

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

**Bio-optical
investigation of
Phytoplankton Production in
the
southern Benguela
ecosystem**

by

Tarron Lamont

Thesis Presented for the Degree of
DOCTOR OF PHILOSOPHY

**Department of Oceanography
University of Cape Town**

August 2011



Supervisors: Dr. R.G. Barlow (Bayworld Centre for Research & Education)
Prof. F.A. Shillington (University of Cape Town)

Acknowledgements

I have the pleasure of expressing my gratitude to the following individuals, without whose contribution, this work would not have been possible:

My supervisors, Dr. Ray Barlow (Bayworld Centre for Research and Education – BCRE), and Prof. Frank Shillington (University of Cape Town – UCT) provided unwavering support and guidance throughout this study.

The officers and crew of the *F.R.S. Africana* provided excellent and efficient support during the research surveys.

The technical staff of DEA: Oceans & Coasts, especially Heather Sessions, Hassan Ismail, and Kobus Britz, provided assistance with laboratory analyses.

Financial support for this study was provided by the Benguela Environment Fisheries Interaction and Training (BENEFIT) Program, the National Research Foundation (NRF), and the Oceans and Coastal Research branch of the Department of Environmental Affairs (DEA).

Special thanks goes to my family (Marcel, Jason, Shannon, Jean-Pierre, and Renardo) whose continual love, encouragement, and patience with my moods and complaints, gave me the strength which supported me throughout this adventure. Mom, wherever you are, I hope this see this. I finally did it!

Table of Contents

Acknowledgements	i
Table of Contents	ii
List of Figures	iv
List of Tables	vii
Abstract	viii
Chapter 1 – General Introduction	1
1.1. Rationale and Key Questions.....	3
1.2. Thesis Structure	6
1.3. Review of the Southern Benguela ecosystem	7
1.3.1. Hydrography	7
1.3.2. Phytoplankton Biomass and Composition.....	10
1.3.3. Primary Production	12
1.3.4. Factors affecting Phytoplankton Biomass and Primary Production	14
Chapter 2 – In situ Phytoplankton Production and Physiology	21
2.1. Introduction.....	21
2.2. Methods	25
2.2.1. Study area and sampling	25
2.2.2. Phytoplankton biomass and Pigment composition	26
2.2.3. Phytoplankton light absorption coefficients	30
2.2.4. Irradiance at the sea surface and in the water column	30
2.2.5. Photosynthesis-Irradiance (P-E) experiments	31
2.2.5.1. Irradiance in the incubator	33
2.2.5.2. Photosynthesis-Irradiance (P-E) parameters	33
2.2.6. Primary Production estimation	37
2.3. Results and Discussion	38
2.3.1. Hydrography	38
2.3.2. Phytoplankton biomass, Pigment composition, and Primary Production.....	46
2.3.3. Photosynthetic Parameters	51
2.3.4. Relationships between Photosynthetic parameters and Environmental variables	58
2.3.5. Relationships between Phytoplankton biomass, Primary Production, and the environment.....	62
2.4. Summary and Conclusions	67
Chapter 3 – Comparison of in situ and satellite-derived Primary Production	69
3.1. Introduction.....	69

3.2. Methods	72
3.2.1. Hydrographic and Primary Production measurements	72
3.2.1. Primary Production Modelling.....	72
3.3. Results and Discussion	74
3.3.1. PP estimated using in situ data.....	74
3.3.2. PP estimated using ocean colour data	78
3.4. Summary and Conclusions	80
Chapter 4 – Long-term patterns of remotely-sensed Primary Production	81
4.1. Introduction.....	81
4.2. Methods	83
4.3. Results	85
Sea Surface Temperature	85
Chlorophyll <i>a</i>	89
Primary Production	92
4.3. Discussion and Conclusions	97
Seasonal and Latitudinal Variability	97
Interannual Variability	99
Chapter 5 – Discussion	103
Bibliography	111

List of Figures

Figure 1.1. The Benguela Ecosystem (from Shannon 2006).	8
Figure 2.1. Idealised curve of specific photosynthetic rate as a function of irradiance. The maximum photosynthetic rate, P_s , light saturation parameter, E_k , the quantum efficiency of photosynthesis, α , and the coefficient of photoinhibition, β , are indicated.	22
Figure 2.2. Maps illustrating the distribution of PP stations across the southern Benguela during (a) October 2006, and (b) May 2007. ETOPO2 bathymetry contours are indicated as black dotted lines.	25
Figure 2.3. Emission spectrum for the tungsten-halogen lamp.	36
Figure 2.4. Maps of weekly averaged (a, b) MODIS Aqua Sea Surface Temperature ($^{\circ}\text{C}$), and (c, d) Quikscat wind speed (m s^{-1}) for the southern Benguela during October 2006. ETOPO2 bathymetry contours (50, 100, 200, 300, 400, and 500 m) are indicated as black dotted lines. The white diamonds on (a, b) indicate the locations of the primary production stations. The arrows on (c, d) indicate the wind direction.	39
Figure 2.5. Maps of weekly averaged (a, b) MODIS Aqua Sea Surface Temperature ($^{\circ}\text{C}$), and (c, d) Quikscat wind speed (m s^{-1}) for the southern Benguela during May 2007. ETOPO2 bathymetry contours (50, 100, 200, 300, 400, and 500 m) are indicated as black dotted lines. The white diamonds on (a, b) indicate the locations of the primary production stations. The arrows on (c, d) indicate the wind direction.	40
Figure 2.6. Weekly averaged geostrophic currents overlaid onto sea surface height anomalies for (a) 15 – 21 October 2006, and (b) 22 – 28 October 2006. ETOPO2 bathymetry contours (50, 100, 200, 300, 400, and 500 m) are indicated as black dotted lines. The white diamonds indicate the locations of primary production stations.	41
Figure 2.7. Vertical temperature ($^{\circ}\text{C}$) distribution along a transect through the PP stations during (a) October 2006, and (b) May 2007. The white line across each profile indicates the depth of the euphotic zone (z_{eu}).	42
Figure 2.8. Relationship between the depth of the euphotic zone (z_{eu}) and the upper mixed layer depth (z_{uml}). The solid black line indicates where $z_{\text{eu}} = z_{\text{uml}}$	44
Figure 2.9. Profiles of inorganic nitrogen and silicate (mmol m^{-3}) at PP stations during October 2006 and May 2007.	45
Figure 2.10. Integrated total chlorophyll <i>a</i> (TChl <i>a</i>) concentration (mg m^{-2}) and integrated primary production ($\text{g C m}^{-2} \text{d}^{-1}$) at primary production stations during October 2006 and May 2007.	49
Figure 2.11. Integrated Diagnostic and Photo-Pigment indices at primary production stations during October 2006 and May 2007.	50

Figure 2.12. Map indicating the position of stations where dark bottle disintegrations per minute (DPM) contributed significantly to light bottle DPM's. ETOPO2 bathymetry contours are indicated as thin black lines.	51
Figure 2.13. Relationship between P_s^B (mg C [mg chla] ⁻¹ h ⁻¹) and α^B (mg C [mg chla] ⁻¹ h ⁻¹ [μmol m ⁻² s ⁻¹] ⁻¹) for all stations sampled during October 2006 and May 2007, (a) including outliers, and (b) excluding outliers. The solid line indicates the relationship for October, while the dashed line indicates the relationship for May.	52
Figure 2.14. Vertical profiles of TChla (mg m ⁻³) and photosynthesis rates (mg C m ⁻³ h ⁻¹) for all stations sampled during October 2006 and May 2007.	56
Figure 2.15. Vertical profiles of photosynthetic parameters, α^B (mg C [mg chla] ⁻¹ h ⁻¹ [μmol m ⁻² s ⁻¹] ⁻¹), P_s^B (mg C [mg chla] ⁻¹ h ⁻¹), and E_k (μmol m ⁻² s ⁻¹) for all stations sampled during October 2006 and May 2007. ...	57
Figure 2.16. Relationships between α^B (mg C [mg chla] ⁻¹ h ⁻¹ [μmol m ⁻² s ⁻¹] ⁻¹), P_s^B (mg C [mg chla] ⁻¹ h ⁻¹), E_k (μmol m ⁻² s ⁻¹) and temperature (a, b, c), and inorganic nitrogen concentrations (d, e, f) during October 2006 and May 2007.	60
Figure 2.17. Relationships between α^B (mg C [mg chla] ⁻¹ h ⁻¹ [μmol m ⁻² s ⁻¹] ⁻¹), P_s^B (mg C [mg chla] ⁻¹ h ⁻¹), E_k (μmol m ⁻² s ⁻¹) and z/z_{eu} (a, b, c), and between (d) a_{ph} (440), (e) TChla, (f) PP and z/z_{eu} during October 2006 and May 2007.	61
Figure 2.18. Relationship of TChla (mg m ⁻³) and photosynthesis (mg C m ⁻³ h ⁻¹) with (a) temperature (°C), (b) NO ₃ +NO ₂ (mmol m ⁻³), and (c) silicate (mmol m ⁻³).	64
Figure 2.19. Integrated Primary Production (g C m ⁻² d ⁻¹) plotted as a function of integrated TChla (mg m ⁻²) for (a) October and May pooled, (b) October and May separately, and as a function of surface TChla (mg m ⁻³) for (c) October and May pooled, (d) October and May separately.	65
Figure 2.20. Integrated TChla (mg m ⁻²) plotted as a function of surface TChla (mg m ⁻³), for October 2006 and May 2007.	66
Figure 3.1. Comparison of in situ measured PP with modelled PP (g C m ⁻² d ⁻¹) during (a) October 2006 and (b) May 2007.	75
Figure 3.2. Relationships between in situ measured PP (g C m ⁻² d ⁻¹) and PP modelled using the (a, b) VGPM and, (c, d) Eppley-VGPM, during October 2006 and May 2007.	75
Figure 3.3. Percentage difference between in situ measured PP and modelled PP (g C m ⁻² d ⁻¹) during (a) October 2006, and (b) May 2007.	76

Figure 3.4. (a) Comparison, and (b) percentage difference between in situ measured PP with modelled PP ($\text{g C m}^{-2} \text{d}^{-1}$) during October 2006 and May 2007.	78
Figure 4.1. Bathymetric map of the Southern Benguela. The dark solid line indicates a 200 km wide area, while the dashed lines indicate the three latitudinal transects.	84
Figure 4.2. Monthly means (a, c, e) , and anomalies (b, d, f) of SST ($^{\circ}\text{C}$), chlorophyll <i>a</i> (mg m^{-3}), and PP ($\text{g C m}^{-2} \text{d}^{-1}$) averaged over a 200 km wide area along the southern Benguela coast.	86
Figure 4.3. Hovmöller plots of the latitudinal (a) mean SST ($^{\circ}\text{C}$) and (b) SST anomalies ($^{\circ}\text{C}$) for the southern Benguela ecosystem between 29°S and 34.3°S , averaged over 200 km.	87
Figure 4.4. The Niño 3.4 Index.	88
Figure 4.5. Hovmöller plots of the latitudinal mean (a) and anomalies (b) of chlorophyll <i>a</i> (mg m^{-3}) in the southern Benguela ecosystem between 29°S and 34.3°S , averaged over 200 km.	90
Figure 4.5. (continued) Hovmöller plots of the latitudinal mean (c) and anomalies (d) of PP ($\text{g C m}^{-2} \text{d}^{-1}$) in the southern Benguela ecosystem between 29°S and 34.3°S , averaged over 200 km.	91
Figure 4.6. Hovmöller plots of PP ($\text{g C m}^{-2} \text{d}^{-1}$) for the 200 km wide (a) Cape Peninsula, (b) St Helena Bay, and (c) Namaqua transects.	95
Figure 4.7. Hovmöller plots of PP anomalies ($\text{g C m}^{-2} \text{d}^{-1}$) for the 200 km wide (a) Cape Peninsula, (b) St Helena Bay, and (c) Namaqua transects.	96

List of Tables

Table 2.1. Symbols, names, formulae, and selected taxonomic designations for chlorophylls, carotenoids, pigment sums, and pigment indices (Barlow et al. 2005, 2006, Jeffrey and Vesk 1997).	29
Table 2.2. Symbols, definitions, and units for phytoplankton biomass, light, P-E relationships, and Primary Production.	35
Table 2.3. PAR incident at the sea surface (SPAR), euphotic zone depth (z_{eu}), upper mixed layer depth (z_{uml}), and vertical attenuation coefficients (K_d) during October 2006 and May 2007.	43
Table 3.1. In situ measured P_s^B ($\text{mg C} [\text{mg chl}a]^{-1} \text{h}^{-1}$) and modelled P_{opt}^B ($\text{mg C} [\text{mg chl}a]^{-1} \text{h}^{-1}$).	77
Table 3.2. In situ and satellite chlorophyll a (mg m^{-3}), surface temperature ($^{\circ}\text{C}$), and Photosynthetically Available Radiation ($\text{E m}^{-2} \text{d}^{-1}$).	79

Abstract

Investigations of in situ and satellite Primary Production (PP) were undertaken across the continental shelf of the southern Benguela ecosystem. In situ ^{14}C measurements of PP were obtained during two research surveys in October 2006 (mid-spring) and May 2007 (late autumn), and a 13-year time series of satellite Sea Surface Temperature (SST), chlorophyll a and PP was used to examine seasonal and interannual signals. Cross-shelf differences indicated low biomass and PP in newly upwelled water along the coast, higher biomass and PP in the mid-shelf region, while lower values were observed at and beyond the shelf edge. Latitudinal variations showed consistently higher biomass and PP in the St. Helena Bay area compared to the Namaqua shelf and off the Cape Peninsula. Seasonal differences were evident, with higher PP observed in situ during mid-spring, ranging from $0.71 - 6.98 \text{ g C m}^{-2} \text{ d}^{-1}$, and lower in late autumn, varying from $0.70 - 3.35 \text{ g C m}^{-2} \text{ d}^{-1}$. Satellite estimates were slightly lower, ranging from $0.5 - 6 \text{ g C m}^{-2} \text{ d}^{-1}$ throughout the time series. Interannual variations showed chlorophyll a decreasing from 1997 to 2002, followed by a steady increase until 2005, after which higher levels were maintained for the remainder of the time series. A clear decreasing trend in the maximum summer PP was observed from 1997 to 2003, and again from 2007 to 2010, while PP during 2004 and 2005 was typically above-average and was associated with higher than normal biomass and SST during a prolonged period of El Niño conditions.

Irradiance was found to be the primary environmental variable influencing vertical variations in PP, and while no definitive relationship could be established with nutrients, an optimal temperature range of $12-16 \text{ }^\circ\text{C}$ was identified for elevated biomass and PP. Phytoplankton adaptation to environmental variability was characterised by increased P_s^{B} (maximum photosynthesis) and E_k (light saturation) under elevated temperatures and irradiance, while no clear relationships were evident for α^{B} (photosynthetic efficiency). Comparisons of measured and modelled PP showed that Vertically Generalised Production Model (VGPM) estimates most closely matched the in situ measurements, while the Eppley and Eppley-VGPM estimates were considerably different. Although satellite models captured seasonal changes in PP, accuracy was noted to vary between October and May. Parameterisation of $\text{P}_{\text{opt}}^{\text{B}}$ (maximum photosynthetic rate) was the primary cause of the differences between measured and modelled PP, suggesting that the temperature-dependant modelling of $\text{P}_{\text{opt}}^{\text{B}}$ may be regionally specific and might vary seasonally.

Chapter 1 – General Introduction

Physical processes related to the global energy and water cycles, and the associated biological and chemical processes which control biogeochemical cycles are central to the understanding of climate. In upwelling areas, biogeochemical cycling plays an important role in supporting and determining the level of oceanic primary production (PP), and small changes in biogeochemical conditions could result in major changes in biogeochemical pathways and ultimately in the trophic structure of food webs (Fréon et al. 2009). Among these biogeochemical cycles, the oceanic carbon cycle is of particular importance, and its understanding has been a major goal in biological oceanography since the mid 19th century (Barber and Hilting 2002, Stocker et al. 2001).

Autotrophic organisms, including phytoplankton and bacteria, play a critical role in a number of key marine processes. Marine phytoplankton form the first link in the trophic interactions of marine food webs (Behrenfeld and Falkowski 1997 a, b) and fix large quantities of atmospheric carbon dioxide (CO₂) via the ocean-atmosphere interface and transfer it to the deep ocean, thereby decreasing atmospheric CO₂ concentrations (Demarcq et al. 2008, Huntley et al. 1991, Longhurst 1991, Wefer and Fisher 1991, Siegenthaler and Sarmiento 1993). The circulation of the ocean, the solubility pump, and the biological pump are the primary controls acting on the marine carbon cycle.

Thus, the physical processes, photosynthesis and the export of organic carbon from the upper 100 m of the ocean (euphotic zone) as dissolved inorganic carbon (DIC), dissolved organic carbon (DOC) or particulate organic carbon (POC), due to sedimentation or grazing by zooplankton, are key components in the cycling of carbon in the oceans (Berger et al. 1989, Falkowski et al. 1998, Moore III et al. 2001) and are fundamental to understanding the role of the oceans in regulating global climate. By influencing variables such as gas solubility and fluxes, climate variability plays an important role in affecting the interaction between the ocean surface and the lower atmosphere in coastal upwelling systems (Fréon et al. 2009).

Approximately half of the global biospheric net PP can be attributed to marine phytoplankton and thus long-term changes in oceanic PP may have significant impacts on the global carbon cycle (Behrenfeld et al. 2001, Gregg et al. 2003a). The Intergovernmental Panel on Climate Change (IPCC) estimated the known global sinks of CO₂, noting that the errors in the estimation of the oceanic sink were very large (Houghton

et al. 1996). Considerable efforts have been made to describe and understand carbon fixation at global as well as regional scales (Antoine et al. 1996, Balkanski et al. 1999, Basterretxea and Arístegui 2000, Falkowski et al. 1998, Field et al. 1998, Houghton et al. 1990, Longhurst et al. 1995, Morán and Estrada 2001). Estimates of gross PP vary from 27.1 Gt C y⁻¹ (Eppley and Peterson 1979) to 50.2 Gt C y⁻¹ (Longhurst et al. 1995), up to as much as 103 Gt C yr⁻¹ (Bender et al. 1994). The range of estimates indicates that there is still great uncertainty about the magnitude of global PP. Accurate estimation of phytoplankton biomass and PP are fundamental to understanding oceanic carbon cycles and the biological and ecological processes related to fisheries in coastal ecosystems, as well as the coupling of pelagic ecosystems to regional- and basin-scale hydrodynamic forcing.

Coastal upwelling ecosystems constitute approximately 2 - 3 % of the global ocean and yet they are responsible for the largest proportion of the global oceanic PP (Antoine et al. 1996, Hill et al. 1998). In the east Atlantic and east Pacific oceans, upwelling ecosystems are responsible for 20 - 30 % of the total fish catches of the world (FAO Marine Resources Service FRD 2005). The vertical advection of deeper nutrient-rich water into the euphotic zone during upwelling largely determines the overall productivity of these ecosystems (Joint et al. 2002, Prentice et al. 2001). With regard to fisheries productivity, the Benguela has been ranked second among upwelling ecosystems globally (Hutchings 1992).

Climate change and natural variability have significant implications for the productivity of upwelling ecosystems, and the high levels of spatio-temporal variability in fish abundance and catches is a constant challenge to the management of these ecosystems (Caddy and Cochrane 2001, Moore III et al. 2001). The lack of adequate spatial and temporal information on the interactions between the physical environment, phytoplankton, and fish leads to a poor understanding of the functioning of such marine ecosystems (Fréon et al. 2005, Drapeau et al. 2004, Pecquerie et al. 2004).

Environmental variability is thought to play an important role in the variability of fish recruitment and thus it is essential that this variability be studied within the context of physical-biological-ecological interactions (Huggett et al. 2003, Parada et al. 2003, 2008). Investigating the seasonal and interannual variability of environmental variables, particularly phytoplankton biomass and primary productivity, can provide important information on the distribution and recruitment strength of fish resources (Roy et al. 2007, van der Lingen et al. 2006).

1.1. Rationale and Key Questions

A better understanding of the global carbon cycle necessitates global observations that enable the determination of the sources and sinks of carbon, and there is a need for further study of the fundamental biological processes and their interaction with the environment (Moore III et al. 2001). In the Benguela ecosystem, phytoplankton communities exhibit high variability in their photosynthetic response due to the complex and dynamic water-column physics. For this reason, PP is expected to be highly variable in time and space.

PP is not only dependant on changes in phytoplankton biomass, but the variations in the photosynthetic parameters are also important (Lorenzo et al. 2005). Global- and regional-scale models of PP are generally based on a mechanistic understanding of the basic processes controlling photosynthesis in marine environments. The complexity of these models requires validation, which necessitates that numerous measurements of biomass, PP, and the photosynthetic parameters be made accurately across the world's ocean (Babin et al. 1994).

