Phytoplankton Studies in the KwaZulu-Natal Bight

by

Aadila Omarjee

Submitted in fulfilment of the academic requirements for the degree of Master of Science in the School of Biological & Conservation Sciences, University of KwaZulu-Natal, Durban

DECEMBER 2012

As the candidate's supervisor I have approved this thesis for submission.

Signed: 

Name: Dr Albertus J. Smit

Date: 30 November 2012

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Abstract

The KwaZulu-Natal Bight is an important area along the South African east coast, stretching 160 km north from Scottsburgh to St Lucia (Lutjeharms *et al*., 2000). The Bight is of interest to the region as the area contains some distinct physical features, which are presumed to drive the ecological functioning of the shelf ecosystem through their role in nutrient sources. These include the Tugela River, the second largest river in South Africa in terms of outflow, and the Agulhas Current that forms an outer border at the edge of the continental shelf.

Phytoplankton interacts with the majority of essential ecological networks and therefore greatly influences marine ecosystems. To this end, it is necessary to understand their ecophysiological rate processes – particularly those that are influenced by the dominant nutrient inputs to the Bight. The overall aim of this project is therefore to provide an insight into the sources of nutrients driving phytoplankton productivity in the Bight.

Synoptic surveys were conducted to provide an indication of the distribution of Total Suspended Solids (TSS), Particulate Organic Matter (POM) and phytoplankton in the Bight, while focussed experiments used stable isotopes to examine the rate processes involving C and N acquisition, as well as sources of N available in the surface water.

Concentration of particulate organic phosphorus and nitrogen were found to be higher in the wet season when compared to the dry season. During the wet season a large variation in chlorophyll-*a* fluorescence was observed across the Bight, while natural abundance isotope data indicated a seasonal change in the nutrient source available. For the wet season nutrient concentration varied with site and depth, however uptake rates ($\mu g\ N.l^{-1}.h^{-1}$) measured using ^{15}N tracer additions were not significantly different with site and depth. Alternatively, the dry season showed a significant difference between site in surface waters. In the wet season the mid shelf area had the highest uptake rate and phytoplankton biomass while the Richards Bay north site dominated, with regard to the previously mentioned factors, in the dry season. At the time of the experiments, neither the Durban eddy nor the upwelling cell were present, and hypotheses regarding the importance of these physical features in driving phytoplankton nutrient acquisition could not be assessed. However, a notable difference in uptake rate between the wet and dry seasons was observed, and this difference is likely due to the fluvial sources of nutrients from the Tugela and many other rivers entering the KZN coast, which are absent during the dry season.

The results indicate that terrestrial nutrient sources play a major role in influencing nutrient concentrations on the Bight, and hence influence the nearshore ecosystem of the region.

Preface

The experimental work described in this thesis was carried out in the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Durban, from January 2010 to November 2012, under the supervision of Dr. Albertus J. Smit.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

Declaration 1 - Plagiarism declaration

I, Aadila Omarjee declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
    a. Their words have been re-written but the general information attributed to them has been referenced
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Declaration 2 - Publications

No publications.

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Acknowledgements

I would like to dedicate this thesis to my dad. Without your encouragement I would not be where I am today. I miss you every day. I would also like to thank my mum for her love, support and most importantly, the bountiful and delicious, food during those late nights on campus.

Albertus Smit, though it has been an emotional journey for us, I am the biologist you have moulded me to be, and I am truly grateful for that. Without your confidence in my abilities, and your constant assertion that I can do better, I would not be handing my MSc to this high standard. Thank you.

Another much deserved thank you to Ander de Lecea, Lisa de Charmoy, Travis Kunnen and Johan van der Molen for all their help in the field and off, it is sincerely appreciated. Ander, you were always there to lend a shoulder to cry on and to help me solve problems along the way, a special thank you to you. To the team working on the Natal Bight project, thank you for your input and guidance, as well as gladly sharing your data. To the technical team at UKZN, especially Krishna Govindsamy (Kay), Sagaran Kasavan, Nisha Singh and Jay Rambaran, for help with building, finding and sharing equipment, thank you. I also appreciate the time you took to give me advice on the methods and instruments I needed. I would like to thank ACEP-II for providing funding for my project, as well as the logistic and administrative support they provided. A special thank you to Sean Fennessy and Angus Paterson for ensuring that I was financially secure throughout my thesis. Thank you to the crew of the *FRV Algoa*, your help and efficiency enabled the trips to be both successful and fun.

A special thank you to the amazing Nicola Carrasco, your presence on campus always motivated me. More than that, thank you for your help and guidance, which you provided on a daily basis. Natasha Rambaran, you were there for me at a very difficult time in my life. Were you not there, I doubt that this thesis would be complete. Thank you for your love and all the help you gave me. A huge thank you to my sisters, Naseera Amod Omarjee and Sumaiya Omarjee, for your encouragement, the example you set and your sarcasm, all of which motivate me to excel in everything I do. An additional thank you to Naseera for volunteering to be my editor, one day I will learn how to use a comma. To my aunts, the ladies of Islamic Guidance and my true friends, I am grateful for all the support you provided for me, physically, emotionally and financially. I love you all and, everyday, I appreciate having you in my life.

CHAPTER 1

INTRODUCTION

1. INTRODUCTION

1.1. General overview

The province of KwaZulu-Natal is situated on the east coast of South Africa. The region encloses an important shelf environment, the KwaZulu-Natal Bight (henceforth termed "the KZN Bight"). It stretches 160 km north from Scottsburgh, which is situated just south of Durban, to St. Lucia, just north of Richards Bay (Lutjeharms *et al*., 2000, Figure 1.1). The Bight has a wide continental shelf, which extends 40 km off the Tugela River mouth region at its widest point (Lutjeharms *et al*., 2000) and has a maximum depth of about 50 m to about 100 m in the northern and southern parts of the Bight, respectively (Lutjeharms. 2006). The nature of the Bight, specifically with respect to its narrow width and reduced depth, creates a coastal region where strong winds can greatly perturb the coastal, benthic and neritic portions of the ecosystem (Lutjeharms, 2006).

KwaZulu-Natal (KZN) receives 80 % of its rain between the months of October and March, rendering it extremely seasonal (Nel, 2002); the resulting fluvial runoff enters the ocean via 73 rivers and estuaries along this stretch of coast, and is expected to play a crucial role in the ecosystem processes in the nearshore region (Begg, 1978; Allanson and Baird, 1999). The Tugela River, the second largest river in South Africa in terms of outflow (Begg, 1978), is possibly the most important river in the region. Besides the many fluvial drivers and the strong coupling with the wind regime of the region, the Agulhas Current is the defining feature of the KZN coastline, especially in terms of the oceanography of the region. This current forms the outer boundary at the edge of the continental shelf of the area, and hence also the Bight. The movement of the Agulhas Current causes cold nutrient rich water, generally found at 150 to 250 m deep, to be upwelled in the St. Lucia and Richards Bay area and eddies to be formed around Durban (Lutjeharms, 2006; Figure 1.1).

This study forms a part of larger ACEP II project. ACEP is the acronym for the African Coelacanth Ecosystem Project and aims to understand the processes that drive the functioning of the South West Indian Ocean ecosystem by integrating the physical and biological sciences. The study on the KZN Bight functioning is a smaller part of the ACEP II project. ACEP II has five basic aims: 1) to investigate how the transport of nutrients and sediment across the Bight are facilitated by physical oceanographic and geological processes; 2) to determine the relative importance of material derived from fluvial processes and those originating from Agulhas Current mediated processes (i.e. the St Lucia upwelling and cyclonic Durban lee eddy) on the Bight; 3) to study the ecology and biodiversity of the shelf; 4) to establish levels of assimilation, recycling and transformation of particulate and dissolved materials in the Bight; 5) and to integrate the data collected into a combined bio-energetic ecosystem model.

This ACEP II programme achieved its aims through an integrated, multidisciplinary and cost- and time-efficient sampling program. Studies were conducted on dermersal fish, macrobenthos, zooplankton, phytoplankton, and bacteriofauna. Food webs were pieced together using stable isotopes, and a coupled biophysical model assimilating all data was produced. The scope of this dissertation is part of the phytoplankton studies, which together spans Aim 2 and a portion of Aim 4. The phytoplankton studies are compartmentalised into three sections: 1) phytoplankton productivity and pigment studies conducted by Dr. Ray Barlow and Tarron Lamont; 2) phytoplankton taxonomic composition and biomass by Dr. Johan van der Molen; and 3) this study, an investigation into the nitrogen acquisition ecophysiology by Aadila Omarjee, under the supervision of Dr. A.J. Smit.

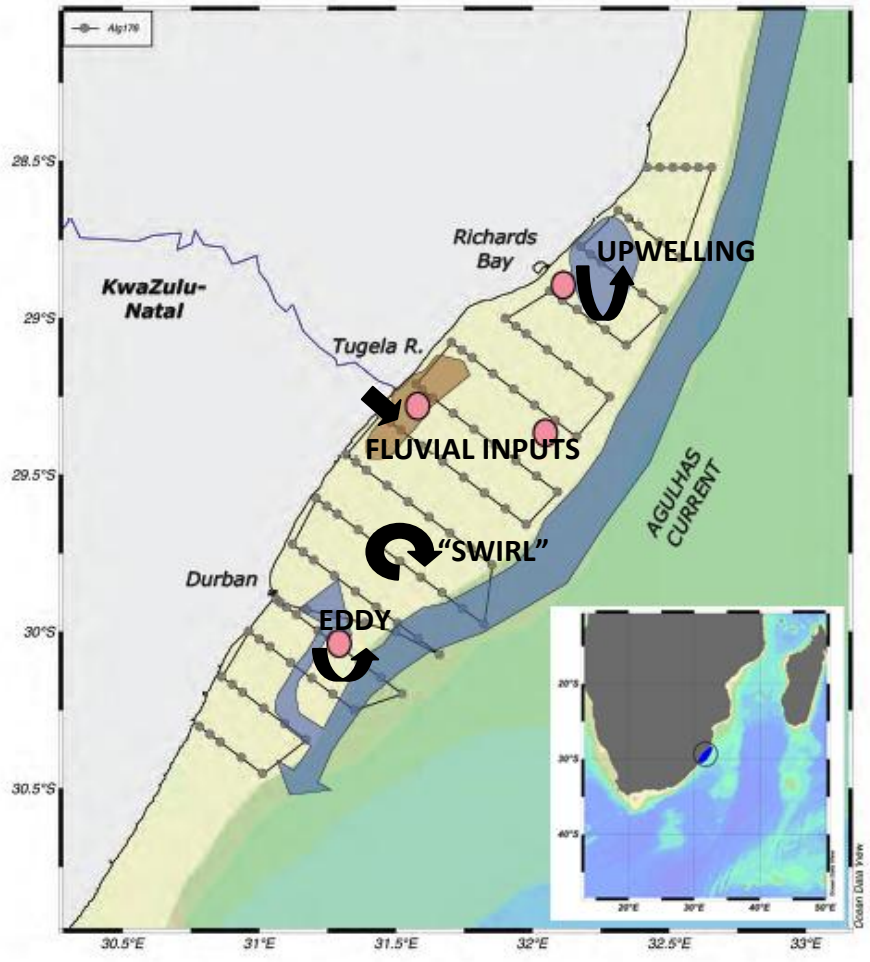

Figure 1.1. A conceptual model of the ecosystem drivers in the KZN Bight region, including its major features, as well as the synoptic (grey circles) and focus (pink circles) sampling station and sites. Black arrows indicate the nutrient sources into the system.

1.2. Physical environment

1.2.1. Regional climate

An area's climate influences the biological processes that occur in the associated ecosystems (Allanson and Baird, 1999). Along the KZN coast, summer temperatures range between 25 – 28 ºC and winter temperatures around 23 ºC (Jury, 1998). Rainfall has a great influence on the riverine runoff, influencing coastal ecosystems though freshwater additions, which bring associated terrigenous nutrients and other particulate materials. Mean annual rainfall in KZN is around 1000 mm with approximately 70 % of this in the summer season (Day, 1981; Allanson and Baird, 1999; Nel, 2009). In February, rainfall was found to be 125 mm, which when compared to 25 mm in winter is extremely high (Jury, 1998; Nel, 2009). Hunter (1988) stated that January was the peak of the wet season and August the peak of the dry season. Mean monthly precipitation in these months are 118 mm and 39 mm for January and August respectively (Hunter, 1988). For the year of study specifically, February had the highest rainfall and August the lowest, at 157.99 and 0.51 mm respectively (Table 1.1).

Table 1.1. Total precipitation (mm) and mean wind speed (km.h^{-1}) at the Louis Botha weather station for the year 2010 (Available online at: www.tutiempo.net/en/climate/Durban_Louis_Botha/2010/685880.htm).

Month	Total precipitation (mm)	Mean wind speed (km.h^{-1})	Month	Total precipitation (mm)	Mean wind speed (km.h^{-1})
January	110.98	15.5	**July**	1.53	10.5
February	157.99	16	**August**	0.51	13.2
March	22.87	14.4	**September**	7.87	16.2
April	8.89	14.1	**October**	18.35	14.5
May	32.25	11.5	**November**	21.06	16.8
June	9.39	11.2	**December**	49.77	13.2

Wind plays an important role in coastal systems, especially shallow waters, as it reduces stratification by causing waters to mix, inducing wave action, and in some geographical locations may cause upwelling (Pearce *et al*., 1978; Allanson and Baird, 1999). The east coast is dominated by westerly winds throughout the year, although easterly winds comprise a high percentage of the wind in the summer season (Allanson and Baird, 1999). However, a coastal low pressure system causes a change in the dominant wind direction to north-northeasterlies at Durban (Schumann, 1988; Allanson and Baird, 1999). KZN experiences a cyclone season from November to May, during which time four to five tropical cyclones generate high waves in the north of the coastline (Allanson and Baird, 1999).

These waves influence the fluvial sources of nutrients in the Bight. Waters in the upper layer of the KZN Bight are directly related to synoptic winds in the area, rendering the area being described as well mixed (Pearce *et al*., 1978).

1.2.2. The coastline

Some of the most important fluvial drivers of the KZN region in terms of annual contributions to freshwater, sediment and nutrient fluxes to the Bight area are the St. Lucia Estuary, the Mfolozi River, Richards Bay Harbour, Durban Bay and the Tugela River (Hutchings *et al*., 2010). However, the other 68 rivers that discharge into the Bight should be noted, as they may have a cumulative influence on the Bight dynamics.

The St. Lucia Estuary is the largest estuarine system in Africa as it covers approximately 80 % of the total estuarine area in KZN (Begg, 1978). Net mean annual run-off is 567 – 633 × 10^6 m^3 (Begg, 1978). The Mfolozi River used to form a tributary to the St. Lucia estuary, it was once artificially diverted (Begg, 1978) but has since been reconnected (N. Carrasco pers. comm.). The Mfolozi estuary is the second largest draining basin in KZN with a catchment size of between 9,918 – 11,318 km^2 and a mean annual run-off of 729 × 10^6 m^3 (Begg, 1978). Hutchings *et al*. (2010) determined the mean annual run-off to be 887.3 × 10^6 m^3 with a median inorganic nitrogen concentration of 7.1 $\mu mol.l^{-1}$, several years later. Both of these outlets may form a source of nutrients into the KZN Bight. However, the St. Lucia estuary is currently undergoing a severe drought, a situation that started in 2002, and the estuary has since been closed (N. Carrasco pers. comm.). The Mhlatuze River, with a catchment size of 4,268 – 4,489 km^2, drains into the Richards Bay Harbour (Begg, 1978). The Harbour forms a nutrient trap with the mangroves contributing to the nutrient level (Begg, 1978). Mean annual run-off from Richards Bay Harbour is approximately 616 × 10^6 m^3 with a median inorganic nitrogen load at 20.5 $\mu mol.l^{-1}$ in the Mhlatuze (Begg, 1978; Hutchings, 2010). The Umbilo and Mhlatuzana Rivers with a cumulative catchment size of 180 km^2 drains into the Durban Harbour (Begg, 1978). In 2009, the Durban Bay catchment was 264 km^2 (Forbes and Demetriades, 2005). It is apparent that industrial pollution flows into the harbour through storm water outlets and river canals and that untreated domestic sewage has been released at the harbour mouth affecting nutrient concentrations of the waters surrounding it (Begg, 1978). Nutrient concentrations in Durban harbour can range from 7 – 15 $\mu mol.l^{-1}$ for dissolved inorganic nitrogen, 7 – 0.5 $\mu mol.l^{-1}$ for dissolved inorganic phosphorous and 75 – 10 $\mu mol.l^{-1}$ for silicate (CSIR, unpublished). Another source of pollution entering the Bight is through two pipelines off Richards Bay as well as another two outside Durban. Effluent from these pipelines may have an influence on nutrients in the north of the Bight. The Mgeni estuary should also be noted as a potential driver, even though it experiences a mean annual runoff of 707 × 10^6 m^3, it is subjected to a considerable amount of pollution, increasing the nutrient levels within the estuary (Cooper *et al*., 1992; Allanson and Baird, 1999). Ammonium, nitrate and orthophosphate

concentrations measured in the Mgeni were as high as 83, 124 and 129 µmol.l^{-1} respectively (Cooper *et al*., 1992).

The Tugela River is the greatest contributor of freshwater to the nearshore region in KZN. It is the largest river on the KZN coastline and the second largest in South Africa. The Tugela has a catchment area of 28,702 km^2 (Allanson and Baird, 1999). With 5,071 × 10^6 m^3 as the mean annual run-off, the river can be expected to significantly influence the dynamics of the adjacent oceanic waters (Begg, 1978; Allanson and Baird, 1999). Whitfield and Harrison (2003) noted the mean annual runoff as 3,865 × 10^6 m^3 25 years later. Average yearly flow rates for the Tugela were approximately 138 m^3.sec^{-1} in 1997 and 225 m^3.sec^{-1} in 1999 (Whitfield, 2000). Discharge at the Tugela changes seasonally. There is a wet high flow season from November to March, and a dry low flow season lasting from April to October (Oliff, 1964). Discharge rates in winter and summer are at approximately 73.6 and 481 m^3.sec^{-1} respectively (Oliff, 1964). Later studies found the mean annual outflow rate of the Tugela to be 3865 × 10^6 m^3 (Hutchings *et al*., 2010). These outlets have the potential to influence nutrient characteristics in the Bight, thus influencing the phytoplankton ecophysiology.

The Tugela River mouth is situated in the central Bight, and the freshwater plume resulting from the river influences the water column characteristics of the inshore portion of the Bight in this region (Meyer *et al*., 2002). In the estuary a survey found no nitrate in the surface water but concentration of 0.78 and 1.29 µmol.l^{-1} at the bottom (Cooper *et al*., 1992). Orthophosphate concentrations here ranged between 0 – 0.29 µmol.l^{-1} and 0.16 – 0.32 µmol.l^{-1} in the surface and bottom depths respectively (Cooper *et al*., 1992). Meyer *et al*. (2002) also noted that the central KZN Bight is well mixed, at least as data from the period of his sampling seem to indicate. The mouth of the Tugela River was found to have higher concentrations of phosphate, at 0.77 µmol.l^{-1}, and silicate, at 4.0 µmol.l^{-1}, as compared to the rest of the central KZN Bight (Table 1.1; Meyer *et al*., 2002). A later study by Hutchings (2010) stated that the Tugela has a median inorganic nitrogen concentration of 21.4 µmol.l^{-1} with an estimated load of 1160 t.y^{-1}.

It was emphasised in a report from the CSIR, studying the influence of the terrestrial freshwater outflow on the nearby coast, that the KZN Bight functions as an integrated ecosystem (van Ballegooyen, 2007). The model produced in the report illustrated that no specific river had a major influence on the ecosystem except for the Tugela. Furthermore it explained that a combination of fluvial nutrient sources, including the rivers and estuaries on the KZN coast, had an influence on productivity in the KZN Bight. The report concluded that there needs to be further study in the region to determine the true extent of the influence of these terrestrial sources on the marine environment in the KZN region.

Table 1.2. A summary of nutrient concentrations determined in Meyer *et al*. (2002).

Bight region	Depth (m)	Nitrate ($\mu mol.l^{-1}$)	Phosphate ($\mu mol.l^{-1}$)	Silicate ($\mu mol.l^{-1}$)
Southern	10	0.15 – 1.65	0.35 – 0.65	2.66 – 4.05
	30	0.18 – 1.89	0.37 – 0.59	2.83 – 4.05
	75	0.18 – 13.45	0.46 – 5.43	3.03 – 10.73
	125	18.33	1.59	13.60
Central	10	1.01 – 1.86	0.48 – 0.72	3.50 – 4.69
	25	-	0.5	3.0
Tugela	25	-	0.77	4.0
Northern	10	0.15 – 15.30	0.35 – 1.64	2.52 – 9.41
	50	0.18 – 18.27	0.37 – 1.39	2.40 – 12.22

1.2.3. Hydrography

The Agulhas Current is fed largely by the South West Indian Ocean sub-gyre, along with the Mozambique Channel, Mozambique Current and East Madagascar Current. The Agulhas Current is fully formed at around 30 ºS, from where it borders the KZN continental shelf, continuing to flow southwards and eventually forming a retroflection with most of the current returning east. Flowing at a rate of 1.5 $m.s^{-1}$ along the KZN Bight, this large-scale oceanographic feature introduces different waters into the KZN Bight area (Lutjeharms, 2006; Figure 1.2).

The KZN Bight water consists of South Indian Subtropical Surface Waters and Indian Tropical Surface Water (Lutjeharms *et al*., 2000). The Tropical Surface Water is characterised by salinities and temperatures from 35.0 to 35.5 and 20 to 28º C, respectively (Lutjeharms, 2006).

The movement of this current, as well as the bathymetry of the continental shelf, results in upwelling and gyres forming in the northern and southern areas of the KZN Bight, respectively (Schumann, 1988). The water generated to the surface significantly influences the ecophysiology of the biota in the Bight, as it is colder and nutrient rich which can then be used by phytoplankton in the presence of light in the euphotic zone. This topographically-induced upwelling occurs where the sharp bend in the coastline causes water to be pulled to the surface; this type of upwelling differs from coastal upwelling found in on the West Coast of South Africa, which is caused by the Ekman transport interacting with the Benguela Current, resulting in very high levels of primary production, with values of 500 g $C.m^{-2}.year^{-1}$ and some more than double that (Behrenfeld and Falkowski, 1997; Carr and Kearns, 2003; Trujillo and Thurman, 2005; Figure 1.3; Figure 1.4). Lutjeharms *et al*. (2000) noted these features: upwelling was found in the north of the KZN Bight with water of higher salinity,

nutrients and chlorophyll-*a* values, as well as lower temperatures (Figure 1.2). On comparison of temperature and nitrate concentrations, the beginning of a cyclonic pulse in the southern regions of the KZN Bight was found (Lutjeharms *et al*., 2000). Both these features have a marked effect on the nutrients being introduced to these areas (Schumann, 1988).

ADCP data from the cruises completed in 2010, Voyage 175 and 177 using the *FRV Algoa*, indicated another possible source of nutrients into the KZN Bight (Roberts pers. comm.). A "swirl" (*sensu* Roberts) of water bringing up cold nutrient rich water was observed in the middle shelf area (Roberts pers. comm.; Figure 1.1). This resulted in high chlorophyll-*a* concentrations at 2.65 mg.m^3 in the mid shelf area with productivity values ranging between 7 – 10 g C.m^2.d^{-1} (Lamont and Barlow, unpublished).

