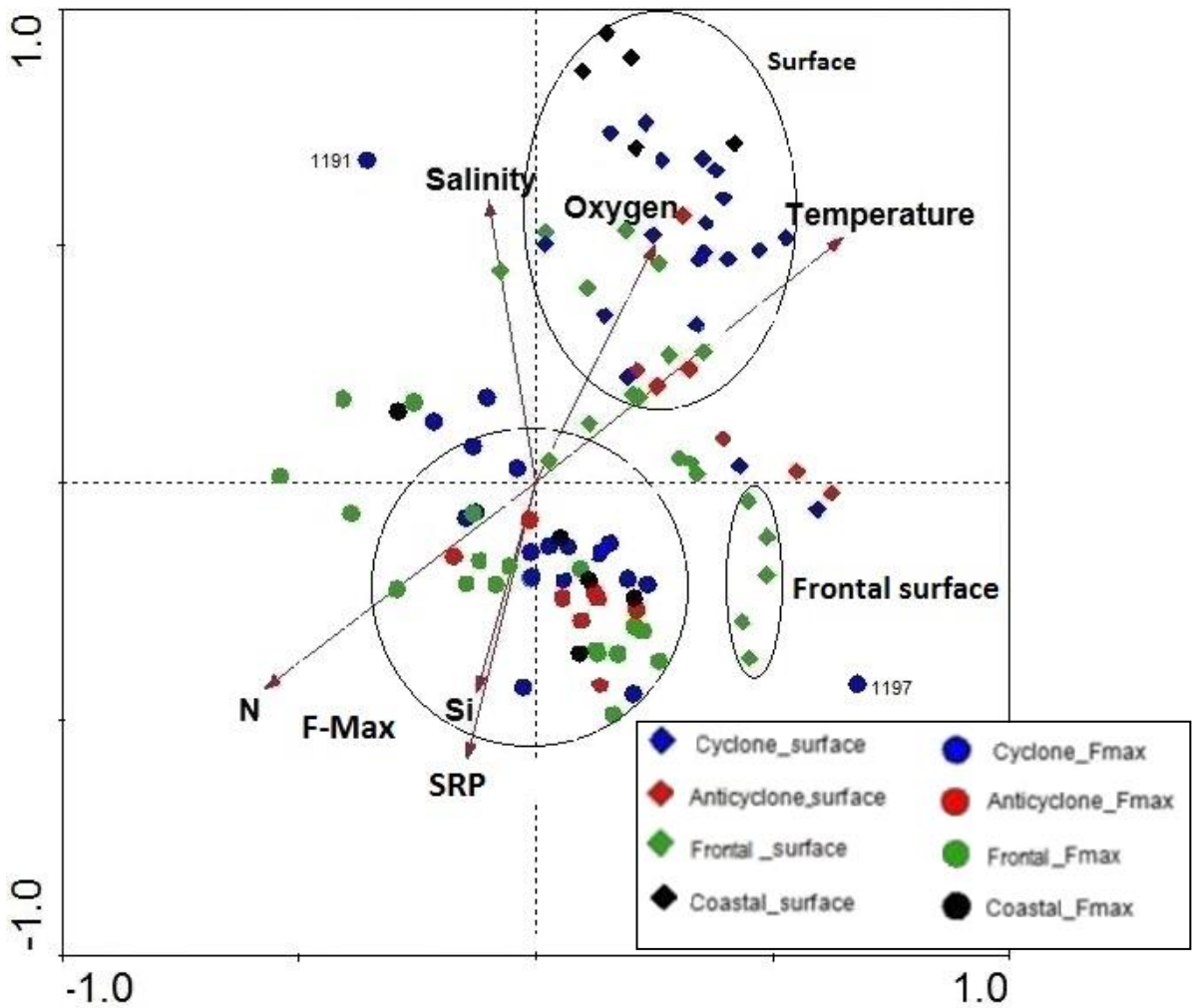

Figure 5.3 Canonical Correspondence Analyses of samples constrained by environmental variables.

5.4 Discussion

5.4.1 Environmental variability

There are more significant environmental variable differences between surface and *F*-max waters than between mesoscale features. This result is significant as it is reflected in the phytoplankton communities. We can assume that the environmentally variable differences between surface and *F*-max created two relatively distinct habitats at these depths in the water column thus encouraging phytoplankton community differences. Phytoplankton is indirectly affected by the vertical stratification of salinity (Sin and Wetzel 2002). Salinity between *F*-max and surface waters showed significant differences within the anti-cyclone, cyclone and coastal systems sampled. As expected, all nutrients correlated negatively to dissolved oxygen concentration and temperature.

5.4.2 Species composition

Studies of *Emiliania huxleyi* from various parts of the world's oceans have indicated that temperature is an important factor in controlling the organism's calcification but not its distribution (Smetacek 2001; Paasche 2002; Frada et al., 2009). Gregg and Casey (2007) state that ecologically, competition for light and nutrients is the main determinant of coccolithophorids distributions. *E. huxleyi* is the most abundant coccolithophorid species and although considered to be an oceanic species can be a very important species in coastal waters (Winter et al., 1994). The dominance of *E. huxleyi* in this study (29.5% of all species counted across all sites) is not surprising due to its general abundance and wide distribution of the species in the world's oceans. *E. huxleyi* is said to be exceptionally cosmopolitan and often dominates coccolithophorid assemblages (Bratbak et al., 1993).

Koning et al. (2001) found the diatom *Thalassionema nitzschioides* (15.5% of all species counted in the present study) to dominate upwelling regions of the Indian Ocean along the coast of Somalia where high loads of dissolved silicate and other nutrients become available when upwelling in the ocean starts in the early summer months. *T. nitzschioides* is known to be able to tolerate variable conditions and is often associated with upwelling regions with increased nutrient loading (Schuette and Schrader 1981; Romero et al., 1999). Investigations on the water column off the Portugal coast by Abrantes and Moita (1997) revealed diatoms to be the most important contributor by an order of magnitude in increased phytoplankton biomass concentrations during upwelling conditions compared to coccolithophorids. *T. nitzschioides* exhibited its most abundant presence within frontal *F*-max samples in the present study. The frontal zones between cyclonic and anti-cyclonic mesoscale features are distinguished by high mixing rates due to the systems `colliding` into one another. The frontal zones in the present study showed highly variable temperatures throughout with minimum and maximum temperatures reaching 21.85ºC and 29.52ºC respectively.