Photosynthetic rates are controlled by a variety of factors, among which irradiance is a key regulator (Behrenfeld and Falkowski 1997a, b, Kirk 1994). Knowledge of the variability in the relationship between photosynthesis and irradiance in natural phytoplankton populations allows for the determination of the influence of various environmental factors on the efficiency with which phytoplankton convert light into chemical energy (Marañón and Holligan 1999, Platt et al. 1992, Longhurst et al. 1995). It also provides the parameters needed to estimate PP from various satellite models (Antoine et al. 1996, Joint et al. 2002, Platt and Sathyendranath 1988, Tilstone et al. 2003, 2005).

The dependence of photosynthesis on irradiance can be determined and analysed with the Photosynthesis-Irradiance (P-E) relationship. Generally, the P-E relationship is determined by the incubation of water samples at a range of irradiances over a fixed time period. The resulting parameters derived from this relationship are then applied to models which quantitatively estimate rates of PP. The P-E relationship is crucial in measuring, modeling and predicting phytoplankton photosynthesis, and in evaluating the physiological state of phytoplankton.

Accurate measurement and simulation of this relationship is of major importance to further our understanding of the biology and ecology of phytoplankton and their role in the global

carbon cycle. Unfortunately, relatively few studies of PP and measurements of photosynthetic parameters have been undertaken in the Benguela ecosystem, in comparison to other ecosystems. During the Atlantic Meridional Transect (AMT)-6 cruise, 11 P-E measurements were made across the Benguela upwelling system to compare Fast Repetition Rate Fluorometer (FRRF)-derived photosynthetic parameters with those derived from radiocarbon measurements (Aiken et al. 1998). Along a transect off Lambert's Bay, Mitchell-Innes et al. (2000) used 21 radiocarbon-derived P-E measurements to verify primary productivity estimates derived from natural fluorescence.

In the context of global climate change, it is particularly important to gain a better understanding of the scales of variability in biological productivity as well the sensitivity of upwelling ecosystems to environmental influences (Lutjeharms et al. 2001). Bio-optical models based on mechanistic linkages between optical properties of the water column, light penetration, and phytoplankton PP are a useful tool in the spatial and temporal assessment of the biological and ecological variability inherent to oceanic and coastal ecosystems and also offers a platform for comparison between a variety of ecosystems. Use of this tool can be extended to fisheries management and stock assessment, and the exploration of new fisheries.

Synoptic measurements of the ocean, provided by operational ocean colour satellite sensors, over large spatial and temporal scales, are becoming increasingly important in the management of coastal resources. The continuously evolving capabilities of satellite sensors and data processing procedures, presents a promising tool for the development and application of fisheries management and forecasting techniques. Satellite estimates of phytoplankton biomass and PP allow for the large scale evaluation and description of the contribution of the oceanic biosphere to the global carbon cycle. The combined use of field measurements and remotely sensed data allows the investigation and understanding of the physical and biogeochemical processes regulating PP in coastal ecosystems across local, regional and global scales.

This study aims to evaluate various existing models for the estimation of PP in the southern Benguela ecosystem, and to investigate the photophysiological responses of phytoplankton to changes in environmental conditions. Currently available in situ methodology (Arbones et al. 2000, Barlow et al. 1997, Tilstone et al. 2003, 2005, Lorenzo et al. 2004, 2005, Marañón and Holligan 1999) was used for the estimation PP from field data, and to investigate and describe the relationships between phytoplankton composition

and photophysiology, photosynthetic parameters, PP, and the environment. The following key questions will be addressed: (1) What is the spatial and temporal variability in phytoplankton production in the southern Benguela ecosystem? (2) What are the physiological mechanisms that govern the variability in primary production? (3) What is the influence of environmental variables (irradiance, temperature, nutrients) on phytoplankton photosynthesis? (4) How do satellite estimates of PP compare to each other and to in situ estimates? (5) What are the spatial and temporal patterns of PP observed from ocean colour data?

University of Cape Town

1.2. Thesis Structure

A review of the hydrography and phytoplankton production of the southern Benguela ecosystem is provided in Section 1.3. of this chapter. Chapter 2 details the estimation of photosynthetic parameters and primary production (PP) using Photosynthesis-Irradiance (P-E) experiments. Chapter 3 investigates how well ocean colour model PP estimates compare with each other and with in situ PP and examines the factors responsible for the differences in PP estimates. Chapter 4 uses a 13-year time series of satellite Sea Surface Temperature (SST), chlorophyll *a* and PP to investigate the seasonal and interannual variations across the southern Benguela ecosystem, and Chapter 5 synthesises the findings of this research.

University of Cape Town

1.3. Review of the southern Benguela ecosystem

1.3.1. Hydrography

The Benguela upwelling ecosystem (Figure 1.1.) extends along the southwestern coast of Africa. It consists of the Benguela Current, which comprises the equatorward limb of the South Atlantic Subtropical gyre, and an upwelling system extending southward from about Cape Frio (18 °S) to Cape Agulhas (34 °S) (Shillington 1998). The Benguela is one of the four major coastal upwelling systems of the global ocean and is unique in that it is bordered by warm water on both the equatorward and poleward ends (Hardman-Mountford et al. 2003, Shillington et al. 2006).

On the equatorward end between 15 - 17 °S, the permanent Angola-Benguela surface front separates warm Angolan Current water from the cooler Benguela upwelling system and shows some seasonal and interannual variability in its position (Field and Shillington 2006, Mackas et al. 2006, Meeuwis and Lutjeharms 1990, Nelson and Hutchings 1983, Shannon 1985, Shannon et al. 1987, Shannon and Nelson 1996, Veitch et al. 2006). A strong warming trend has been noted at the northern and southern boundaries, with a cooling trend observed close inshore in the southern Benguela (Hutchings et al. 2009). Similarly, Belkin (2009) and Demarcq (2009) observed a slow but steady warming throughout the Benguela ecosystem.

In the south, the upwelling system is terminated by the Agulhas Retroflexion region between 36 - 37 °S. Warm subtropical water is introduced to the Cape Basin in the form of warm-core eddies (Agulhas rings) with an average diameter of ~ 200 km and filaments shed from the Agulhas Retroflexion (Brundrit and Shannon 1989, Duncombe Rae 1991, Garzoli et al. 1999, Lutjeharms and van Ballegooyen 1988, Nelson et al. 1998, Shannon et al. 1990, Lutjeharms 2006, Zahn 2010). These mesoscale features have been shown to occasionally impact on the upwelling system (Duncombe Rae 1991, Duncombe Rae et al. 1992, Hardman-Mountford et al. 2003) by contributing to the offshore loss of fish eggs and larvae (Hutchings et al. 1998) and by influencing phytoplankton distribution (Carr 2002, Demarcq et al. 2007, Rossi et al. 2008).

Using fifteen years of satellite altimetry to investigate eddy activity in the four major eastern boundary upwelling ecosystems, Chaigneau et al. (2009) showed that cyclonic and

anticyclonic eddies are generated along continents and propagate westward with velocities which increase toward the equator. Long-term trends in eddy activity suggested a sensitivity of upwelling ecosystems to global change, and the strongest interannual variability in eddy generation and associated eddy activity was observed in the Benguela ecosystem. The presence of cyclonic eddies along the upwelling front in the southern Benguela was shown to be recurrent throughout the year (Rubio et al. 2009), suggesting that these eddies play a significant role in exchanges of energy, nutrients, and biological material between the open ocean and coastal regions. Due to strong mesoscale activity offshore of the shelf edge, a strong offshore gradient of eddy kinetic energy exists in the Benguela system, particularly in the southern part (Veitch et al. 2009). The influence of the Agulhas Current Retroflexion on the intraseasonal variability in the southern Benguela was noted by Chavez and Messié (2009).

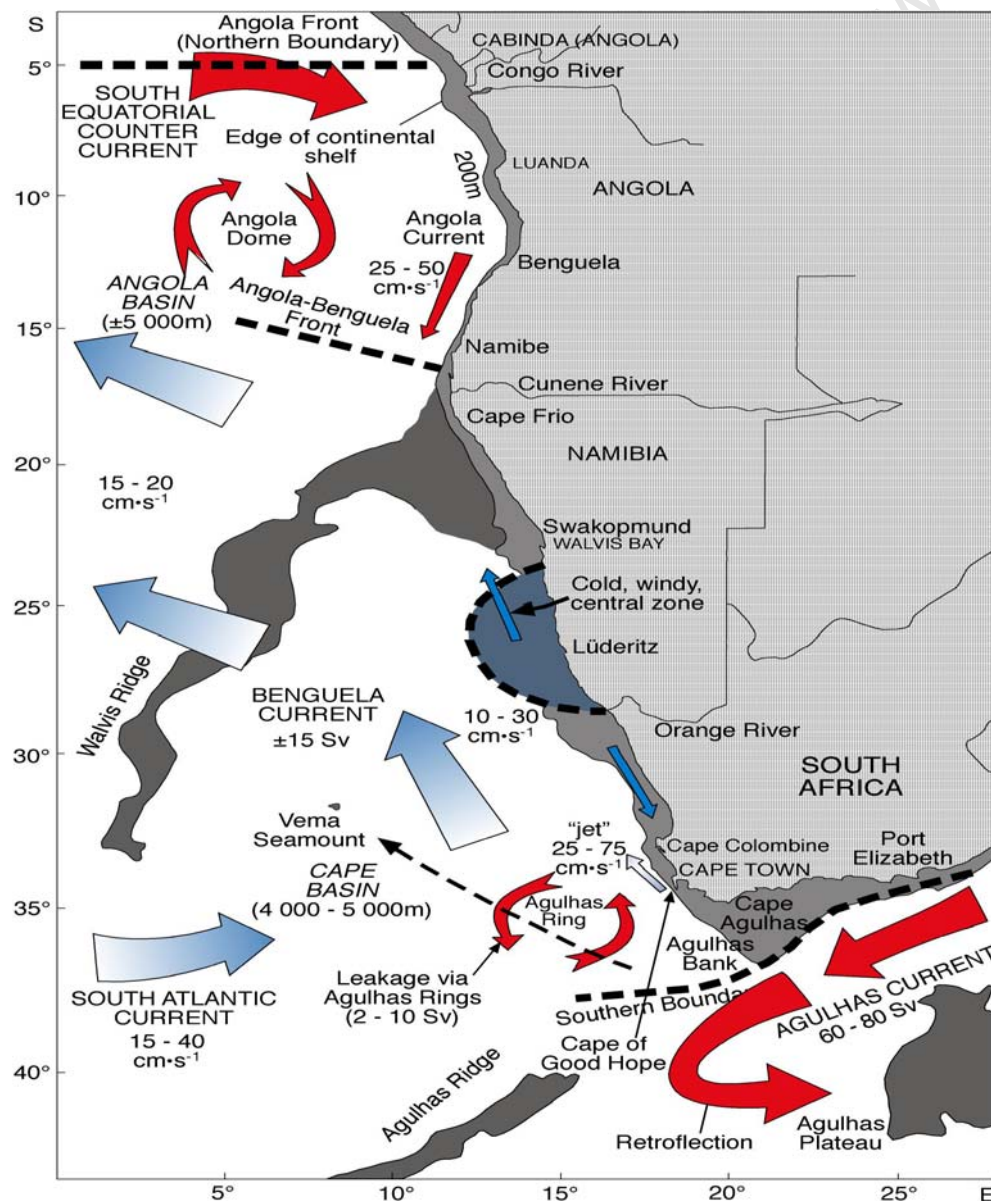


Figure 1.1. The Benguela Ecosystem (from Shannon 2006).

Due to the complex interaction between local physical oceanographic features and remote oceanographic processes, the Benguela is subject to substantial seasonal and interannual variability, which significantly influences the biological resources of the region (Weeks et al. 2006). Nelson (1992) suggested that inertial and five-day periods are important frequencies with regard to PP in the Benguela ecosystem. The extent and intensity of the wind-driven coastal upwelling which dominates the ecosystem is primarily controlled by the prevailing wind and pressure fields, the orientation of the coastline, and the topography (Hardman-Mountford et al. 2003, Nelson and Hutchings 1983, Rykaczewski and Checkley 2008, Shannon and Nelson 1996, Shillington 1998). The combination of these controlling factors results in the formation of upwelling cells at specific locations. Characteristics of the principle upwelling cells have been described in detail by various authors (Nelson and Hutchings 1983, Shannon 1985, Lutjeharms and Meeuwis 1987, Hutchings 1992, Shannon and Nelson 1996).

The perennial upwelling cell in the vicinity of Lüderitz (27 °S) is the most intense in the system and comprises an environmental barrier that essentially divides the Benguela into the northern and southern subsystems. The southern Benguela extends south from the Orange River Mouth (28.6293 °S; 16.4533 °E) to Cape Agulhas (34.8256 °S; 20.0135 °E) (Duncombe Rae 2005, Lett et al. 2007, Shannon 1985, Shannon et al. 2003, Veitch et al. 2009). The main frequencies of variability in the northern and southern Benguela are different, probably indicating the differences in the dominant forcing mechanisms (Demarcq et al. 2007). Reason et al. (2006) and Colberg and Reason (2007) described the major modes of climate variance in the South Atlantic ocean.

In the southern Benguela, polar frontal systems exert a greater influence on the wind field resulting in strong northwesterly to southwesterly winds with a period of 3 - 10 days which suppresses upwelling during winter. Upwelling-favourable winds are maximum during spring and summer (Andrews and Hutchings 1980, Preston-Whyte and Tyson 1988, Shannon and Nelson 1996). This variation in the prevailing wind field produces short-lived and highly seasonal upwelling events (Risien et al. 2004). A well defined frontal zone usually coincides with the shelf edge, and upwelling filaments with a lifespan of a few days to several weeks are generally orientated perpendicular to the coast (Shannon and Nelson 1996).

The area between Cape Point (34.3534 °S; 18.4889 °E) and Cape Agulhas comprises the western part of the Agulhas Bank, which is an important habitat and spawning ground for

commercial pelagic and demersal fish species (Probyn et al. 1992). Roy et al. (2007) described an eastward shift in the distribution of anchovy spawner biomass over a period of two decades from the western to the eastern Agulhas Bank, and attributed this shift to enhanced coastal upwelling east of Cape Agulhas. Investigation of the spatial and temporal patterns of chlorophyll *a* and PP may support the hypothesis of an environmentally mediated shift in the distribution of anchovy spawner biomass.

1.3.2. Phytoplankton Biomass and Composition

As a consequence of upwelling, phytoplankton biomass and PP is generally high. Various studies in the Benguela have described the long-term mean trends (Carr 2002, Carr and Kearns 2003, Demarcq et al. 2003, Demarcq 2009, Thomas et al. 2001, Thomas et al. 2003, Weeks et al. 2006). Two classifications of phytoplankton blooms are recurrent and predictable in upwelling regions. In coastal waters, an annual diatom bloom occurs as winter translates to spring and irradiance conditions become optimal. As a consequence of the pulsating nature of upwelling events, a series of small localised diatom blooms continually occur throughout the upwelling system, varying in intensity and duration in response to the wind forcing (Smayda and Trainer 2010).

Local physical factors, such as the orientation of the coastline, occurrence of headlands, and the shelf width, introduce additional temporal and spatial variability to biomass and PP estimates (Thomas et al. 2003). Maximum chlorophyll concentrations usually coincide temporally with the seasonal maximum in upwelling and are found downstream of upwelling cells, while lower concentrations are associated with the centre of upwelling cells (Thomas et al. 2001, Thomas et al. 2003, Weeks et al. 2006). The lowest biomass concentrations in the Benguela ecosystem are found at the Lüderitz upwelling cell (Demarcq et al. 2003).

In the southern Benguela, phytoplankton biomass is generally maximum between 20 - 80 km offshore, although blooms have been noted to extend over 100 km offshore subsequent to periods of intense upwelling (Brown et al. 1991, Weeks et al. 2006). Fischer et al. (2009) noted that chlorophyll was transported about 400 km offshore in an upwelling filament off Mauritania. In the Benguela, chlorophyll concentrations of less than 1 mg m⁻³ and high nutrients are generally found in recently upwelled water (< 10 °C), while chlorophyll in maturing upwelled water (10 - 12 °C) ranges between 1 - 20 mg m⁻³ with

nitrate concentrations of 2 - 15 mmol m⁻³. Aged upwelled water (12 - 16 °C) is typically characterised by chlorophyll concentrations of 1 - 30 mg m⁻³ and nitrates of < 2 mmol m⁻³ (Barlow 1982a, b, c). Brown and Hutchings (1987a, b) found that phytoplankton blooms typically last for approximately a week, developing for three days and declining over the next four.

As a result of the high PP, and consequent high biomass blooms, the southern Benguela ecosystem is susceptible to blooms of harmful algae (Pitcher and Pillar 2010). Typically, the high productivity of the southern Benguela has generally been attributed to large cell-sized phytoplankton such as diatoms, which tend to dominate in coastal upwelling systems (Hutchings et al. 1995, Shannon and Pillar 1986). However, Pitcher et al. (1998) have demonstrated the importance of a range of dinoflagellates which comprise the bulk of harmful algal blooms (HABs) in upwelling ecosystems (Pitcher and Pillar 2010). Harmful algae are known to form widespread and persistent blooms during late summer in stratified waters on the west coast (Pitcher and Boyd 1996, Probyn et al. 2000, Pitcher et al. 1998). The influence of windstress on the dynamics of the upper mixed layer is important in affecting the composition of phytoplankton communities and in determining the surface circulation which, in turn, determines the transport and distribution of blooms (Pitcher and Nelson 2006).

HABs influence the upwelling ecosystem by introducing toxins which impact negatively on marine and human life (Botes et al. 2003, Fawcett et al. 2007). As a result of the high respiratory demand of settling organic matter which follows bloom decay, high biomass blooms may cause rapid oxygen consumption which can lead to hypoxia and anoxia (Pitcher et al. 2008, Pitcher and Weeks 2006, Pitcher and Cockcroft 1998), and in some rare cases, to the production of hydrogen sulphide (Weeks et al. 2002, 2004, Matthews and Pitcher 1996). In the southern Benguela, the occurrence of hypoxic water has been linked solely to the decay of dense phytoplankton blooms (Monteiro and van der Plas 2006) and has resulted in periodic mass mortalities of shellfish and rock lobster (Pitcher and Weeks 2006). These impacts are most significant in nearshore areas where the orientation of the coastline and bottom topography influences water stratification and retention (Pitcher and Pillar 2010).

In combination with the varying cycles of wind forcing, these factors significantly influence the productivity of the shelf by favouring the presence of various algal groups (Figueiras et al. 2006). Factors which influence the development, maintenance and decline

of HABs, and changes in species composition have been studied over a broad range of spatial and temporal scales (Pitcher et al. 1993, Pitcher et al. 1995, Pitcher et al. 1998, Pitcher and Boyd 1996, Probyn et al. 2000, Pitcher and Calder 2000, Pitcher and Nelson 2006, Pitcher et al. 2010, Trainer et al. 2010). Mitchell-Innes et al. (2000) examined the biomass and productivity of dinoflagellate blooms and found that the saturation of photosynthesis in diatom-dominated communities occurred at higher irradiances, up to $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$, while dinoflagellate-dominated communities saturated at lower irradiances, up to $750 \mu\text{mol m}^{-2} \text{s}^{-1}$.

1.3.3. Primary Production

Estimates of PP are essential to understanding biological processes in the ocean, such as the removal of carbon from the atmosphere, and trophic interactions in marine food webs. A number of measurements of PP and bacterioplankton production have been made in the southern Benguela (Brown 1984, Brown and Field 1985, Brown and Hutchings 1987a, b, Lucas et al. 1987, Mitchell-Innes et al. 2000, Painting et al. 1989, Shannon and Pillar 1986, Verheye-Dua and Lucas 1988). Most of the PP in the Benguela occurs over the shelf, the area of which increases and decreases along the coastline according to the width of the shelf (Koné et al. 2005, Pitcher et al. 1992, Weeks et al. 2006). Demarcq (2009) noted that the productivity of most eastern boundary upwelling systems showed an increasing trend from 1998 to 2007, while offshore, the global primary biomass decreased.

Total PP can be separated into new and regenerated production, depending on the source of nitrogen used (Waldron and Probyn 1992). New production results from the uptake of new nitrogen which is introduced into the system through the atmosphere, riverine input, and through the upwelling of nutrient rich water onto the shelf. Regenerated production occurs due to the uptake of nitrogen from metabolic recycling (ammonia and urea) in the surface waters, which becomes available when wind-driven upwelling eases (Waldron and Probyn 1992, Probyn 1992). Efficient phytoplankton production requires the alternate stabilisation and destabilisation of the water column (Legendre 1981). Inshore, biomass is high and nitrate is the primary source of the nitrogen taken up by phytoplankton, while further offshore the phytoplankton is mainly supported by regenerated nitrogen from urea and ammonia (Probyn 1985).