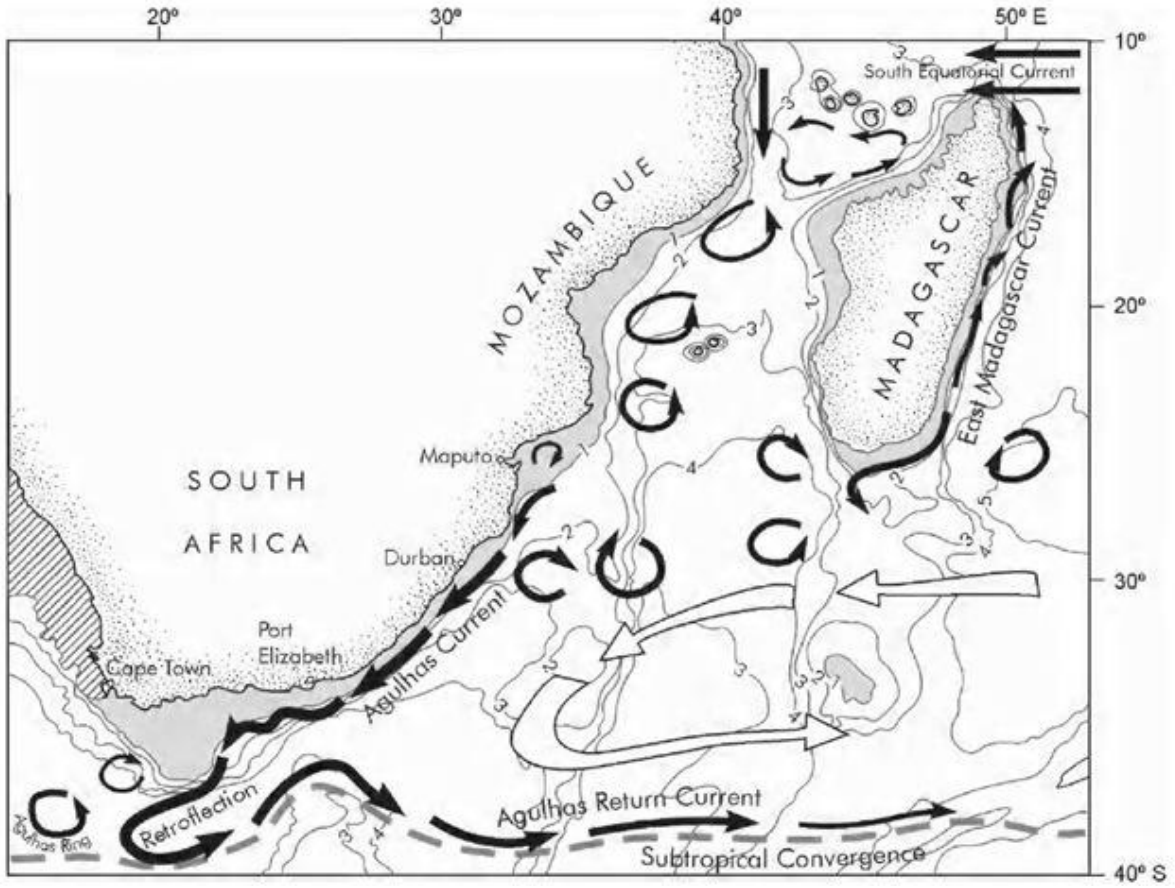

Figure 1.2. A map indicating the movement of the Agulhas Current along the east coast of Africa (Lutjeharms, 2007).

The major feature affecting nutrient concentration in the Durban region is a recurrent eddy. When the eddy is not present, the surface layer is well mixed with higher concentrations of nitrogen below 60 m. When present, the eddy results in cold nutrient rich water being drawn upward, increasing nitrate concentrations in the surface regions to between 2.22 and 2.32 µmol.l^{-1} (Burchall, 1968; Carter and d'Aubrey, 1988). Later literature shows, the water of the southern KZN Bight to be well mixed

for the first 30 m (Table 1; Meyer *et al*., 2002). Meyer *et al*. (2002) noted warm water with low nutrient concentrations closer inshore with a positive horizontal nutrient gradient, with the highest concentrations at the continental shelf edge. A coastal plume inshore moving northward was further noted (Meyer *et al*., 2002). Meyer *et al*. (2002) added that there was a cyclonic eddy present in the offshore region of the northern KZN Bight, which is further proven by the distribution of nutrients with a core of higher nutrients found in the centre of the eddy (Table 1.2).

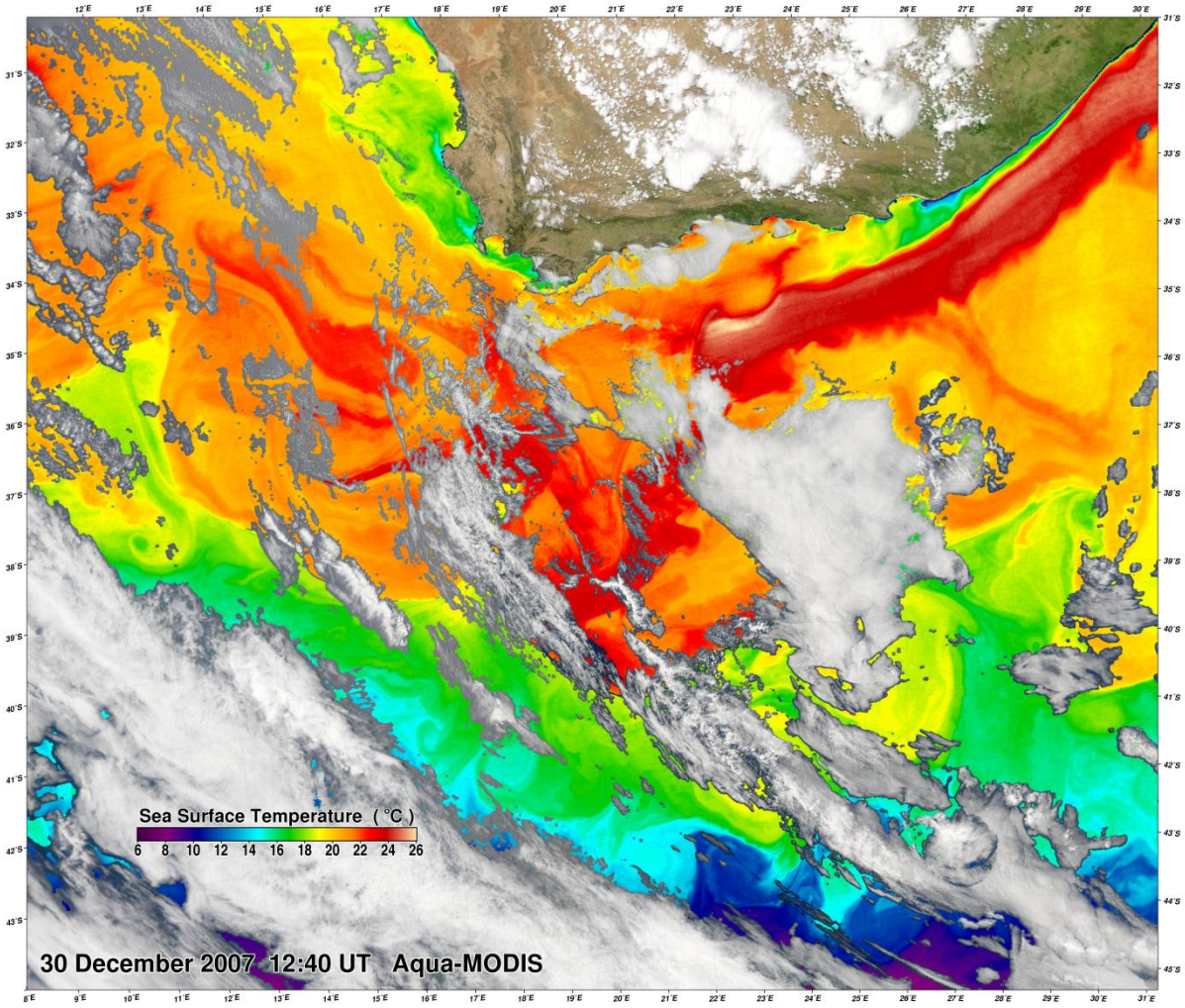

Figure 1.3. Aqua-MODIS graph showing the sea surface temperature along the South African Coast with the red colour on the east coast being the Agulhas current (available online: http://oceandata.sci.gsfc.nasa.gov/MODISA/L2/2007/364/) .

We are unsure how frequently the Durban eddy occurs, but it has been suggested by Harris (1964) that the eddy is present approximately 50 % of the time; according to a recent study, the eddy was present 55 % of the time (Guastello pers. comm.). The eddy was found to be present for an average of eight days but the duration ranged from 3 – 19 days. When the eddy was present, there was a notable increase on nutrient concentrations (~ 15 mmol.l^{-1}) and a decrease in the nutricline depth (Carter and

d'Aubrey, 1988; Lutjeharms, 2006). Although the change in nutrient concentrations was noted during the eddy's presence, Lutjeharms (2006) states that "it has not been shown to affect primary productivity or the biogeography of other organisms" in the KZN Bight.

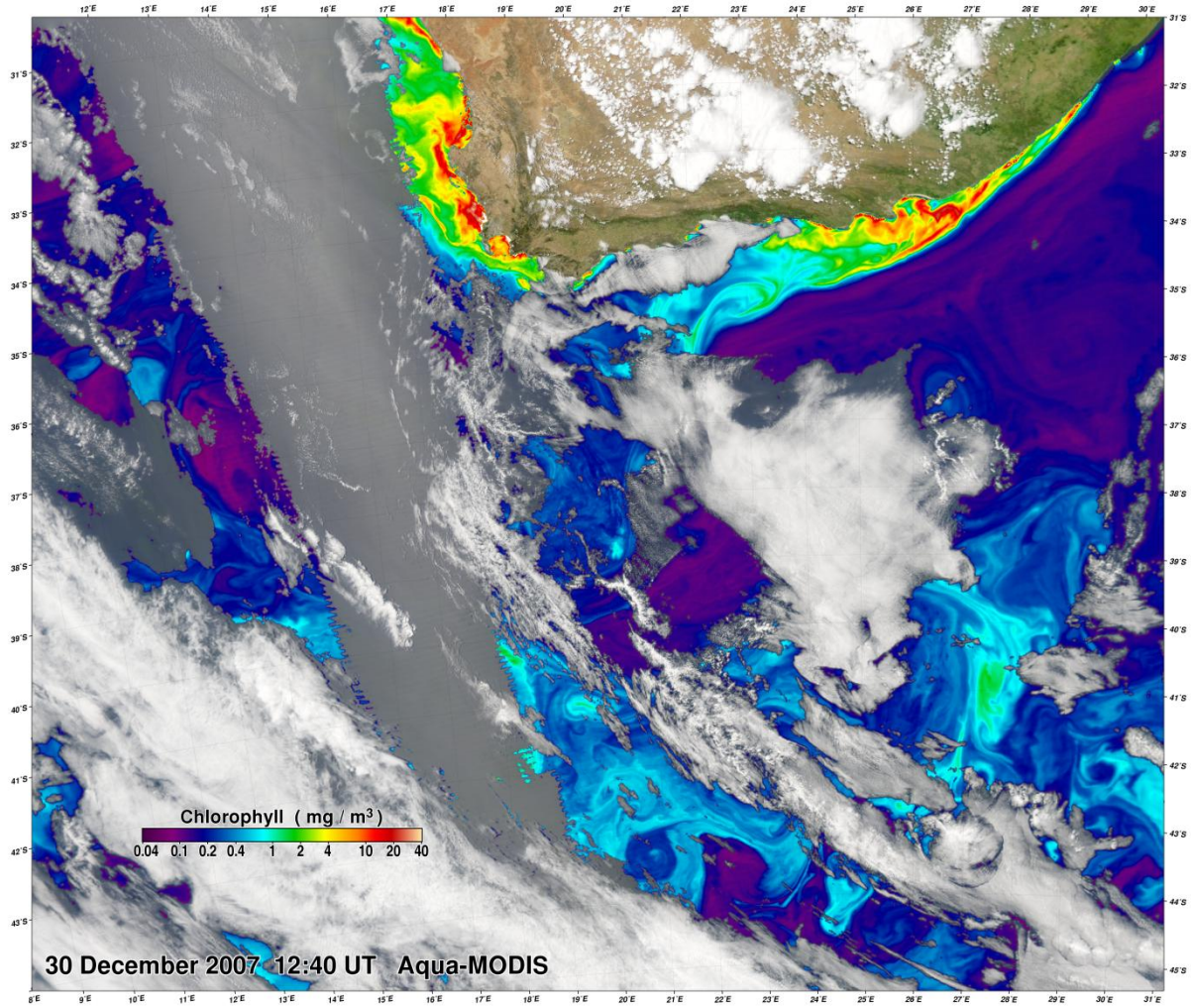

Figure 1.4. Aqua-MODIS graph showing the chlorophyll-*a* concentration along the South African Coast (available onlinehttp://oceandata.sci.gsfc.nasa.gov/MODISA/L2/2007/364/).

The Agulhas Current, with its low nutrient concentration, is responsible for a negative horizontal gradient in nutrient concentration, moving from Richards Bay offshore (Carter and d'Aubrey, 1988; Meyer *et al*., 2002; Oliff, 1973; Pearce, 1977). A large vertical gradient in nutrient concentration was also present due to periodic upwelling found in the area (Carter and d'Aubrey, 1988; Meyer *et al*., 2002). Older literature indicates that the topographically driven upwelling causes surface nitrate concentration to increase between 1.0 - 7.0 µmol.l^{-1} (Lutjeharms, 1989; Oliff, 1973). According to Oliff (1973), Richards Bay estuary has a small influence on the near shore with an average concentration of 20 µmol.l^{-1} (Begg, 1973); once the dilution factor was taken into account a maximum

increase of 1 μmol.l^{-1} was expected (Carter and d'Aubrey, 1988). Meyer *et al*. (2002) later also found distinct vertical and horizontal gradients (Table 1.1).

1.3. Phytoplankton ecology

Phytoplankton interacts with the majority of essential ecological networks and therefore significantly influences marine ecosystems. Accordingly, it is necessary to understand the ecophysiological processes, such as primary productivity and nutrient uptake, that occur within them. Morris (1980) states that there is a link between the physical environment and the physiology of phytoplankton, where the photosynthetic characteristics of a microalgal population reflects a change in the environment with a small time lag.

Carbon, nitrogen and phosphorus are essential elements that are needed for algal growth (Naldi and Wheeler, 2002). Carbon is generally taken up in the bicarbonate (HCO_3^-) form while nitrogen can be taken up by phytoplankton either actively or passively, in several forms, namely: ammonium (NH_4^+), nitrite (NO_2^-) and nitrate (NO_3^-) (Taylor *et al*., 1998). Urea and amino acids are also forms of nitrogen available for uptake by phytoplanton. These nutrients are assimilated into cells where they are used to aid in growth. Because these nutrients are essential in growth, an understanding of the process of nutrient uptake is therefore imperative.

The relationship between uptake rate and productivity needs to be explained, as both terms can be used to describe the ecophysiological processes that were measured, in this study. In order for phytoplankton to increase in biomass, nitrogen needs to be taken up, because it forms a part of the amino acids (Dugdale and Goering; 1967; Chenl and Durbin, 1994). Carbon and nitrogen concentrations are taken up by phytoplankton, according to the Redfield Ratio (C:N = 106:16), and it can thus be deduced that nitrogen and carbon uptake are coupled (Dugdale and Goering, 1967; Feliatra and Bianchi, 1993). Because carbon uptake is equivalent to productivity, nitrogen uptake can be referred to as productivity due to their parallel relationship. Although under certain conditions the stoichiometry may not follow this relationship, it is generally considered an acceptable comparison.

Morris (1980) initially observed that phytoplankton utilise nitrate over other nitrogenous compounds but later found that nitrate is only used when the combination of ammonium and urea is unable to saturate uptake. Replenishing of the euphotic zone by upwelling and terrestrial nutrient input may result in the nitrogenous nutrient pool being dominated by nitrate (Morris, 1980). Nitrite is found in concentrations much lower than nitrate, but at low oxygen concentrations, increases to more substantial levels (Morris, 1980). Consumption and reduction of nitrite, from nitrite to ammonium, was found to be completed by phytoplankton over bacteria in the near surface oceanic waters (Wada and Hattori, 1971). Furthermore, it was found that phytoplankton was capable of using nitrite as equivalent to nitrate in a growth medium (Eppley and Rogers, 1970). Harrison and Davis (1977),

studying a natural population of marine phytoplankton, found that at low concentrations of nitrate, 1 – 2 μmol.l^{-1}, both nitrate and nitrite ions were removed at similar rates. In oceanic waters, with no pollution, ammonium concentrations are relatively low when compared to other nutrients (Morris, 1980). Eppley *et al*. (1969) found that ammonium was preferentially taken up over nitrate until the concentration of ammonium in the water drops below 0.5 μmol.l^{-1} in the diatom *Ditylum brightwellii* and the dinoflagellate *Gonyaulax polyedra*. Nitrate and more so ammonium, are assimilated at a faster rate than nitrite and these nutrients are thus taken up preferentially over nitrite. Urea and amino acids are also taken up preferentially over nitrite. Inorganic nutrient concentrations provide information on the potential for phytoplankton growth, to identify water masses, as well as to provide a biological account of the water (Carter and d'Aubrey, 1988). This was indicated in several studies in the KZN Bight (Carter and d'Aubrey, 1988; Carter and Schleyer, 1988; Lutjeharms, 2000; Meyer *et al*., 2002. Carter and d'Aubrey (1988) found that the nutrients showed a spatial and temporal variability, which was also concluded by Meyer *et al*. (2002). It has been established that upwelling of nutrient rich water can shape phytoplankton productivity, spatially and temporally (Carter and d'Aubrey, 1988; Carter and Schleyer, 1988; Lutjeharms, 2000; Meyer *et al*., 2002).

Uptake rate is a function of the nutrient concentration, light, and temperature in the surrounding medium. Waters rich in dissolved inorganic carbon (DIC), nitrogen (DIN) and phosphorous (DIP) will affect the rate of nutrient uptake in phytoplankton (Naldi and Wheeler, 2002). Enhancing environmental nutrient concentrations often alleviates the limitation of DIN, resulting in accelerated DIC acquisition or primary productivity (Borum and Sand-Jensen, 1996). The response in phytoplankton can be measured as sustained uptake over the course of hours (Dy and Yap, 2001), and should be correlated with environmental nutrient status, as these nutrients may explain the underlying patterns observed (Borum and Sand-Jensen, 1996).

The stable isotope method allows for a more direct measurement of nutrient uptake, through accumulation, as the amount of the stable isotope collected in the sample is measured (McCarthy and Eppley, 1972). Additionally, this method allows an estimate of primary production, as the ratio of nitrogen to carbon uptake is related (Dugdale and Wilkerson, 1986). The isotope method has the advantage of a high sensitivity and shorter incubation times (Naldi and Wheeler, 2002), although as concentrations of nutrients are very low in oceanic samples large periods of time will be needed in order to note a significant difference.

1.3.1 Phytoplankton ecology of the KZN Bight

Productivity

The Oceanographic Research Institute (ORI) produced a series of reports discussing primary productivity on the continental shelf off Durban. The first report sampled in 50 fathoms (91.44 m) off

the harbour entrance. *In situ* primary production was only measured between May and November but showed great variability (Burchall, 1968 b). Primary production, in the surface waters, ranged from 1.05 mg $C.m^{-3}.day^{-1}$ in May to 14.14 mg $C.m^{-3}.day^{-1}$, at the bottom, in July. The month of October showed high primary production in the surface, at 52.25 mg $C.m^{-3}.day^{-1}$, but showed lower production at the bottom with a value of 0.25 mg $C.m^{-3}.day^{-1}$. No set conclusions regarding the factors controlling primary production were drawn from this study. Further studies of primary production found mean carbon uptake rates to be 17 – 942 mg $C.m^{-3}.day^{-1}$ in the euphotic zone throughout the KZN Bight and surrounding coastal waters (Burchall, 1968 a). Another study measured extremely high primary production values, at 3000 mg $C.m^{-3}.day^{-1}$ were found at 49 m south-east of the Tugela mouth (Ryther *et al*., 1966). The high values found by Ryther *et al*. (1966) were attributed to the high rate of terrestrial inputs from the Tugela River introducing nutrients into the KZN Bight. Burchall (1968 a) found highest primary production south-east of the Tugela mouth at 119 mg $C.m^{-3}.day^{-1}$. The study hypothesised that it was due to terrestrial inputs from along the coast.

A later study on phytoplankton productivity was conducted along the entire Agulhas Current stretching from Delagoa Bay to Mauritius around the coast to Cape Agulhas and down to Marion Island (Mitchell-Innes, 1967). Primary production near the KZN Bight was found to be 84 mg $C.m^{-3}.day^{-1}$ at the surface (Mitchell-Innes, 1967), decreasing to 4.32 and 0.24 mg $C.m^{-3}.day^{-1}$ at 28 and 66 m respectively (Mitchell-Innes, 1967). Although only one sampling site in this study pertains to the KZN Bight, it is important to note that this study found photosynthetically available radiation (PAR) as the major factor influencing primary productivity (Mitchell-Innes, 1967).

The KZN Bight was again studied by Oliff (1973) and Schleyer (1981) who focussed attention to the upper regions of the KZN Bight due to the upwelling in the region. Primary production rates measured were 43.2 and 307.2 mg $C.m^{-3}.day^{-1}$ at 10 m and 1 m, respectively, in the southern end of the KZN Bight (Oliff, 1973; Schleyer, 1981). These higher values over short periods of time are indicative of upwelling in the region. A recent study by Barlow *et* al. (2010) found a primary productivity to range between 0.3 – 3.7 mg $C.m^{-3}.day^{-1}$ in the KZN Bight and areas south of the KZN Bight. Although these values are high they do differ from the Benguela upwelling systems with primary production values of 500 g $C.m^{-3}.year^{-1}$, which averages to 1.37 mg $C.m^{-3}.day^{-1}$, n and some values are more than double that (Carr and Kearns, 2003; Behrenfeld and Falkowski, 1997). This is because these two currents experience different levels of nutrient availability.

Chlorophyll-a biomass

Carter and Schleyer (1988) found chlorophyll-*a* concentrations to range between 0.3 – 3.9 $mg.m^{-3}$ in the Durban eddy region of the KZN Bight. Later studies found chlorophyll-*a* concentrations to be below 0.5 $mg.m^{-3}$ in the Durban eddy area (Lutjeharms, 2000). The Richards Bay upwelling area was found to have chlorophyll-*a* concentrations ranging between 1.0 – 1.5 $mg.m^{-3}$ (Lutjeharms, 2000). The

higher chlorophyll-*a* concentrations are likely due to nutrient inputs. Other similar systems, such as the Delogoa Bight, experience chlorophyll-*a* concentration ranging between 0.6 – 1.3 $mg.m^{-3}$. The biomass found along our east coast is much lower than that of the west coast. Chlorophyll-*a* concentrations in the Benguela upwelling region on the west coast of South Africa were found to be as high as 9 $mg.m^{-3}$ (Verheye-Dua and Lucas, 1988) with later studies indicating values from 5 – <15 $mg.m^{-3}$ depending on the season (Carr and Kearns, 2003). A maximum chlorophyll-*a* concentration of 117 $mg.m^{-3}$ has recently been noted in the Benguela ecosystem (Barlow and Lamont, 2012). The reason for the difference between the regions, is that the west coast experiences much higher nutrient concentrations than the KZN Bight which has been described as being oligotrophic (Vreheye-Dua and Lucas, 1988; Bustamante *et al*., 1995; Carr and Kearns, 2003).

Species composition

A study was conducted on phytoplankton species diversity along the Agulhas current region in 1969 (Thorrington-Smith, 1969). The study established that all sites were diatom dominated with dinoflagellates not reaching more than 2.3 % of the cells counted. Another study by Carter and Schleyer (1988) reiterated this finding when it determined that the Durban eddy region was dominated by diatoms. The site situated off the Tugela River mouth had the largest variety of species while the one furthest from the coast had the fewest, although all the areas were dominated by diatoms (Thorrington-Smith, 1969). The study stated that the type of upwelling in a system not only affects the amount of phytoplankton in a system, but also the presence or absence of a species (Thorrington-Smith, 1969).

Barlow *et al*. (2008) conducted a study on phytoplankton in both the KZN and Delagoa Bight. The study focussed on determining the functional groups of plankton found in this area using pigments. It was determined from this study that flagellates were located throughout both Bight systems and further they had the highest biomass of all the phytoplankton functional groups detected (Barlow *et al*., 2008). Flagellates were found in temperatures of between 18 – 24 ºC, whereas diatoms dominated in colder upwelled waters with temperatures less than 22 ºC and high phytoplankton biomass (Barlow *et al*., 2008). Prokaryote biomass was found to increase in warmer waters greater than 22 ºC (Barlow *et al*., 2008). Knowledge of the broad phytoplankton communities present related to their habitat temperature may enable us to determine the nutrient sources influencing productivity in the KZN Bight.

1.4. The current study

1.4.1. ACEP aims

To recap, the aims of the KZN Bight project were:

1) To determine the relative importance of material derived from fluvial processes and those originating from the Agulhas Current – the St Lucia upwelling and cyclonic Durban lee eddy on the Bight. This aim can be further broken down:
   - To quantify the contribution of the Agulhas Current to the nutrient fluxes in the Bight.
   - To quantify the nutrient fluxes through the biota and environment.

2) To establish levels of assimilation, recycling and transformation of materials in the Bight. This major aim can be unravelled into smaller components:
   - To determine the stoichiometry (C:N:P) of the biota in the KZN Bight.
   - To make use of stable isotope analysis to provide input for food web studies, as well as ecosystem models.

1.4.2. Aims of this study

Using the ACEP aims as a guideline, the aims of this project were drawn up. The overall aim of this thesis is to provide an insight into which nutrient source is driving phytoplankton productivity in the KZN Bight. It can be broken down into the following three aims:

1) To determine the distribution of particulate organic matter (POM) along the KZN Bight.
   - POM content of water forms a good indicator of productivity in the euphotic zone (Charpy, 1985) thus an understanding of distribution of these nutrients will allow us to determine the relative importance of nutrient sources in the KZN Bight region.
   - It can be hypothesised that there will be higher concentrations of POM along areas of higher phytoplankton biomass, as well as at terrestrial output regions.
   - Data from here will be introduced into flux models being completed by a member of the KZN Bight Project.
   - Data will also used to explain patterns seen in other studies as part of the project, as well as aid in an understanding of the results used to explain the second aim of this project.
2) To examine the influence of fluvial and oceanic nutrient sources on phytoplankton ecophysiology.
   - These findings in combination with other ACEP data allowed us to determine the relative importance of nutrient sources in the KZN Bight region.