The diatom *Pseudo-nitzschia* sp. A (12.5% of all species counted in the present study) are said to be a cosmopolitan genus occurring in tropical, polar and coastal waters in oceans all around the world (Hasle et al., 1996; Hasle 2002). *Pseudo-nitzschia* is known to produce blooms in an extensive range of locations. A short list of the dominant diatoms found within an anti-cyclonic eddy in the south-eastern Indian Ocean by Thompson et al. (2007): *Chaetoceros* (Ehrenberg, 1844); *Nitzschia* sp. (Hassall, 1845); *Thalassionema* (Grunow ex Mereschkowsky, 1902); *Pseudo-nitzschia* (H. Peragallo, 1900); *Cyclotella* (Kützing) Brébisson, 1838; *Nitzschia longissima* (Brébisson in Kützing) Ralfs in Pritchard, 1861 and *Guinardia striata* (Stolterfoth) Hasle, 1997. The genus has a wide range for peak growth and is capable of surviving in salinities between 6 and 48 psu and temperatures ranging from

5°C to 30°C (Lundholm et al., 1997; Thessen et al., 2005). It is not surprising then that the diatom *Pseudo-nitzschia* was found to be one of the dominant diatoms in the present study as an anti-cyclonic eddy dominated the Mozambique Channel during the MC08A cruise. Another diatom, *Bacteriastrum furcatum* which represented 7% of all species counted in the present study is widely distributed in the world's oceans but does not often dominate phytoplankton populations (Round et al., 1990). This species of diatom showed its strongest presence within the anti-cyclone.

The change in relative abundance of *Deutschlandia anthos* between *F*-max (5.8%) and surface waters (23%) was the most discernible change in the phytoplankton community within the anti-cyclones sampled. The deepest *F*-max found was situated in the anti-cyclone and was at a depth of 100.6 metres.

Surface waters within the frontal zone were dominated by *T. nitzschioides*, whereas at *F*-max *E. huxleyi* dominated. *T. nitzschioides* represented a much smaller percentage of the total number of phytoplankton cells sampled in *F*-max compared to surface waters. The isolated dominance of *T. nitzschioides* was the only instance where *E. huxleyi* was found not to dominate surface or *F*-max waters throughout all mesoscale features sampled. Surface water within the frontal zone contained significantly lower concentrations of dissolved inorganic nitrogen than *F*-max waters. The reduced nitrogen levels at surface waters may be explained by the dominance of diatoms which have considerably higher minimum quota for nitrogen and higher carbon-specific nitrate uptake rates compared to coccolithophorids such as *E. huxleyi* (Litchman et al., 2007).

Previous studies have revealed coccolithophorids to be important contributors to the total phytoplankton population in coastal upwelling environments during periods of upwelling relaxation and decreased silicate concentrations (Sournia et al., 1970; Giraudeau et al., 1993; Ziveri and Thunell 2000). In eutrophic conditions, coccolithophorids are usually outcompeted by diatoms (Schmidt et al., 2006). Contrary to the statements made above, the coccolithophorid *E. huxleyi* dominated phytoplankton communities in coastal waters which had higher nutrient concentrations than the cyclone, anti-cyclone and frontal systems sampled. The nutrient conditions found in the coastal zone may have been brought about either by freshwater input from the mainland (Lutjeharms 2006a; Tew-Kai and Marsac 2009) or by upwelling which is said to be common on the western side of the Mozambique Channel (Tew-Kai and Marsac 2009). One explanation for the dominance by *E. huxleyi* within the coastal zone is that the increased nutrient levels may have been a recent occurrence and diatoms present in the water column had not yet had time enough to synthesise the nutrients.

5.4.3 Functional Group Spatial Trends and Relationships

Coccolithophorids are thought to be an important contributor to phytoplankton communities in the ocean (Broerse et al., 2000). Coccolithophorids are frequently found to be more abundant than other phytoplankton groups in warm, oligotrophic waters (Ziveri and Thunell 2000; Broerse et al., 2000). Nutrient depletion and increased stabilisation within a recently diatom dominated water column is known to create an environment that is suitable for coccolithophorids (Margalef 1978). The relatively strong diatom presence across a majority of the sample sites suggests that these diatom species may well have dominated the photic zone within the various mesoscale features prior to sampling. If this was the case then the diatoms may have reduced nutrient levels within the photic zone creating an environment more suitable for coccolithophorid growth (i.e: *E. huxleyi).*

5.4.4 Spatial Trends in Species Richness and Diversity

The relatively strong dominance of *E. huxleyi* in coastal waters may have attributed to the low species richness and diversity found in that system. The cyclonic mesoscale features sampled contained the highest species richness and diversity and were not dominated as strongly by *E. huxleyi* when compared to the coastal waters. In a study carried out by Broerse et al. (1998) *E. huxleyi* was found to be the main contributor to the numerical annual coccolith flux (with 69% and 72%, respectively) at both the subtropical and temperate stations sampled.

5.4.5 Community Analyses

The marginal grouping of the diatom species *Thalassionema nitzschioides, Pseudo-nitzschia* sp.A, *Pseudo-nitzschia* sp.B, *Thalassiosira* sp.C*, Thalassiosira sp.E, B. furcatum, Guinardia cylindrus, Nitzschia closterium, Hemiaulus hauckii,* and *Nitzschia braarudii* suggests that these species occurred within similar habitats and reacted similarly to a dominant environmental variable. In a study undertaken by Abrantes in 1988 it was found that smaller species of the genus *Thalassiosira* occurred in areas of regular upwelling where the availability of nutrients is generally more constant (Abrantes 1988). *Thalassiosira* species form gelatinous masses and seem to be most prominent in coastal waters where upwelling occurs (Hasle 1976). In general, the results obtained from the species analyses are vague with regards to deciphering species groupings The reason for this could be that the mesoscale features contained the same species and communities and the only difference

was most likely in the richness and diversity of individual species that responded favourably to the specific conditions found at the time of sampling.