Some of the total production in the euphotic zone is lost through passive sinking of phytoplankton. In the long term, high phytoplankton biomass in the Benguela ecosystem is unsustainable on regenerated production only (Waldron and Probyn 1992, Probyn 1992). Fernández et al. (2009) showed that, off Peru, PP is driven by new nitrate through upwelling as well as by regenerated nitrogen in the form of ammonium or nitrate generated through nitrification in the near-surface layer. It is thus the introduction of new nitrogen into the system, and hence new production that sustains phytoplankton populations and constitutes the sink for atmospheric carbon in the Benguela upwelling system. The determination of new production at global as well as regional scales is thus crucial to understanding the role of the oceans as a carbon sink.

Waldron and Probyn (1992) estimated annual new production in the Benguela (northern and southern) to be $0.649 \text{ g C m}^{-2} \text{ day}^{-1}$ during 1987, while Shannon and Field (1985) estimated the rate of productivity (new and regenerated) in the southern Benguela to be $2.8 \text{ g C m}^{-2} \text{ day}^{-1}$. Brown et al. (1991) estimated a total PP of $1.2 \text{ g C m}^{-2} \text{ day}^{-1}$ and $2 \text{ g C m}^{-2} \text{ day}^{-1}$ for the northern and southern Benguela, respectively. Mitchell-Innes et al. (2000) demonstrated a close match between PP estimates determined by natural fluorescence and those from ^{14}C experiments, and estimated productivity to range from $0.8 \text{ g C m}^{-2} \text{ day}^{-1}$ in newly upwelled water to $12.3 \text{ g C m}^{-2} \text{ day}^{-1}$ during a red tide event in the nearshore zone. Further offshore, the estimated productivity ranged from $2.4 - 4 \text{ g C m}^{-2} \text{ day}^{-1}$. Messié et al. (2009) reported that the Benguela system had levels of nitrate supply and potential new production similar to those found in the Humboldt and the Canary systems.

Upwelling ecosystems act as carbon sinks due to the high fixation of CO_2 by phytoplankton, which exceeds community respiration over the long term. However, since cold upwelled water releases CO_2 when warmed at the surface, upwelling systems may also be sources for CO_2 . González-Dávila et al. (2009) concluded that south of 20°S in the southern Benguela, surface waters acted as a sink of CO_2 , suggesting higher biological activity as a result of increased upwelling intensity and intrusion of seawater with a lower inorganic carbon content from the Agulhas Bank. Continental shelf waters have been reported to have a limited capacity to store absorbed carbon, and thus most of the carbon has to be exported to the open ocean or into the sediments.

Benthic processes within the sediment and at the sediment-water interface are critical components of the biogeochemical cycling in coastal upwelling systems, yet their role is poorly understood due to their variability and complexity (Fréon et al. 2009). Liu et al.

(2000) estimated that 7 - 27 % of the global biological pump can be attributed to the export of PP from the shelf, with the contribution of upwelling systems comparatively higher than non-upwelling continental margins. Waldron et al. (1998) estimated that 0.2×10^{13} g C year⁻¹ of new production in the southern Benguela is exported to the open ocean. Swart et al. (2007) provide evidence of the export of particulate organic carbon and particulate organic nitrogen from the shelf to the continental slope in the southern Benguela, and estimated that 2.9×10^{13} g C year⁻¹ sank over the continental shelf while 2.0×10^{13} g C year⁻¹ was either exported toward the slope or absorbed into the sediments.

1.3.4. Factors affecting Phytoplankton Biomass and Primary Production

The relationship between environmental factors and biological production is crucial to understanding the variability in the productivity of an ecosystem. Dynamic and constantly fluctuating upwelling ecosystems present an unstable environment for phytoplankton growth. Variations in photosynthesis and PP in the ocean are complex and have been attributed to factors such as stratification, turbulence, temperature, available nitrogen, light intensity and the spectral quality of light in the water column, phytoplankton size and diversity, as well as the physiological state of phytoplankton populations (Smayda 2010 a, b, Platt and Jassby 1976, Harding et al. 1986, Harrison and Platt 1980, Platt et al. 1992, Kyewalyanga et al. 1998, Gallegos et al. 1983, Lewis et al. 1984, Falkowski 1981, Côté and Platt 1984, Malone 1980, Gallegos 1992, Platt et al. 1993).

The structure of the pelagic food web and the interactions between its various components strongly influences the productivity of upwelling ecosystems. Strong mesoscale variability in pico- and nano-plankton communities along the NW African coastal transition zone was observed to alter the ratio of autotrophic to heterotrophic plankton, thereby modifying the carbon pathways within the food web (Baltar et al. 2009). Landry et al. (2009) showed a good agreement between experimentally derived estimates of phytoplankton community growth and micro- and meso-zooplankton grazing, accounting for 91 % of the variability observed in ambient chlorophyll *a* concentrations over time scales of 3 – 5 days. González et al. (2009) showed that euphausiids exerted a top-down control over phytoplankton communities and modulated the flux of sedimenting organic carbon in the Humboldt upwelling system.

More than one variable may be acting on photosynthetic parameters at any one time and it is often difficult to discern the effect of one from the effect of another (Lohrenz et al. 1994). Eppley et al. (1985) included day length in their multiple linear regression to model integral production. The mechanisms and processes affecting the dynamics of phytoplankton biomass and productivity in the Benguela have been described by various authors (Shannon 1985, Lutjeharms and Stockton 1987, Lutjeharms et al. 1991, Shannon and Nelson 1996, Shillington 1998, Hardman-Mountford et al. 2003). A good description of the response of plankton to specific upwelling events in the southern Benguela has been provided (Barlow 1982a, b, c, 1984a, b, Brown 1984, Brown and Field 1986, Brown and Hutchings 1987a, b, Hutchings et al. 1995, Mitchell-Innes and Walker 1991, Pitcher et al. 1992, Shannon and Pillar 1986).

In upwelling regions, the variation in PP is dependant on the strength of vertical advection and the duration of stratification. Generally, high and continual vertical advection reduces PP due to high turbulence and water column mixing, offshore movement of phytoplankton, and may cause the Ekman layer to deepen below the euphotic zone (Marra 1980b, Nelson 1992). Since the light levels found at the base of the euphotic zone are very low, any phytoplankton mixed down there would not photosynthesize and grow. Instead, only respiration and nutrient consumption would be evident.

Phytoplankton have developed mechanisms to adapt to such perturbations and allow them to take advantage of available niches in their environment. Such adaptations include the adjustment of cellular concentrations and composition of photosynthetic pigments and the use of organic nutrients to supplement growth under unfavourable conditions. During weak upwelling, PP increases since phytoplankton have a longer residence time under optimal light and nutrient conditions. The duration of stratification is critical in increasing or decreasing PP (Tilstone et al. 1999). Long periods of stratification can result in lower PP due to nutrient consumption and limitation and due to the sedimentation of phytoplankton from the euphotic zone. The alternation between high winds and well mixed water columns, and stratification and water column heating have been reported to yield high PP as long as light and nutrients are not limiting (Brown and Field 1986, Legendre 1981).

Ware (1992) reported a linear relationship between PP and Ekman transport. Carr (2002) found that PP was most related to Ekman transport and not correlated to Sea Surface Temperature (SST). Harrison and Platt (1980) showed that temperature was a dominant environmental variable accounting for 40 % of the observed variation in assimilation

number. On a theoretical basis, Eppley (1972) described a logarithmic relationship between temperature and assimilation number, although, the linear fit described by Platt and Jassby (1976) and various other authors is statistically more acceptable, considering the variability in field data. Demarcq (2009) showed that the long-term relationship between sea surface temperature and chlorophyll *a* biomass estimates were not significant in upwelling systems, but that upwelling-favourable winds were highly correlated with the observed trends in phytoplankton biomass.

Carr and Kearns (2003) showed multiple factors affecting PP but that large-scale circulation resulting in nutrient sufficiency accounted for up to 60 % of the variance in production, while local physical forcing (Ekman transport) and temperature variability only explained 18 %. Through hydrodynamic modelling, Lett et al. (2006) found that enrichment was a dominant process and enhanced retention occurred in two small regions (off the Orange River and in St. Helena Bay) in the southern Benguela, and over a large area (east of 23 °E) on the central and eastern Agulhas Bank. The physical mechanisms of enrichment and retention would serve to enhance PP in those regions. Observations of elevated phytoplankton (Hutchings et al. 2009, Weeks et al. 2006) and zooplankton (Huggett et al. 2009) biomass supports the St. Helena Bay area as a region of enhanced retention.

Physical and nutrient regimes are tightly coupled and it is often difficult to distinguish their individual effects on species succession and changes in biomass and PP (Tilstone et al. 2000). The relationship between nutrient concentration and phytoplankton production in the oceans is highly dynamic. Ability of phytoplankton cells to photosynthesise is strongly dependant on their ability to assimilate sufficient carbon, nitrogen and phosphorus, as well as minor nutrients in the surrounding water. The environment in which phytoplankton grow is significantly modified by their growth and over a period of a few days, assemblages may move from a situation of nutrient excess to nutrient depletion.

Marine phytoplankton are well adapted to and are efficient in the assimilation of nutrients at very low concentrations. Low nutrient concentrations may limit the total population biomass but may not necessarily reduce the growth rate of phytoplankton cells. When nutrients are in excess much higher phytoplankton biomass is attained, but unless nutrients are continuously replenished, the phytoplankton growth reduces nutrient concentrations eventually leading to nutrient limitation (Joint et al. 2001). The reported increase in the magnitude of HAB events has been linked to the availability of nutrients (Anderson et al.

2002, Glibert et al. 2005) and these events are often associated with anthropogenic eutrophication (Anderson et al. 2008, Glibert et al. 2005, 2006).

In coastal upwelling systems, nitrogen (N) is often described as the primary limiting nutrient for phytoplankton growth (Wilkerson and Dugdale 2008), although silicate (Si) has been shown to be important in altering phytoplankton community composition (Kudela 2008). Although iron (Fe) has been identified as an important limiting micronutrient, especially in high-nutrient, low-chlorophyll (HNLC) regions of the ocean, terrigenous (through riverine or aeolian supply) input may counteract deficits in coastal environments. The Redfield ratio of 106 C: 16 N: 1 P is important to understand how phytoplankton respond to episodic nutrient enrichment in upwelling ecosystems. However, the interpretation of these ratios is often complicated by the rapid recycling of these elements in upwelling systems (Andrews and Hutchings 1980, Chapman and Shannon 1985). It is well established that there is a negative correlation between temperature and nitrate concentrations in the ocean and it has been suggested that this relationship may be used as an index of productivity (Brown and Henry 1985, Kirk 1994).

The ratio of new to total production, known as the f-ratio, has been shown to increase asymptotically with an increase in nitrate concentration (Platt and Harrison 1985, Harrison et al. 1987). Eppley and Peterson (1979) demonstrated that f-ratios increased non-linearly with total production, reaching a maximum value of 0.5 in productive upwelling regions. However, the determination of reliable f-ratios is not an easy task and often yields highly variable results (Platt and Harrison 1985). Probyn (1992) demonstrated that ammonia concentrations and cell size have an important influence on f-ratios which may have some bearing on the potential new production in upwelling systems. By applying an appropriate f-ratio to estimates of total production, Sathyendranath et al. (1991) estimated new production from satellite data.

Physical and temporal variations in upwelling and stratification cycles influences phytoplankton composition and succession (Blasco et al. 1980, Brink et al. 1980, Mann 1992). Diatom domination has been associated with upwelling events and high nutrient input into the euphotic zone (Barber and Smith 1980, Jones and Halpern 1981). The temporal evolution from upwelling to stratification is marked by a change from small-celled diatoms to medium-sized mixed diatoms and culminates in flagellates which are better adapted to maintaining buoyancy under low mixing conditions (Legendre 1990, Mann 1993, Smith et al. 1983). Within each stage of succession from diatoms to

flagellates, there are short-term changes in diatom genera that are associated with specific hydrographic events and nutrient regimes, and these changes in diatom assemblages are reflected in patterns of carbon fixation (Gallegos 1992, Lohrenz et al. 1994).

Small diatoms such as *Skeletonema costatum* and *Thalassiosira nana* have high growth rates and productivity and are typically associated with turbulent upwelled water, while medium-sized diatoms such as *Ceratauline*, *Chaetocerus*, *Lauderia*, *Coscinodiscus*, and *Thalassionema* have lower growth rates and productivity and often succeed the smaller diatoms (Margalef 1958). The spatial distribution of phytoplankton ultimately results from the interactions between physical processes such as growth, mortality and predation, but it is difficult to evaluate which of these has the greatest influence on phytoplankton succession and variations in biomass and PP.

In the marine environment, phytoplankton experience changes in ambient irradiance over a broad range of time scales. Some of these changes are categorised as systematic, such as diurnal and seasonal cycles in solar elevation, while others are often treated as stochastic, such as changes in weather and turbulent mixing of phytoplankton cells in the water column (Legendre et al. 1993). The biological adjustment of phytoplankton to light intensity (photoadaptation) is reflected in the response of photoadaptive parameters to changes in ambient irradiance. These parameters include the chemical composition of phytoplankton, ratios of photosynthetic pigments, photosynthetic capacity, the *in vivo* fluorescence yield of chlorophyll *a*, and algal growth rates, and do not all respond to changes in irradiance at the same rate (Harris 1980, Laws and Bannister 1980, Falkowski and Wirick 1981, Falkowski 1980, 1981, Hitchcock 1980, Marra 1980a, Prézelin and Matlick 1980). For some algal cells, the relationship between irradiance and photosynthesis is not fixed, but adjusts according to changes in the ambient irradiance experienced by the cells over time (Lewis and Smith 1983).

Such adaptive responses are ecologically important because of the inherent non-linearity in the relationship between photosynthesis and light. Seasonal variations in incident solar radiation are important in explaining some of the variation in assimilation numbers since maximum photosynthetic rates may to some extent be determined by the magnitude and duration of light exposure, especially over time scales of hours or less. At lower irradiances, cells are able to photosynthesise at a greater rate than cells at higher irradiance (Anning et al. 2000). This may be due to a dilution of photosynthetic pigments which results from an increase in cellular carbon throughout the day at high irradiances. The

ability of a cell to increase its carbon content may be related to its size, and many cells are known to increase their volume at higher irradiances, thereby increasing their photosynthetic capacity at higher irradiances (Thompson et al. 1991). At high light, carbon-specific photosynthesis is also regulated by electron transport due to a shift in control from the Calvin cycle to the electron transfer chain (Geider et al. 1996).

The cell size distribution of primary producers acts as a major controlling factor of the community structure, metabolism, and trophic organisation of the pelagic ecosystem (Banse 1976, Chisholm 1992, Fenchel 1974, Legendre and Le Fèvre 1989, Legendre and Rassoulzadegan 1996, Li 2002, Malone 1980, Rodríguez 1994). It also influences the fate of biogenic carbon through photosynthesis and PP, in relation to the physical structure of the water column and the associated light and nutrient regimes (Banse 1976, Geider et al. 1986, Platt et al. 1993, Hood et al. 1992). Platt and Jassby (1976) showed that, generally, high assimilation numbers were related to low mean cell volumes, and Malone (1977) observed similar patterns in mean cell size.

Communities dominated by large-size phytoplankton typically have a large potential to export organic matter to upper trophic levels through a short food chain, and to adjacent systems. In contrast, communities dominated by small-size phytoplankton are characterised mainly by complex microbial food webs that favour the recycling of organic matter within the euphotic layer (Cermeño et al. 2006). Several authors have argued that when interspecific variability is taken into consideration, the relationship between phytoplankton cell size and growth rate becomes weaker and highly variable (Banse 1982, Blasco et al. 1982, Chisholm 1992, Tang 1995). Studies have shown that, in productive coastal ecosystems characterised by diverse phytoplankton communities, large-size phytoplankton can sustain higher rates of carbon-specific and chlorophyll *a*-normalised photosynthesis than small-size phytoplankton (Claustre et al. 2005, Cermeño et al. 2005a, b, Crosbie and Furnas 2001, Furnas 1991, Frenette et al. 1996, Jochem 2003, Legendre et al. 1993, Tamigneaux et al. 1999, Hashimoto and Shiomoto 2002, Uitz et al. 2008). In contrast, Marra et al. (2007) shows that smaller phytoplankton have higher maximum photosynthetic rates than larger-sized phytoplankton.

This is ecologically significant since it represents a physiological basis to explain why large phytoplankton become dominant in resource-saturated environments. Size is thus an ecologically important variable of the structure and function of food webs by having a strong influence on the efficiency of transfer and the fate of carbon to higher trophic levels

(Michaels and Silver 1988, Legendre and Le Fèvre 1989, Iriarte et al. 2000). However, the interpretation of the chlorophyll *a*-normalised photosynthesis depends on the carbon-to-chlorophyll *a* ratio, which has been reported to vary with environmental conditions and cell size and phyletic affiliation (Taylor et al. 1997, Finkel et al. 2004). In an approach which linked size class specific photosynthetic rates to the optical absorption of phytoplankton, Hirata et al. (2009) suggested that, due to a greater spatial extent, the production in nano-plankton dominated communities may be larger than those in which microplankton dominate. However, communities dominated by microplankton were shown to have a larger photosynthetic rate per unit volume.

Small-size phytoplankton are an important fraction (35 - 60 %) of the total autotrophic biomass and may account for over 50 % of the daily PP in oligotrophic regions, and 25 - 30 % of daily PP in more productive regions (Li et al. 1983, Platt et al. 1983, Takahashi and Bienfang 1983, Joint and Pomroy 1983, 1986, Tremblay and Legendre 1994). The biomass and production of small phytoplankton cells tends to remain relatively constant, but their relative contribution at a community level is highly variable and dependant on the dynamics of large phytoplankton cells which tend to bloom whenever light and nutrient conditions are adequate (Chisholm 1992).

An increase in the biomass of small-size phytoplankton is usually rapidly followed by an increase in biomass and activity of small herbivores which exert a strong grazing control on these populations. In contrast, large phytoplankton are grazed upon by mesozooplankton with longer generation times than those of phytoplankton (Banse 1992, Kiørboe 1993). The uncoupling between phytoplankton (prey) and zooplankton (predators) has been suggested as an explanation of why large phytoplankton become dominant in resource-saturated environments (Kiørboe 1993).

Chapter 2 – In situ Phytoplankton Production and Physiology

2.1. Introduction

The photophysiological responses of phytoplankton vary as a function of irradiance, temperature, nutrient concentrations, and physical processes. Among these, irradiance is a key variable. The relationship between phytoplankton and irradiance is crucial to understanding the physiology and ecology of phytoplankton (Behrenfeld and Falkowski 1997a, b, Kirk 1994). Photosynthetic rates and irradiance have a non-linear relationship which can be determined by incubating a series of subsamples, drawn from a single seawater sample, against a gradient of light, at a temperature as close as possible to natural conditions (Sakshaug et al. 1997).

Photosynthetic-Irradiance (P-E) relationships have been used for a long time to compute depth-integrated production, and to determine spatial and temporal variations in assimilation numbers and light-limited photosynthesis rates. They have also been used to investigate the physiological status of algal populations with changing environmental conditions, and to estimate parameters for algal growth modelling (Talling 1984, Vollenweider 1974, Falkowski 1981, Côté and Platt 1984, van Straten and Herodek 1982).

The major parameters (Figure 2.1.) derived from this relationship include α (the initial slope of the P-E curve), P_s (the maximum photosynthetic rate), and β (the negative slope of the P-E curve beyond the optimal light intensity). P_s is a measure of the photosynthetic capacity of phytoplankton, while α is a measure of the quantum efficiency of photosynthesis. β is the coefficient of photoinhibition and represents the decline of photosynthesis at saturating irradiances. Additional parameters, such as E_k (the light saturation parameter), can also be derived. E_k describes the optimal light intensity for balance between the light and dark reactions of photosynthesis (i.e. it is the light intensity at the onset of photosynthetic saturation). It is independent of biomass and is often used as an indication of photoacclimation (Henley 1993, Laws et al. 2002, Sakshaug et al. 1997).

By way of these parameters, which describe useful physiological characteristics of phytoplankton, P-E curves provide important information on the spatial and temporal variations of the environmental effects on algal physiology (Arbones et al. 2000, Platt and Jassby 1976, Prézelin et al. 1987, Prézelin and Glover 1991). P-E parameters are also used as input into bio-optical models which attempt to predict changes in the rates of phytoplankton growth and photosynthesis, and they reflect the underlying biophysical, biochemical, and metabolic processes that regulate photosynthesis (Laws and Bannister 1980, Lewis et al. 1985, Geider et al. 1986, Bidigare et al. 1987, Platt and Sathyendranath 1988, Smith et al. 1989, Baker et al. 1990, Fasham et al. 1990, Falkowski and Raven 1997).