- It can be hypothesised that an input of nutrients would result in an increase in nitrate concentration which, in turn, would result in an increase in productivity (Brylinsky and Mann, 1973; Dortch, 1990; Borum and Sand-Jensen, 1996; Cochlan and Bronk, 2001; Kockum *et al*., 2002).

3) To use daily results of both uptake and chlorophyll-*a* concentration to provide an understanding of the oceanographic processes that drive productivity in the KZN Bight.
    - A daily perspective will provide an insight into biomass and production changes, which might not be observed when comparing results statistically.

1.4.3. Structure of this thesis

This thesis is structured in order to help accomplish this overall aim, while not being redundant in the different chapters. This study is broken down into three aims as seen in the introduction. The first two chapters, being the introduction and methods and materials respectively, are combined for all three aims. This prevents the repetition of information because the information provided in these sections are needed for all the aims. Chapter three is the results and discussion, is divided three sections, one for each aim. The results and discussion presented is kept to one chapter, due to the large volume of data presented which could prove difficult to follow if discussed separately from the results. The overall aim is addressed specifically in the conclusion.

CHAPTER 2

METHODS AND MATERIALS

2. METHODS

Two cruises were conducted in the wet and dry season along the KZN Bight (29°36.826 S; 31°24.777 E). The first cruise, sampling the wet season, occurred from the 22/01/2010 – 22/02/2010 on Voyage 175 aboard the *FRV Algoa*, while the second cruise, aboard the same vessel Voyage 177, occurred during the dry season from 16/07/2010 – 27/02/2010. For both cruises the ADCP data showed that neither of the oceanographic features, i.e. the upwelling at Richards Bay and the eddy at Durban, was present (Roberts pers. comm.). There was a distinct difference in rainfall between February, which experienced heavy rain, and August, which had low rain (Table 1.2).

Each cruise was comprised of two components, i.e. a synoptic and a focussed part of the cruise. The synoptic study provided an overall picture of the KZN Bight and lasted for approximately two weeks for both the wet and dry season. The focussed studies were conducted at sites chosen in proximity of the major oceanic or fluvial drivers anticipated to exist there, thus allowing the determination of the influence of each of the nutrient sources on phytoplankton ecophysiological characteristics. Spatial coordinates for the synoptic and focus cruise components can be found in Appendix A and B respectively.

At each station water samples were collected using twelve PVC Niskin bottles attached to a rosette housing with a Sea-Bird 911 *plus* CTD (Sea-Bird Electronics, Inc., Bellevue, Washington, USA). The CTD provided the depth and active fluorescence, to determine the fluorescence maximum (F_{max}), in order to electronically fire the Niskin bottles, collecting water at respective depths. A summary linking the methods used to the aims of the study can be found below (Table 2.1.)

Table 2.1. Summary of the aims and objectives of this thesis with the related methods section.

Aim	Objective	Section
To determine the distribution of POM along the KZN Bight.	A synoptic study of the KZN Bight was conducted, concentrating on POM, to provide an overall understanding of the area.	2.1. 2.3.1.1. 2.4.1.
To examine the influence of fluvial and oceanic nutrient sources on phytoplankton ecophysiology.	A study of five focus areas of the KZN Bight was conducted at which ^{15}N uptake experiments were performed over several days. Data from each site was grouped and statistical analysis completed.	2.2. 2.3.1.1. 2.3.1.2. 2.3.2. 2.4.2.
To use daily results of both uptake and chlorophyll-*a* concentration to provide an understanding of the oceanographic processes that drive productivity in the KZN Bight.	A study of five focus areas of the KZN Bight was conducted at which ^{15}N uptake experiments were performed. Data from each sampling day were visually compared.	2.2. 2.3.1.1. 2.3.1.2. 2.3.2. 2.4.3.

2.1. Synoptic study field work

2.1.1. Site selection

The synoptic survey covered the area across the entire KZN Bight region, from Scottsburgh to St. Lucia (Figure 2.1.). Shore-normal transect lines from the shore to the outer edge of the continental shelf ensured a broad and comprehensive spatial coverage of the study region (Figure 2.1.). There were 117 stations sampled in both synoptic cruises.

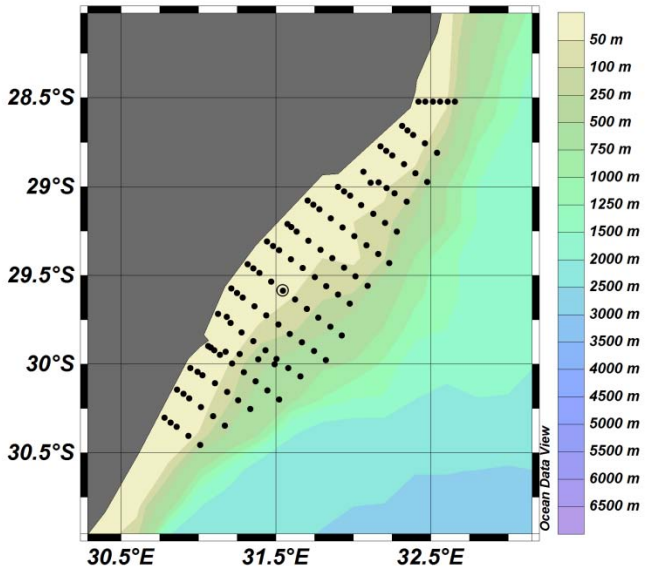

Figure 2.1. Synoptic cruise sampling sites in the KZN Bight.

2.1.2 Quantitative analysis for the synoptic cruise

It is vital when working with isotopes that all nitrogen and carbon are removed from the filtering equipment, filters and storage containers. Thus, all sample bottles and containers were washed with 10 % HCl acid wash and rinsed three times in distilled water. All filters were precombusted at 450 ºC for six hours removing all organics and then weighed to three decimal places.

At each of the 117 stations CTD casts were conducted using a SBE 911 Plus under water unit was used to measure depth (m), temperature (ºC), salinity (PSU), dissolved oxygen levels ($mg.l^{-1}$) and pressure (db). Fluorescence ($mg.m^{-3}$) and backscatter was also determined. Chlorophyll-*a* biomass was later determined using a WET Labs ECO-Fluorometer (Philomath, USA) which measures the direct chl-*a* concentration extracted, using acetone (90 %), from phytoplankton cells.

The cost of analysis of certain parameter forced us to select a subset of 45 out of the 117 stations. Three stations on each line were chosen to provide a broad picture of the study area (Appendix A). Water was collected from each of these 45 discrete stations at three depths (surface, fluorescence F_{max} and bottom). Water volumes of 300 or 500 ml were filtered onto precombusted and pre-weighed 25

mm diameter Whatman GF/F (nominal 0.72 µm) at a pressure of less than < 100 mm Hg. The filters were frozen wrapped in foil sleeves at – 20 º C and stored in Ziploc packets for later particulate organic matter (POM) analysis (yielding TSS, % $CaCO_3$, particulate organic nitrogen (PON) and phosphorous (POP)). All samples were analysed within six months after completion of the cruise.

2.2. Focussed study field work

2.2.1. Site

Four sites *viz*. the Durban eddy, the Tugela mouth, Richards Bay north and Richards Bay south, were chosen in the KZN Bight, due to them being influenced by the proposed nutrient input mechanisms in the area (Figure 1.1). These include the upwelling cell at Richards Bay, the eddy just below Durban and the outflow from the Tugela River. The mid-shelf region of the KZN Bight was found to have high chlorophyll-*a* biomass (as per *in situ* fluorescence measurements) during the synoptic cruise of the wet season, and was included as an additional site for sampling.

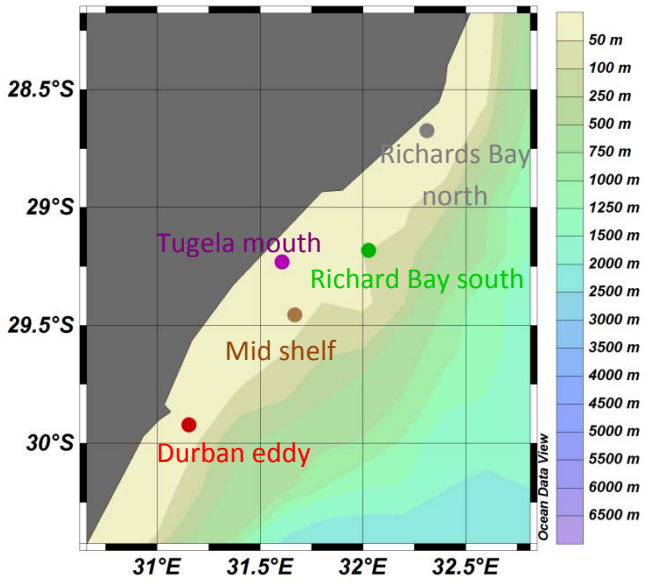

Figure 2.2. The four focus sites sampled along the KZN Bight (Richards Bay north – grey, Richards Bay south – green, Tugela mouth – purple and Durban eddy – red). An indication of the mid shelf sampling site is also included (brown).

2.2.2. Quantitative analysis for the focussed cruise

Once again, the same pre-trip preparation was conducted with all the bottles being washed in 10 % HCl and filter precombusted at 450 ºC for six hours. Seawater was collected from the surface and F_{max} at each focus site (see Appendix D for F_{max} depths). Volumes of 1000 to 2000 ml were filtered onto precombusted and pre-weighed 25 mm diameter Whatman GF/F (nominal 0.72 µm) at a pressure of < 10 mm Hg. The filtrate was stored in 2000 ml Schott bottles and acidified to a pH of 2-3, using 200

µl concentrated HCl (32 %), for later determination of the $\delta^{15}N$ natural abundance values of the DIN contained within the seawater samples. The filters were frozen at - 20 º C in foil folders, and stored in Ziploc packets to determine the isotopic natural abundance values of the POM. Furthermore, another 500 ml was filtered for samples taken at both depths, and the filters kept frozen as above for later POM analysis, in the laboratory at the University of KwaZulu-Natal. All samples were analysed within six months after completion of the cruise.

CTD casts were conducted at each sampling event. Samples were collected at approximately 10:00 SAST, using a SBE 911 Plus underwater unit was used to measure depth (m), temperature (º C), salinity (PSU), dissolved oxygen levels ($mg.l^{-1}$) and pressure (db). Fluorescence ($mg.m^{-3}$) and backscatter was also determined. Chlorophyll-*a* biomass was later determined using a WET Labs ECO-Fluorometer (Philomath, USA) again using acetone (90 %) for extraction of chlorophyll-*a* pigments providing a more accurate estimation of the biomass.

2.2.3. ^{15}N uptake experiments

Nutrients modulate phytoplankton ecophysiological rate processes, influencing spatial patterns in chlorophyll-*a* distribution (Naldi and Wheeler, 2002) and interacting with many biotic and abiotic components – forming a crucial link between the environment and higher tropic positions. The stable isotope method measures nutrient uptake by the amount of the limiting nutrient accumulated into the phytoplankton. Developed approximately 25 years ago, this method uses a chemically labelled nutrient, either ^{15}N for nitrogen, ^{13}C (stable) for carbon or ^{32}S for sulphur (Dugdale and Wilkerson, 1986; Harrison *et al.*, 1989; Naldi and Wheeler, 2002). The rate of uptake is followed by adding the tracer nutrient to the culture medium and subsequently determining the amount of labelled nutrient accumulated in the phytoplankton after uptake at a set incubation time period using isotope ratio mass spectrometry (IRMS) (Cornelisen and Thomas, 2002; Harrison *et al.*, 1989). This method was used to determine uptake rate in my sampling in order to determine if there are oceanic processes influencing the physiology of phytoplankton in the area.

There are factors affecting the accuracy of nutrient uptake experiments that need to be controlled. These are important to consider as they may result in an over or under estimation of the measured uptake rate (Dugdale and Wilkerson, 1986). The upper limit of nutrient uptake is variable and therefore incubation time can affect results as the variability needs to be noted and not assumed or extrapolated (Magnusson *et al.*, 1993). *In vitro* experiments allow for environmental factors to be controlled but prevent the accuracy which the *in situ* experiment provides. For *in vitro* experiments conducted in bottles and beakers, Runcie *et al.* (2003) and Dugdale and Wilkerson (1986) state that the amount of nutrients absorbed by the bottle or beaker itself is negligible and does not need to be considered. The initial concentration of the nutrients is important to note when performing an experiment. When nutrient concentrations are low, around the limit of analytical detection, an

enrichment experiment that disturbs the current nutrient regime will not be able to provide accurate information on the sufficiency of the nutrients in the environment (Morris, 1980).

In order to complete aim two, to examine the influence of fluvial and oceanic nutrient sources on phytoplankton ecophysiology, ^{15}N uptake experiments were performed. These experiments were conducted at each of the focus sites because they had either an oceanic or fluvial feature that introduces nutrients into the KZN Bight, allowing us to determine the influence of each of the nutrient sources on productivity. Oceanographical studies moves away from statistical analysis and discusses generalised patterns seen in data. Statistical analysis requires replicates which are often not available when studying large scale marine ecosystems. It is for that reason that I have decided to look at both a combined statistical comparison of nitrate uptake, to determine if there are differences at each site, as well as a daily perspective of both the nitrate and ammonium uptake rates of phytoplankton at the focus sites, to provide an idea of potential nutrients sources in the KZN Bight.

Water from the surface and F_{max} was filled directly into 1000 ml polycarbonate bottles directly from the Niskin bottles for the wet season. Alternatively, in the dry season, water was collected in a 25 litre drum, to homogenise the sample, before filling the polycarbonate bottles. Five bottles were enriched with 99 atom-% ^{15}N-NO_3^- from $NaNO_3$, to a concentration of 1.0 μmol.l^{-1} (Dugdale and Wilkerson, 1986; Harrison *et al.*, 1989; Naldi and Wheeler, 2002). It is important to note that the higher nitrate concentration in the experiment as compared to the natural environment may form a possible source of bias in the uptake results. A further two bottles were wrapped in foil and served as dark controls for each depth. The enriched nitrogen served as a tracer as it is taken up and assimilated into the phytoplankton cells. A further three bottles were enriched with ^{15}N-NH_4^+ from NH_4Cl to a concentration of 1.0 μmol.l^{-1} (Brylinsky and Mann, 1973; Dortch, 1990; Borum and Sand-Jensen, 1996; Cochlan and Bronk, 2001; Kockum *et al*., 2002). The enriched nitrogen will serve as an indicator of ammonium uptake by the phytoplankton but again the higher ammonium concentration in the experiment may affect the uptake results. The bottles were randomly placed in an incubator with circulating surface seawater for approximately six hours (Dugdale and Wilkerson, 1986; Harrison *et al.*, 1989; Naldi and Wheeler, 2002). Oceanic sampling is subject to good weather and thus the number of days sampled fluctuated between sites and seasons (Appendix C). Each day of incubations served as a replicate for the experiment, which allowed us to determine which nutrient was taken up, at the focus sites, in order to determine if there aree major influencing factors on the physiology of phytoplankton in the area.

After the incubation period, the water was filtered onto precombusted 25 mm diameter Whatman GF/Fs and frozen, in foil sleeves, at – 20 ° C for isotopic analysis. Another 500 ml was stored in Schott glass bottles for ammonium diffusion analysis and acidified to a pH of 2-3 using 200 μl 32 % HCl.

2.3. Laboratory analysis

At the laboratory in the University of KwaZulu-Natal, the GF/Fs were dried at 60 ºC for 24 hours, and TSS was measured by mass difference before and after filtration. $CaCO_3$ was removed by acidification with a 2 % HCl solution to prevent it having an effect on $\delta^{13}C$-values.

2.3.1. POM

POM is formed from a combination of detritus, dissolved organic matter flocculation, phytoplankton biomass and sloppy feeding (Lee and Cronin, 1984; Golladay, 1997). The distribution of POM can thus be described as a function of *in situ* production and heterotrophic decomposition in the euphotic zone and heterotrophic decomposition alone in the deeper waters (Lee and Cronin, 1984). Suspended particles play a major role in nutrient cycling since they serve as a transport agent through which nutrients are able to move (Tanimoto and Hoshika, 1997). It allows for the vertical transport of nutrients from the euphotic zone to the deep ocean (Lathja and Michener, 1994). POM forms a link between up- and downstream communities trophically forming one ecosystem (Golladay, 1997).The first aim, determining POM distribution along the KZN Bight, will allow us to determine the relative importance of nutrient sources in the area.

2.3.1.1. PON and POP

PON and POP were then determined from the GF/F by digestion, using a wet oxidation method according to Raimbault *et al*. (1999). In order to complete a digestion, filters containing the POM were placed in Teflon digestion flasks (Nalgene) with 30 ml Milli-Q water. After 3.75 ml of an oxidising reagent was added, which consisted of 30 g disodium tetraborate dissolved in 250 ml Milli-Q water (at 50 ºC), after which 15 g of potassium peroxodisulfate was added and dissolved by stirring. Oxidation reagent of desired volume was made every day to prevent crystallisation. Digestion was completed in an autoclave at 120 ºC for 30 minutes. The resultant solutions of the digestion, which contain inorganic nutrients, were analysed using a Skalar San $^{++}$ continuous flow analyser. One set of initial controls was conducted which included a precombusted filter, Milli-Q water and oxidising reagent.

2.3.1.2. Isotopic POM

The filters were packaged into 12 x 6 mm tin capsules (OEA laboratories, Cornwell, UK) and placed into multiwall trays for transportation. POM for isotopic analysis of both the natural abundance levels and after incubations (i.e. enriched samples) were conducted using isotope ratio mass spectrometry (IRMS). Both levels were determined in order to i) use the natural abundance values to determine the major nutrient source to phytoplankton; ii) to use the values along with nitrogen regeneration rates, in the calculation, to work out uptake rate. For the natural abundance POM, $\delta^{15}N$ and $\delta^{13}C$ values were determined. For the enriched POM filters from the incubations, the atom-% of ^{15}N and ^{13}C was determined in the IRMS.

2.3.2. ^{15}N filtrate

Nitrogen in the form of NO_3^- was extracted from the filtrate of both the natural abundance (before incubation) and enriched incubation samples (after incubation). The extraction was conducted according to the ammonium diffusion method by Sigman *et al*. (1997). These values were later used in the calculations for uptake rate.

The method begins with an addition of 1500 mg precombusted MgO (600 ºC for 6 hours) to 500 ml of the filtrate, which was then heated in an oven for five days, at 65 ºC, to convert DON to NH_4^+. The samples were then evaporated to dryness, at 95 ºC, to allow the NH_4^+ in the sample to evaporate. The salts were then re-dissolved to a volume of 100 ml using Milli-Q water. Devarda's alloy (375 mg) was then added to the re-dissolved solution to convert NO_3^- to NH_4^+ which would dissolve into an acidified diffusion packet (1 cm ø GF/D sandwiched between two Mitex Teflon membranes). The diffusion process was allowed to occur for four days at 65 ºC and on a shaker table for nine days. Packets were then acid washed, dried and packaged into tin capsules (12 X 6 mm, from OEA laboratories, Cornwell, UK) before Isotope Ratio Mass Spectrometry (IRMS) analysis. Three replicate controls were conducted with each batch of samples analysed, which only replaced the sample water with Milli-Q water, providing a comprehensive blank value.

2.4. Data analysis

2.4.1. Aim 1

Graphs of the synoptic sampling were created using Ocean Data View 4©. TSS, PON were compared between treatment and site as well as site and depth using two-way ANOVAs in Prism GraphPad 5®. POP was not compared, as there was not enough data for statistical comparison.

2.4.2. Aim 2

Data from the enriched samples were calculated as atom percent (At %) using the following equation (Fry, 2006):

$$\text{At \%} \quad \frac{\left(100 \;\; R_{std} \;\; \left[\frac{\delta_{sam}}{1000} \;\; 1\right]\right)}{\left(1 \;\; \left[R_{std} \;\; \left\{\frac{\delta_{sam}}{1000} \;\; 1\right\}\right]\right)}$$

Where R_{std} refers to the world standards, for which for nitrogen is atmospheric N_2. δ_{sam} refers to the value measured by the IRMS, and is reported in parts per thousand (‰). It is calculated using the following equation (Fry, 2006):

$$\delta_{sam} \quad \left(\left[\frac{R_{sam}}{R_{std}}\right] \;\; 1\right) \;\; 1000$$

Uptake rates were then calculated using the isotope dilution model of Gilbert *et al*. (1982). This model was selected as it accounts for the change in enrichment concentration and uptake rate throughout the experiment. It uses an exponential decay curve to account for the change in ^{15}N, within the sample, with time (*R*). *R* is calculated using the following equation:

$$R \quad —(1\ \exp[\quad])$$

Here R_o refers to the ^{15}N atom percent of the aqueous fraction at time zero and *t* the time incubated of (Gilbert *et al*., 1982). δ values of R_o were provided from the IRMS and then converted into atom percent using the first equation provided in this section. *k* is used to account for the change in uptake rate related to the change in the concentration of nutrients in the sample and can be calculated using the following equation:

$$-\frac{\ln\left(\frac{R_t}{R_0}\right)}{t}$$

Uptake rate (ρ) was calculated using the following equation:

$$\left(\frac{^{15}\text{N atom \% excess}}{\text{t ime of incubation}}\right)$$

Where atom percent excess refers to the atom percent of the sample, subtracted by the atom percent of the substrate, and *PN* refers to the particulate nitrogen in the sample. Details of the equations used can be found in Appendix E.

Visual representation and statistical analysis of the data was then completed. Ocean Data View 4© was used to plot distribution graphs of the nutrient concentrations in the focus cruise, providing a view of the nutrients with site and depth. Prism GraphPad 5® was then used to statistically compare the difference in POM and TSS measured at the focus site. The two-way ANOVA has allowed a preliminary assessment of the influence of processes on the focus site. Nitrate uptake was compared between treatment and site, as well as site and depth using two-way ANOVA's in Prism GraphPad 5. Statistics for the dry season do not include the Richard Bay south and Tugela mouth sites, as there was not enough data present. Assumptions of the ANOVA comparing uptake rates were met except for the wet season surface data, which was log transformed and the data reanalysed. These results comparing uptake rate, along with two-way ANOVAs comparing the environmental conditions with depth and site, provides a further understanding of underlying processes driving production in the KZN Bight. The assumptions were met for most of the samples. For nitrite, concentrations for the wet season and PAR for both seasons were square root transformed and reanalysed. Transformation was unsuccessful for nitrite concentration in the dry season and it was therefore not statistically compared.

Statistical comparisons were not made between the seasons, as a lack of funding did not allow for replication. However, visual comparisons of the data were made to assess the influence of terrestrial nutrient sources on production. It can be inferred from a difference between seasons, that runoff due to rainfall affects phytoplankton production in the KZN Bight.

Multivariate analyses were used to provide a good visual representation of the data as well as a better understanding of the environmental influence on the physiological processes. Principal component analyses (PCA) were completed, using Primer version 6©, in order to compare environmental conditions for both the wet and dry seasons. The data were first normalised and the analysis completed. The factors compared where inorganic nitrogen (nitrate and nitrite) phosphorous and silicate concentration, temperature, salinity, dissolved oxygen and PAR. Non-metric multi-dimensional scaling (nMDS) plots were created using the biological data. This included chlorophyll-*a* concentration, nitrate uptake rate for both seasons. The nMDS plot overlaid with the results of a cluster diagram provides a visual image of the separation of sites according to the biological components. The BIOENV analysis was then completed in PRIMER to determine which environmental variables significantly influence biological data. The data were first normalised and a Bray-Curtis and Euclidian distance resemblance matrix was created for the biological data and environmental data respectively. The BIOENV analysis uses combinations of the environmental variables to find the highest Spearman rank correlation between the two matrices.

2.4.3. Aim 3

Nitrate uptake rates were calculated using the equations in Section 1.4.2. of the methods and materials sections while ammonium uptake rates were calculated using the Dugdale and Goering (1967) model . Prism GraphPad 5® was then used to create the graphs in order to visually compare the data.

CHAPTER 3

RESULTS AND DISCUSSION

3. RESULTS AND DISCUSSION

3.1. Particulate organic matter (POM) distribution

The first aim of my study is to discuss the POM distribution along the KwaZulu-Natal Bight (KZN Bight). The results in this section are reported and discussed according to site, depth and season. A comparison of these three variables will allow us to determine nutrient input points. Furthermore, with season in particular, a comparison will allow us to determine the influence of river outflow into the KZN Bight system and thus determine terrestrial influence in the area.