The distribution of coccolithophorids is closely related to the concentrations of nitrate and phosphate (Young 1994). The controls of nitrate and phosphate on coccolithophorid populations is complicated by the fact that they are K-selected and are usually found in oligotrophic conditions (Brand 1994). Hulbert (1983) suggests that when *E. huxleyi* is found to dominate a specific community, the species does not force other coccolithophorids to change in concentration by out-competing them for nutrients but instead a balance is struck between the species present and their specific nutrient needs related to the nutrients available in the water column at that time.

Overall, distinct differences were discernible between surface and *F*-max communities. Little differences however, were detectable among *F*-max samples within oceanographic features, unlike the surface samples, where the frontal zone separated out. Differences in the physico-chemical drivers of surface and *F*-max communities were also evident, with salinity, temperature and oxygen correlating with surface communities, and the measured nutrients appearing to drive those of the *F*-max. The frontal zone surface community drivers were however less clear. The position of the *F*-max outliers was likely a result of specific features associated with those sampling sites. High rates of physical mixing, variability in *F*-max depth as well as human error in sampling may well have attributed for the outlier.

6 Summary

Correlations between physico-chemical variables and phytoplankton distribution revealed that vertical distribution in the water column (*F*-max vs. surface) played an important role in phytoplankton community structure.

The oligotrophic conditions that dominated the Mozambique Channel during the MC08A cruise were expected (Lee 1980; Machu and Garcon 2001; Martin et al., 2001). Physico-chemical parameters coupled with chlorophyll *a* concentrations helped identify cyclonic upwelling processes which brought nutrients into the euphotic zone.

Phytoplankton community structure differed significantly between *F*-max (depth at which maximum chlorophyll *a* is found) and the surface thus confirming the hypothesis that there would be a difference in phytoplankton community structure between surface and *F*-max. All other hypotheses were unsubstantiated. Phytoplankton community structure did not differ significantly between oceanographic features which contradicted the hypothesis that phytoplankton community structure would differ between oceanographic features. An explanation may be that the physico-chemical variables between oceanographic features were not significantly different and therefore did not provide unique habitats. *Emiliania huxleyi* dominated *F*-max and surface water in the cyclonic eddies rejecting the hypothesis that cyclonic eddies would be dominated by diatoms.

The overall dominance of *E. huxleyi* in the Mozambique Channel during November/December of 2009 suggests that phytoplankton in these waters may be affected by ocean acidification due to the susceptibility of such calcifiers (*E. huxleyi*) to ocean acidification (Smith et al., 2012). On the contrary, results in other studies (Iglesias-Rodriguez et al., 2008) have indicated elevated calcification in phytoplankton under similar conditions. Smith et al., (2012) continues by stating that the observation made by Beaufort et al., (2011) where the most heavily calcified morphotype (*E. huxleyi*) dominated waters when conditions where most acidic is contrary to earlier predictions and raises further questions regarding the future of coccolithophores in a high-CO^2 world.

Phytoplankton biomass in surface water of the cyclonic eddies were significantly higher than in surface waters within the anti-cyclonic eddy. Both these system types had similar phytoplankton diversity which did not verify the hypothesis that there would be less phytoplankton species diversity within the cyclonic eddies compared to the anti-cyclonic eddy.

The grouping of the diatoms *Thalassionema nitzschioides, Pseudo-nitzschia* sp.A, *Pseudo-nitzschia* sp.B, *Thalassiosira* sp.C*, Thalassiosira sp.E, Bacteriastrum furcatum, Guinardia cylindrus, Nitzschia closterium, Hemiaulus hauckii,* and *Nitzschia braarudii* revealed the only discernible `species grouping`. These diatoms are expected to have been found within similar physical environmental conditions and would have potentially had preference to common nutrients and nutrient concentrations. Distribution patterns of species and of ecologically defined groups supports the hypothesis that diatom species and assemblages are good indicators of the changing character of an upwelling system (Abrantes 1988).

The difference between surface and *F*-max communities were most likely driven by the fact that physico-chemical variables differed between the two depths. Relatively consistent physico-chemical parameters probably attributed to there being no significant differences in phytoplankton community structure in general between oceanographic features.

6.1 Future Research Requirements

Due to the generally oligotrophic characteristics of the Mozambique Channel during the summer months (Lee 1980; Machu and Garcon 2001; Martin et al., 2001), and the difficulties associated with sampling phytoplankton in these conditions, the methods used to collect phytoplankton in this study could be improved. Instead of only deploying Niskin bottles, a phytoplankton net pulled vertically through the photic zone and horizontally along the surface when steaming slowly at each station (to concentrate samples) would have captured more species. The surface chlorophyll *a* satellite imagery data used to identify oceanographic features in this study would be insufficient if used on its own in an attempt to describe phytoplankton community structure, as *F*-max was situated at approximately 50-80 metres below the surface waters. Satellite imagery is an invaluable tool when used to identify surface water features as it is rapid and can be used to ‘sample’ broad regions. Therefore, using surface chlorophyll satellite imagery (coupled with geostrophic and SST data) to identify oceanographic features in the Mozambique Channel and then sampling those specific areas identified *in-situ*, would provide an accurate method with regards to identifying episodic events which influence primary productivity in the Mozambique Channel. This method was used during the MC08A cruise and the *in-situ* physico-chemical and biological data did suggest that the oceanographic features identified were indeed present in the water column. Size fractionation of chlorophyll *a* proved to be an essential element of the study as there were variations in dominance between the three fractions sampled (pico-, nano-, microphytoplankton). The total chlorophyll *a* data may have revealed basic

insights into the biological processes at work in the Mozambique Channel during the MC08A cruise, but without the size fractionated component, some insights may have been lost.