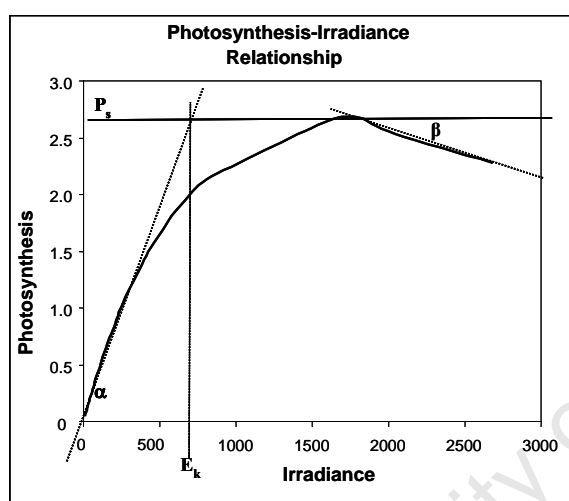


Figure 2.1. Idealised curve of specific photosynthetic rate as a function of irradiance. The maximum photosynthetic rate, P_s , light saturation parameter, E_k , the quantum efficiency of photosynthesis, α , and the coefficient of photoinhibition, β , are indicated.

Since photosynthesis, and hence primary production (PP), occurs throughout the euphotic zone, more accurate estimates of PP would be obtained by integration through the euphotic zone. However, successful integration of PP through the water column requires knowledge of the vertical distribution of phytoplankton. Ocean colour remote sensing enables the estimation of chlorophyll *a* as a measure of phytoplankton biomass over large geographical areas. This estimate, however, is limited to the near-surface phytoplankton distribution since ocean colour sensors are only able to integrate through the upper 20 % of the euphotic zone (Richardson et al. 2002), depending on the extinction of light through the water column.

Most operational satellite models used for the estimation of phytoplankton biomass assume a uniform vertical profile, and are thus unable to account for the variations in the vertical distribution of phytoplankton (Andre 1992). Computations of PP from satellite data tend to underestimate PP because the contribution of subsurface chlorophyll maxima is disregarded (Sathyendranath et al. 1995). Satellite estimates of PP thus require additional information from the vertical distribution of phytoplankton through the euphotic zone (Morel and Berthon 1989). In coastal regions, particularly upwelling areas such as the Benguela, dynamic physical conditions result in substantial spatial and temporal variability in phytoplankton biomass distribution. Consequently, the shape of chlorophyll *a* profiles is affected (Brown and Hutchings 1987a, Bailey and Chapman 1991, Demarcq et al. 2008, Pitcher et al. 1992, Richardson et al. 2002).

Traditionally, PP is computed using models which incorporate broad-band photosynthetic parameters and light. These models assume that all light wavelengths in the photosynthetically active radiation (PAR) part of the spectrum (400 - 700 nm) are absorbed with the same efficiency by phytoplankton. However, the absorption of light is strongly wavelength dependent (Bricaud and Stramski 1990). The use of non-spectral models of light attenuation and photosynthesis can overestimate computations of daily PP in the water column by as much as 50 % or more (Sathyendranath et al. 1989, Platt and Sathyendranath 1991). The use of spectral models, which incorporate the wavelength dependency of phytoplankton absorption, has greatly improved the accuracy of PP estimates (Kyewalyanga et al. 1992, Morel 1991).

The extent to which spatial and temporal variations in hydrography affect broad-band and spectral models of PP, particularly in relation to light limitation, is poorly understood in the Benguela ecosystem. Modelling carbon fixation in specific biogeochemical provinces and improving PP estimates from remotely-sensed data thus requires an understanding of the variations of photophysiology in relation to changes in environmental conditions, and an assessment of the variables that influence PP (Sathyendranath et al. 1995, Behrenfeld and Falkowski 1997a).

This chapter investigates the spatial and temporal variations in primary production on the continental shelf of the southern Benguela ecosystem and attempts to understand the physiological response of phytoplankton communities to changing environmental conditions. The key questions addressed in this study are: (1) What is the spatial and temporal variability of in situ primary production on the continental shelf? (2) What are the

physiological mechanisms which govern the variations in primary production? and (3)
What is the effect of environmental variables on phytoplankton photosynthesis?

2.2. Methods

2.2.1. Study area and sampling

Several research surveys were conducted on the continental shelf of the southern Benguela during 2006 - 2007. The first survey took place between 16 - 30 October 2006, and the second during 14 - 29 May 2007. Figure 2.2. illustrates the distribution of stations across the southern Benguela shelf for each of the surveys conducted. At each station, sampling for primary production and physiological experiments was conducted around midday at three to five depths throughout the euphotic zone. Stations were selected to measure daily rates of PP during periods of maximum irradiance at the sea surface.

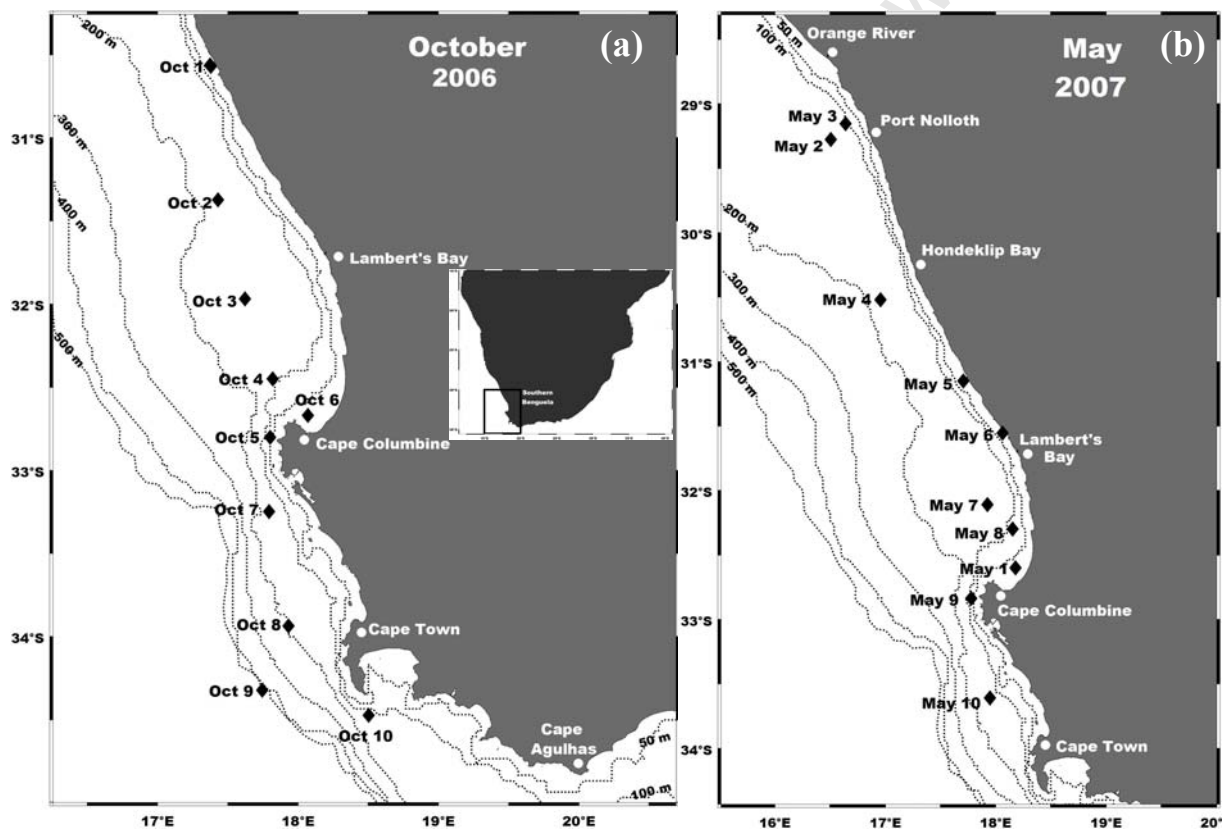


Figure 2.2. Maps illustrating the distribution of PP stations across the southern Benguela during (a) October 2006, and (b) May 2007. 2-minute Gridded Global Relief (ETOPO2) bathymetry contours are indicated as black dotted lines.

Profiles of temperature, salinity, fluorescence, photosynthetically available radiation (PAR), and the PAR incident at the surface were recorded using a Seabird SBE 19 CTD. Seawater samples were collected at selected depths between 3 – 60 m, according to the vertical distribution of fluorescence, using black carboys to prevent light shock to the

phytoplankton. Photosynthesis-Irradiance (P-E) experiments were conducted on board, while samples were collected for the analysis of phytoplankton absorption spectra, pigment composition, and nutrients. Nutrient samples were stored frozen at -80 °C for later analysis ashore. Macro-nutrients (nitrate, nitrite, silicate, phosphate) were determined with standard techniques (Mostert 1983) using an Astoria-Pacific Auto Analyser.

Maps of MODIS Aqua Sea Surface Temperature (SST), Quikscat wind speeds, and geostrophic current velocities overlaid onto sea surface height anomalies were used to describe the hydrographic conditions during the cruise periods. SST data was acquired from the Ocean Biology Processing Group at NASA's Goddard Space Flight Center (<http://oceancolor.gsfc.nasa.gov>), while wind speeds were obtained from CERSAT, at IFREMER (<http://www.ifremer.fr/cersat/en/data/data.htm>) and altimetry data was distributed by Aviso, with support from Cnes (<http://www.aviso.oceanobs.com/duacs/>).

2.2.2. Phytoplankton biomass and Pigment composition

Although chlorophyll *a* is the dominant pigment in phytoplankton cells, chlorophylls *b* and *c*, and various photosynthetic carotenoids contribute significantly to the light-harvesting capacity of phytoplankton. In addition to these photosynthetic pigments, phytoplankton cells also contain photoprotective carotenoids, which serve to protect the cells against high irradiances that may damage the photosynthetic apparatus (Kirk 1994). Certain key pigments are useful signatures for various phytoplankton groups and the analysis and interpretation of phytoplankton pigments provides important chemotaxonomic information on community structure.

To harvest phytoplankton for pigment analysis, seawater samples of 0.5 - 2 L, depending on the concentration of suspended material, were filtered through 25 mm Whatman GF/F filters and stored in liquid nitrogen for later analysis ashore. With the aid of ultrasonication, phytoplankton pigments were extracted into acetone and clarified by centrifugation. Analysis of pigments was achieved by Reverse-phase High Performance Liquid Chromatography (HPLC) (Barlow et al. 1997), using a 5 µm HyPURITY C8 column, a Varian ProStar ternary high-pressure pump, a Thermo Electron AS3000 autosampler, a Thermo Electron UV6000 diode array absorbance detector, and the ChromQuest chromatography software.

Chlorophyll *a* and *trans-β* apo-8' carotenal internal standards were obtained from Sigma-Aldrich Ltd. and other pigment standards were purchased from the DHI Institute for Water and Environment, Denmark. The method enabled the separation of mono- and divinyl chlorophyll *a*, zeaxanthin and lutein, and achieved partial separation of mono- and divinyl chlorophyll *b*. Pigments were detected at two wavelengths (440 nm and 665 nm) and identified on the basis of retention time and online diode array spectra. The limits of detection were on the order of 0.001 mg m⁻³.

Phytoplankton populations are comprised of a considerably large range of groups (Jeffrey and Vesk 1997), and distinguishing each individual group complicates data interpretation and visualization. To facilitate data interpretation, it is useful to extract only the most relevant pigment biomarkers. In this study, phytoplankton groups were selected on the basis of their significance in the ecosystem, according to Barlow et al. (2005, 2006, 2007, 2008). Using Diagnostic Pigment (DP) indices that were defined as the sum of seven selected biomarker pigments as outlined in Table 2.1., four major phytoplankton groups, namely diatoms, peridinin-containing dinoflagellates, small flagellates and prokaryotes, were characterised and designated as Diat_{DP}, Din_{DP}, Flag_{DP}, and Prok_{DP}, respectively. The relative proportion of each group to the total biomass is defined in Table 2.1.

Diatoms and dinoflagellates (5 - 200 μm) were characterised as the most important phytoplankton groups and were identified by Fucoxanthin (Fuc) and Peridinin (Per), respectively. Several pigment biomarkers (Hex, But, All, Chl_b) were collectively identified as small flagellates (generally < 20 μm). This group included prymnesiophytes, chrysophytes, cryptophytes and green flagellates (including prasinophytes). It is noted that some cryptophytes and green flagellates are known to exceed a size of 20 μm (Jeffrey and Vesk 1997). Prokaryotic cyanobacteria (generally < 2 μm), such as *Prochlorococcus* and *Synechococcus*, was indicated by the pigment Zeaxanthin (Zea) (Moore et al. 1995). Throughout the shelf region of the southern Benguela, divinyl chlorophyll *a* and *b* were not detected in any of the samples. This is in accordance with previous studies in the southern and northern Benguela ecosystems, where no divinyl chlorophyll *a* and *b* was detected (Barlow et al. 2005, 2006).

The varying contribution of chlorophylls and carotenoids to the total pigment pool was assessed by Photo-pigment indices. Chlorophyll's are reported as total chlorophyll *a* concentration (TChl_a) and the sum of chlorophyll *b* and *c* were reported as Chl_{bc}. TChl_a was estimated as the sum of chlorophyll *a*, chlorophyllide *a*, and chlorophyll *a* allomers

and epimers. Carotenoids were proportioned into photosynthetic (PSC) and photoprotective carotenoids (PPC). Photosynthetic carotenoids included peridinin, 19'-butanoyloxyfucoxanthin, fucoxanthin, and 19'-hexanoyloxyfucoxanthin. Photoprotective carotenoids comprised violoxanthin, diatoxanthin, alloxanthin, diadinoxanthin, zeaxanthin, lutein, and $\beta\beta$ - and $\beta\varepsilon$ -carotene. The photo-pigment indices were symbolised as $TChla_{TP}$, $Chlbc_{TP}$, PSC_{TP} , PPC_{TP} , and derived as shown in Table 2.1.

Table 2.1. Symbols, names, formulae, and selected taxonomic designations for chlorophylls, carotenoids, pigment sums, and pigment indices (Barlow et al. 2005, 2006, Jeffrey and Vesk 1997).

<u>Symbol</u>	<u>Pigment</u>	<u>Designation</u>	
Chla	Chlorophyll <i>a</i> (plus allomers and epimers)	Chlorophytes	
Chlb	Chlorophyll <i>b</i>		
Chlc ₁	Chlorophyll <i>c</i> ₁		
Chlc ₂	Chlorophyll <i>c</i> ₂		
Chlc ₃	Chlorophyll <i>c</i> ₃		
Chlidea	Chlorophyllide <i>a</i>		
All	Alloxanthin	Cryptophytes	
But	19'-Butanoyloxyfucoxanthin	Chrysophytes	
Caro	ββ-Carotene plus βε-Carotene	Diatoms	
Diad	Diadinoxanthin		
Diato	Diatoxanthin		
Fuc	Fucoxanthin		
Lut	Lutein		
Hex	19'-Hexanoyloxyfucoxanthin		Prymnesiophytes
Per	Peridinin		Dinoflagellates
Viol	Violaxanthin		Cyanobacteria
Zea	Zeaxanthin		
	<u>Pigment sum</u>		<u>Formula</u>
TChla	Total Chlorophyll <i>a</i>	Chla + Chlidea	
Chlbc	Sum of Chlorophyll <i>b</i> and <i>c</i>	Chlb + Chlc ₁ + Chlc ₂ + Chlc ₃	
PPC	Photoprotective carotenoids	All + Caro + Diad + Diato + Lut + Viol + Zea	
PSC	Photosynthetic carotenoids	But + Fuc + Hex + Per	
TP	Total pigments	TChla + Chlbc + PPC + PSC	
DP	Diagnostic pigments	All + But + Chlb + Fuc + Hex + Per + Zea	
	<u>Pigment index</u>	<u>Formula</u>	
TChla _{TP}	Total chlorophyll <i>a</i> to total pigments	TChla/TP	
Chlbc _{TP}	Chlorophylls <i>b</i> and <i>c</i> to total pigments	Chlbc/TP	
PPC _{TP}	Photoprotective carotenoids to total pigments	PPC/TP	
PSC _{TP}	Photosynthetic carotenoids to total pigments	PSC/TP	
Diat _{DP}	Diatom proportion of DP	Fuc/DP	
Dino _{DP}	Dinoflagellate proportion of DP	Per/DP	
Flag _{DP}	Flagellate proportion of DP	(All + But + Chlb + Hex)/DP	
Prok _{DP}	Prokaryote proportion of DP	Zea/DP	

2.2.3. Phytoplankton light absorption coefficients

The absorption of light by phytoplankton varies with changes in photoacclimation and the structure of communities, and is influenced by pigment packaging and cellular pigment composition (Bricaud et al. 2004, Stæhr et al. 2004). Phytoplankton absorption is strongly related to chlorophyll *a* concentration (Bricaud et al. 2004), primary production (Lee et al. 1996, Marra et al. 2007) and physiology (Aiken et al. 2008). It is thus a critical variable in bio-optical models of phytoplankton production and for the interpretation of satellite ocean colour data.

Phytoplankton samples for absorption analysis were collected by filtering 0.5 – 2 L of seawater through 25 mm Whatman GF/F filters and stored in liquid nitrogen for later analysis ashore. The optical density of the total particulate material, a_p , was measured at 1 nm bandwidth from 400-750 nm by the quantitative filter technique of Tassan and Ferrari (1995), using a GBC Cintra 404 spectrophotometer and the Cintral V2.1 software. The spectrophotometer was equipped with a barium-coated integrating sphere, and light was detected by a built-in photomultiplier tube at the base of the sphere. Optimal performance of the sphere across the 200-800 nm wavelength range was provided by spectralon reference disks. A set of five filters were moistened with pre-filtered artificial seawater and read as blanks. The optical density of the non-algal (detrital) material was measured on the same filters after pigment extraction by bleaching with sodium hypochlorite over 24 hours.

All spectra were corrected by subtracting the average blank spectra, and by subtracting the absorbance values at 750 nm from all other wavelengths. A pathlength amplification factor of 2 was used to correct for scattering according to Roesler (1998). Phytoplankton absorption spectra (a_{ph} , m^{-1}) were estimated by subtracting the detrital absorption (a_d) from the total particulate absorption spectra (a_p). Chlorophyll-specific absorption ($m^2 mg^{-1}$) was calculated according to: $a_{ph}^* = a_{ph} / TChla$

2.2.4. Irradiance at the sea surface and in the water column

The photosynthetically available radiation incident at the sea surface (SPAR) and profiles of available radiation through the water column (PAR) was measured simultaneously using a QSR-2000 Hemispherical Quantum Scalar Reference Sensor, and a QSP-2000 Quantum

Scalar Sensor, respectively. The PAR profile was used to determine the depth of the euphotic zone (z_{eu} , metres). Attenuation coefficients, K_d (m^{-1}), were calculated through a linear regression of the natural log of PAR versus depth, according to the following equation (Kirk 1994): $\ln E_d(z) = -K_d z + \ln E_d(0)$

where: $E_d(0)$ are the values of the downwelling PAR just below the surface, $E_d(z)$ are the values of the downwelling PAR at depth z metres, K_d is the average vertical attenuation coefficient over the depth interval from 0 to z metres (m^{-1}).

The depth of the euphotic zone (z_{eu} , metres) was defined as the depth of 1 % of the surface irradiance (Morel 1988). The depth of the upper mixed layer (z_m , metres) was determined as the depth where a change in density, σ_t , of $\geq 0.05 \text{ kg m}^{-3}$ was first observed over a 5 m depth interval (Lorenzo et al. 2002, Morán and Estrada 2005, 2001). The ratio z/z_{eu} was derived as an index of the relative irradiance at the sampled depth (z).

2.2.5. Photosynthesis-Irradiance (P-E) Experiments

To examine the vertical changes in photosynthetic parameters within the euphotic zone, water samples were collected at five depths and Photosynthesis-Irradiance (P-E) experiments were conducted in linear incubators. A total of 93 P-E curves were measured across the shelf area of the southern Benguela ecosystem during two surveys (October 2006 and May 2007). The incubators consisted of two channels, each housing fifteen sub-samples in 75 ml Corning tissue culture flasks, 3 openings for water circulation, and a light-tight cover. Culture bottles were linearly arranged to provide a gradient of light and nylon mesh filters were used to further attenuate the light to yield lower irradiances at the rear of the channel.