3.1.1. A synoptic view

A synoptic view of total suspended solids (TSS) surface waters , during the wet season, reveals amounts of *ca*. 25 mg.l^{-1} just off the Tugela River mouth near the coast, with a smaller amount of approximately 20 mg.l^{-1} at the Richards Bay south/north region (Figure 3.1a). The dry season showed the opposite pattern with less TSS at the surface waters off the Tugela River mouth region at *ca.* 20 mg.l^{-1} but more at the Richards Bay area, with 25 mg.l^{-1} TSS at the southern area of the KZN Bight (Figure 3.1b). The F_{max} depth showed a different pattern between the seasons, with TSS of between 30 – 35 mg.l^{-1} just off Richards Bay, and the dry season with 15 – 25 mg.l^{-1} spread all along the KZN Bight (Figure 3.1c and 3.1d). The bottom depth, of around 40 m, at the Richards Bay area had approximately the same amounts of TSS for both seasons at 30 mg.l^{-1} (Figure 3.1e and 3.1f). Fluvial runoff from rivers introduce suspended solids into the coastal areas of the KZN Bight (Day, 1981). The input from the Tugela River, with a mean annual runoff of 5,071 × 10^6 m^3, in particular, would explain the TSS patterns noted with higher amounts of TSS at the mouth of the river (Begg, 1978; Allanson and Baird, 1999). This was reiterated in a paper by de Lecea *et al.* (Unpublished), using natural abundance isotope data, it was determined that the TSS found in the KZN Bight originated from the Tugela River.

Particulate organic nitrogen (PON) concentration showed an interesting pattern with season. Higher concentrations of PON are found in the surface waters of the wet season, but with patchy distribution, while the dry season waters had moderate concentrations, but spread over the KZN Bight (Figure 5).The wet season surface waters had values as high as 25 µg.l^{-1} while the dry seasons waters highest values did not exceed *ca.* 15 µg.l^{-1}. The surface waters showed two “hot spots” for PON in the wet season just south of the Tugela River mouth and, southerly, just off the edge of the shelf, with values of approximately 20 µg.l^{-1}, which shifted south and decreased slightly, by approximately 0.005 µg.l^{-1}, in concentration in the dry season waters. Lower in the water column, there were higher amounts of PON found just north of Richards Bay, at approximately 35 µg.l^{-1}. The same “hot spot”, found in the surface waters, of the southerly region, can once again be seen, in the in the F_{max} waters of the wet season with values as high as *ca.* 20 µg.l^{-1} (Figure 3.2c). The bottom depth waters shows differences

in the amount of PON available between the seasons with values of up to 80 $\mu g.l^{-1}$ for the wet season and a maximum of 15 $\mu g.l^{-1}$ in the dry season (Figure 3.2e and 3.2f). For the wet season there are three areas with higher concentrations, at values ranging between 20 – 80 $\mu g.l^{-1}$ (Figure 3.2e). One at the coast near Richards Bay, one that was seen in the surface and F_{max} depths and, finally, one that seems to emanate of the coast at the Tugela River mouth region moving northerly in the centre of the KZN Bight (Figure 3.2e). The concentrations of PON seen in the KZN Bight are slightly higher but in a similar range to other coastal areas. The coast of the eastern North Pacific experienced a range of 0.6 – 10. 9 $\mu g.l^{-1}$ (Loh and Bauer, 2000) as well as the oligotrophic Hawaiian coast with a concentration of 5.7 $\mu g.l^{-1}$ (Laws *et al*., 1984). The southern Bight of the North sea, is also shallow with a depth of 30 m and like the KZN and is subjected to terrestrial inflow. In the southern bight of the North Sea PON in the water had a wide range, from 21 to 308 $\mu g.l^{-1}$ (Lancelot and Billen, 1984). This value was again higher than that seen in the KZN Bight, although the lower end of the range did overlap with concentrations seen in the KZN Bight. The wide range seen at the southern bight of the North Sea was take over several months and could be expressive of nutrient inputs in the system during that period (Lancelot and Billen, 1984).

The Mfolozi River discharges nutrients just north of the KZN Bight (Day, 1981). With the Agulhas Current, this water could be drawn southward, introducing the PON found just north of Richards Bay, explaining the high values seen in the region. When sampling, there was an extreme colour change in the water, from blue to murky brown, just outside the Mfolozi. However, the two pipelines introducing pollutants to the coastline outside Richards Bay could be a potential explanation for the higher TSS and POM values in the area. Another potential reason for the high PON in the area, could be due to resuspension of the sediment through wind forcing, as it is a shallow area. The dry season waters showed areas with slightly raised PON concentrations just along the coast in the northern and southern areas of the KZN Bight, with a small area in the Durban eddy region showing concentrations of around 10 $g.l^{-1}$ (Figure 3.2f). The elevated levels of particulate organic nitrogen found in the deeper waters of the KZN Bight, as compared to the surface and F_{max} depth for the wet season, are likely due to the heavier particulates sinking to the bottom of the water column (Wakeham *et al*., 1984).

Particulate organic phosphorous (POP), in the water column, again shows this pattern of extremely high concentrations with values up to 20 $\mu g.l^{-1}$ in the wet season, when compared to the dry season with concentrations only reaching a maximum of around 5 $\mu g.l^{-1}$ (Figure 3.3). Water in the wet season showed higher amounts of POP at the Tugela River mouth region, as high as *ca.* 20 $\mu g.l^{-1}$, also found in the centre of the KZN Bight, as well as similar concentrations in the mid shelf area with a few localities of high concentrations in the north of the KZN Bight (Figure 3.3a). In the dry season, waters showed a concentration of around 1 – 2 $\mu g.l^{-1}$ at the Tugela River mouth region and north of it along the coast (Figure 3.3b). This level of high organic material in the Tugela mouth region, also seen in

PON concentrations, would be due to the higher production and decomposition generally found in estuarine environments, which are then released into the coast (Lee and Cronin, 1984). POP concentration was generally high, at 20 $\mu g.l^{-1}$, for water in the F_{max} depth in the wet season, except around Durban and parts of the northern area of the KZN Bight, where concentrations dropped to as low as 0 $\mu g.l^{-1}$ (Figure 3.3c). Again, concentrations were very low in F_{max} waters with a maximum of around 3$\mu g.l^{-1}$ for the dry season moving along the north of the coastline (Figure 3.3d). The same basic pattern was seen at the bottom waters as the F_{max} depth for both seasons (Figure 3.3e and 3.3f), although the dry season showed an extension of POP, at concentrations of *ca.* 1.5 $\mu g.l^{-1}$, moving further off the coastline and concentration of 2.5 $\mu g.l^{-1}$ of POP in the mid shelf area (Figure 3.3f). The values of POP found along the KZN Bight were much lower than in other coastal and Bight systems. POP concentration in eastern North Pacific waters, a costal system, ranged between 28 – 324 $\mu g.l^{-1}$ (Loh and Bauer, 2000) while the oligotrophic Hawaiian coast had a value as high as 433 $\mu g.l^{-1}$ (Laws *et al*., 1984). POP in KZN Bight waters was also lower than Southern Bight of the North Sea which had concentrations ranging between 3 – 92 $\mu g.l^{-1}$ (van der Zee and Chou, 2005). As seen with PON values earlier this area is extremely variable which explains the wide range seen in the study region (Lancelot and Billin, 1984; van der Zee and Chou, 2005). The Bight system seems to have lower phosphorous concentrations than other systems as also seen in the inorganic results presented in Section 3.2. The pattern seen with particulate organic phosphorous showed a different pattern to organic nitrogen with higher concentrations throughout the water column as opposed to higher values in the bottom depths. This may be due to phosphorous being released swiftly from dead material, and assimilated in the surface waters, before the opportunity to sink deeper (Harvey, 1960; Menzel and Ryther, 1964).

There is a notable difference in salinity with season in surface waters (Figure 3.4). The surface waters of the KZN Bight in the wet season shows lower salinities at the Tugela River mouth, running down to the mid shelf region (Figure 3.4a). Lower salinities are also found in waters at Richards Bay and along the coast, at the bottom edge of the KZN Bight. For the bottom depth, a small area showed a lower salinity just at Richards Bay (Figure 3.4b). On the other hand, the dry season, showed salinities of around 35.5 throughout KZN Bight at the surface (Figure 3.4b). Water sampled from the bottom depth indicated a decrease in salinity with depth along the edge of the continental shelf off the KZN Bight (Figure 3.4d). These lower salinities are indicative of the Agulhas current which has a salinity of between 34.5 – 35.5 (Lutjeharms, 2010).

Flow rates at the Tugela River mouth decrease from approximately 225 $m^3.sec^{-1}$ to 138 $m^3.sec^{-1}$ between seasons, which would result in a considerable decrease in output from the wet and dry season (Whitfield, 2000). This difference would also be mimicked for the other rivers along the coastline, as

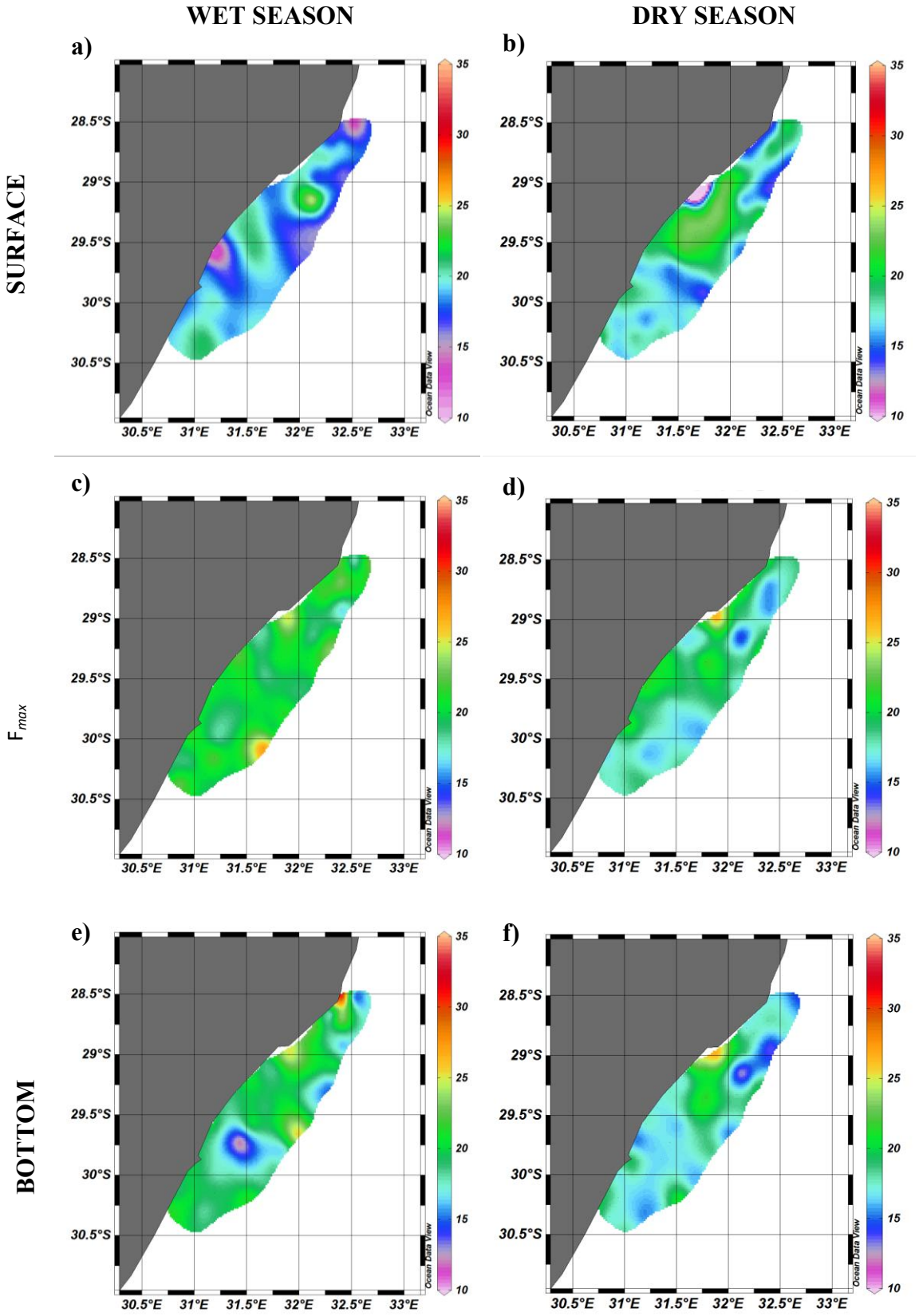

Figure 3.1. Interpolated contour maps depicting TSS (mg.l^{-1}) at the a& b) surface, c & d) F_{max} and e & f) bottom depths for the wet and dry season respectively.

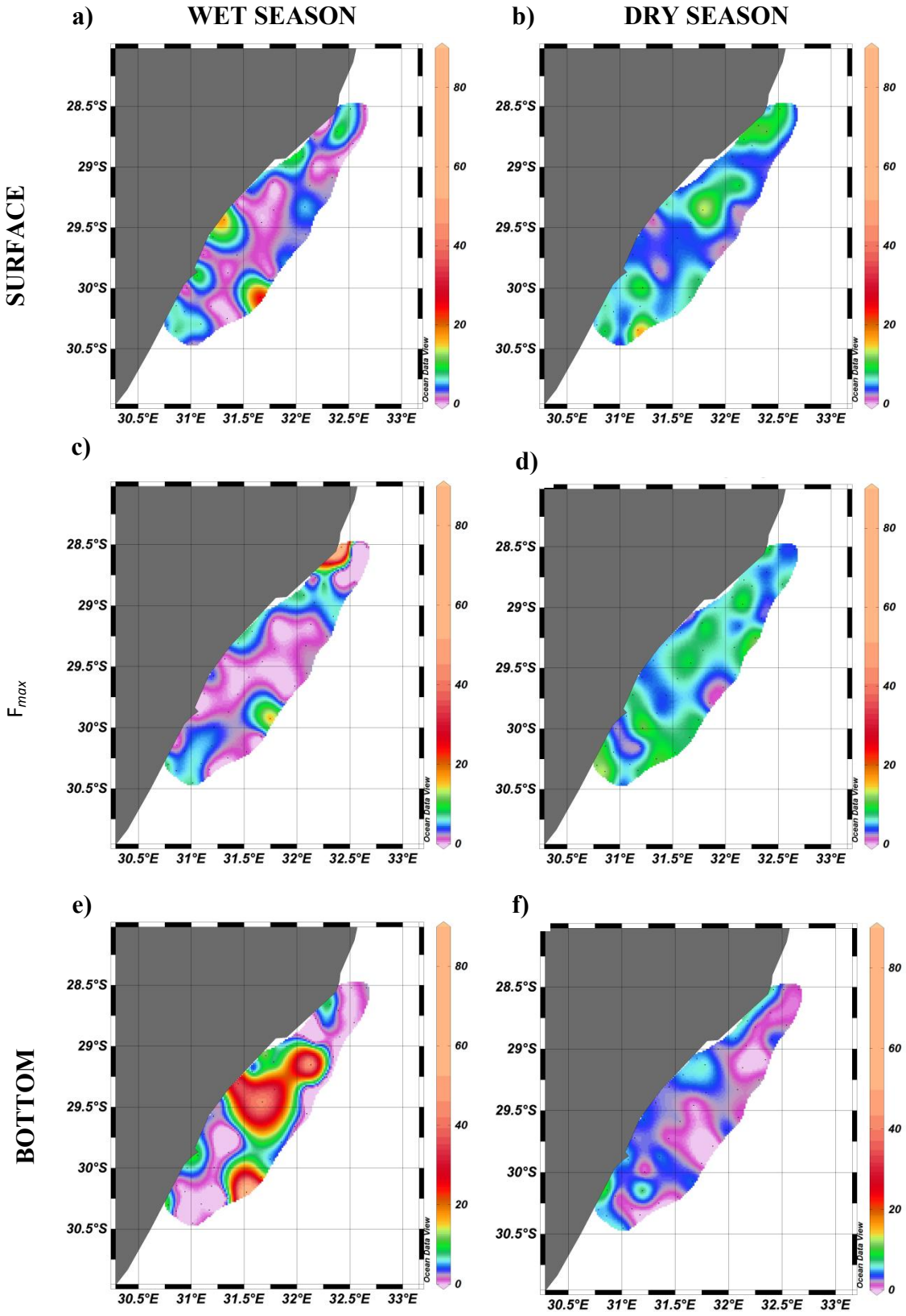

Figure 3.2. Interpolated contour maps depicting particulate organic nitrogen (ug.l^{-1}) at the a & b) surface, c & d) F_{max} and e & f) bottom depths for the wet and dry season respectively.

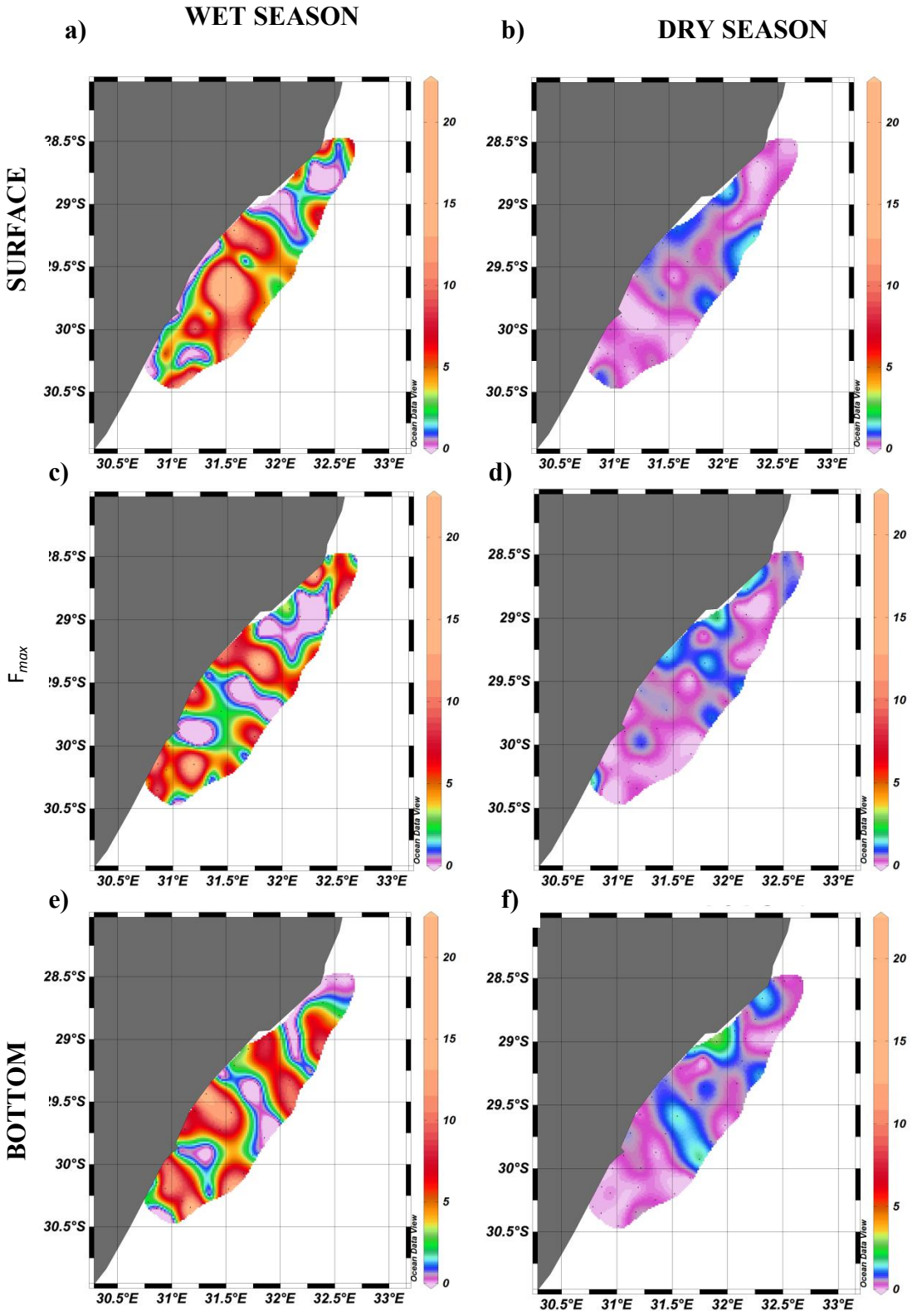

Figure 3.3. Interpolated contour maps depicting particulate organic phosphorous (ug.l^{-1}) at the a & b) surface, c & d) F_{max} and e & f) bottom depths for the wet and dry season respectively.

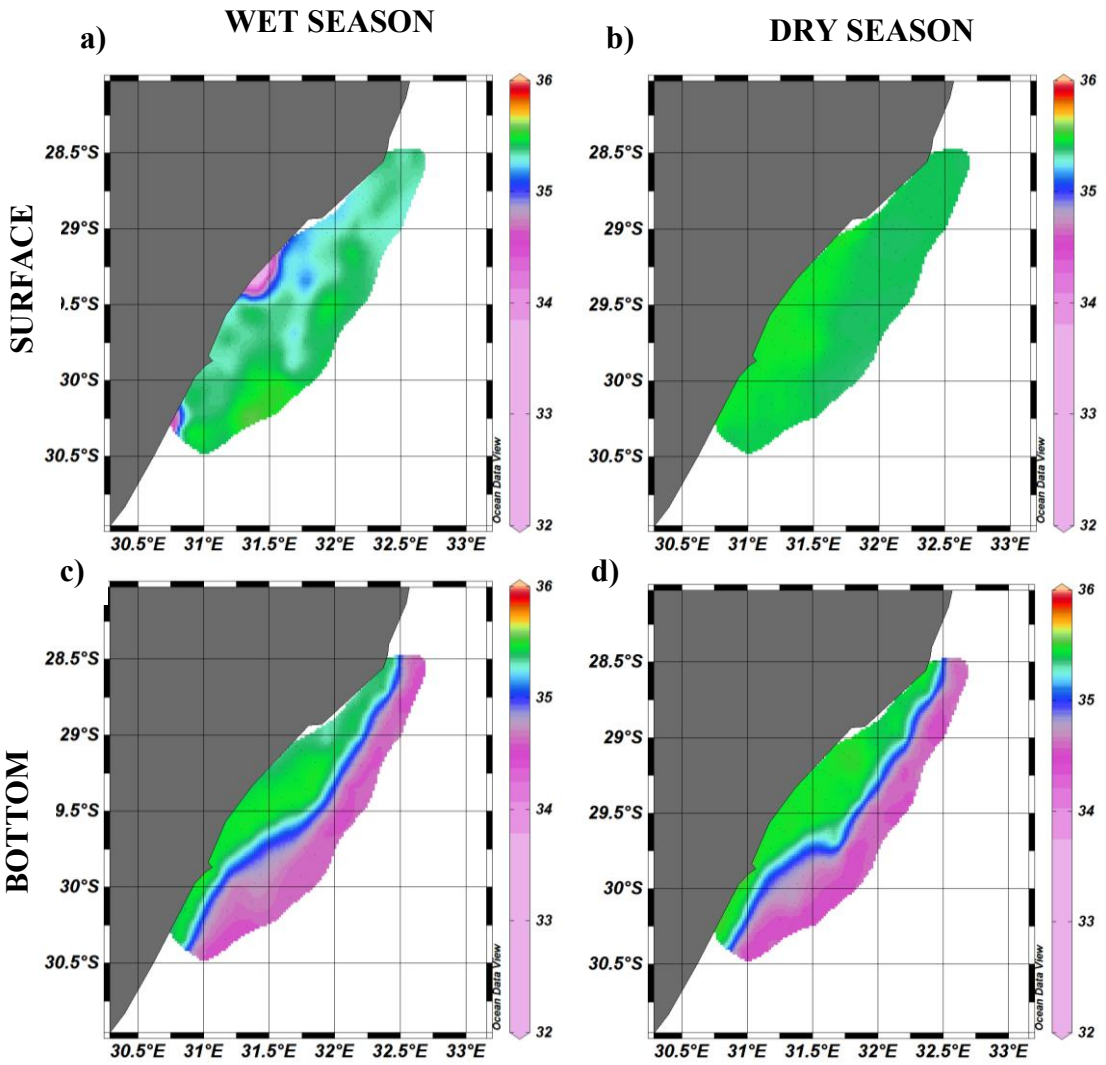

Figure 3.4. Interpolated contour maps depicting salinity at the a & b) surface, c & d) bottom depths for the wet and dry season respectively.

a decrease in rainfall between the wet and dry seasons would influence the flow rates in the river (Day, 1981). Salinity graphs, presented for the wet season, show the reach of freshwater along most of the KZN Bight area, which is not seen at all in the dry season (Figure 3.4). This change in outflow rates would explain the decrease in TSS at the surface depth between seasons (Lambert *et al*., 2009). It would also explain the difference in the amount of particulate organic nitrogen and phosphorous, which decrease dramatically between the wet and dry season (Lambert *et al*., 2009). It can be deduced that particulate organic nitrogen and phosphorous introduced are from fluvial sources due to the differences noted with season.