Long term monitoring of the quantity of freshwater as well as the nutrient concentrations of freshwater entering the Mozambique Channel from the African mainland coupled with long term knowledge of the consistency of mesoscale eddies within the channel should allow for a better understanding of primary production within the channel. The effect of ENSO on the seasonality of mesoscale eddies travelling through the Mozambique Channel as well as the ENSO seasonality of chlorophyll observed in the channel should not be overlooked.

The study demonstrated that phytoplankton communities were influenced by the variations in physico-chemical parameters between surface and *F*-max, and that these physico-chemical variations superseded those imposed by individual oceanographic features as a whole. That is to say that future studies should focus on physico-chemical and phytoplankton relationships between surface and *F*-max waters.

The species composition and community aspect of the study allowed for a slightly more in-depth knowledge of phytoplankton in the Mozambique Channel. *Emiliania huxleyi*, a common and cosmopolitan coccolithophorid species (Bratbak et al., 1993; Broerse et al., 2000; Cortés et al., 2001; Boeckel and Baumann 2008; Frada et al., 2009) accounted for nearly one-third of all species counted across all sites. This dominance gives a clue as to what one might expect in future studies undertaken in the Mozambique Channel during the summer months. Phytoplankton species composition and community structure is an essential component of primary production and cannot be overlooked. The main disadvantage of undertaking species composition for a monitoring programme is that it is costly and time consuming. It is therefore suggested that for future studies, the dominant phytoplankton species be focused on in order to save time and money. In terms of indicator species, a potential link between the genus *Thalassiosira* and areas of upwelling in the Mozambique Channel may also be of interest for any future studies.

This study could potentially be repeated in winter and other seasons to determine if similar community structures occur and whether the same environmental drivers are still relevant. Aspects to look into would be whether coccolithophorids dominate throughout the year or whether the community patterns noted in this study are specific to the physic-chemical parameters recorded.

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APPENDIX A

Table A1: Species list and classification according to Tomas et al., (1997).

Class	Order	Suborder	Family	Species		CANOCO Abbreviation	Authority
Prymnesiophyceae	Isochrysidales		Gephyrocapsaceae	*Emiliania*	*huxleyi*	*Eme_hux*	(Lohmann) Hay & Mohler, 1967
				Gephyrocapsa	*oceanica*	*Gep_oce*	Kamptner, 1943
	Coccosphaerales		Calciosoleniaceae	*Calciosolenia*	*murrayi*	*Cal_mur*	Gran (in Murray & Hjort, 1912)
			Coccolithaceae	*Oolithotus*	*fragilis*	*Ool_fra*	(Lohmann) Martini & C.Müller, 1972
			Halopappaceae	*Halopappus*	*adriaticus*	*Hal_adr*	Schiller, 1914
			Rhabdosphaeraceae	*Discosphaera*	*tubifer*	*Dis_tub*	(Murray & Blackman) Ostenfeld, 1900
				Rhabdosphaera	*claviger*	*Rha_cla*	Murray & Blackman, 1898
			Syracosphaeraceae	*Deutschlandia*	*anthos*	*Deu_ant*	Lohmann, 1912
				Syracosphaera	*histrica*	*Syr_his*	Kamptner, 1941
				Umbellosphaera	*irregularis*	*Umb_irr*	Paasche, 1955
Bacillariophyceae	Biddulphiales	Coscinodiscineae	Thalassiosiraceae	*Planktoneilla*	spp.	*Pla_spp*	Schütt, 1892
				Thalassiosira	sp. A	*Tha_A*	Lebour 1930 emend. Hasle 1973
				Thalassiosira	sp. B	*Tha_B*	
				Thalassiosira	sp. C	*Tha_C*	
				Thalassiosira	sp. D	*Tha_D*	
				Thalassiosira	sp. E	*Tha_E*	
		Rhizosoleniineae	Rhizosoleniaceae	*Rhizosolenia*	spp.	*Rhi_spp*	Brightwell, 1858
				Guinardia	*cylindrus*	*Gui_cyl*	(Cleve) Hasle, 1996
		Biddulphiineae	Hemiaulaceae	*Hemiaulus*	*hauckii*	*Hem_hau*	(Grunow) Van Heurck, 1882
			Chaetocerotaceae	*Bacteriastrum*	*furcatum*	*Bac_fur*	Shadbolt, 1854
	Bacillariales	Fragilariineae	Thalassionemataceae	*Thalassionema*	*nitzschioides*	*Tha_nit*	(Grunow) Mereschkowsky, 1902
		Bacillariineae	Naviculaceae	*Navicula*	sp. A	*Nav_A*	Bory de Saint-Vincent, 1822
				Navicula	sp. B	*Nav_B*	
				Navicula	sp. C	*Nav_C*	
				Navicula	sp. D	*Nav_D*	
			Bacillariaceae	*Fragilariopsis*	*spp.*	*Fra_spp*	Hustedt in Schmidt emend. Hasle 1993
				Pseudo-nitzschia	sp. A	*Pse_A*	H. Peragallo 1900
				Pseudo-nitzschia	sp. B	*Pse_B*	
				Nitzschia	*braarudii*	*Nit_bra*	Hasle, 1960
				Nitzschia	*closterium*	*Nit_clo*	(Ehrenberg) W. Smith, 1853
				Nitzschia	sp. A	*Nit_A*	Hassall, 1845
				Nitzschia	sp. B	*Nit_B*	
				Nitzschia	sp. C	*Nit_C*	
				Nitzschia	sp. D	*Nit_D*	
				Nitzschia	sp. E	*Nit_E*	
Dinophyceae	Prorocentrales		Prorocentraceae	*Prorocentrum*	*gracile*	*Pro_gra*	Schütt, 1895
			Dinophysiaceae	*Phalacroma*	*rotundatum*	*Pha_rot*	(Claparède & Lachman) Kofoid & Michener, 1911
	Dinophysiales			*Phalacroma*	*spp.*	*Pha_spp*	Stein, 1883
	Gonyaulacales		Ceratiaceae	*Ceratium*	*spp.*	*Cer_spp*	Schrank, 1973