The incubators were illuminated through a glass window at the front by 50W, 12V tungsten-halogen lamps with a dichroic reflector and a Deco glass cover (Arbones et al. 2000, Figueiras et al. 1999). A Portable Laboratory Quantum Scalar Irradiance Metre (Biospherical Instruments, QSL-2101) connected to a data logger (LOGGER-2100) was used to measure the photosynthetic available radiation (E_{PAR}). The irradiance metre uses a 1.3 cm diameter Teflon sphere to collect irradiance in 3.8 pi steradians of solid angle (i.e. light is measured from almost all directions around the sphere). E_{PAR} at each position in the incubator was measured by inserting the Teflon sphere into each bottle containing

water. Despite the fact that the sphere never completely fills the space in the bottles, the PAR measurements can be regarded as relatively reliable, assuming that the angular distribution of light is constant from one position to another within the incubator (Babin 1994). The samples were incubated at fifteen different irradiances, varying between a maximum of $\sim 2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ to a minimum of $\sim 20 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Lorenzo et al. 2005, Marañón and Holligan 1999).

Bottles were inoculated with 10 μCi ($3.70 \times 10^5 \text{ Bq}$) of ^{14}C labelled bicarbonate (Arbones et al. 2000, Tilstone et al. 2003, 2005, Lorenzo et al. 2002, 2004, 2005) and incubated for 2 hours commencing within 30 minutes of sampling. Three bottles were used as a control and completely covered with aluminium foil to measure dark ^{14}C fixation. All manipulations were carried out under low light conditions to prevent light shock to the phytoplankton. Before each experiment, all bottles were cleaned following JGOFS protocols so as to reduce any possible trace metal contamination (Sakshaug et al. 1997).

Samples were refrigerated by a system of recirculating water pumped through a refrigeration unit with a digital controller to maintain the incubation temperature as close as possible to the in situ temperature. After incubation, the suspended material was filtered onto 25 mm GF/F filters under low vacuum pressure and then exposed to concentrated HCl fumes for 2 hours in order to eliminate any unincorporated inorganic ^{14}C . The short period of exposure to HCl fumes was chosen to minimise possible losses of organically bound carbon. After fuming, each filter was immersed in 8 ml of scintillation cocktail and stored.

Radiocarbon activity (^{14}C disintegrations per minute – DPM) was determined on a Beckman LSC 6500 liquid scintillation analyser using an internal standard to correct for quenching. Dark bottle DPM's were averaged, and then subtracted from light bottle DPM's to correct for non-photoautotrophic carbon fixation, which could represent a significant portion of the light bottle DPM values (Banse 1992). Due to the relatively short incubation periods, ^{14}C -based primary productivity was presumed to refer to gross carbon uptake as defined by Sakshaug et al. (1997). DPM counts were converted to hourly photosynthesis rates ($\text{mg C m}^{-3} \text{h}^{-1}$) following Parsons et al. (1984):
$$P = \frac{(R_s - R_B) * W}{R * N}$$

where: **P** is the rate of photosynthesis ($\text{mg C m}^{-3} \text{h}^{-1}$), **R_s** is the total activity of the filtered sample, corrected for quenching (DPM), **R_B** is the total activity of the dark bottle, corrected for quenching (DPM), **W** is the weight of the dissolved inorganic carbon

concentration (carbon dioxide) in the samples (mg C m^{-3}), \mathbf{R} is the total activity of the added ^{14}C (DPM), and \mathbf{N} is the duration of the incubation (hours).

\mathbf{W} can be approximated according to $\mathbf{W} = 12000 * \mathbf{TC}$, where: - \mathbf{TC} (total carbon dioxide) equals $0.96 * \mathbf{CA}$, \mathbf{CA} (carbonate alkalinity) equals $0.05 * \mathbf{TA}$, and \mathbf{TA} (total alkalinity) equals $0.067 * \mathbf{salinity}$. Hourly production rates ($\text{mg C m}^{-3} \text{ h}^{-1}$) were normalised to HPLC-determined chlorophyll a concentrations (mg chla m^{-3}) to provide chlorophyll a specific production ($\text{mg C mg}^{-1} \text{ chla h}^{-1}$) (Kyewalyanga et al. 1997, Bouman et al. 2000).

2.2.5.1. Irradiance in the incubator

The photosynthetically available radiation (PAR) at each position in the incubator, \mathbf{E}_{PAR} , was measured by inserting the irradiance metre into every bottle. It was assumed that the quality of the incident light did not significantly change along the length of the incubator (Arbones et al. 2000, Babin et al. 1994, Figueiras et al. 1999). The spectral irradiance used for broad-band P-E relationships, $\mathbf{E}_q(\lambda)$, at each position in the incubator was calculated by multiplying the relative mean spectrum of the tungsten-halogen lamp, $\mathbf{E}_N(\lambda)$, by the corresponding PAR irradiance, \mathbf{E}_{PAR} , at each location (Kyewalyanga et al. 1997, Lorenzo et al. 2002, 2004), using the equation:

$$\mathbf{E}_q(\lambda) = \mathbf{E}_N(\lambda) * \mathbf{E}_{\text{PAR}}$$

2.2.5.2. Photosynthesis-Irradiance (P-E) parameters

The light-limited slope, the maximum photosynthetic rate, and the coefficient of photoinhibition

Shipboard P-E experiments were conducted by incubating phytoplankton samples according to the procedure described above in section 2.2.5. Broad-band P-E parameters, the light-saturated chlorophyll specific rate of photosynthesis, \mathbf{P}_s^{B} ($\text{mg C [mg chla]}^{-1} \text{ h}^{-1}$), the light-limited slope, α^{B} ($\text{mg C [mg chla]}^{-1} \text{ h}^{-1} [\mu\text{mol m}^{-2} \text{ s}^{-1}]^{-1}$), and the coefficient of photoinhibition, β^{B} ($\text{mg C [mg chla]}^{-1} \text{ h}^{-1} [\mu\text{mol m}^{-2} \text{ s}^{-1}]^{-1}$) were estimated by fitting the chlorophyll-normalised hourly production rates to the continuous exponential model of

Platt et al. (1980) using least squares regression. Superscript ^B indicates that parameters are normalised to chlorophyll *a*.

$$P_z^B = P_s^B \left[1 - \exp\left(-\alpha^B * \frac{E_{PAR}}{P_s^B}\right) \right] * \exp\left(-\beta^B * \frac{E_{PAR}}{P_s^B}\right)$$

where: P_z^B is the chlorophyll specific rate of photosynthesis ($\text{mg C} [\text{mg chla}]^{-1} \text{h}^{-1}$), P_s^B is the chlorophyll specific light-saturated rate of photosynthesis (i.e. the hypothetical maximum value of P_z^B at saturating irradiances) in the absence of photoinhibition ($\text{mg C m}^{-3} \text{h}^{-1}$), α^B is the chlorophyll specific light limited slope ($\text{mg C} [\text{mg chla}]^{-1} \text{h}^{-1} [\mu\text{mol m}^{-2} \text{s}^{-1}]^{-1}$), β^B is the chlorophyll specific coefficient of photoinhibition ($\text{mg C} [\text{mg chla}]^{-1} \text{h}^{-1} [\mu\text{mol m}^{-2} \text{s}^{-1}]^{-1}$), E_{PAR} is the PAR incident at each location in the incubator ($\mu\text{mol m}^{-2} \text{s}^{-1}$).

In order to avoid any bias in the choice of model, the Platt et al. (1980) model was systematically used for all P-E curves, regardless of whether photoinhibition was apparent or not. When β^B equals zero, the model of Platt et al. (1980) is equivalent to the exponential model of proposed by Webb et al. (1974), which does not include a photoinhibition parameter. Predictions of photosynthesis resulting from P-E models such as Webb et al. (1974), Platt et al. (1980), and Jassby and Platt (1976) approach net production (i.e. gross production minus autotrophic respiration) since they contain parameters which are determined by short-term ¹⁴C incubations.

Frenette et al. (1993) found that there are systematic differences in P_s^B , α^B , and β^B estimated from the models of Webb et al. (1974) and Platt et al. (1980). α^B is particularly sensitive to the choice of model. This stems from forcing mathematical functions with different curvatures to the data. Currently, there are no published protocols which make recommendations as to the precision and accuracy of results obtained for P-E parameters (Sakshaug et al. 1997). This is because P-E parameters are estimated from several different measurements and thus lack an absolute reference. For the purposes of comparison, all the models used in study are presented in similar notation and units. The notation used to describe the primary production models is summarised in Table 2.2.

Table 2.2. Symbols, definitions, and units for phytoplankton biomass, light, P-E relationships, and Primary Production.

<u>Symbol</u>	<u>Definition</u>	<u>Unit</u>
Phytoplankton biomass		
chl_a	Chlorophyll <i>a</i> concentration	mg m ⁻³
Tchl_a	Total chlorophyll <i>a</i> concentration	mg m ⁻³
Light		
a_p(λ)	Phytoplankton spectral absorption coefficient	m ⁻¹
\bar{a}_p	Unweighted, spectral mean photosynthetic absorption of phytoplankton	m ⁻¹
\bar{a}_T	Mean photosynthetic absorption of phytoplankton weighted by the shape of the emission spectrum of the tungsten-halogen lamp	m ⁻¹
PAR	Photosynthetically available radiation	μEinsteins m ⁻² s ⁻¹
SPAR	Photosynthetically available radiation incident at the sea surface	μEinsteins m ⁻² s ⁻¹
K(λ)	Spectral attenuation coefficient for the water column	m ⁻¹
z_{eu}	Depth of the euphotic zone	m
z_{uml}	Depth of the surface mixed layer	m
z_{E_k}	Depth where PAR equals E _k	m
Photosynthesis-Irradiance relationships		
E_{PAR}	Photosynthetically available radiation at each position in the incubator	μmol m ⁻² s ⁻¹
α*	Chlorophyll specific light limited slope	mg C [mg chl _a] ⁻¹ h ⁻¹ [μmol m ⁻² s ⁻¹] ⁻¹
P_s*	Chlorophyll specific light saturated rate of photosynthesis	mg C m ⁻³ h ⁻¹
P_z*	Chlorophyll specific rate of photosynthesis	mg C [mg chl _a] ⁻¹ h ⁻¹
β*	Chlorophyll specific coefficient of photoinhibition	mg C [mg chl _a] ⁻¹ h ⁻¹ [μmol m ⁻² s ⁻¹] ⁻¹
X	Correction factor for α*	dimensionless
I_T(λ)	Incident irradiance (from the tungsten-halogen lamp) at λ in the incubator	μmol m ⁻³ s ⁻¹
E_{kPAR}	Spectral light saturation parameter for PAR available to phytoplankton	μmol m ⁻³ s ⁻¹
φ_m	Maximum quantum yield of photosynthesis	mol C [mol photons] ⁻¹
Primary Production		
∑PP_{PAR}	Daily integrated water column primary production computed using PAR	mg C m ⁻² d ⁻¹

The light-saturated rate of photosynthesis, P_s^B (also known as the assimilation number), is independent of wavelength and can thus be obtained by fitting the data to broad-band PAR or to PUR (photosynthetically usable radiation) without distinction (Lorenzo et al. 2004). Since $\alpha(\lambda)$ is wavelength dependant, values of the initial slope, α^B , estimated from broad-band models need to be corrected for bias due to the spectral quality of the incident irradiance (Dubinsky et al. 1986, Kyewalyanga et al. 1997). The emission spectrum of the tungsten-halogen lamp (Figure 2.3.) is not spectrally neutral, but is strongly wavelength dependent. It has an emission minimum in the blue and a maximum in the red part of the spectrum.

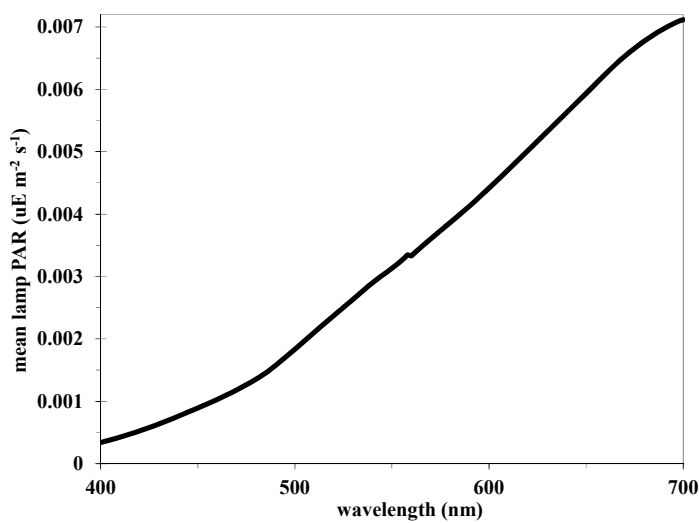


Figure 2.3. Emission spectrum of the tungsten-halogen lamp.

To correct for the bias introduced by the shape of the emission spectrum of the tungsten-halogen lamps, the initial slope, α^B , was multiplied by a correction factor, $X = \frac{\overline{a_p}}{a_T}$. The correction factor is based on the absorption spectrum of phytoplankton and assumes that the maximum quantum yield of photosynthesis, $\phi_m(\lambda)$, is spectrally flat. X is dimensionless and is defined as the ratio of the unweighted, spectral mean photosynthetic absorption of phytoplankton, $\overline{a_p}$, to the mean photosynthetic absorption of phytoplankton weighted by the shape of the emission spectrum of the tungsten-halogen lamp, $\overline{a_T}$ (Babin et al. 1994, Bouman et al. 2000, Dubinsky et al. 1986, Kyewalyanga et al. 1997, Schofield et al. 1990).

The unweighted, spectral mean photosynthetic absorption of phytoplankton was

determined as $\overline{a_p} = \frac{\int_{\lambda=400}^{700} a_p(\lambda) d\lambda}{\int_{\lambda=400}^{700} d\lambda}$, where $a_p(\lambda)$ is the phytoplankton absorption coefficient

at λ . The weighted mean absorption, which accounts for the spectral quality of the

tungsten-halogen lamp, $\overline{a_T}$, was determined as $\overline{a_T} = \frac{\int_{\lambda=400}^{700} a_p(\lambda) I_T(\lambda) d\lambda}{\int_{\lambda=400}^{700} I_T(\lambda) d\lambda}$, where $I_T(\lambda)$ is the

incident irradiance (from the tungsten-halogen lamp) at λ in the incubator.

The spectral light saturation parameter

The spectral light saturation parameter for PAR ($\mu\text{mol m}^{-3} \text{s}^{-1}$) derived from broad-band P-

E relationships (Figueiras et al. 1999, Lorenzo et al. 2002, 2004) is given by: $E_k = \frac{P_s^B}{\alpha^B}$

The light saturation parameter is the intercept between the slope of the P-E curve and the maximum photosynthetic rate. It indicates the irradiance at which control of photosynthesis passes from light absorption and photochemical energy conversion to reductant utilisation (Sakshaug et al. 1997). It may be used as a convenient indicator of photoacclimation in phytoplankton.

2.2.6. Primary Production estimation

The daily integrated water column primary production, $\sum \text{PP}$ ($\text{mg C m}^{-2} \text{d}^{-1}$), was estimated using the formulation of Platt et al. (1980). This model uses E_{PAR} , chlorophyll *a* and the broad-band photosynthetic parameters to calculate $\sum \text{PP}$ (Tilstone et al. 2003). Daily primary production rates were calculated by multiplying hourly rates by the number of daylight hours (Varela et al. 2005). Vertical integration over the five sampled depths was carried out using the trapezoidal rule. These calculations only provide an estimate of daily gross primary production, and no attempt was made to correct for losses of carbon as a result of respiration or grazing.

2.3. Results and Discussion

Investigations of phytoplankton photosynthesis, pigments and absorption, and support hydrographic measurements were undertaken across the continental shelf of the southern Benguela during October 2006 and May 2007. Photosynthesis-irradiance (P-E) parameters and primary production were estimated from a total of 93 P-E experiments conducted over a range of depths at 20 stations. Phytoplankton community structure was assessed using pigment signatures and TChla concentrations were interpreted as a measure of the phytoplankton biomass. Relationships between phytoplankton biomass, pigment indices, absorption, photosynthetic parameters, primary production, and environmental variables are presented here.

2.3.1. Hydrography

The spatial distribution of satellite Sea Surface Temperature (SST) showed typical patterns expected for the southern Benguela during mid-spring (October) (Figure 2.4.a,b) and late autumn (May) (Figure 2.5.a,b). A large gradient between inshore and offshore temperatures was observed during May, ranging from 12 °C at the coast to 20 °C further offshore (Figure 2.5.a,b). During October, this gradient was slightly weaker, with temperatures ranging between 12 °C and 18 °C throughout most of the region. Higher temperatures, up to 21 °C, were observed only in the southern part of the region (Figure 2.4.a,b) and were associated with the presence of an Agulhas ring, indicated by the large positive sea surface height anomaly centred at about 36 °S; 15 °E (Figure 2.6).

Satellite altimetry (Figure 2.6.) showed that this anticyclonic feature moved northward and influenced the outer part of the shelf off the Cape Peninsula. Such features have been shown to periodically interact with the upwelling system by influencing phytoplankton distribution and contributing to the offshore advection of fish eggs and larvae (Duncombe Rae et al. 1992, Hutchings et al. 1998, Rossi et al. 2008).

Equatorward, upwelling-favourable winds during October (Figure 2.4.c,d) resulted in intense upwelling, as indicated by the presence of cool water (Figure 2.4.a,b) along the coast throughout the region. The predominantly south-easterly wind observed during 16 – 22 October yielded more enhanced upwelling, with the cooler water extending further offshore, while the upwelled water was confined in a narrower band along the coast during 23 – 30 October when the wind exhibited a slightly more westerly component.

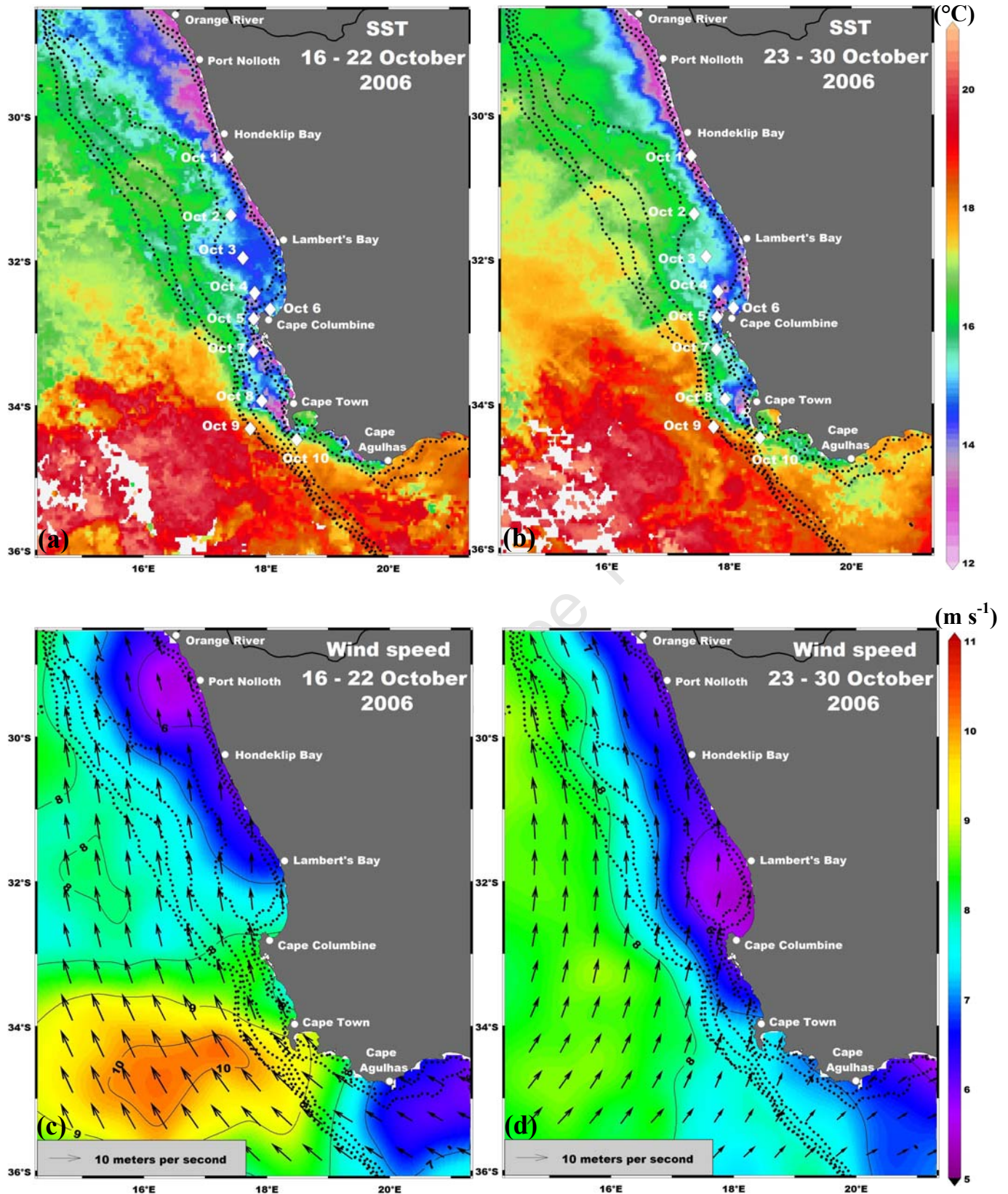


Figure 2.4. Maps of weekly averaged (a, b) MODIS Aqua Sea Surface Temperature ($^{\circ}\text{C}$), and (c, d) Quikscat wind speed (m s^{-1}) for the southern Benguela during October 2006. 2-minute Gridded Global Relief (ETOPO2) bathymetry contours (50, 100, 200, 300, 400, and 500 m) are indicated as black dotted lines. The white diamonds on (a, b) indicate the locations of primary production stations. The arrows on (c, d) indicate the wind direction.