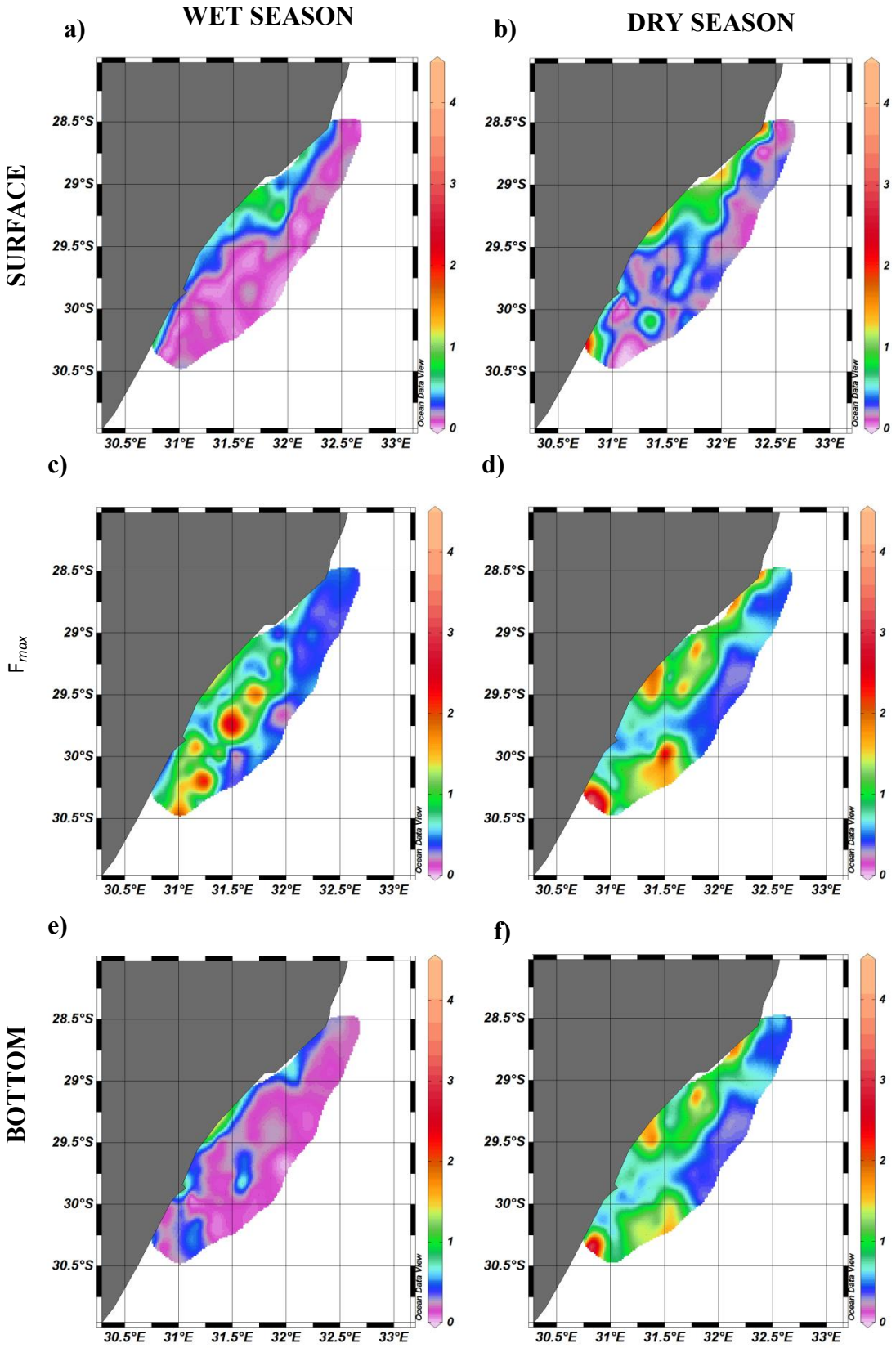

Figure 3.5. Interpolated contour maps depicting chlorophyll-a (mg.m-3) at the a & b) surface, c & d) Fmax and e & f) bottom depths for the wet and dry season respectively.

Chlorophyll-*a* did not show the same pattern as PON and POP. Generally, a larger biomass of chlorophyll-*a* was seen throughout the water column in the dry season, as compared to the wet season (Figure 3.5). This was also found in oligotrophic Northwest Mediterranean waters where POM concentration did not relate to chlorophyll-*a* (Doval *et* al., 1999). Concentrating on the wet season, values of between 0.5 – 1.0 $mg.m^{-3}$ were found close to water in the coastline, which extended slightly south of Richards Bay (Figure 3.5a). These chlorophyll-*a* concentrations were similar to that found by Meyer *et* al. (2002) who noted low concentrations in the south end of the Bight. Phytoplankton at the F_{max} depth showed a bloom in the mid shelf area, as well as south of Durban (Figure 3.5c). These values ranged as high as 4 $mg.m^{-3}$ (Figure 3.5c). The bloom seen in the mid shelf was unusual as previous literature indicated the central Bight to not be highly productive with chlorophyll-*a* concentrations of between 0.1 – 0.5 $mg.m^{-3}$ (Meyer *et al*., 2002). Values of around 1 $mg.m^{-3}$ were noted in the waters around the Tugela River mouth region (Figure 3.5c). Waters at the bottom depth in the wet season had low chlorophyll-*a* biomass, ranging between 0 – 0.5 $mg.m^{-3}$, except in waters at the Tugela River mouth region at 1.5 $mg.m^{-3}$ (Figure 3.5e). In the dry season, the chlorophyll-*a* biomass was highest in waters along the coastline, with concentrations up to 2 $mg.m^{-3}$, from Richards Bay to the Tugela River for all three depths measured (Figure 3.5b, d and f). Notable blooms (1– 3 $mg.m^{-3}$) were also found in waters at the edge of the KZN Bight near and south of Durban (Figure 3.5b, d and f). The results indicate no strong relationship and the hypothesis that chlorophyll-*a* biomass would result in an increase in POM, can neither be rejected nor accepted. Along terrestrial areas there is an increase in particulate organic nutrients, at the same regions with higher chlorophyll-*a* biomass, but the pattern with season showed a higher biomass in the dry season compared to the wet season, opposite to the pattern seen in the particulate organic matter. The data was thus inconclusive and further studies need to be conducted in order to determine the underlying influencing factors of both chlorophyll-*a* and particulate organic nutrients.

3.1.2. Focussed studies

Analysis of the focus studies showed a similar pattern as the synoptic survey. Waters in the wet season showed significant differences between site for both TSS and PON (Figure 3.6a: $p_{site} = 0.0134$; Figure 3.6c: $p_{site} = 0.0134$), but no significant difference between depth (Figure 3.6a: $p_{depth} = 0.0784$; Figure 3.6c: $p_{depth} = 0.9317$). A Tukey test found TSS at the Durban eddy site to be significantly different from the Richards Bay north site, and PON from waters in the mid shelf site to be significantly different from both Richards Bay sites. A significant interaction effect was found for TSS in the wet season (Figure 3.6a: $p_{interaction} = 0.0385$). Although not statistically compared, POP concentration in the water showed a difference between the northerly and southerly sites (Figure 3.6e). The dry season showed no significant difference in site and no significant interaction effect, but differed significantly with depth (Figure 3.6b: $p_{site} = 0.7091$, $p_{depth} = 0.0436$, $p_{interaction} = 0.8660$). PON for the dry season showed no significant differences between site and depth, as well as, no significant

interaction effect (Figure 3.6d: $p_{site} = 0.7091$, $p_{depth} = 0.0436$, $p_{interaction} = 0.8660$). Again, no statistical comparison was made for POP in the dry season, but it can be noted that there appears to be a difference between the sites and depths (Figure 3.6f).

Natural abundance isotope values, again, showed the same pattern as the particulate organic nutrient concentrations (Figure 3.7). Significant differences between sites for both $\delta^{13}C$ and $\delta^{15}N$ in the wet season but no difference in the dry season (Figure 3.7a: $p_{site} = 0.0007$; Figure 3.7c: $p_{site} = 0.1415$). Furthermore, $\delta^{13}C$ and $\delta^{15}N$ showed no interaction effects as well as no significant differences between depth for the wet season (Figure 3.7a: $p_{depth} = 0.6728$, $p_{interaction} = 0.1823$; Figure 3.7c: $p_{depth} = 0.4340$, $p_{interaction} = 0.2365$). The dry season showed no significant differences between depth and site, as well as no significant interaction between the two factors for both $\delta^{13}C$ and $\delta^{15}N$ (Figure 3.7b: $p_{site} = 0.\ 1415$, $p_{depth} = 0.1960$, $p_{interaction} = 0.\ 6388$; Figure 3.8d: $p_{site} = 0.7789$, $p_{depth} = 0.1450$, $p_{interaction} = 0.5049$).

The mid shelf site may be receiving particulate organic nutrients from terrestrial sources, which then exits the KZN Bight in horizontal strips to the edge of the sampling area. This pattern is more prominent in the POP concentrations. It would be expected that during upwelling or when an eddy is present, that higher levels of particulate organic nutrients would be present as heavier decomposing material from deeper depths would be driven upwards. Unfortunately, the eddy at Durban, as well, as the upwelling cell at Richards Bay was not present during the sampling (Roberts pers. comm.). The higher particulate organic phosphorous levels seen in the surface layer of the wet season could be due to an oceanographic feature, the “swirl”, present at the time bringing up nutrients from the deeper waters (Roberts pers. comm.). Although, this proposed mechanism should have been evident in the PON signal as well but was only evident in deeper waters. The low concentration of particulate organic nutrients in the Durban eddy region can also be explained by the absence of the oceanic process at the time of sampling.

Results from the focus cruise emulate results from the synoptic cruise. It was found that there was a significant difference between sites for TSS and PON concentration in the wet season. Runoff high in particulate organic nutrients would explain the TSS, as well as the PON difference in the wet season. The KZN Bight is a shallow area with a depth range of about 50 m to 100 m in the northern and southern parts of the KZN Bight (Lutjeharms. 2006). This shallow depth, along with wind, was expected to have an influence on the TSS in the KZN Bight, but the significant separation with site in the wet season indicates that this is not probable. There was no significant difference found for the dry season, which, when contrasted with the differences found in the wet season, may be explained by the

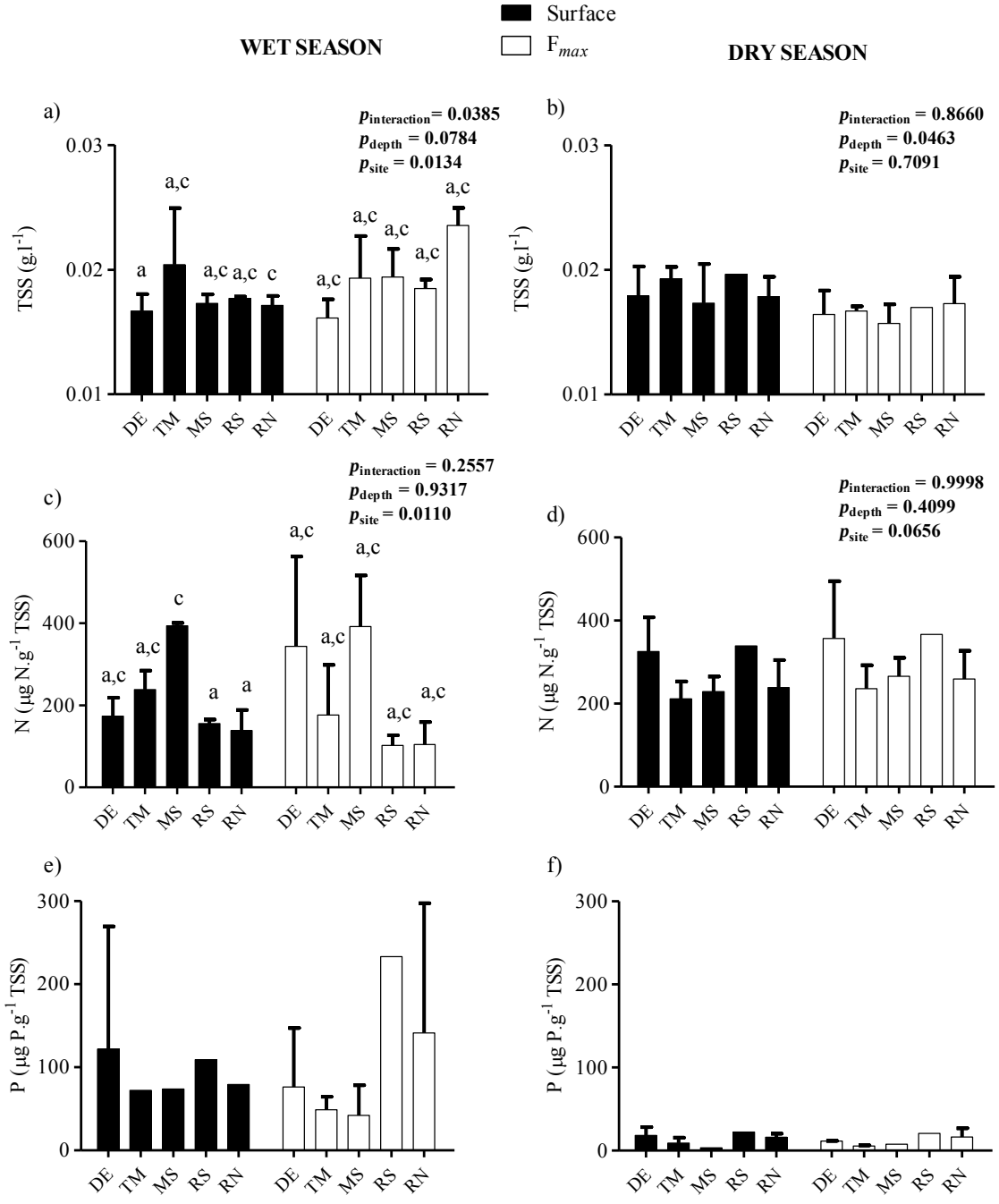

Figure 3.6. TSS (g.l-^{1}) determined during the a) wet and b) dry seasons, particulate organic nitrogen (µg N. g^{-1} TSS) for the c) wet and d) dry season and particulate organic phosphorous (µg P. g^{-1} TSS) for the e) wet and f) dry seasons focus sites of the KZN Bight. Similar letters above the bars indicate no significant difference.

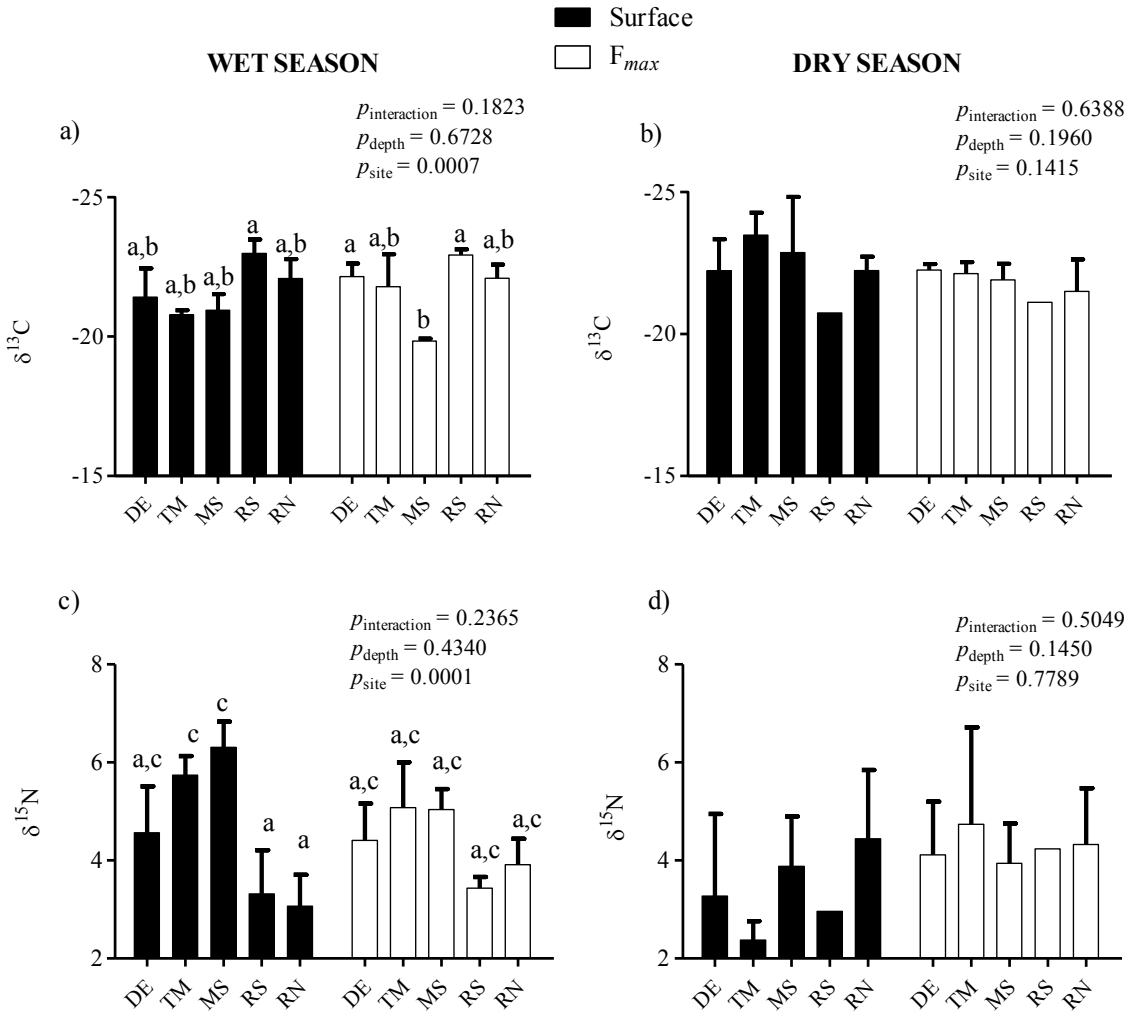

Figure 3.7. Natural abundance values of a) δ^{13}C in the wet season, b) δ^{13}C dry season, c) δ^{15}N in wet season and d) δ ^{15}N in the dry season for the focus sites of the KZN Bight (DE– Durban eddy, TM– Tugela River mouth, MS– Mid shelf, RN–Richards Bay north, RS– Richards Bay south. Similar letters above the bars indicate no significant difference.

influence of the fluvial sources explained earlier. Although, it needs to be noted that during the focus cruise POP decreased dramatically from wet to dry season, but this is not seen for PON. This may be explained by the fact that nitrogen is more refractory to decomposition than phosphorous (Harvey, 1960).

The differences seen in the wet season indicate that the southerly sites are different from the Richards Bay sites. Input from the Tugela, and potentially other rivers in the south of the KZN Bight seemed to form a separation between the northerly and southerly sites. Stable isotopes provide an insight into trophic position using δ^{15}N and to determine food sources using δ^{13}C (Peterson and Fry, 1987). Lower δ^{13}C indicate a terrestrial source while higher, an oceanic source. The isotope results as well as the POM results indicate a separation in the northerly and southerly sites. The isotope results indicate that the southerly sites are influenced more from terrestrial sources, with the lower δ^{15}N and δ^{13}C, while

the northerly sites are more influenced by oceanic sources, with the higher delta values, which can be clearly seen in the $\delta^{13}C$ of the wet season (Peterson and Fry, 1987).

The N:P ratios were extremely different in the wet and dry season (Table 3.1). In the mid shelf area the surface N:P ratio was 5:1 but this changed to 59:1 in the dry season (Table 3.1). Similar ratios are seen at the Tugela mouth and Durban eddy sites. The Richards Bay sites had a 1:1 in the wet season and was quite similar to the Redfield ratio, at 15:1, in the dry season (Redfield *et al*., 1958). These ratios indicate that the more southerly sites are deficient of phosphorous in the dry season while the northerly sites have abundant nitrogen and phosphorus for phytoplankton growth in both seasons (Redfield *et al*., 1958; Doval *et al*., 1999). It can be deduced that the southerly sites more likely receive nutrients from fluvial sources in the wet season which is not present in the dry season, hence the phosphorous deficiency in the system during that period.

Table 3.1. N:P ratios for the wet and dry season for both depths sampled of the focus study site in the KZN Bight.

	Wet season		**Dry season**	
Site	Surface	F_{max}	Surface	F_{max}
Durban eddy	8:1	25:1	18:1	36:1
Tugela mouth	3:1	5:1	42:1	47:1
Mid shelf	5:1	13:1	59:1	30:1
Richards Bay north	1:1	1:1	15:1	18:1
Richards Bay south	2:1	3:1	16:1	24:1

3.2. Nutrient uptake and associated environmental parameters

The concentrations of nutrients as well as other environmental variables were visually and statistically compared between site and depth to determine if there is an actual difference at the focus sites, as well as, to provide a potential explanation for the nutrient uptake results.

3.2.1. Environmental variables

Nutrient concentrations were measured at the different sites and along the depth profile during sampling. The Durban eddy area was the deepest site and thus showed nutrient concentrations extending to approximately 200 m (Figure 3.8 and 3.9). In the wet season, nitrate and silicate concentrations are highest in waters at the 50 m and 200 m depths in the Durban eddy and mid shelf areas (Figure 3.8a and 3.8d). The concentrations in the water were between 4 – 6 $\mu mol.l^{-1}$ for nitrate and up to 7 $\mu mol.l^{-1}$ for silicate (Figure 3.8a and 3.8d). Water in the Tugela River mouth area had substantially higher nitrite concentrations, up to 2 $\mu mol.l^{-1}$, when compared to the other sites, and also concentrations of up to 6 $\mu mol.l^{-1}$ of silicate in its surface waters (Figure 3.8b and 3.8d). Richards Bay north waters had almost double the concentration of phosphate than the other sites at 2 $\mu mol.l^{-1}$ (Figure 3.8c). There was a shift in nutrient concentration, in the KZN Bight, during the dry season (Figure 3.9). Nitrate and silicate concentrations were highest at the Durban eddy and Richards Bay north waters (Figure 3.9a and 3.9d). Nitrite concentrations were again highest in water within the Tugela River mouth region with the mid shelf region showing the same concentrations at around 0.2 – 0.4 $\mu mol.l^{-1}$ (Figure 3.9c).

No significant difference was found, as well as, no significant interaction effects for the nitrate (Figure 3.10a: p_{site}= 0.3427, p_{depth} = 0.1613, $p_{interaction}$= 0.5466), silicate (Figure 3.10c: p_{site}= 0.4025, p_{depth} = 0.2362, $p_{interaction}$= 0.6342) and phosphate (Figure 3.10d: p_{site}= 0.4337, p_{depth} = 0.2558, $p_{interaction}$= 0.4114) concentrations in the wet season. For the dry season, nitrate and silicate concentrations did not differ with site (Figure 3.10e: p_{site}= 0.4272, p_{depth} = 0.1600, $p_{interaction}$= 0.2477; Figure 3.10g: p_{site}= 0.1569, p_{depth} = 0.9181, $p_{interaction}$= 0.1554; Figure 3.10h: p_{site}= 0.0195, p_{depth} = 0.8268, $p_{interaction}$= 0.1554). Nitrite concentration differed significantly with site for the wet season (Figure 3.10b: p_{site}= 0.0260, p_{depth} = 0.5180, $p_{interaction}$= 0.9842), but was not statistically compared for the dry season.

The nutrients found in the KZN Bight system may have been added naturally or anthropogenically. Naturally, through bacterial decomposition of detritus releasing dissolved inorganic nutrients back into these systems, or anthropogenically through effluent discharge. Meyer *et al*., (2002) found, in the northern area of the KZN Bight, concentrations of nitrate ranging between 0.15 – 15.30 and 0.18 – 18.27 $\mu mol.l^{-1}$ at 10 and 50 m, respectively. The higher end of the range would be indicative of upwelling in the region which our results did not show. For the Durban eddy site, the increase in nutrient concentration with depth allows us to deduce that nutrients were not being driven up to the surface waters with an eddy. This is reiterated when compared to previous studies, which show high

nutrient concentrations when the eddy was present (Burchall, 1968b; Cater and d'Aubrey, 1988; Meyer *et al*., 2002). The nutrient concentrations found in the KZN Bight are not indicative of an oceanic feature introducing nutrients into the area (Figure 3.8 and 3.9). Although, it is important to note that the ADCP data for the cruise, although not presented, also indicated that the eddy was not present at the time of both cruises, which explains the results showing a greater terrestrial influence.