APPENDIX B

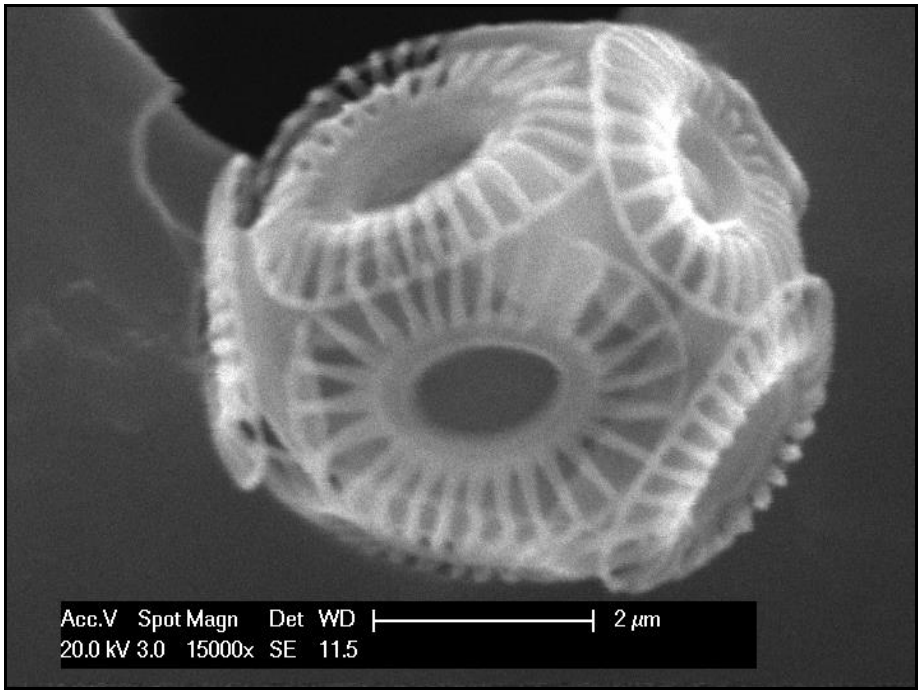

Plate 1: *Emiliania huxleyi* (Lohmann) W.W. Hay & H.P. Mohler

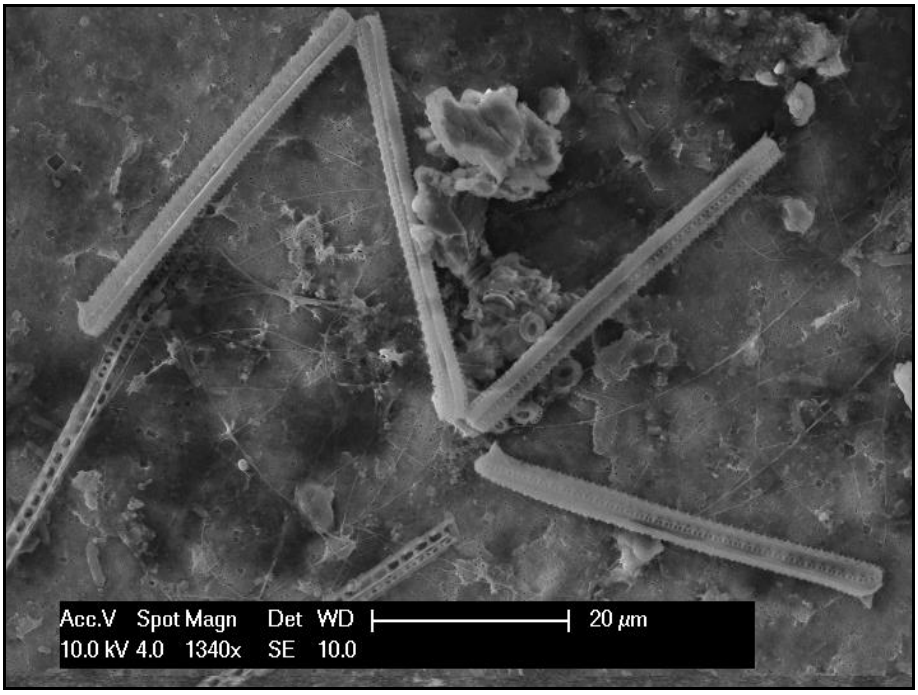

Plate 2: *Thalassionema nitzschoides* (Gunow) Mereschkowsky

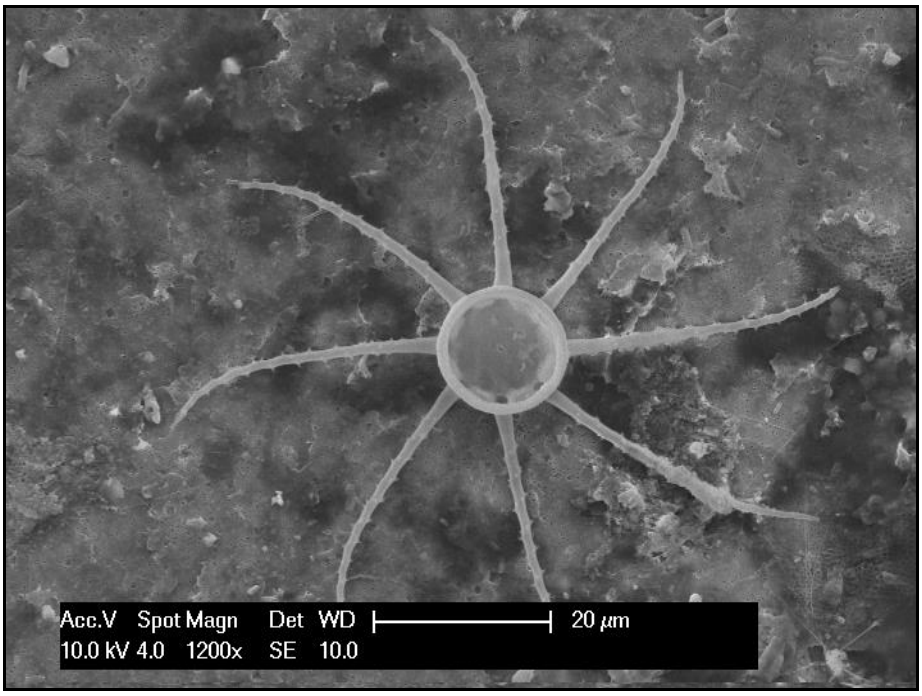