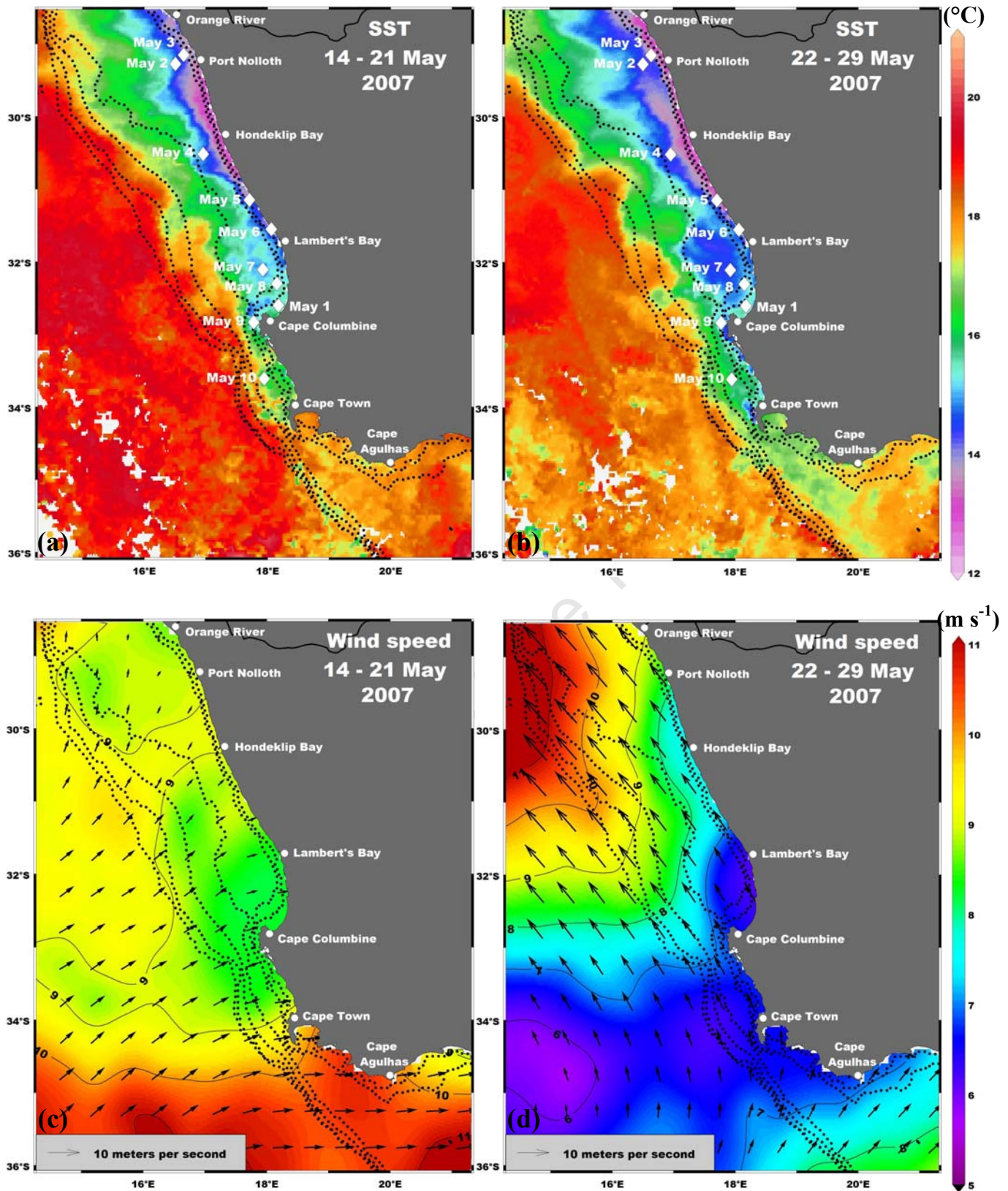


Figure 2.5. Maps of weekly averaged (a,b) MODIS Aqua Sea Surface Temperature ($^{\circ}\text{C}$), and (c,d) Quikscat wind speed (m s^{-1}) for the southern Benguela during May 2007. 2-minute Gridded Global Relief (ETOPO2) bathymetry contours (50, 100, 200, 300, 400, and 500 m) are indicated as black dotted lines. The white diamonds on (a, b) indicate the locations of primary production stations. The arrows on (c, d) indicate the wind direction.

In May, upwelling was generally less intense, with cool water notable only between Cape Columbine and the Orange River (Figure 2.5.a,b). During 14 – 21 May, the strong south-westerly winds were associated the passage of a polar frontal system south of the continent (Figure 2.5.c) and resulted in the suppression of upwelling throughout the region. In the following week (22 – 28 May), a shift in the wind field produced more upwelling-favourable winds that intensified the upwelling north of Cape Columbine (Figure 2.5. b,d).

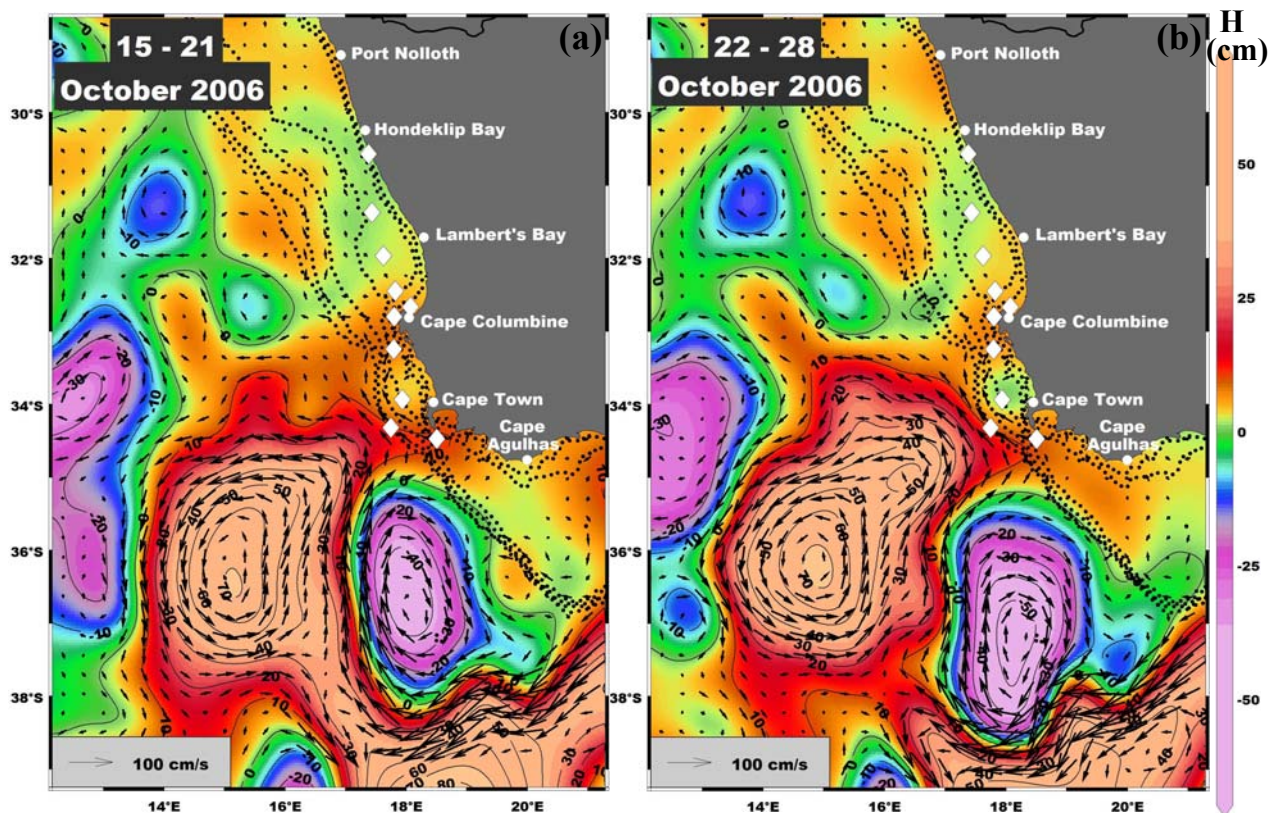


Figure 2.6. Weekly averaged geostrophic currents overlaid onto sea surface height anomalies for (a) 15 – 21 October 2006, and (b) 22 – 28 October 2006. 2-minute Gridded Global Relief (ETOPO2) bathymetry contours (50, 100, 200, 300, 400, and 500 m) are indicated as black dotted lines. The white diamonds indicate the locations of primary production stations.

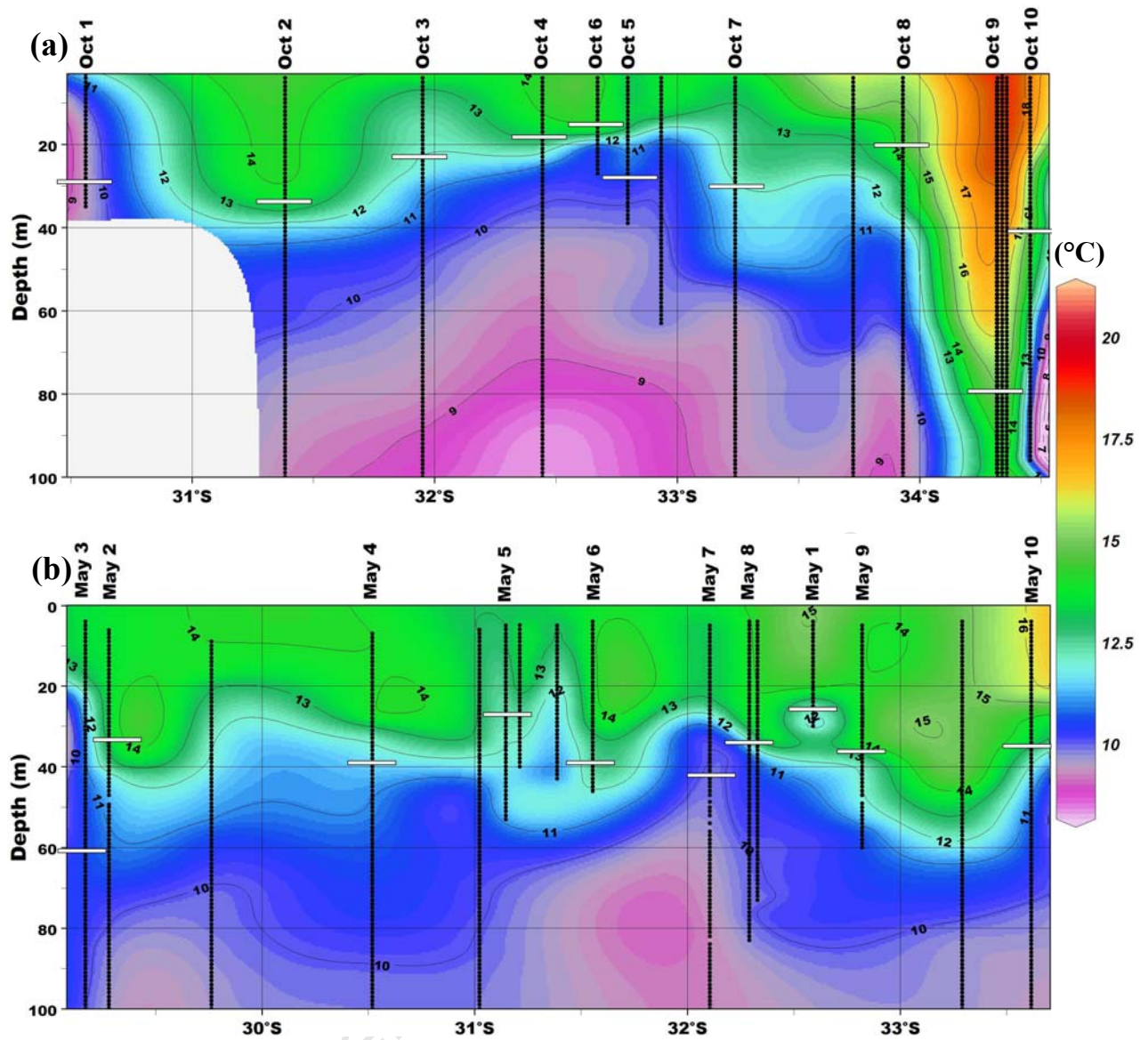


Figure 2.7. Vertical temperature ($^{\circ}\text{C}$) distribution along a transect through the PP stations during (a) October 2006, and (b) May 2007. The white line across each profile indicates the depth of the euphotic zone (z_{eu}).

The vertical structure of temperature indicated a warmer upper mixed layer (z_{uml}), with a wide range of thicknesses (Table 2.3), overlaying cooler upwelled water (Figure 2.7.a,b). Station Oct 1 was the exception, where cooler water penetrated the surface layers indicating active upwelling. Weaker upwelling is notable in the region of station May 5. The upper mixed layer was, on average, deeper and less variable during May (Figure 2.7.b), indicating longer periods of water column stratification and fewer upwelling-favourable winds. No strong thermoclines were evident during the surveys, except at Oct 9 and Oct 10 where an Agulhas ring interacted with the outer part of the shelf, depressing the thermocline and increasing the mixed layer depth (Figure 2.7.a).

Euphotic zone depth (z_{eu}) generally showed greater variability and vertical attenuation coefficients (K_d) were considerably larger during October (Table 2.3.). The deepest z_{eu} and smallest K_d was observed at Oct 9 and was associated with the presence of Agulhas Current water that typically has low phytoplankton biomass (Lutjeharms 2006), possibly accounting for the low attenuation. The highest attenuation of light and shallowest euphotic zones during both October and May were found in the St. Helena Bay region at Oct 6 and May 1. St Helena Bay is well known as an area of enhanced retention (Lett et al. 2006) and is often associated with elevated levels of phytoplankton biomass (Hutchings et al. 2009), which may account for the high attenuation of light and shallow euphotic zones observed in this region.

Table 2.3. PAR incident at the sea surface (SPAR), euphotic zone depth (z_{eu}), upper mixed layer depth (z_{uml}), and vertical attenuation coefficients (K_d) during October 2006 and May 2007.

Station	SPAR ($\mu\text{Einstein m}^{-2} \text{ s}^{-1}$)	z_{eu} (m)	z_{uml} (m)	K_d (m^{-1})
Oct 1	2485.61	18	8	0.24
Oct 2	2538.15	22	30	0.21
Oct 3	2573.28	11	9	0.24
Oct 4	2070.25	12	11	0.23
Oct 5	2350.48	14	16	0.19
Oct 6	2640.45	10	9	0.34
Oct 7	2573.13	20	9	0.22
Oct 8	1412.69	13	9	0.17
Oct 9	1632.69	40	27	0.06
Oct 10	2526.20	27	10	0.12
May 1	2269.85	15	13	0.22
May 2	1282.94	19	32	0.05
May 3	2110.91	20	13	0.06
May 4	2158.10	21	28	0.04
May 5	1893.79	19	13	0.13
May 6	2858.88	21	25	0.14
May 7	2201.50	19	23	0.06
May 8	2201.41	18	29	0.09
May 9	2233.80	21	36	0.12
May 10	2275.60	20	22	0.04

As a result of the seasonal cycle of solar heating, the southern Benguela experienced generally higher irradiance at the sea surface and upwelling-favourable winds were enhanced during October, yielding stronger upwelling. This resulted in the euphotic zone typically extending deeper than the upper mixed layer (Figure 2.8.). At stations Oct 2 and Oct 5, the mixed layer depth exceeded the euphotic zone depth, suggesting that these stations were sampled during periods of relaxed upwelling-favourable winds. During May, there is generally less irradiance available at the sea surface and upwelling-favourable winds are fewer, resulting in the euphotic zone being generally shallower than the upper mixed layer. At stations May 1, May 3, and May 5, euphotic zone depth exceeded upper mixed layer depth, suggesting sampling during periods of active upwelling.

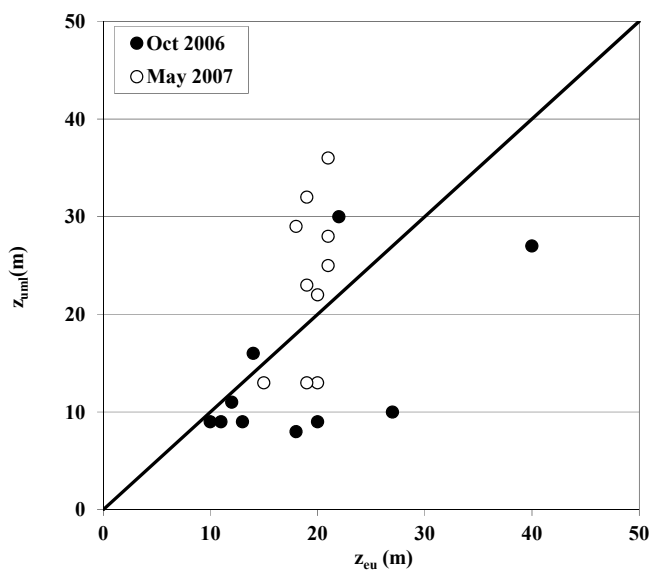


Figure 2.8. Relationship between the depth of the euphotic zone (z_{eu}) and the upper mixed layer depth (z_{uml}). The solid black line indicates where $z_{eu} = z_{uml}$.

Considerable variability in nutrient concentrations was observed during the surveys. Figure 2.9. indicates the nutrient profiles at the PP stations across the southern Benguela during October 2006 and May 2007. Generally, very similar ranges in nitrogen ($NO_3 + NO_2$) and silicate were observed during both cruises, with lower levels in the surface layers and increasing concentrations deeper in the water column. During May, subsurface nutrient levels were more elevated than those observed in October, and the nutricline was on average deeper and more defined, reflecting the seasonal differences in upwelling and nutrient supply to the surface layers. Silicate concentrations were generally higher than nitrogen in the surface layers during October, while the opposite was true at most stations during May. This suggests greater uptake of nitrogen than silicate by the larger phytoplankton biomass during October.