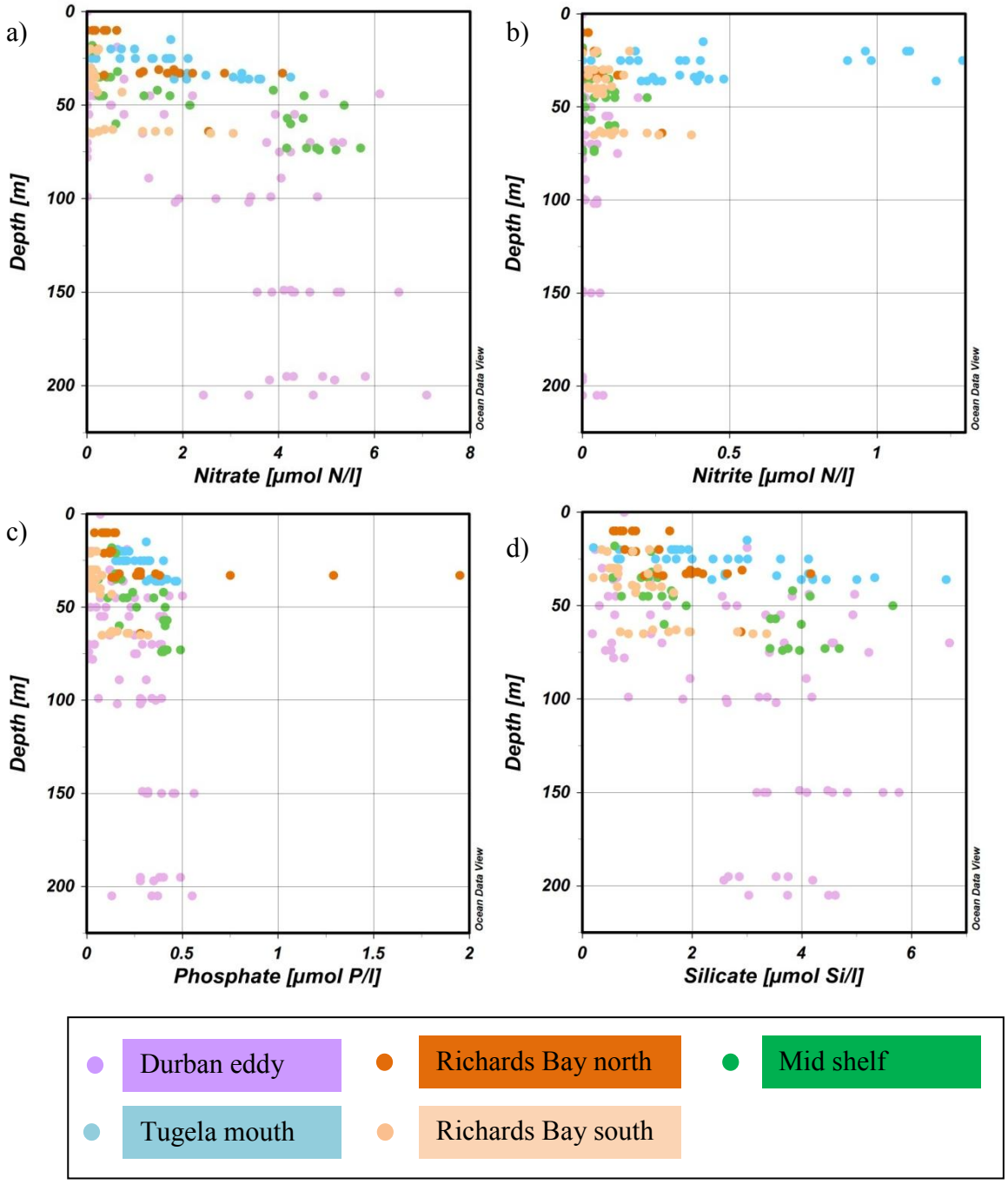

Figure 3.8. Depth profile graphs showing a) nitrate (µmol.l^{-1}), b) nitrite (µmol.l^{-1}), c) phosphate (µmol.l^{-1}) and d) silicate (µmol.l^{-1}) concentrations with depth for all days sampled at the five focus sites for wet season in the Bight.

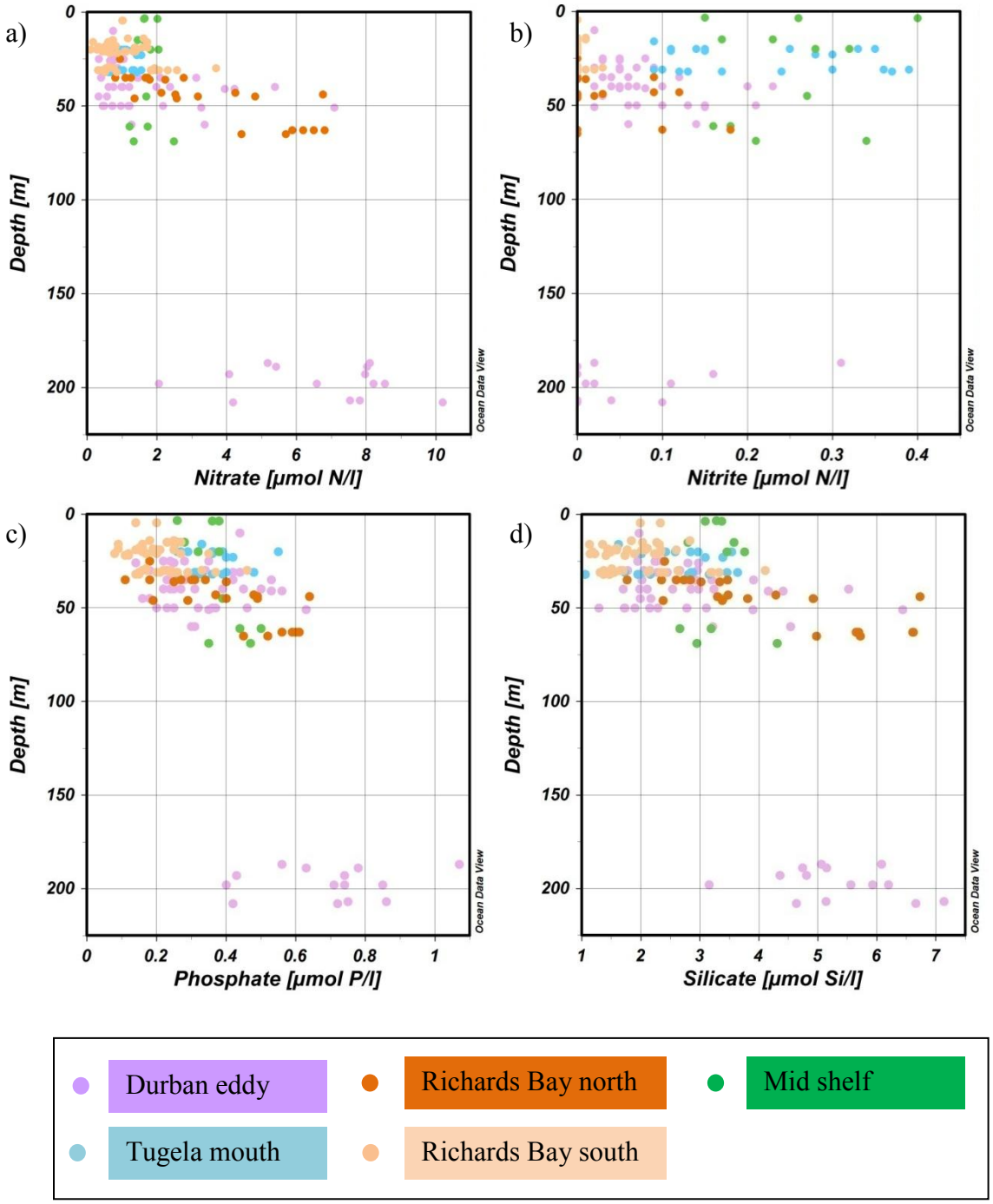

Figure 3.9. Depth profile graphs showing a) nitrate (µmol.l^{-1}), b) nitrite (µmol.l^{-1}), c) phosphate (µmol.l^{-1}) and d) silicate (µmol.l^{-1}) concentrations with depth for all days sampled at the five focus sites for the dry season in the KZN Bight.

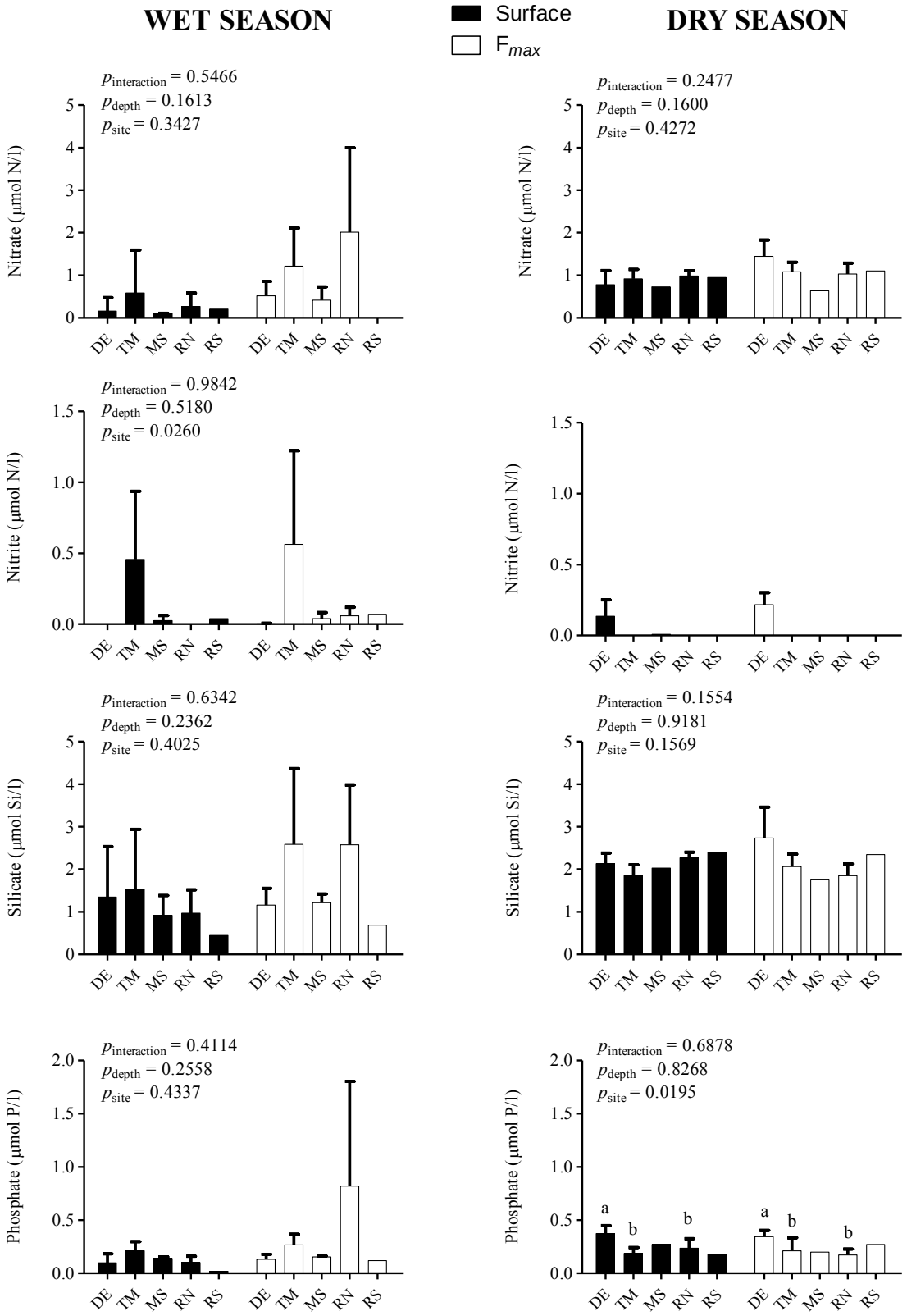

Figure 3.10. Bar graphs showing a) nitrate (µmol.l^{-1}), b) nitrite (µmol.l^{-1}), c) phosphate (µmol.l^{-1}) and d) silicate (µmol.l^{-1}) concentrations with depth for the five focus sites in the KZN Bight for the wet season and showing e) nitrate (µmol.l^{-1}), f) nitrite (µmol.l^{-1}), g) silicate (µmol.l^{-1}) and h) phosphate (µmol.l^{-1}) for the dry season.

The comparison between seasons plays a role in our investigation as to whether oceanic process or fluvial sources affect the KZN Bight dynamics. Phosphate and nitrite concentration vary between the seasons, which poses the question: are these nutrients introduced into the system through fluvial sources due to the influence of changing rainfall pattern affecting output from rivers into coastal waters. The wet season showed a larger variation in the nutrient concentrations between sites, but these variations were not significant (Figure 3.10). The dry season showed significant differences between sites. For nitrite, this might be due to the lower concentrations found at the focus sites, allowing small differences to be significant (Figure 3.10).

Temperature showed a significant difference with depth in the wet season and with site in the dry season (Figure 3.11a: p_{site}= 0.1141, p_{depth} = 0.0002, $p_{interaction}$= 0.1316; Figure 3.11e: p_{site}= 0.0001, p_{depth} = 0.0865, $p_{interaction}$= 0.4993). For the wet season, salinity showed no significant difference but differed with site in the dry season (Figure 3.11b: p_{site}= 0.3599, p_{depth} =0. 6489, $p_{interaction}$= 0.3559; Figure 3.11f: p_{site}= 0.0009, p_{depth} = 0.5921, $p_{interaction}$= 0.5364). There was a significant difference between the focus sites in dissolved oxygen concentration for both the wet and dry season (Figure 3.11c: p_{site}= 0.0007, p_{depth} = 0.0760, $p_{interaction}$= 0.8174; Figure 3.11g: p_{site}= 0.0081, p_{depth} = 0.2685, $p_{interaction}$= 0.0965). Alternatively, PAR showed significant difference with depth for both seasons (Figure 3.11d: p_{site}= 0.4152, p_{depth}< 0.0001, $p_{interaction}$= 0.8182; Figure 3.11h: p_{site}= 0.8880, p_{depth} = 0.0155, $p_{interaction}$= 0.1974).

There was an extreme distinction between the seasons in terms of environmental conditions. In the wet season, the Tugela River had a high outflow rate releasing nutrients into the KZN Bight area (Begg, 1978; Whitfield, 2000). However, there was no distinct difference between the sites indicating well mixed waters. In the dry season, the Tugela River mouth site separated from the others, as well as the mid shelf site. These sites were separated due to dissolved oxygen concentration and salinity. The freshwater flowing out of the Tugela River would explain the separation from the other sites. This water moving in a southerly direction would influence the salinity of the mid shelf site and explain its distinction from the other focus sites. It is interesting to note that it would generally be expected for the wet season to have shown a greater distinction with salinity at the Tugela mouth site, as more freshwater would be flowing out the mouth with the greater rainfall. This could indicate that the KZN Bight was more homogeneous in the wet rather than the dry season. Overall, the environmental variables indicate the same patterns as the nutrient concentrations, showing no true distinction at the Durban eddy and Richards Bay north sites, which would not be expected if there were an oceanic processes present.

3.2.2. Nitrate uptake

When comparing phytoplankton nitrate uptake rates, we found no significant difference between sites and the light and dark treatments for both the surface and F_{max} waters of the wet season (Figure 3.12a: p_{site}= 0.2695, $p_{treatment}$ = 0.3754; Figure 3.12b: p_{site}= 0.2675, $p_{treatment}$ = 0.5845). When taking into account chlorophyll-*a* concentration present at the time of the incubations we found the same significance pattern in uptake rate (Figure 3.12c: p_{site}= 0.2971, $p_{treatment}$ = 0.7353; Figure 3.12d: p_{site}= 0.3927, $p_{treatment}$ = 0.5848). This is indicative of homogenised waters also seen in the wet season environmental variables. Unusually, in the wet season, uptake rates in the dark incubations were higher than uptake rates in the light incubations, while the opposite pattern was see in the dry season following a more standard pattern. This could be attributed to luxury consumption as the enriched spike added to the incubations were of a higher concentration than the substrate (Morris, 1980; Domingues *et al.*, 2011). Overall the maximum uptake rate determined in the KZN Bight was *ca*. 2.63 µg $N.l^{-1}.h^{-1}$, at the Durban eddy, which was much lower than that seen in the Benguela current, which can experience uptake rates as high as 6 – 8 µg $N.l^{-1}.h^{-1}$ (Probyn, 1985; Probyn, 1987). This is expected, as the Benguela is an extremely productive system (Probyn, 1985; Probyn, 1987). Alternatively, the southern bight of the North Sea being a more comparable area experienced uptake rates of 0.43 µg $N.l^{-1}.h^{-1}$ in 1996 and 2.76 µg $N.l^{-1}.h^{-1}$ the following year (Tungaraza *et al*., 2003). These values fall within the same range as the KZN Bight.

Uptake rate of phytoplankton in the dry season, showed a significant difference between sites and treatment in the surface waters but no difference at the F_{max} depth (Figure 3.12e: p_{site}= 0.0360, $p_{treatment}$ = 0.0422; Figure 3.12f: p_{site}= 0.2006, $p_{treatment}$ = 0.2824). The significant difference between treatments for the surface waters of the dry season but not the F_{max} waters was also noted when taking chlorophyll-*a* into account (Figure 3.12g: p_{site}= 0.0009, $p_{treatment}$ = 0.0030; Figure 3.12h: p_{site}= 0.0717, $p_{treatment}$ = 0.1602). The difference noted in the surface waters of the dry season is due to the high uptake rate at the Richards Bay north site in comparison to the Durban eddy and mid shelf sites. There was also no significant interaction effect between site and treatment for the wet season at both depths sampled, however, for the surface waters of the dry season there was a significant interaction effect in waters sampled but not at the F_{max} depth (Figure 3.12a: $p_{interaction}$= 0.3993; Figure 3.12b: $p_{interaction}$= 0.7135; Figure 3.12e: $p_{interaction}$= 0.0450; Figure 3.12f: $p_{interaction}$= 0.2222; Figure 3.12c: $p_{interaction}$= 0.7788; Figure 3.12d: $p_{interaction}$= 0.5764; Figure 3.12g: $p_{interaction}$= 0.0012; Figure 3.12h: $p_{interaction}$= 0.0793). When taking phytoplankton biomass into account extremely low uptake rates not increasing above 2 µg N.mg chl-$a^{-1}.h^{-1}$, in the wet season. The highest uptake rates were found at the Richards Bay north site in the dry season with an uptake rate of 28.52 µg N.mg chl-$a^{-1}.h^{-1}$ in the surface waters and 38.43 µg N.mg chl-$a^{-1}.h^{-1}$ at the F_{max} depth. In a report by Kokkinakis and Wheeler (1987), they studied the coastal waters of Washington and Oregon in the USA, where they compared nitrate uptake

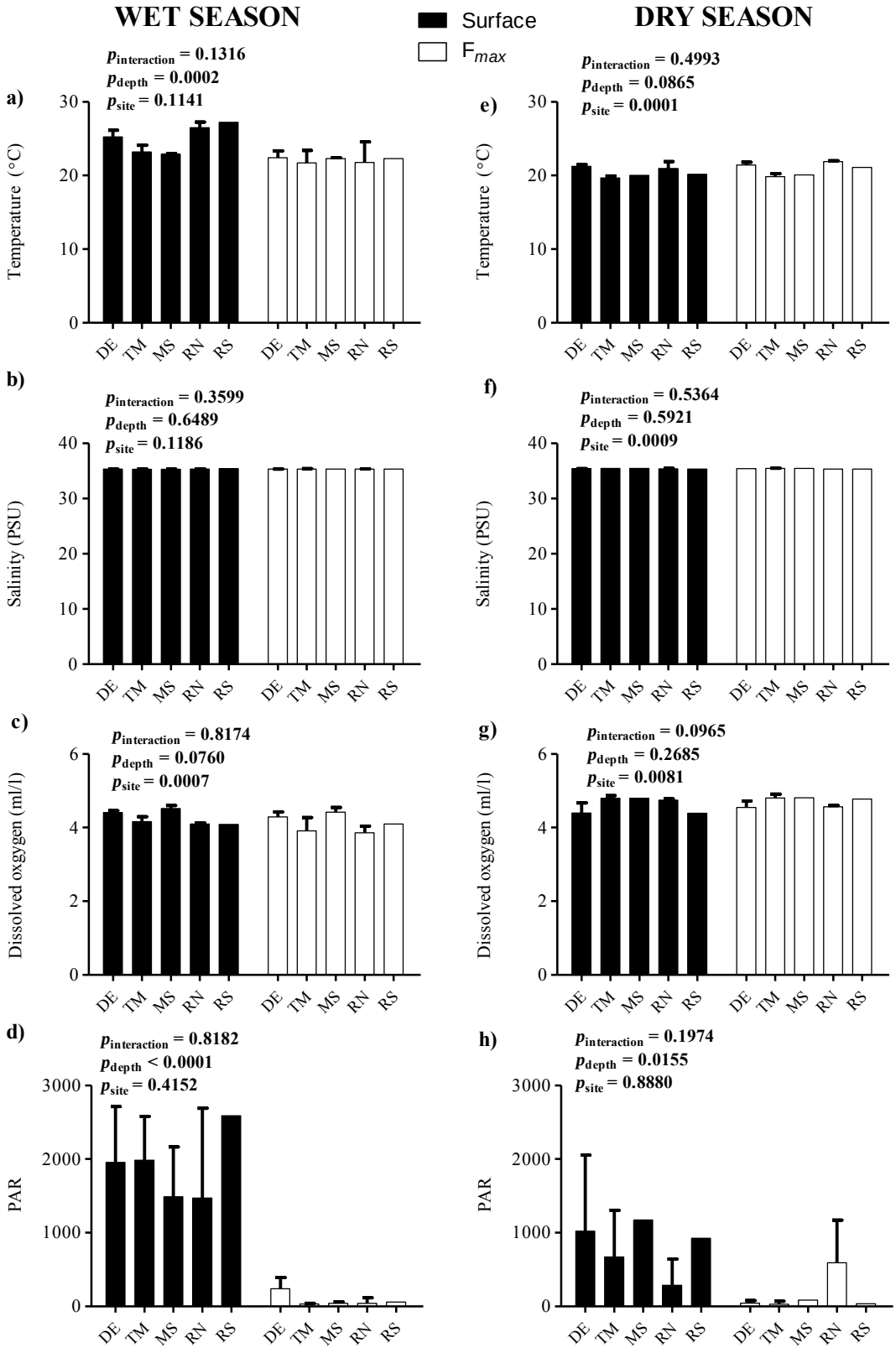

Figure 3.11. Bar graphs showing a) temperature (ºC), b) salinity (PSU), c) dissolved oxygen (ml.l^{-1}) and d) PAR with depth for the five focus sites of the KZN Bight for the wet season and showing e) temperature (ºC), f) salinity (PSU), g) dissolved oxygen (ml.l^{-1}) and h) PAR in the dry season.

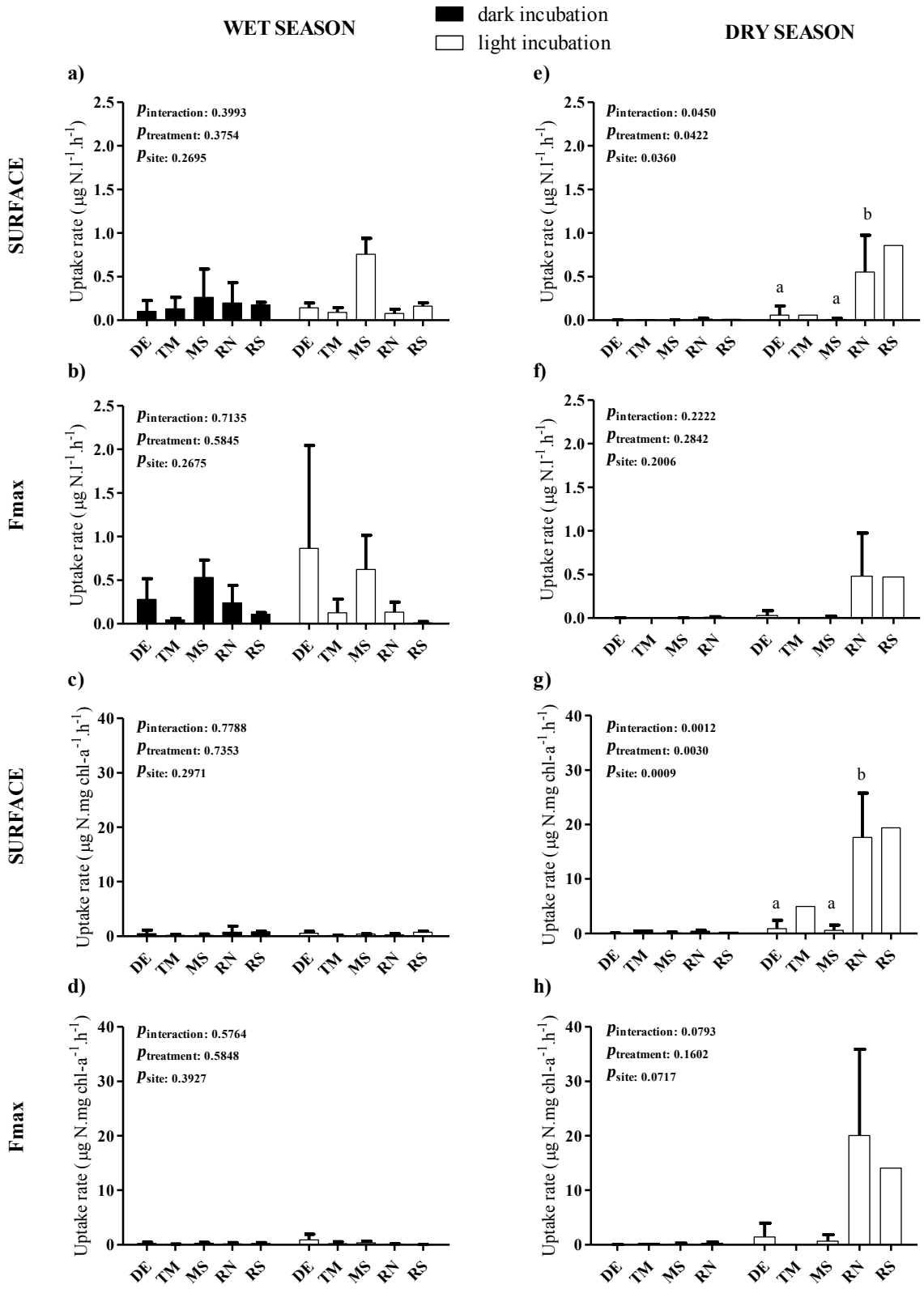

Figure 3.12. Nitrate uptake rates (µg N.l^{-1}.h^{-1}) for the dark and light incubations at the surface in the a) wet and e) dry season and the F$_{max}$ depth in the b) wet and f) dry season. Graphs indicating nitrate uptake rates (µg N. g chl-*a*$^{-1}$.h^{-1}) for the dark and light incubations at the surface in the c) wet and g) dry season and the F$_{max}$ depth in the d) wet and h) dry season. These graphs are for the focus areas (DE– Durban eddy, TM– Tugela mouth, MS– Mid shelf, RN– Richards Bay north, RS– Richards Bay south) of the KZN Bight.

rates by phytoplankton in high (> 20 µmol.l^{-1}) and low (< 5 µmol.l^{-1}) nitrate conditions. They determined an uptake range of 4 – 21 µg N.l^{-1}.h^{-1} in the high nitrate waters and an uptake range of 0.3 – 3.6 µg N.l^{-1}.h^{-1} in the low nitrate waters. The uptake rate range of latter, overlap with the range in the KZN Bight, reiterating the oligotrophic status of the Bight system.