Plate 3: *Bacteriastrum furcatum* Shadbolt

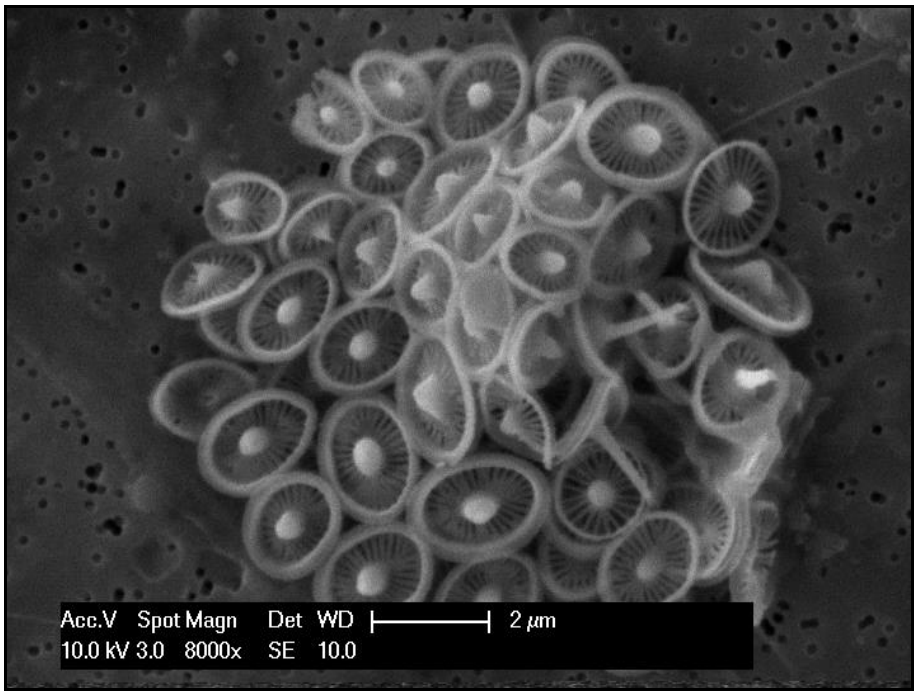

Plate 4: *Deutschlandia anthos* Lohmann 1912

Plate 5: *Discosphaera tubifer* (Murray & Blackman) Ostenfeld

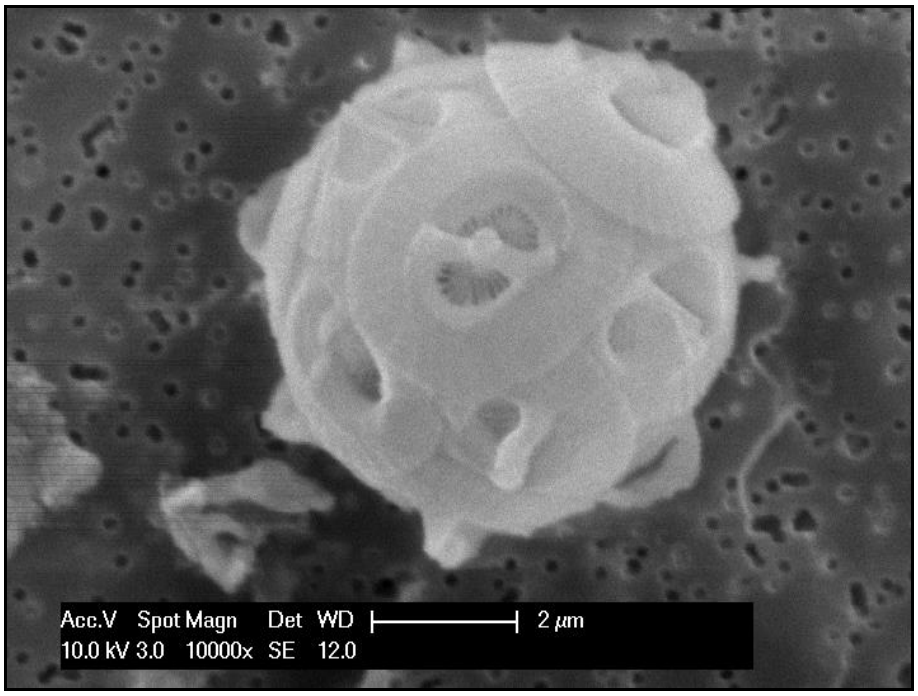

Plate 6: *Gephyrocapsa oceanica* Kamptner