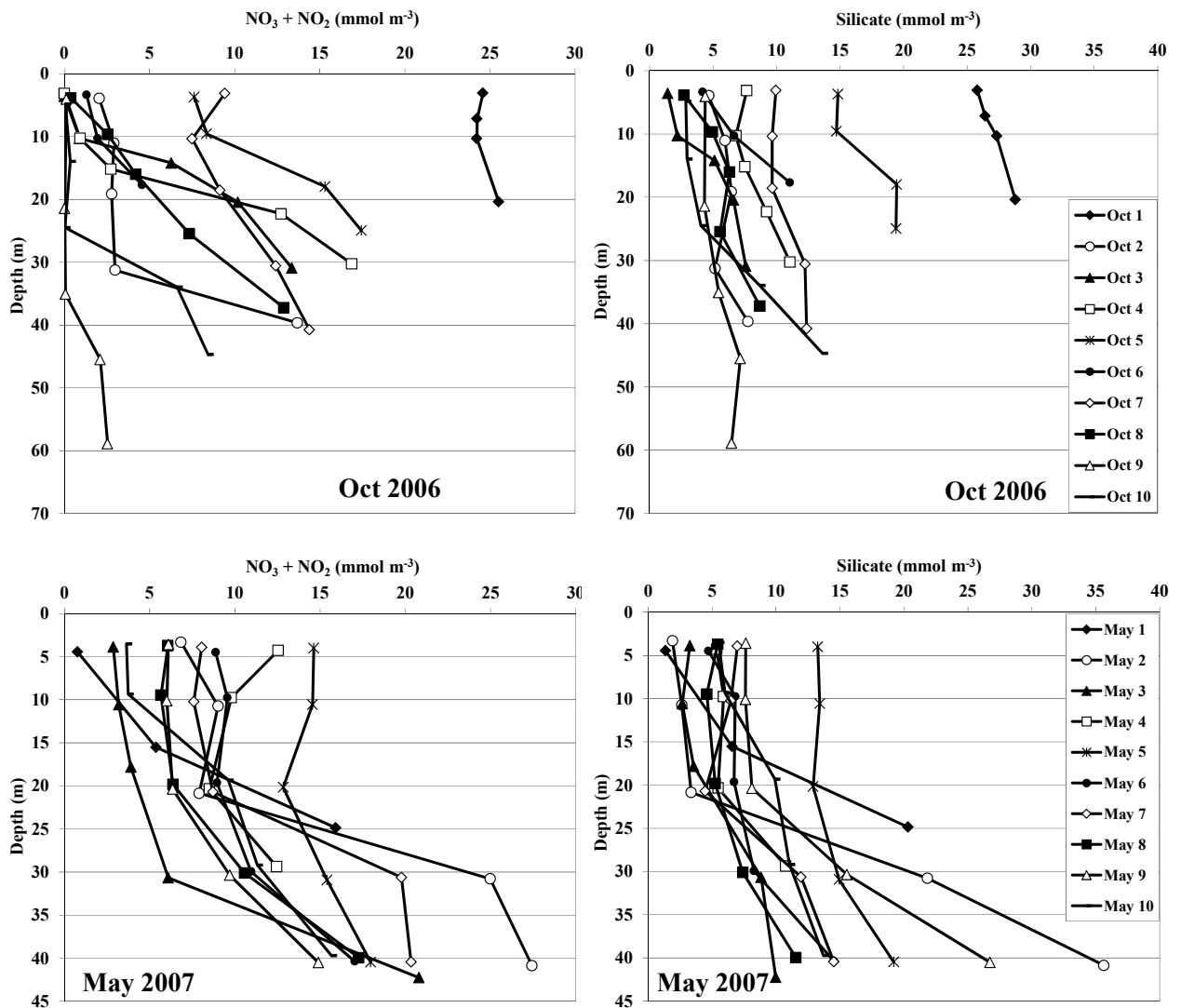


Figure 2.9. Profiles of inorganic nitrogen and silicate (mmol m^{-3}) at PP stations during October 2006 and May 2007.

The highest nutrient concentrations during October were sampled at Oct 1, with very little difference between the surface and lower layers, confirming the active upwelling indicated by the temperature distribution in Figures 2.4.a,b and 2.7.a. The higher K_d observed at this station may be associated with the entrainment of bottom sediment into the water column by the active upwelling. Notably high silicate concentrations were observed at Oct 5, while nitrogen concentrations were considerably lower, suggesting nitrogen uptake by phytoplankton. At Oct 9, silicate concentrations were around 5 mmol m^{-3} throughout the water column, while virtually no nitrogen was detectable in the upper 35 m. The same pattern was noted in the upper 25 m of the water column at Oct 10, indicating that the intrusion of Agulhas Current water was nitrogen-limited. During May, the highest nutrient concentrations in the surface layers was found at May 5 (Figure 2.9.) and was associated with the band of cooler water along the coast (Figure 2.5.a,b).

2.3.2. Phytoplankton biomass, Pigment composition, and Primary Production

Significant variation in phytoplankton biomass and primary production (PP) was observed between cruises and between different stations within cruises across the southern Benguela shelf. In general, higher PP seemed to occur where the phytoplankton biomass was higher, while lower PP was associated with lower biomass. During mid-spring (October), integrated phytoplankton biomass and PP were generally higher, ranging from 21.11 – 366.47 mg m⁻², and 0.71 – 6.98 g C m⁻² d⁻¹, respectively. In late autumn (May), biomass and PP were considerably lower, ranging from 47.92 – 141.82 mg m⁻² and 0.70 – 3.35 g C m⁻² d⁻¹, respectively (Figure 2.10.). The ranges in biomass and PP compare well to previous observations made in the Benguela ecosystem (Barlow et al. 2009, Brown and Field 1986, Mitchell-Innes and Walker 1991, Mitchell-Innes et al. 2000).

Differences in phytoplankton biomass and PP were observed across the shelf, where low biomass and PP was observed in recently upwelled water along the coast, higher biomass and PP occurred in the mid-shelf region, and low biomass and PP were measured at or beyond the shelf edge. Latitudinal variation was also evident, with the lowest values in the upwelling cells (for example, Oct 1) and south of the Cape Peninsula. Similarly, Brown and Field (1986) showed that the rate of primary production (including small initial biomass) is low in newly upwelled waters, increased sharply after the onset of relaxation, and decreased again due to light limitation (self-shading), nutrient depletion, and differences in taxonomic composition of phytoplankton in aged upwelled water.

During both cruises, the highest integrated biomass and PP were observed between Lambert's Bay and the Cape Peninsula, although higher biomass and PP were also noted at May 3. These stations were located in areas with enhanced retention (Lett et al. 2006) and correlates well with previous observations of elevated biomass (Demarcq et al. 2007, Weeks et al. 2006) and PP (Mitchell-Innes et al. 2000). Montecino et al. (2004) observed similar ranges in PP during spring (0.68 – 7.48 g C m⁻² d⁻¹) at coastal and shelf stations in the upwelling system off central Chile, and noted that PP during winter was significantly lower (0.15 – 1.93 g C m⁻² d⁻¹).

During October, maximum biomass and PP were observed at Oct 3, while the lowest was observed at Oct 1 and Oct 9. Oct 3 was located mid-shelf with a deeper upper mixed layer, a relatively shallow euphotic zone, and a surface temperature just below 14 °C. High vertical attenuation of light at this station could be largely attributed to the high

phytoplankton biomass. Oct 1 was located along the coast in newly upwelled (11 °C), nutrient-rich water just south of Hondeklip Bay, while Oct 9 was located further offshore from the Cape Peninsula in warmer (19 °C), nutrient-poorer water with a euphotic zone extending deeper than the upper mixed layer.

Similar to previous studies (Barlow et al. 2001, 2005), integrated diagnostic pigment indices (Figure 2.11.) indicated that phytoplankton communities in the southern Benguela are composed primarily of diatoms and smaller flagellates. Variations in PP are related to community structure, with diatoms typically resulting in higher production (Claustre et al. 2005, Uitz et al. 2008). During October, diatoms dominated the phytoplankton communities by more than 70 % at most stations, while flagellates were more notable in May. Although Oct 9 was dominated by flagellates, the prokaryote proportion was comparatively higher than at the other stations, supporting the finding that the water column at this station was influenced by oligotrophic Agulhas current water. Flagellate dominated stations (Oct 2 and Oct 9) showed slightly decreased proportions of TChla and photosynthetic carotenoid, and slightly elevated proportions of chlorophylls *b* and *c*. This suggests that chlorophylls *b* and *c* played a significant role in light harvesting and photosynthesis in flagellate communities.

The differences in biomass and PP at stations Oct 1, Oct 3, and Oct 9 seem to be mainly due to variable environmental conditions and changing phytoplankton populations. Despite the inorganic nitrogen limitation at Oct 9, PP and biomass was slightly higher than that at Oct 1. This suggests that low temperatures were more limiting to photosynthesis than low nutrient concentrations. Stations Oct 5 and Oct 8 showed very similar levels of primary production, although the biomass at Oct 5 was considerably lower than at Oct 8 and diatoms dominated the phytoplankton population at both stations. The lower biomass at Oct 5 could be due to a more unstable water column, as indicated by the shallower upper mixed layer and higher nutrient concentrations. However, the similar levels of production, suggests differences in photosynthetic response, photo-physiology, and nutrient uptake.

Diatoms were less dominant during May and approximately equal mixtures of diatoms and smaller flagellates were found at four of the stations. Stations May 7 and May 8 showed very similar levels of biomass, but the production at May 8 exceeded that at May 7. The elevated PP at May-8 may have resulted from a more stable water column, as suggested by the slightly deeper upper mixed layer and generally lower nutrient concentrations in the surface layers.

Similar high levels of biomass were observed at May 1 and May 2, but PP at May 1 greatly exceeded that at May 2. Nutrients were sufficient at both stations, while the vertical attenuation of light at May 1 greatly exceeded that at May 2. Both stations were diatom dominated with smaller (< 25 %) proportions of flagellates. Since phytoplankton biomass was similar at both stations, it is likely that other suspended material, such as coloured dissolved organic matter (CDOM) or sediment, contributed to the higher K_d observed at May 1. The lowest integrated biomass was observed at May 9 although this station exhibited the second highest PP during May and was dominated by diatoms. Environmental variables do not account for the observed differences in biomass and PP at these stations and it is likely that differences in photosynthetic rates and phytoplankton photo-physiology were mainly responsible for the observed differences in biomass and PP.

University of Cape Town

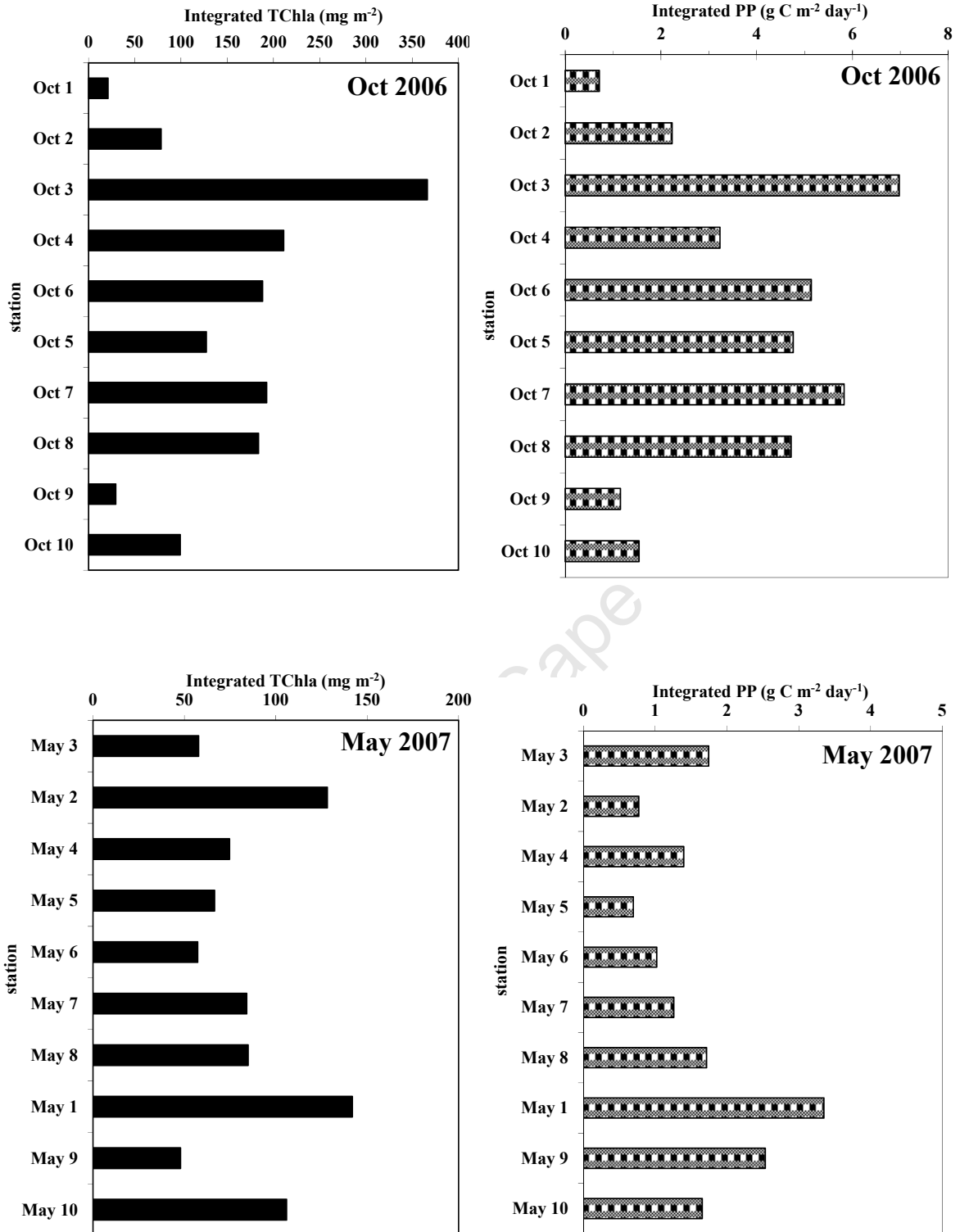


Figure 2.10. Integrated total chlorophyll *a* (TChla) concentration (mg m⁻²) and integrated primary production (g C m⁻² d⁻¹) at primary production stations during October 2006 and May 2007.

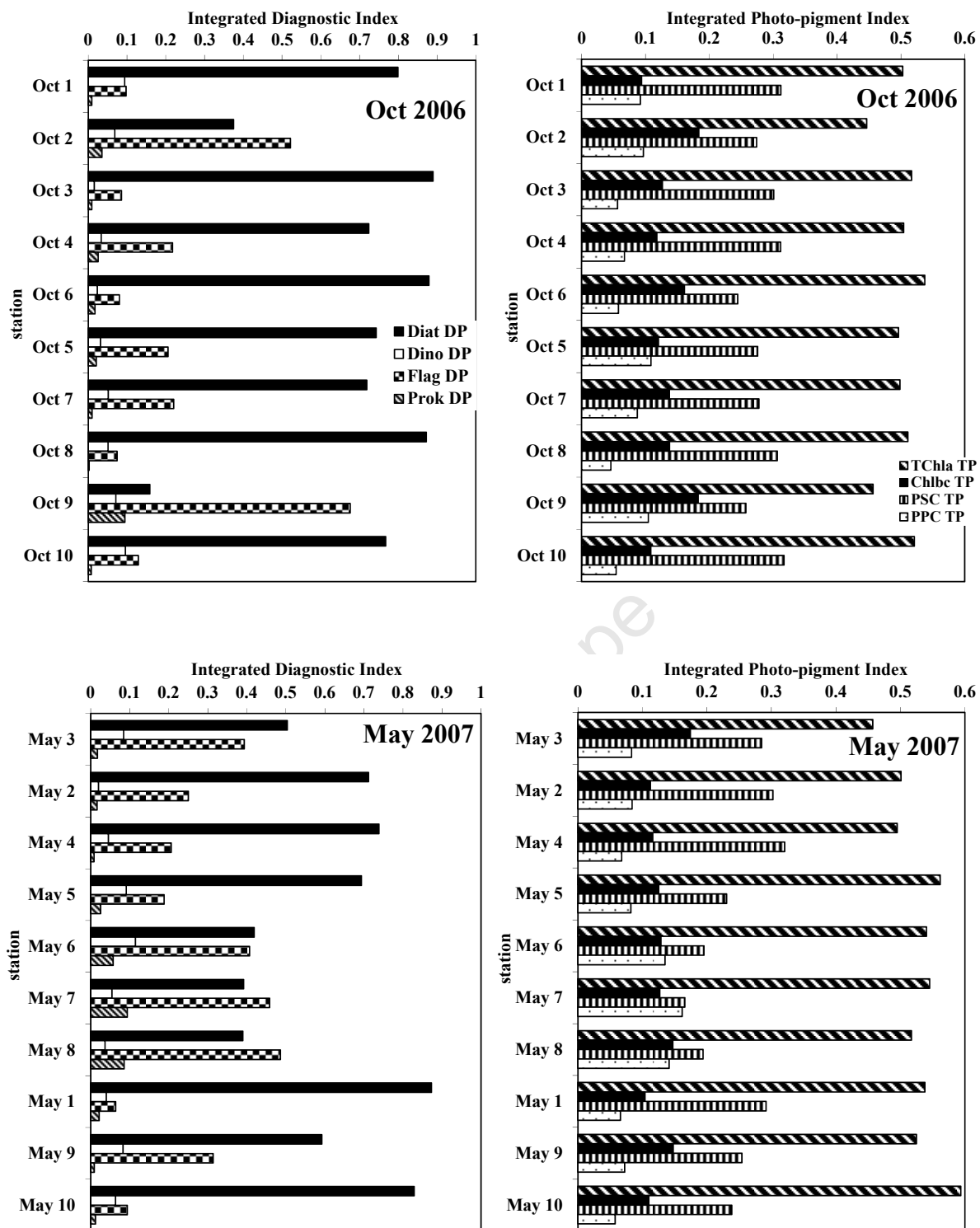


Figure 2.11. Integrated Diagnostic and Photo-Pigment indices at primary production stations during October 2006 and May 2007.

2.3.3. Photosynthetic Parameters

Photosynthetic parameters have been noted to vary among phytoplankton populations of different sizes and composition (Malone 1980, Gallegos 1992). Larger-celled phytoplankton, such as diatoms, have been associated with higher photosynthetic rates and greater efficiency of carbon storage than smaller phytoplankton, such as flagellates or picoplankton (Cermeño et al. 2006, 2005a, b, Claustre et al. 2005, Uitz et al. 2008). The range in production observed here could not be explained solely by variations in environmental variables, nor by phytoplankton biomass and the composition.

P-E parameters were therefore examined to assess their effect on primary production. Three of the P-E curves, one sampled at 30 m at station Oct 4, and two sampled at 40 m during May, were excluded from all computations. During October, the dark bottle DPMs exceeded the highest light bottle DPMs by 30 %. During May, the dark bottle average DPM represented 61 % of the highest light bottle DPM at station May 7, and 42 % at station May 8. TChla for these samples were very low, 0.16 mg m^{-3} at Oct 4, 0.04 mg m^{-3} at May 7, and 0.35 mg m^{-3} at May 8. Despite the low phytoplankton biomass, elevated dark carbon fixation suggested extensive heterotrophic activity in these samples. Interestingly, all of these samples were collected in a similar area between Lambert's Bay and Cape Columbine (Figure 2.12.), which is well known as a retention area in the southern Benguela (Lett et al. 2006, Parada et al. 2003) and has been identified as a region of high zooplankton biomass (Huggett et al. 2009).

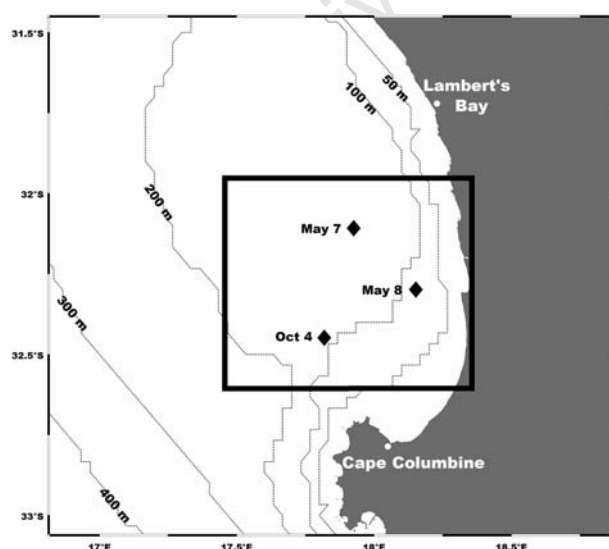


Figure 2.12. Map indicating the position of stations where dark bottle disintegrations per minute (DPM) contributed significantly to light bottle DPM's. 2-minute Gridded Global Relief (ETOPO2) bathymetry contours are indicated as thin black lines.

A further four experiments were excluded from all computations because the photosynthetic parameters were considered to be outliers to the rest of the dataset. These experiments are indicated as open circles (Figure 2.13.a). They were all conducted during May, at 40 m at May 3, and below the euphotic zone at May 9. Pigment indices showed that although diatoms were dominant throughout the water column, the proportion of TChla in the total pigment pool was less than 10% at 40 m at May 3. A temperature of 10.88 °C and PAR of 5.10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was observed at this depth. Below the euphotic zone at May 9, flagellates were dominant, with PSC_{TP} exceeding the TChla_{TP} . A mean temperature of 17.41 °C and mean PAR of 11.29 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was observed below the euphotic zone. Studies have shown that, in productive coastal ecosystems characterised by diverse phytoplankton communities, different sized phytoplankton can sustain different rates of carbon-specific and chlorophyll a-normalised photosynthesis (Claustre et al. 2005, Cermeño et al 2005a,b). It is thus possible that the elevated photosynthetic parameters at station May 9 may be due to a higher efficiency of carbon uptake by flagellates under very low light conditions. The anomalous photosynthetic parameters measured at May 3 may be due to the low proportion of TChla.