When comparing nitrate uptake rates in the light incubations, no significant difference, in site and depth, for the wet season was determined (Figure 3.12a and 3.12c: p_{site}= 0.2189, p_{depth} = 0.5927). Once again, the lack of difference indicates well mixed waters in the wet season. Uptake rate by phytoplankton in the dry season showed a significant difference with site but not depth (Figure 3.12b and d: p_{site}= 0.0175, p_{depth} = 0.4709). Furthermore, no significant interactions between site and depth were found for both seasons (Figure 3.12b: $p_{interaction}$= 0.5031; Figure 3.12c: $p_{interaction}$= 0.9550).

3.2.3. The influence of environmental variables on nitrate uptake

Further comparison using multivariate statistics were used to provide a visual representation of the data. The principal component analysis completed showed no distinct pattern between sites for the wet season (Figure 3.13). There is a small grouping of the Tugela and mid shelf sites according to dissolved oxygen concentration, but generally the KZN Bight seems to be well mixed in this season (Figure 3.13). Alternatively, in the dry season, definite patterns are visible with the three areas sampled separating (Figure 3.14). The Richards Bay sites separate from the group with temperature. The Tugela mouth and mid shelf sites are found to have similar dissolved oxygen levels and salinity, which separates them from the other focus sites. The Durban eddy site is separated from the other focus sites due to its distinct nutrient concentrations. Figure 3.15 contains a combination of the environmental data for both wet and dry seasons and clearly shows the separation of the seasons with dissolved oxygen levels and temperature.

The biological components, including chlorophyll-*a* concentration and nitrate uptake rate, showed a similar pattern as the environmental parameters discussed. The wet season showed no strong distinction between the sites, while the dry season showed two very distinct groups (Figure 3.16 and 3.17). One group consisting of a combination of Richards Bay sites with the Tugela River mouth F_{max} and the mid shelf surface waters, while the other a combination of the Durban eddy sites, with the Tugela River mouth surface and mid shelf site F_{max} waters.

Nutrient uptake rate is influenced by several environmental factors such as temperature, light intensity, salinity, dissolved oxygen and nutrient concentration (Brylinsky and Mann, 1973; Richardson *et al*., 1983; Dortch, 1990; Borum and Sand-Jensen, 1996; Cochlan and Bronk, 2001; Kockum *et al*., 2002). The environmental factor, temperature, plays a role in productivity of phytoplankton (Paerl, 1988; Chenl and Durbin, 1994; Kockum *et al*., 2002). Production is positively influenced by temperature. The reason for this is that temperature influences enzymes that control the

rate of production (Paerl, 1988; Underwood and Kromkamp, 1999; Chenl and Durbin, 1994; Kockum *et al*., 2002). The effect of temperature is coupled with light and cannot be considered solely, as light has an influence on temperature. An increase in temperature, combined with a higher irradiance will normally produce a higher productivity rate (Falkowski and Stone, 1975; Chenl and Durbin, 1994; Kockum *et al*., 2002). Falkowski and Stone (1975) determined that the energy (in the form of ATP) that is used to take up NO_3^- is generated from light. This explains the relationship between productivity and light intensity, where an increase in irradiance will result in higher nitrate productivity. Light intensity can be affected by turbidity and depth; higher turbidity and lower depth would decrease irradiance, therefore decreasing productivity (Falkowski and Stone, 1975; Richardson *et al*., 1983; Chenl and Durbin, 1994; Kockum *et al*., 2002). Nutrient concentrations, temperature, PAR, salinity and dissolved oxygen were compared to determine which environmental variable correlated best with nitrate uptake rate. The BIOENV analysis found that PAR (r = 0.080) had the highest correlation with the biological components for the wet season, however this correlation was weak. Including the option of a maximum of five variables, it was still found that a combination of PAR, nitrite and phosphate concentration (r = 0.114) had the best correlation. For the dry season, it was established that salinity has the highest correlation with the biological components (r = 0.281) when allowing a maximum of one or five trial variables.

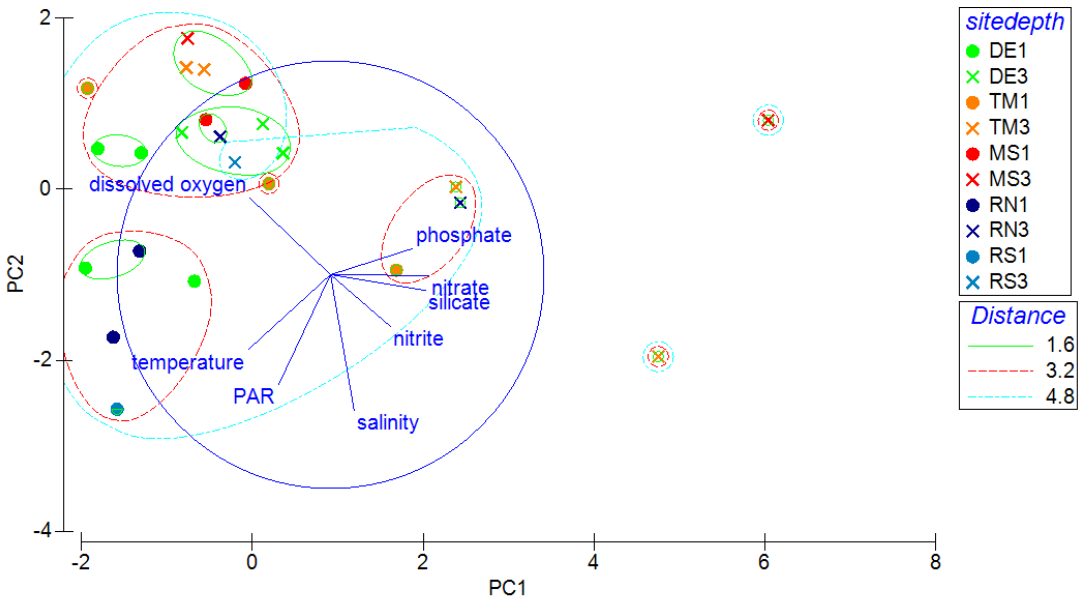

Figure 3.13. Principle component analysis representing the environmental factors for the focus sites (DE– Durban eddy, TM– Tugela mouth, MS– Mid shelf, RN– Richards Bay north, RS– Richards Bay south) and depths (1- surface, 3- F_{max}) in the KZN Bight for the wet season.

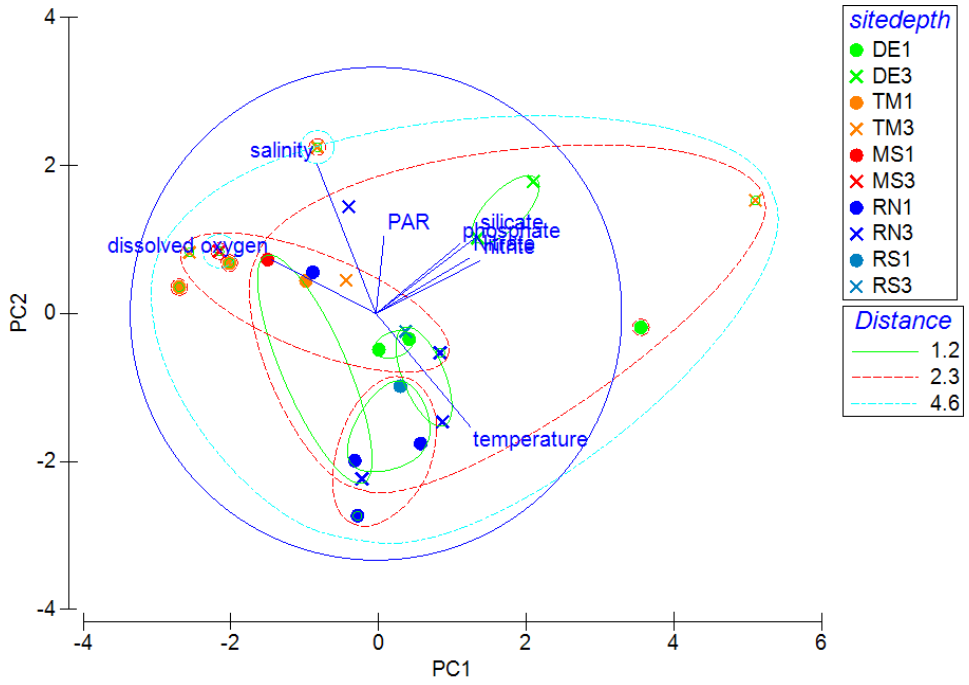

Figure 3.14. Principle component analysis representing the environmental factors for the focus sites (DE– Durban eddy, TM– Tugela mouth, MS– Mid shelf, RN– Richards Bay north, RS– Richards Bay south) and depths (1- surface, 3- F_{max}) in the KZN Bight for the dry season.

The literature has stated that an increase in nitrate concentration results in an increase in productivity (Brylinsky and Mann, 1973; Dortch, 1990; Borum and Sand-Jensen, 1996; Cochlan and Bronk, 2001; Kockum *et al*., 2002), but the BIOENV analysis found PAR and salinity to have the best correlation with uptake rate for the wet and dry season respectively. The hypothesis made that the input of nitrate from the oceanic processes and fluvial sources, on the KZN Bight, would result in an increase in productivity, can thus be rejected. This was because uptake rate was not correlated with nitrate concentration, which would have been expected if nitrate was the influencing factor. It is important to note that although there was a lack of correlation between nitrate and uptake rate, this could be result of nitrate having been removed from the waters by phytoplankton (Brylinsky and Mann, 1973; Dortch, 1990; Borum and Sand-Jensen, 1996; Cochlan and Bronk, 2001; Kockum *et al*., 2002).

Phytoplankton community structure will modulate an ecophysiological response to nutrient additions, although the literature does not seem to indicate that specific species compositions would influence nitrate uptake rate. According to Goldman and Gilbert (1982) most species increase uptake rate but decrease growth rate except for diatoms who are able to sustain high uptake and growth rates simultaneously. Silicate is not a limiting nutrient but would modulate nitrate uptake in diatoms (Kudela and Dugdale, 2000). A study conducted by Barlow *et al*. (unpublished) determined the species composition of the KZN Bight using pigment characteristic. They determined that the

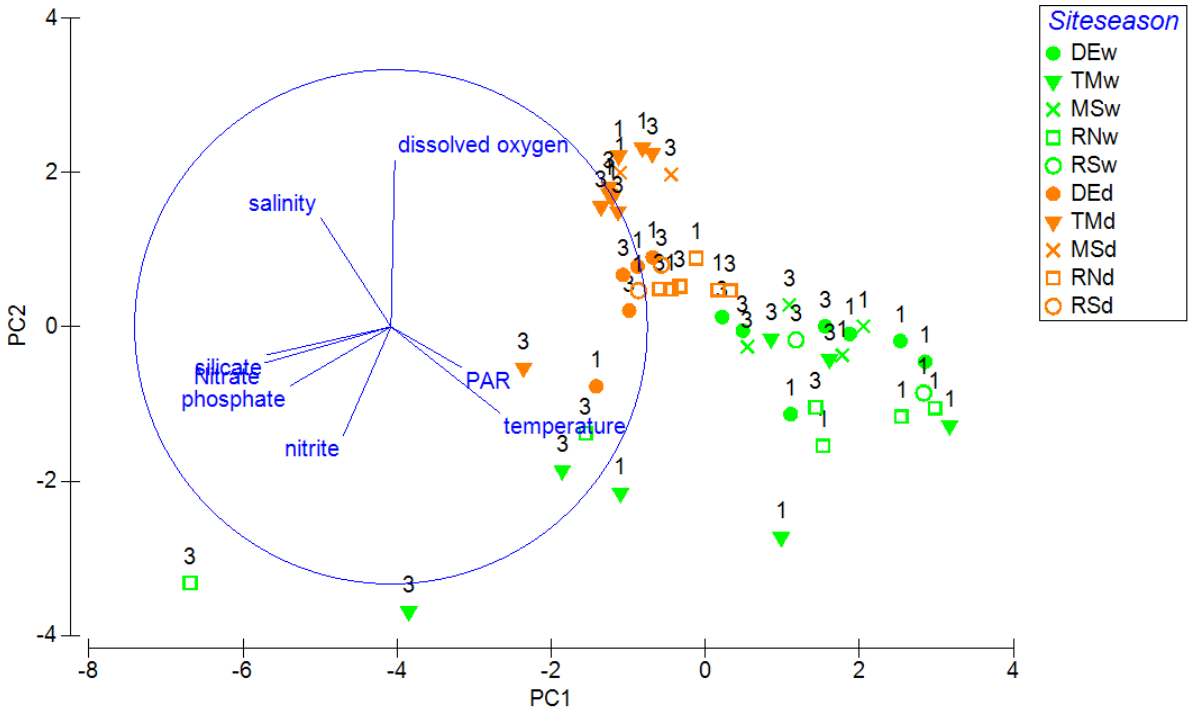

Figure 3.15. Principle component analysis representing the environmental factors for the focus sites (DE– Durban eddy, TM– Tugela mouth, MS– Mid shelf, RN– Richards Bay north, RS– Richards Bay south) in the KZN Bight for both the wet (W) and dry (D) season combined.

southerly sites, these include the Durban eddy, Tugela River mouth and mid shelf sites, were diatom dominated while the two northerly Richards Bay sites were dominated by small flagellates and prokaryotes. Diatoms and flagellates are associated with cooler lower salinity waters, which have usually been upwelled, while prokaryotes with warmer waters with higher salinities (Barlow *et al*., 2008). The separation between the northerly and southerly sites noted here reiterates the separation seen in the natural abundance results (from Section 3.1) as well as the nMDS plot above. The diatoms present in the southerly sites could be explained by the dissipating eddy noted in the wet season bringing up silicate into surface waters. The presence of prokaryotes could be indicative of terrestrial inputs in the Richards Bay area with flagellates signifying upwelled waters in the system.

The range of uptake rates found in the wet season corresponded with that found in the summer season in the Middle Atlantic Bight (Harrison *et al*., 1983). The mid shelf region had a higher chlorophyll-*a* biomass and uptake rate in the wet season, which would explain why it was grouped away from the other sites in the nMNDs analysis (Figure 3.16). For the dry season the nMDS ordination showed a high degree of separation between the northerly and southerly sites (Figure 3.17). This correlates to the statistics in the previous section which indicated a significant difference between uptake rates at Richards Bay north and the southerly sites. It is interesting to note that the drastic decrease in uptake rates in the southerly sites during the dry season, (Figure 3.16). This could indicate that the phytoplankton are not as productive in the dry season as their source of nutrients, in this season, is no

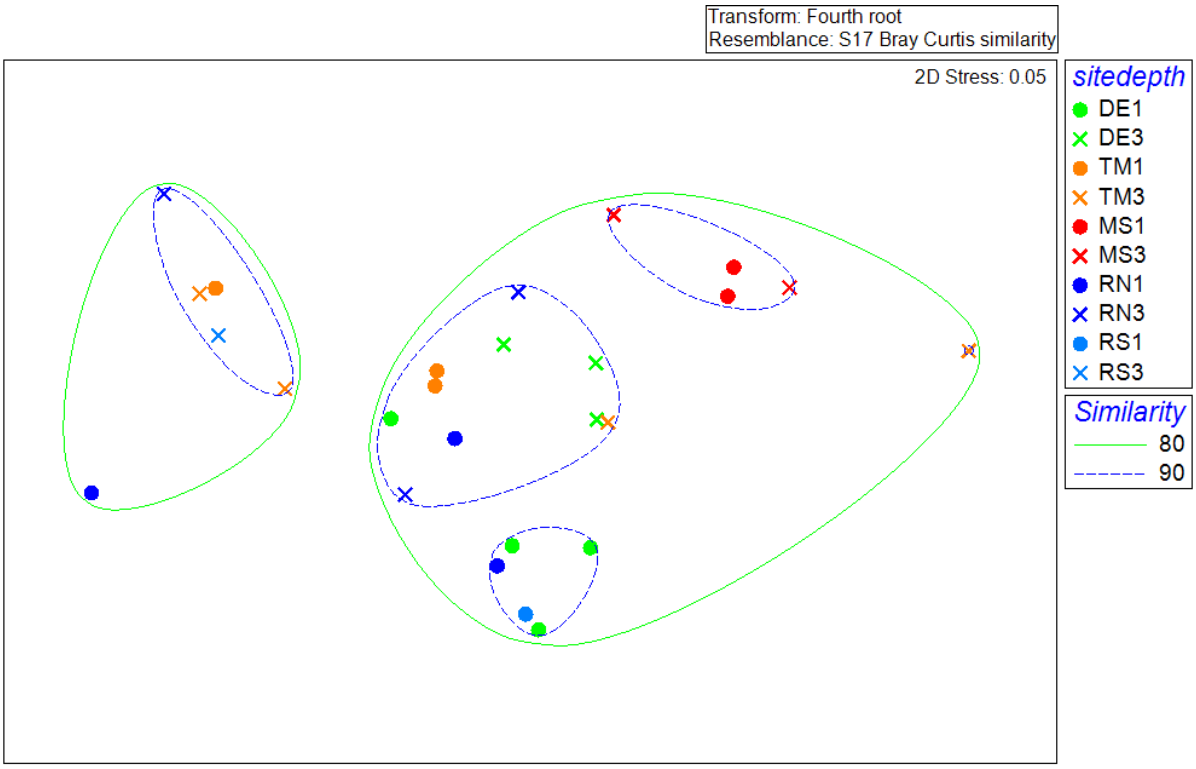

Figure 3.16. nMNDS ordination showing the difference in the biological components between sites and depth for the wet season at the focus sites (DE– Durban eddy, TM– Tugela mouth, MS– Mid shelf, RN– Richards Bay north, RS– Richards Bay south) and depths (1- surface, 3- F_{max}) of the KZN Bight.

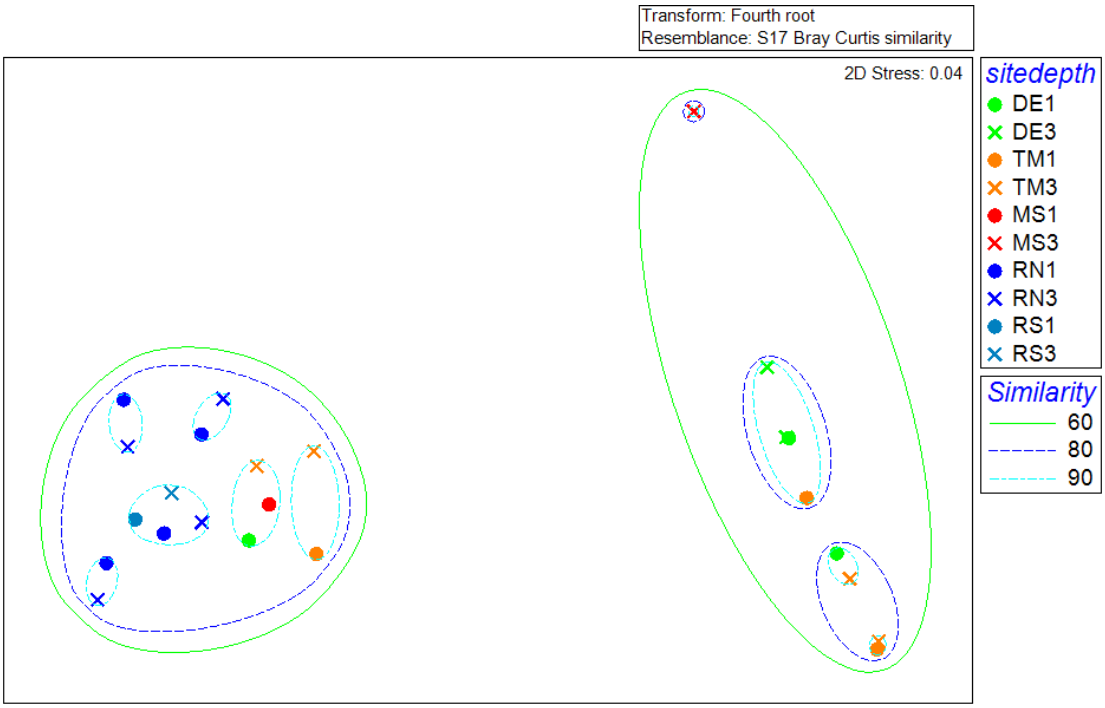

Figure 3.17. nMNDS ordination showing the difference in the biological components between sites and depth for the dry season at the focus sites (DE– Durban eddy, TM– Tugela mouth, MS– Mid shelf, RN– Richards Bay north, RS– Richards Bay south) and depths (1- surface, 3- F_{max}) of the KZN Bight.

longer available. This could be explained by the absence of fluvial sources of nutrients from the Tugela River and many other rivers entering the KZN coast, which decrease during the dry season.

The lack of differences between sites was not expected as it was predicted that the different nutrient sources at the different focus sites would influence the phytoplankton nitrate uptake rate. At the time of the experiment, neither the Durban eddy nor the upwelling cell was present. The absence of these major oceanic features could be a potential explanation for the lack of difference in uptake rate of phytoplankton between sites seen in the wet season. Another potential explanation for this is the homogenized waters, illustrated by the environmental parameters, found in the wet season (Figure 3.13).

The literature available indicates the relationship of nitrate productivity and ammonium concentrations to be inverse, where an increase in ammonium concentration results in a decrease in nitrate productivity (Dortch, 1990; Cochlan and Bronk, 2001; Kockum *et al*., 2002; Dugdale *et al*., 2007). This observation is qualified with the basis that ammonium has a lower energetic cost of assimilation than nitrate (Dortch, 1990; Cochlan and Bronk, 2001; Kockum *et al*., 2002; Dugdale *et al*., 2007). Unfortunately due to problems on the storage of the samples, no data on ammonium concentration was collected. However, ammonium uptake rate results are presented in Section 3.3, as ammonium uptake as an alternative to nitrate, still needs to be considered as a potential explanation for the lack of difference in uptake rate.

3.3. Daily comparison of ammonium and nitrate uptake at the focus sites

The daily comparison of biological parameters in the KZN Bight indicated that the mid shelf region experienced the highest uptake rate in the wet season, at 0.88 μg $N.l^{-1}.h^{-1}$ (Figure 3.18a). Although, when comparing uptake rate per gram chlorophyll-*a*, at approximately 0.94 μg N.mg chl-$a^{-1}.h^{-1}$, the Durban eddy site experienced the highest nitrate uptake rate (Figure 3.18b). The Richards Bay south area also showed a high uptake rate per gram chlorophyll-*a* at 0.9 μg N.mg chl-$a^{-1}.h^{-1}$ (Figure 3.18b). Chlorophyll-*a* biomass determined at the mid shelf site was almost double that found at the other study sites in KZN Bight (Figure 3.18c). Ammonium uptake rate was highest at the Richards Bay south site followed closely by the mid shelf site with uptake rates of 9.27 and 8.43 ng $N.l^{-1}.h^{-1}$, respectively (Figure 3.18d). The dry season, on average, showed a lower nitrate uptake rate for all focus sites except for both the Richards Bay sites, which experienced upta e rates of 1.17 μg $N.l^{-1}.h^{-1}$ in the north and 0.86 μg $N.l^{-1}.h^{-1}$ in the south (Figure 3.19a). The Richards Bay area, both the north and south focus sites, also had the highest chlorophyll-*a* biomass and also the highest ammonium uptake rate in the dry season (Figure 3.19c and d). At the Durban eddy and mid shelf sites, it appears that phytoplankton in these regions were taking up ammonium up preferentially over nitrate, in the dry season (Figure 3.19a and d).