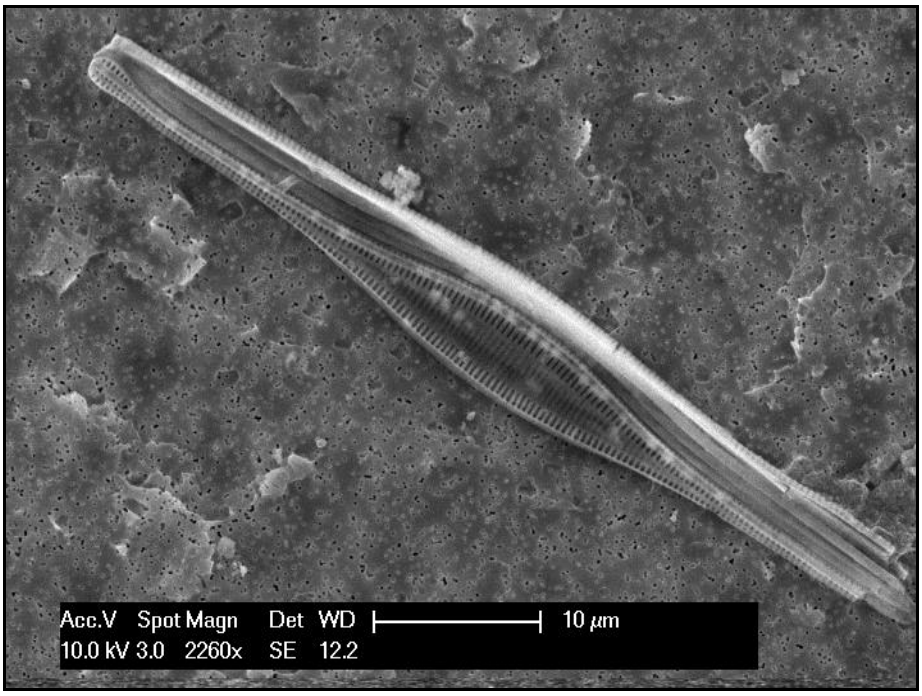

Plate 7: *Nitzschia closterium* (Ehrenberg) W.Smith

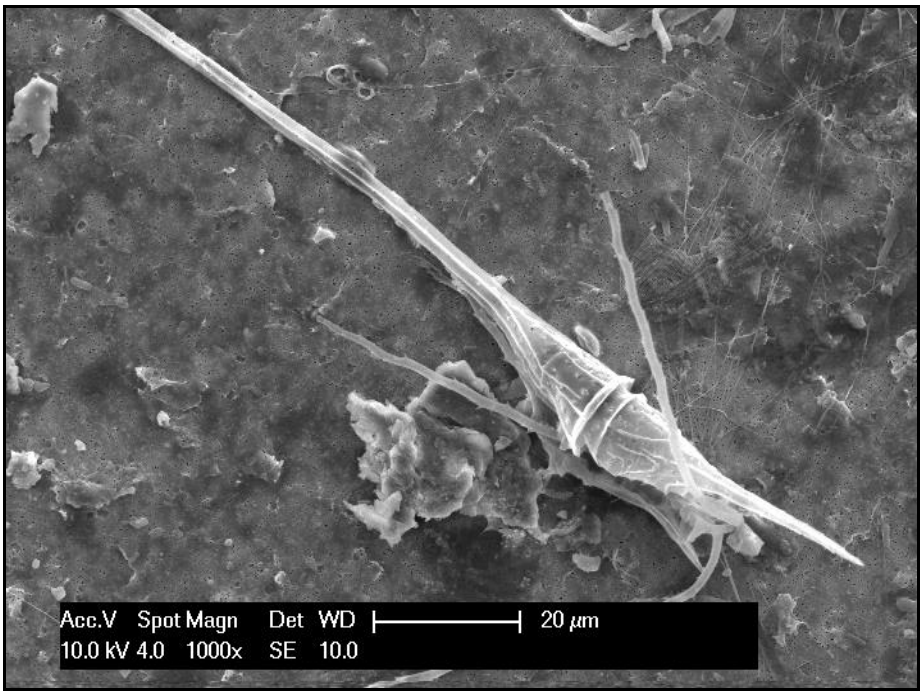

Plate 8: *Ceratium* spp. Schrank, 1793

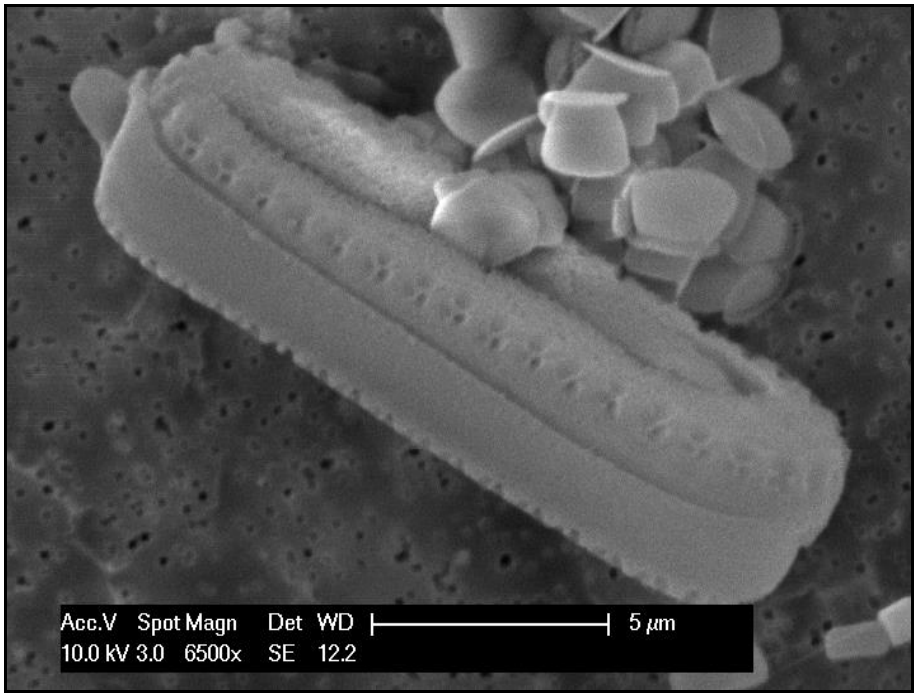

Plate 9: *Guinardia cylindrus* (Cleve) Hasle

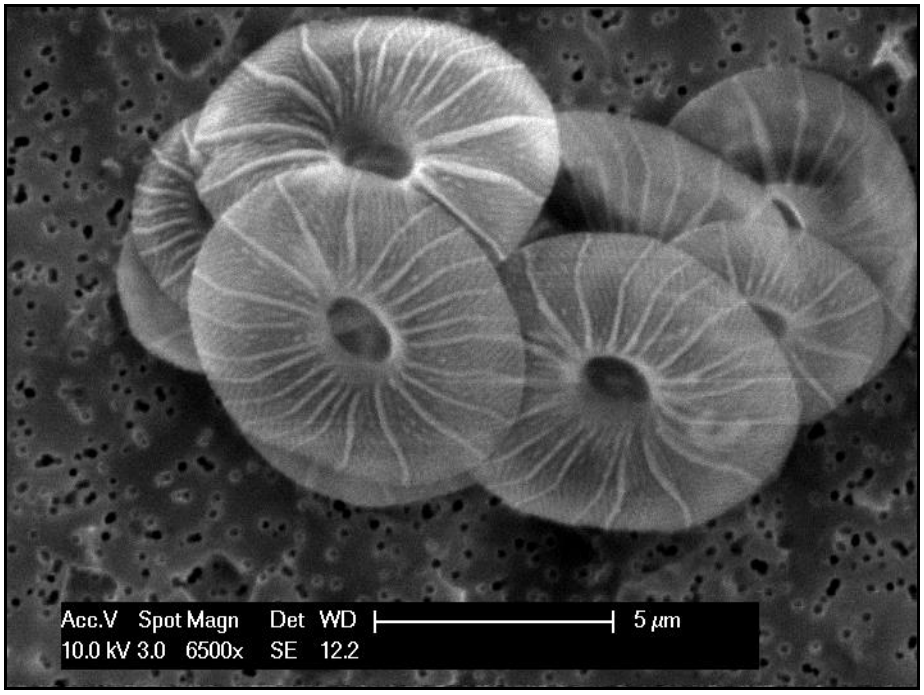

Plate 10: *Umbellosphaera irregularis* Paasche

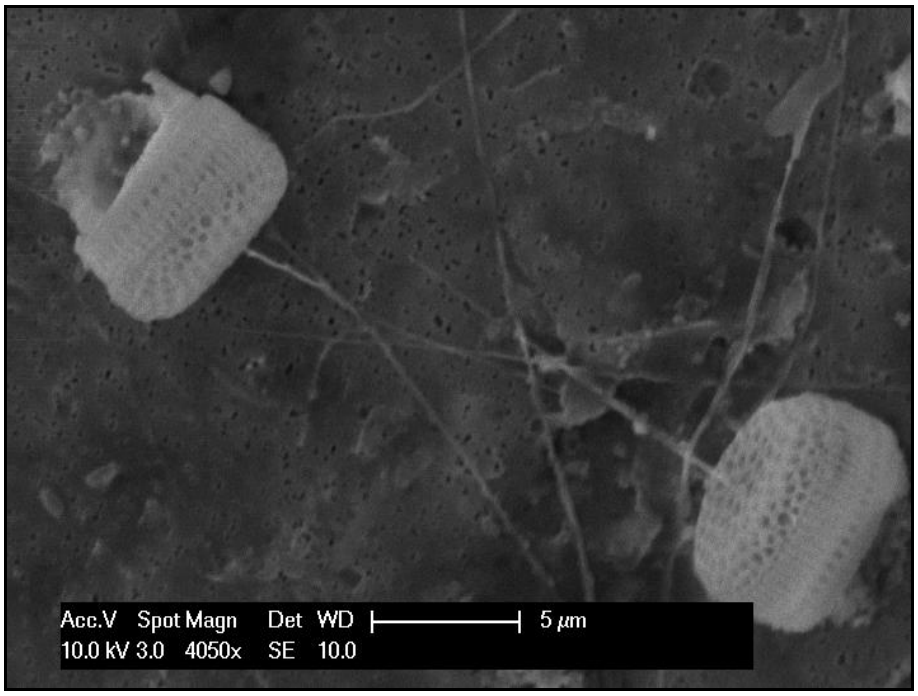

Plate 11: *Thalassiosira* sp.C Cleve, 1873

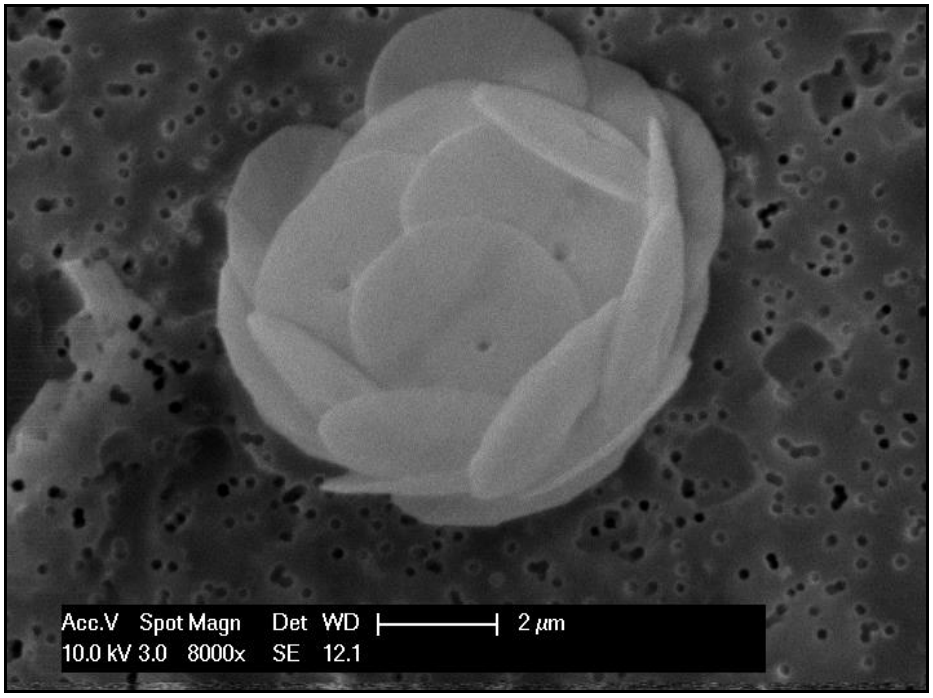

Plate 12: *Oolithotus fragilis* (Lohmann) Martini & C. Müller