The daily perspective of the data clearly indicated high chlorophyll-*a* biomass and uptake rates in the mid shelf area. This mimics the results of high primary production found by Barlow *et al*. (unpublished) in the mid shelf with at a range of 7.22 – 9.89 g C. $m^{-2}.d^{-1}$. The nutrients in this area could be from three potential sources. Firstly, as fluvial inputs from the Tugela River moving onto the shelf, secondly from upwelling in the north of the Bight driven south with the Agulhas current and lastly as a result of the newly proposed "swirl" oceanographic feature in the mid shelf area itself. Although the exact source cannot be confirmed, looking at the data presented in the first section, a visual representation of the outflow of the Tugela on the mid shelf area is seen, as well as the natural abundance data, indicated a terrestrial nutrient source. Phytoplankton at the Richards Bay sites indulged in ammonium, as well as nitrate as a source of nitrogen. Eppley *et al*. (1969) found that ammonium was preferentially taken up over nitrate, until the concentration of ammonium in the water drops below 0.5 μmol.l^{-1}. This is because it is requires less energy to be converted to proteins compared to nitrate. Probyn *et al*. (1995) measured a maximum ammonium concentration of 25 μg.l^{-1} along the Eastern Agulhas Bank. The paper indicated the higher ammonium concentration and thus uptake in the region is likely due an oceanic processes upwelling nutrients. It is important to note the persistent presence of the "bloom" in both wet and dry season, for all days, is indicative of a constant nutrient source as opposed to a short term process. In oceanic waters, with no pollution, ammonium concentrations are relatively low compared to other nutrients (Morris, 1980). The slightly elevated levels could be explained by effluent discharge from pipelines that may play a role in adding nutrients into the system. However, in the context of the greater KZN Bight area its role is most likely minute.

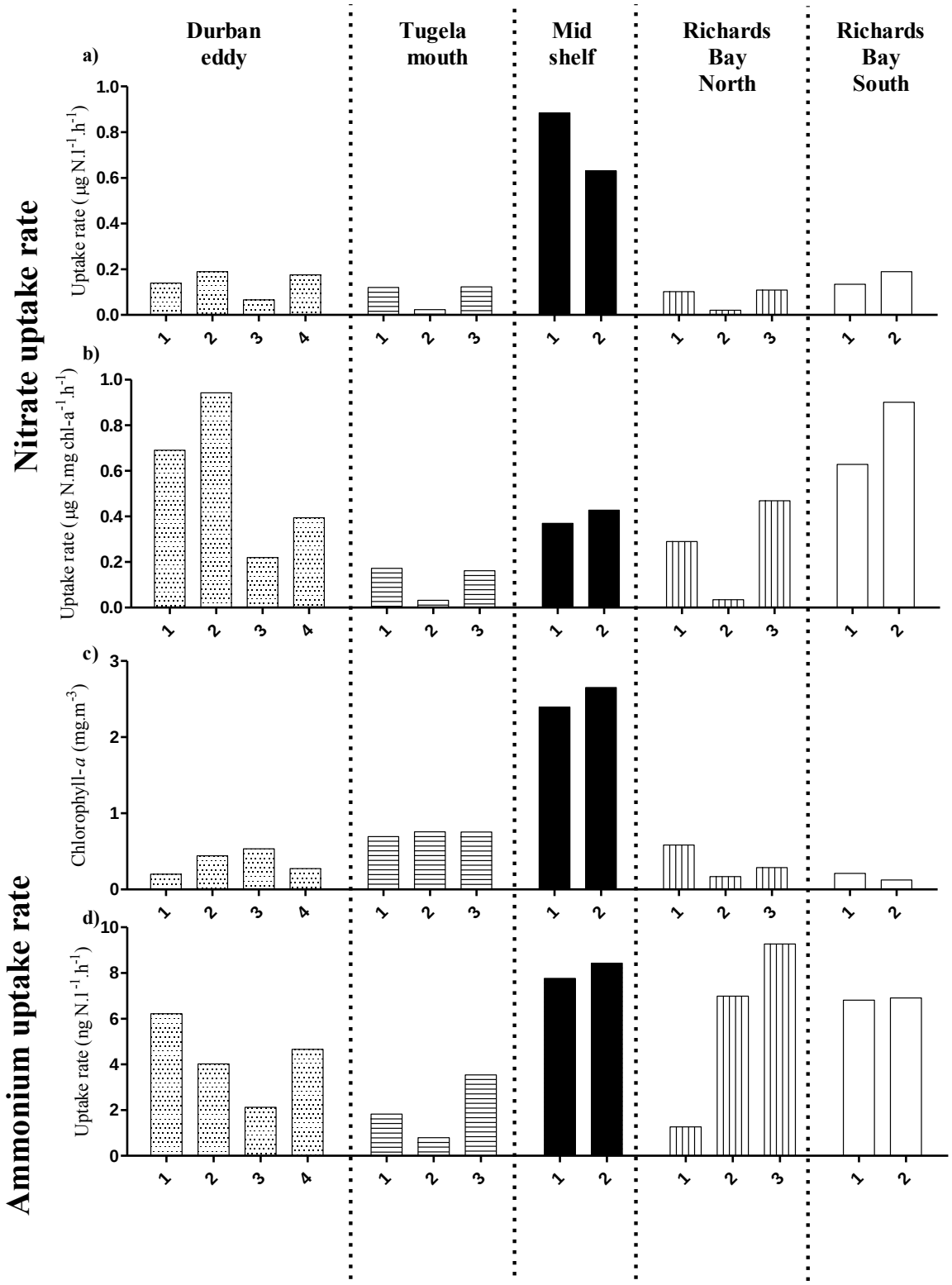

Figure 3.18. Surface water comparison of daily a) nitrate uptake rates (µg N.l.h^{-1}) b) uptake rates taking into account chlorophyll-*a* (µg N.g chl-*a*$^{-1}$.h^{-1}) c) chlorophyll-*a* (mg.m^{-3}) d) ammonium uptake rate (ng N.l.h^{-1}) in the focus areas of the KZN Bight for the wet season.

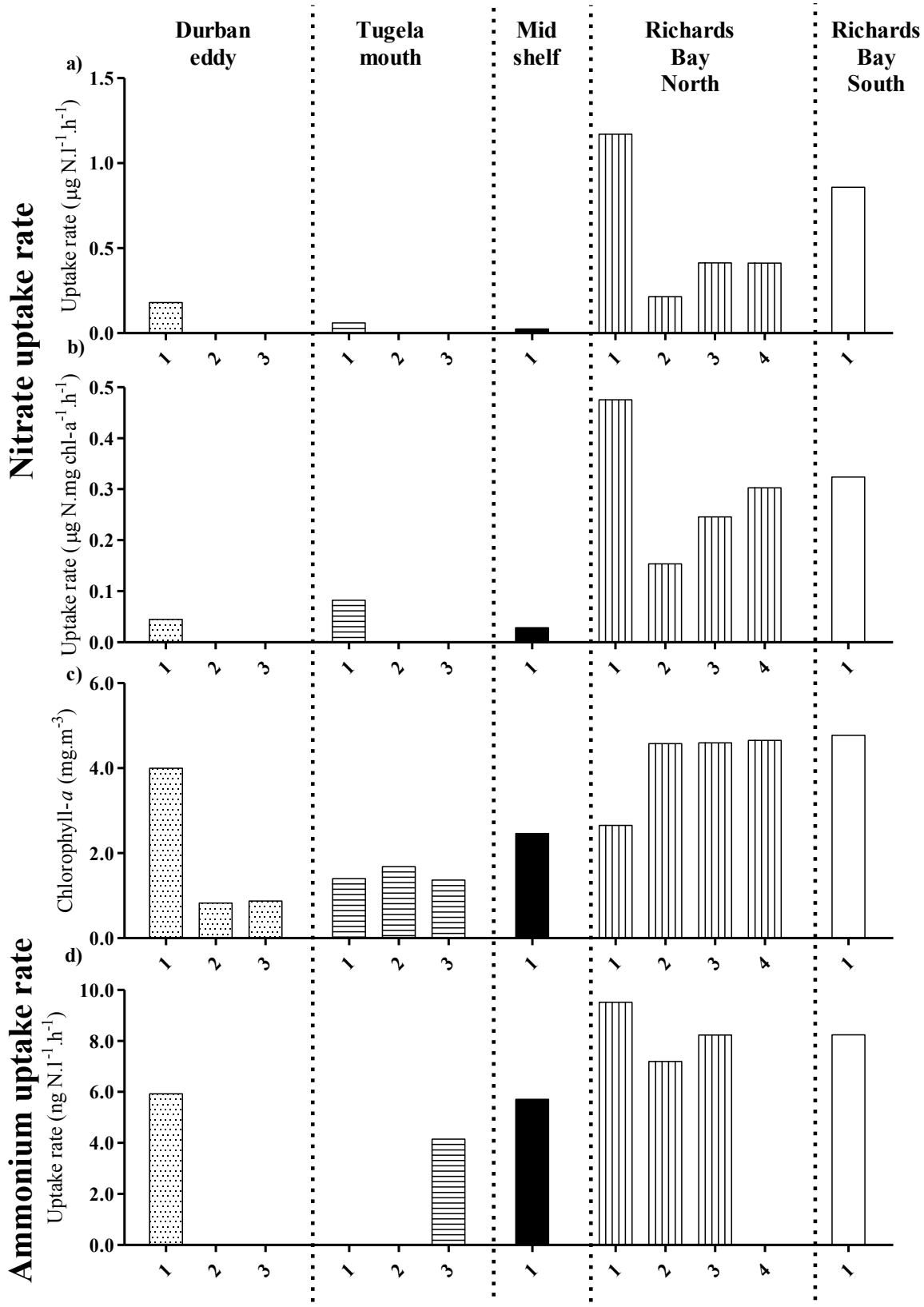

Figure 3.19. Surface water comparison of daily a) nitrate uptake rates (µg N.l.h^{-1}) b) uptake rates taking into account chlorophyll-a (µg N.g chl-a^{-1}.h^{-1}) c) chlorophyll-*a* (mg.m^{-3}) d) ammonium uptake rate (ng N.l.h^{-1}) for the focus areas of the KZN Bight in the dry season.

4. CONCLUSION

To recap, previous studies in the KZN Bight system described it as an area with a wide and shallow continental shelf subjected to the outflow of 73 rives and estuaries and bounded by the Agulhas system bringing nutrient rich waters on to the shelf. With this knowledge ACEP II developed five basic aims: 1) to investigate how the transport of nutrients and sediment across the KZN Bight are facilitated by physical oceanographic and geological processes; 2) to determine the relative importance of material derived from fluvial processes and those originating from the Agulhas Current – the St Lucia upwelling and cyclonic Durban lee eddy - on the KZN Bight; 3) to define the ecology and determine the biodiversity on the shelf; 4) to establish levels of assimilation, recycling and transformation of materials in the KZN Bight; 5) and to integrate the data collected into a combined bio-energetic ecosystem model. From these aims, the aims of my project were derived.

There were three aims in this study: 1) to determine the distribution of POM along the KZN Bight; 2) to examine the influence of fluvial and oceanic nutrient sources on phytoplankton ecophysiology; 3) to see daily results of both uptake and chlorophyll-*a* concentration, providing an understanding of the oceanographic processes which drive productivity in the KZN Bight. To summarise the results associated with these aims, the first hypothesis was testing if chlorophyll-*a* biomass would result in an increase in POM. This hypothesis was neither rejected nor accepted due to inconclusive patterns noted. However, a distinct pattern with season was noted, with a higher POM biomass noted in the wet rather than in the dry season. The second hypothesis, that the input of nitrate from the oceanic processes and fluvial sources, on the KZN Bight, would result in an increase in productivity was rejected, because there were no strong correlations between the nutrient and uptake rate. The last section of the results looking at a daily perspective of uptake rate in the KZN Bight, found no distinct differences between days but a difference between sites and seasons was noted. Overall, the KZN Bight maintains a notable diatom dominated biomass of phytoplankton spread over the area that is able to support the system (Barlow *et al*., unpublished). The southerly sites seem to be driven by another nitrate source compared to the northerly sites as it experienced a higher uptake rate in the dry season whereas the southerly sites experienced higher nitrate uptake in the wet season. Furthermore, there seems to be a source of ammonium in the Richards Bay area present in both the wet and dry season allowing for ammonium uptake in the region.

The overall aim of this project was to provide an insight into which nutrient source is driving phytoplankton productivity in the KZN Bight. These results, as summarised above, points in the direction that terrestrial sources play a major role in influencing nutrient concentrations on the KZN Bight in the wet season. The difference in uptake rate in the northerly sites between the wet and dry season reiterate that these areas productivity is fuelled by terrestrially sourced nutrients. This is not a

new idea, as the theory that estuaries produce more dissolved and particulate matter than can be used or decomposed in that surrounding and that they export this matter into the coastal marine environment, is nown as the "outwelling" hypothesis (Winter and Baird, 1991). A study in the Swartkops Estuary concluded that it played a role in outwelling and was able to support productivity on the inshore regions of the coast (Baird, 1987). Later studies by Winter *et al*. (1996) concluded that 4755 tons of carbon was exported from the Swartkops Estuary annually, which would then be available for primary production in the coast. Later literature found that inputs from nutrient rich estuaries are likely to promote primary production in phytoplankton (Whitfield and Bates, 2007). However, Whitfield and Bates (2007) went on to state that further work needs to be conducted in the surf-zone to determine the true influence of the estuaries. Fisheries studies in the KZN Bight area have also hypothesised that the Tugela River has a major influence on productivity in the system (Lambert *et al*., 2009; Hutchings *et al*., 2010).

The terrestrial sources of nutrients could either be naturally, such as the Tugela and the many other rivers in the KZN Bight area or anthropogenically, from one of the many outlet pipes discharging in the KZN Bight area, as often algal blooms can be seen along the plumes at these pipes (Lutjeharms *et al*., 2000). Further work needs to be conducted in order to confirm these conclusion as the volume flowing from these pipes may be miniscule when taking into account the grater Bight area. Natural abundance of isotopes should be collected from within the estuary, the surf zone and further offshore, as well as from the effluent pipes and all would need to be compared. This will provide a clear indication of the influence of terrestrial sources and further, whether it is the outflow of rivers or of the effluent that is playing a major role in influencing phytoplankton biomass in the region. Furthermore, studies need to be conducted when the eddy at Durban and the upwelling at Richards Bay are present. These results could be compared with results from this study and would help clarify the true influence of these oceanic processes on the production within the KZN Bight.

In summary, the phytoplankton within the KZN Bight system are adapted to a variable environment. **T**he KZN Bight is an oligotrophic environment that receives spurts of nutrients throughout the year from oceanographic processes and a large input of nutrients from terrestrial inflow, mainly during the wet season (Lutjeharms *et al*., 2000, Lutjeharms, 2006). These inputs, influencing productivity in the region are most likely from natural fluvial inputs. However, to confirm this and to determine the magnitude of the influence further work needs to be conducted in the KZN Bight area.

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5. REFERENCES

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APPENDICES

6. APPENDIX A

Table 6.1. Station numbers and position of the synoptic sampling sites.

station grid #	latitude DMS			longitude DMS			Decimal degrees	
	deg	min	sec	deg	min	sec	latitude	longitude
1-1	30	18	6.1200	30	46	51.6000	-30.3017	30.7810
1-3	30	21	6.5454	30	51	28.8776	-30.3518	30.8580
1-5	30	27	7.3922	31	0	43.7862	-30.4521	31.0122
2-1	30	8	34.8000	30	51	45.0000	-30.1430	30.8625
2-3	30	11	35.2298	30	56	21.8326	-30.1931	30.9394
2-5	30	17	36.0853	31	5	35.8484	-30.2934	31.0933
2-6	30	20	36.5110	31	10	13.0673	-30.3435	31.1703
3-1	29	59	52.8000	30	57	42.1200	-29.9980	30.9617
3-3	30	2	53.2338	31	2	18.5491	-30.0481	31.0385
3-5	30	8	54.0973	31	11	31.7553	-30.1484	31.1922
3-7	30	14	54.9553	31	20	45.5205	-30.2486	31.3460
4-1	29	53	45.6000	31	3	39.6000	-29.8960	31.0610
4-4	29	59	46.4718	31	12	51.9978	-29.9962	31.2144
4-8	30	11	48.1990	31	31	18.3913	-30.1967	31.5218
6-1	29	43	15.6000	31	7	19.2000	-29.7210	31.1220
6-5	29	52	16.9200	31	21	6.5425	-29.8714	31.3518
6-9	30	4	18.6609	31	39	31.5512	-30.0719	31.6588

station grid #	latitude DMS			longitude DMS			Decimal degrees	
	deg	min	sec	deg	min	sec	latitude	longitude
7-1	29	34	30.0000	31	12	32.4000	-29.5750	31.2090
7-5	29	43	31.3320	31	26	18.5468	-29.7254	31.4385
7-9	29	55	33.0890	31	44	41.9474	-29.9259	31.7450
8-1	29	26	6.0000	31	18	56.1600	-29.4350	31.3156
8-5	29	35	7.3434	31	32	41.1686	-29.5854	31.5448
8-9	29	47	9.1157	31	51	3.0384	-29.7859	31.8508
9-1	29	18	25.5600	31	26	33.0000	-29.3071	31.4425
9-5	29	27	26.9139	31	40	16.9757	-29.4575	31.6714
9-9	29	39	28.7000	31	58	37.4564	-29.6580	31.9771
10-1	29	12	36.0000	31	34	22.8000	-29.2100	31.5730
10-5	29	21	15.1344	31	47	11.0279	-29.3542	31.7864
10-9	29	33	16.9318	32	5	30.3935	-29.5547	32.0918
11-1	29	4	37.2000	31	42	10.8000	-29.0770	31.7030
11-3	29	7	37.6589	31	46	44.7340	-29.1271	31.7791
11-7	29	19	39.4809	32	5	1.6682	-29.3276	32.0838
12-1	29	0	3.6000	31	54	3.6000	-29.0010	31.9010
12-5	29	9	4.9786	32	7	45.1308	-29.1514	32.1292
12-7	29	15	5.8910	32	16	53.4600	-29.2516	32.2815

station grid #	latitude DMS			longitude DMS			Decimal degrees	
	deg	min	sec	deg	min	sec	latitude	longitude
13-1	28	54	48.0000	32	3	48.0000	-28.9133	32.0633
13-3	28	58	24.0000	32	9	48.0000	-28.9733	32.1633
13-6	29	5	12.4599	32	20	33.7943	-29.0868	32.3427
14-1	28	46	19.2000	32	10	30.0000	-28.7720	32.1750
14-3	28	49	19.6671	32	15	3.1331	-28.8221	32.2509
14-5	28	55	20.5972	32	24	9.7265	-28.9224	32.4027
15-1	28	39	25.2000	32	18	46.8000	-28.6570	32.3130
15-3	28	42	25.6701	32	23	19.6344	-28.7071	32.3888
15-5	28	48	26.6063	32	32	25.6283	-28.8074	32.5405
16-1	28	31	12.0000	32	25	8.4000	-28.5200	32.4190
16-3	28	31	12.0000	32	30	48.9606	-28.5200	32.5136
16-6	28	31	12.0000	32	39	19.8015	-28.5200	32.6555

7. APPENDIX B

Table 7.1. The position of the focus sites sampled.

station	latitude DMS			longitude DMS			Decimal degrees	
	deg	min	sec	deg	min	sec	latitude	longitude
Durban eddy	29	55	28.5600	31	9	18.3600	-29.9246	31.1551
Tugela mouth	29	16	48.8400	31	40	38.2800	-29.2794	31.6773
Mid shelf	29	27	26.2800	31	40	18.1200	-29.4573	31.6717
Richards Bay north	28	40	30.0000	32	18	43.2000	-28.6750	32.3120
Richards Bay south	29	6	25.2000	32	2	42.0000	-29.1070	32.0450

8. APPENDIX C

Table 8.1. The number of days samples at the focus sites of the KZN Bight for cruises completed in the wet and dry seasons.

Wet season cruise	# of days sampled	Dry season cruise	# of days sampled
Durban eddy	4	**Durban eddy**	3
Tugela mouth	4	**Tugela mouth**	3
Mid shelf	2	**Mid shelf**	1
Richards Bay north	3	**Richards Bay north**	4
Richards Bay south	2	**Richards Bay south**	1

9. APPENDIX D

Table 9.1. The F_{max} depths for sites sampled in the focus leg of the wet season.

Grid #	Depth [m]
DE-001	35
DE-002	38
DE-003	35
DE-004	30
DE-005	45
DE-006	29
DE-007	20
DE-008	24
DE-009	19
DE-010	24
TM-001	19
TM-002	15
TM-003	20
TM-004	16
TM-005	15
TM-006	15
MS-001	21
MS-002	22
MS-003	18
MS-004	20
MS-005	15
RN-001	21
RN-002	20
RN-003	33
RN-004	33
RN-005	32
RN-007	34

RS-001	43
RS-002	51
RS-003	52
RS-004	65
RS-005	65
RS-006	50

Table 9.2. The F_{max} depths for sites sampled in the focus leg of dry season.

Grid #	Depth [m]
DE-004	21
DE-006	26
DE-010	24
TM-002	11
TM-004	17
TM-006	11
MS-001	36
MS-002	20
RN-002	15
RN-004	18
RN-006	18
RS-003	26

10.APPENDIX E

Table 10.1. The breakdown of the equations used to calculate nitrate uptake rate.

parameter	unit	equation	reference	variables	unit
PN (Particulate organic nitrogen at T_0)	µg N			Given	
t (time incubated)	hrs	t_6-t_0			
R_t (^{15}N atom % in the seawater at T_t)	At%	$\text{At \%} \quad \frac{\left(100 \quad R_{std} \quad \left[\frac{\delta_{sam}}{1000} \quad 1\right]\right)}{\left(1 \quad \left[R_{std} \quad \left\{\frac{\delta_{sam}}{1000} \quad 1\right\}\right]\right)}$			
k		$- \frac{\ln\left(\frac{R_t}{R_0}\right)}{t}$	Gilbert *et al*., 1982	R_t	At%
				T	hrs
Spike of ^{15}N into the bottle at T_0					
F (Fractional abundance of the spike)		$^{13}F \quad ^{15}N\left(^{1} \quad N \quad ^{15}N\right)$	Hayes, 2004		
Molar concentration of the spike	µmoles	$m_x \quad \frac{m \ (F \quad F \ )}{m \ (F \quad F \ )}$ Where k = spike x = sample m = moles	Hayes, 2004	Spike of ^{15}N into the bottle at T_0	
				F	
Natural abundance of nitrogen in particulate fraction at T_0	δ	$\delta_{sam} \quad \left(\left[\frac{R_{sam}}{R_{std}}\right] \quad 1\right) \quad 1000$		Given – from filters	
Molar concentration of the seawater at T_0	µmol.l			Given – from ammonium diffusion	
R_0	δ	$\delta_{sam} \quad \left(\left[\frac{R_{sam}}{R_{std}}\right] \quad 1\right) \quad 1000$		Molecular concentration of the seawater at T_0	µmol.l^{-1}
				Natural abundance of nitrogen in particulate fraction at T_0	δ
				Molecular concentration of the spike	µmoles
R_0 (^{15}N in seawater at T_0)	At%	$\text{At \%} \quad \frac{\left(100 \quad R_{std} \quad \left[\frac{\delta_{sam}}{1000} \quad 1\right]\right)}{\left(1 \quad \left[R_{std} \quad \left\{\frac{\delta_{sam}}{1000} \quad 1\right\}\right]\right)}$		R_0	δ
R		$R \quad \frac{R_0}{t}(1 \quad \exp[\quad t])$	Gilbert *et al*., 1982	R_0	At%
^{15}N atom % of particulate at t_0	At%	$\text{At \%} \quad \frac{\left(100 \quad R_{std} \quad \left[\frac{\delta_{sam}}{1000} \quad 1\right]\right)}{\left(1 \quad \left[R_{std} \quad \left\{\frac{\delta_{sam}}{1000} \quad 1\right\}\right]\right)}$		From filter	
^{15}N atom % of the particulate nitrogen at t_6	At%	$\text{At \%} \quad \frac{\left(100 \quad R_{std} \quad \left[\frac{\delta_{sam}}{1000} \quad 1\right]\right)}{\left(1 \quad \left[R_{std} \quad \left\{\frac{\delta_{sam}}{1000} \quad 1\right\}\right]\right)}$		From fiter	
atom % excess	At%	$A\%E \quad \text{atom \%}_{sample} \quad \text{atom \%}_{substrate}$	Gilbert *et al*., 1982	^{15}N atom % of particulate at t_0	At%
				^{15}N atom % of the particulate nitrogen at t_6	At%
P –Nitrate uptake rate	µg N.l^{-1}/h^{-1}	$\left(\frac{^{15}\text{N atom \% excess}}{R \quad \text{time of incubation}}\right) \quad PN$	Gilbert *et al*., 1982	atom % excess	At%
				R	
				T	hrs
				PN	µg N