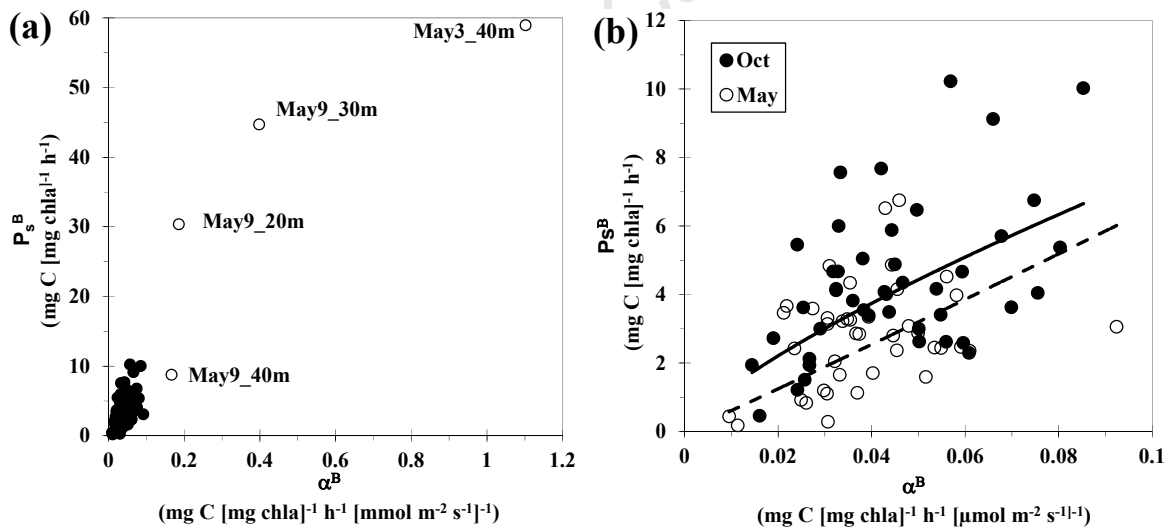


Figure 2.13. Relationship between P_s^{B} ($\text{mg C} [\text{mg chla}]^{-1} \text{h}^{-1}$) and α^{B} ($\text{mg C} [\text{mg chla}]^{-1} \text{h}^{-1} [\mu\text{mol m}^{-2} \text{s}^{-1}]^{-1}$) for all stations sampled during October 2006 and May 2007, (a) including outliers, and (b) excluding outliers. The solid line indicates the relationship for October, while the dashed line indicates the relationship for May.

For the remaining experiments (Figure 2.13.b), α^{B} and P_s^{B} ranged over one and two orders of magnitude, from 0.01 – 0.09 $\text{mg C} [\text{mg chla}]^{-1} \text{h}^{-1} [\mu\text{mol m}^{-2} \text{s}^{-1}]^{-1}$, and 0.18 – 10.22 $\text{mg C} [\text{mg chla}]^{-1} \text{h}^{-1}$, respectively, for pooled data from both cruises. Mean values of α^{B} were

0.045 and 0.038 mg C [mg chla]⁻¹ h⁻¹ [μmol m⁻² s⁻¹]⁻¹, respectively for October and May, while the mean P_s^B for October was 4.41 and 2.81 mg C [mg chla]⁻¹ h⁻¹ for May. The light-saturation parameter, E_k, varied from 9.15 – 226.71 μmol m⁻² s⁻¹, with a mean value of 103.73 μmol m⁻² s⁻¹ for October and 75.52 μmol m⁻² s⁻¹ for May. Although α^B values during October were higher than those during May, the difference was not significant (T = 1.55, P = 0.125). Conversely, P_s^B (T = 3.99, P = 0.00015) and E_k (T = 2.86, P = 0.0053) were significantly higher during October than in May. Although the relationship was not strong, P_s^B and α^B tended to be positively related (Figure 2.13.b) for both cruises and indicated that in general, phytoplankton with a lower photosynthetic efficiency (α^B) tended to exhibit lower maximum photosynthetic rates (P_s^B), and vice versa.

The variability of photosynthetic parameters for the Benguela was comparable to other coastal upwelling regions. In the Canary – NW African coastal transition zone, Basterretxea and Arístegui (2000) reported α^B values ranging from 0.003 – 0.075 mg C [mg chla]⁻¹ h⁻¹ [μmol m⁻² s⁻¹]⁻¹ and P_s^B ranging from 0.60 – 13.02 mg C [mg chla]⁻¹ h⁻¹ in the mixed layer and at the chlorophyll maximum. They noted that photosynthetic responses in the mixed layer and at the chlorophyll maximum became progressively similar on the continental shelf where mixing processes were enhanced and coastal upwelling increased. Aguirre-Hernández et al. (2004) observed seasonal differences in photosynthetic parameters in the southern region of the California Current off Baja California, with P_s^B ranging from 3 – 11 mg C [mg chla]⁻¹ h⁻¹ and α^B from 0.004 – 0.028 mg C [mg chla]⁻¹ h⁻¹ [μmol m⁻² s⁻¹]⁻¹ during summer. They observed significantly lower P_s^B and α^B during autumn, ranging from 0.5 – 5 mg C [mg chla]⁻¹ h⁻¹ and 0.005 – 0.010 mg C [mg chla]⁻¹ h⁻¹ [μmol m⁻² s⁻¹]⁻¹, respectively.

Tilstone et al. (2003) found that photosynthetic parameters and primary production were significantly greater during summer upwelling than in spring and winter in the northwest Iberian ecosystem. They also observed that photosynthetic parameters and primary production were significantly lower during summer stratified conditions. Montecino et al. (2004) showed that photosynthetic parameters were significantly higher during non-upwelling conditions in winter than during spring upwelling, and noted a larger variability in α^B in winter.

Figures 2.14. and 2.15. illustrate that TChla, photosynthetic rates, α^B , P_s^B , and E_k varied with depth at all stations and also exhibited greater ranges in October than in May. The highest biomass for October was, on average, three times greater than in May, while the highest photosynthesis rates were twice as high. Although subsurface maxima in TChla were observed at most stations in October, the maximum photosynthesis rates were always found at the surface, with a sharp decline at depth. During May, TChla was more evenly distributed through the upper layers, while photosynthesis rates exhibited a similar decline with depth, as observed in October.

Although phytoplankton biomass contributed to the spatial variability in PP, as indicated by the general correspondence between integrated TChla and PP (Figure 2.10.), the mismatch between profiles of photosynthesis rates and biomass suggested that chlorophyll *a* was not the primary variable controlling vertical variations in photosynthesis rates. Decoupling between chlorophyll *a* and PP could result from phytoplankton assemblages exhibiting high and variable carbon to chlorophyll *a* ratios (Basterretxea and Arístegui 2000) and when zooplankton communities exert rapid grazing control on the produced biomass. Mesoscale and smaller scale physical processes, such as the penetration of light down the water column, and mixing, would also control the vertical distribution of biomass and PP.

Although subsurface maxima in photosynthetic parameters were observed at several stations, P_s^B and E_k tended to be higher at the surface and decrease with depth. α^B showed considerable variability but tended to be lower at the surface and increase with depth, with subsurface maxima observed at numerous stations. During October, the highest α^B (Figure 2.15.) was measured in the surface waters at Oct 3, corresponding to the highest photosynthesis rate (Figure 2.14.). The low biomass and PP at Oct 1 could thus be attributed to low photosynthetic activity associated with colder, upwelled water.

Although the integrated biomass at Oct 5 was lower than at Oct 8, these stations showed similar levels of integrated PP. α^B , P_s^B , and E_k were higher at Oct 8, indicating that the phytoplankton were better adapted to higher light intensities. This suggests that although both these communities were photosynthetically active, the phytoplankton at Oct 5 may have been less efficient at storage of organically-bound carbon at higher light intensities.

E_k values at Oct 9 and Oct 10 were considerably higher than at the other stations, indicating an adaptation to higher light intensities. These stations exhibited high P_s^B but relatively low α^B in the surface layers, and vice versa deeper in the water column. Such a pattern is typical of stratified oligotrophic waters (Babin et al. 1996, Bouman et al. 2000) and has commonly been interpreted as photo-acclimation to the light field (Cullen et al. 1992, Falkowski 1980).

Although May 1 and May 2 exhibited similar biomass levels, the highest PP observed during May was measured at May 1 while PP at May 2 was significantly lower. α^B values at these two stations were not significantly different, but surface P_s^B and E_k at May 1 was considerably greater than at May 2. This indicated that phytoplankton at May 1 was better adapted to the higher irradiance in the surface layers than at May 2.

Very similar levels of biomass were observed at May 7 and May 8, but photosynthetic rates and integrated PP were greater at May 8 and can be explained by higher subsurface P_s^B and α^B at this station. E_k values indicated that phytoplankton at May 8 was adapted to higher light intensities than at May 7. Although May 9 had the lowest integrated biomass, the second highest photosynthetic rates were observed at this station during May. This can be attributed to very high P_s^B in the surface layers, and significantly higher subsurface α^B and P_s^B (Figure 2.15.), corresponding to a population change from diatoms in the surface layers to smaller flagellates dominating at depth. Although a reasonably high biomass and PP were measured at station May 10, α^B and P_s^B were relatively low, suggesting that the phytoplankton biomass was possibly in a stationary phase of growth.

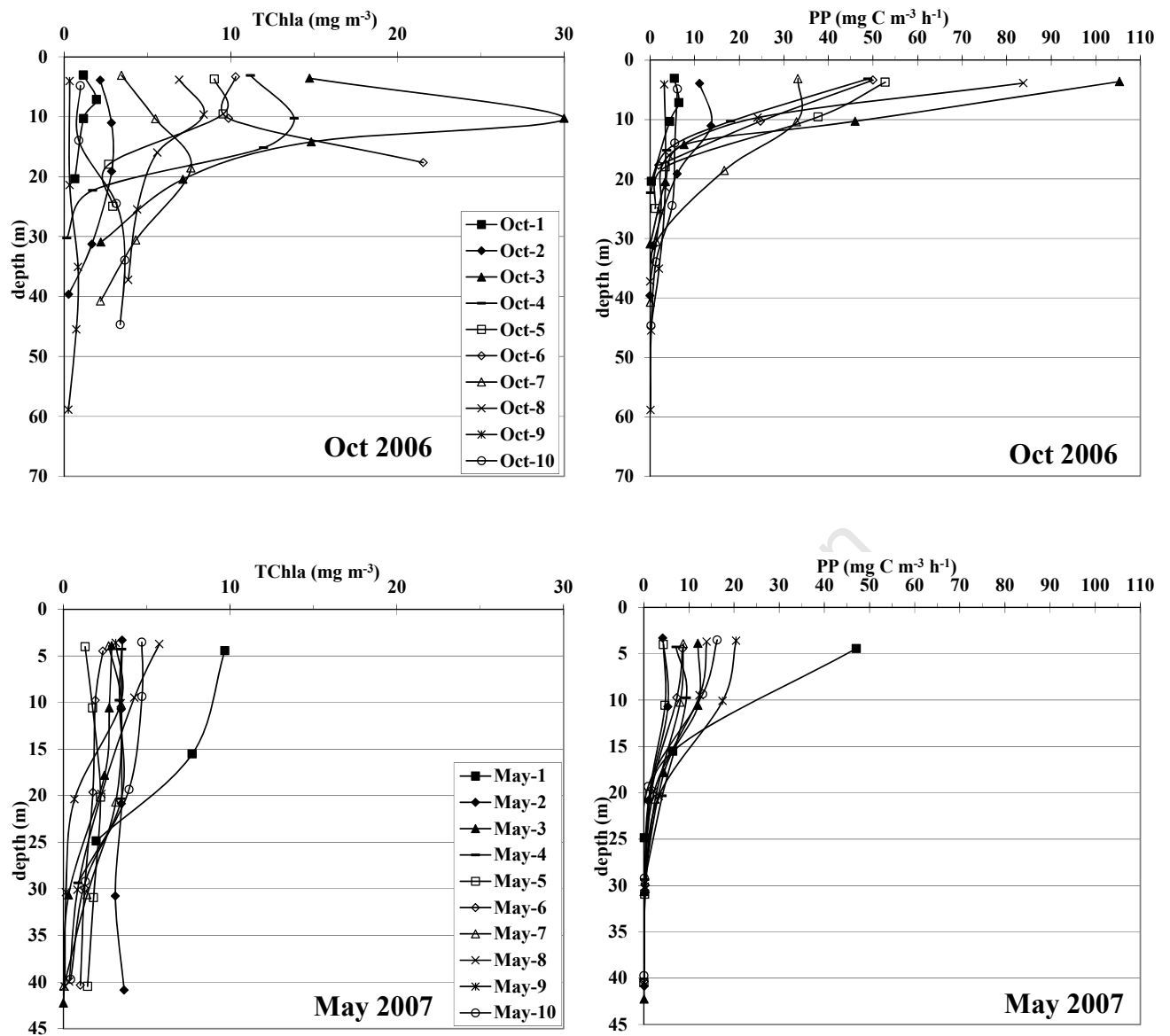


Figure 2.14. Vertical profiles of TChla (mg m^{-3}) and photosynthesis rates ($\text{mg C m}^{-3} \text{h}^{-1}$) for all stations sampled during October 2006 and May 2007.

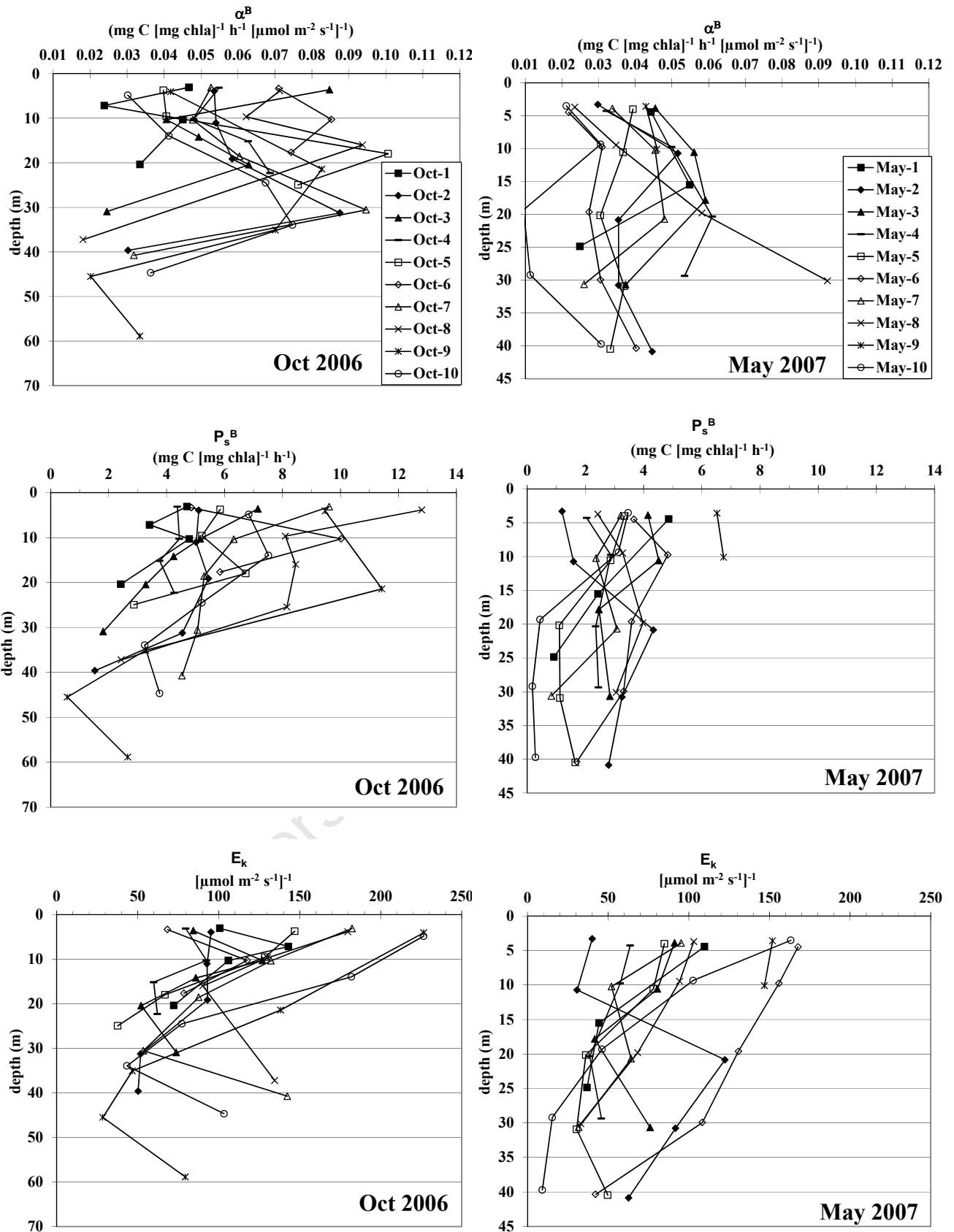


Figure 2.15. Vertical profiles of photosynthetic parameters, α^B (mg C [mg chla]⁻¹ h⁻¹ [μmol m⁻² s⁻¹]⁻¹), P_s^B (mg C [mg chla]⁻¹ h⁻¹), and E_k (μmol m⁻² s⁻¹) for all stations sampled during October 2006 and May 2007.

2.3.4. Relationships between Photosynthetic Parameters and Environmental Variables

It has been suggested that variability in photosynthetic parameters can be explained by environmental factors such as light intensity and spectral quality (Falkowski et al. 1981, Côté and Platt 1984, Platt and Jassby 1976, Kyewalyanga et al. 1998) and nutrient availability (Falkowski et al. 1998, Platt et al. 1992, Sathyendranath et al. 1995). While some authors found significant correlations between photosynthetic parameters and nitrate concentrations (Bouman et al. 2000, Marañón and Holligan 1999), others noted weak relationships (Bouman et al. 2005, Claustre et al. 2005). In the absence of significant variations in available light and nutrients, temperature is recognised to have a strong influence on P_s^B (Geider and MacIntyre 2002, Tilstone et al. 2003). Various authors (Bouman et al. 2005, Eppley 1972, Harrison and Platt 1980, Kyewalyanga et al. 1998) have shown that temperature was the dominant environmental variable accounting for observed variations in P_s^B , with higher temperatures associated with higher values of P_s^B (Lorenzo et al. 2004, 2005).

Figure 2.16. shows the relationships between temperature, inorganic nitrogen concentrations, and the photosynthetic parameters measured in the southern Benguela during October and May. While higher values of P_s^B and E_k tended to be associated with higher temperatures and lower nutrient concentrations, the relationships were weak and merely reflected the uptake of nutrients during photosynthesis in upwelled waters that have warmed. α^B seemed to be largely unaffected by changes in temperature and nutrients.

Sampling period as well as the depth of sampling could also affect photosynthetic parameters. Each survey was characterised by different means of total incident irradiance; 2480.34 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during October and 2078.68 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during May. Sampling depths differed between stations and seasons because depths were chosen according to the fluorescence profile. Thus, the ratio between the depth of sampling and the euphotic zone depth (z/z_{eu}) was used as an index of the relative irradiance in the water column. Various authors (Barlow et al. 2010, Uitz et al. 2008) found that this index was useful in assessing the photo-physiological adaptation of phytoplankton.

The relationships between photosynthetic parameters and z/z_{eu} are presented in Figure 2.17. There was a clear tendency for P_s^B and E_k to decrease with increasing z/z_{eu} , and

although higher values of α^B were observed subsurface, no clear relationship was evident. This is in contrast to the studies of Barlow et al. (2010) and Uitz et al. (2008), which reported an increase in α^B with increasing z/z_{eu} . The pattern of decreasing E_k and P_s^B with increasing z/z_{eu} reflects the adaptation of phytoplankton to changing light levels and agrees with the well-established positive relationship between irradiance and P_s^B (Geider and MacIntyre 2002, Behrenfeld et al. 2001, Tilstone et al. 2003). Similar patterns in E_k and P_s^B were reported by Uitz et al. (2008). There was also a tendency for a_{ph} (440) to decrease as z/z_{eu} increased, reflecting greater absorption of light by phytoplankton at higher irradiances in the upper part of the water column.

In a survey of the coastal transition zone off northern California, Hood et al. (1992) observed significant differences in the phytoplankton P-E response, and attributed this to changes in taxonomic composition, physiological condition, and light history of the cells. In the southern Benguela, phytoplankton are continually re-distributed within the upper mixed layer as a result of the frequency of wind-induced upwelling and mixing events. The response of photosynthetic parameters to changing light intensities may reflect photoacclimation and photoadaptation processes that are faster than the rates of vertical mixing (Cullen and Lewis 1988). Figure 2.17.e indicates that a reasonable amount of biomass was sampled at depths below the euphotic zone (indicated by $z/z_{eu} > 1$), while photosynthesis rates decreased dramatically below the euphotic zone (Figure 2.17.f). Irradiance thus appeared to be the primary variable influencing the vertical variability in photosynthetic rates in the southern Benguela ecosystem.

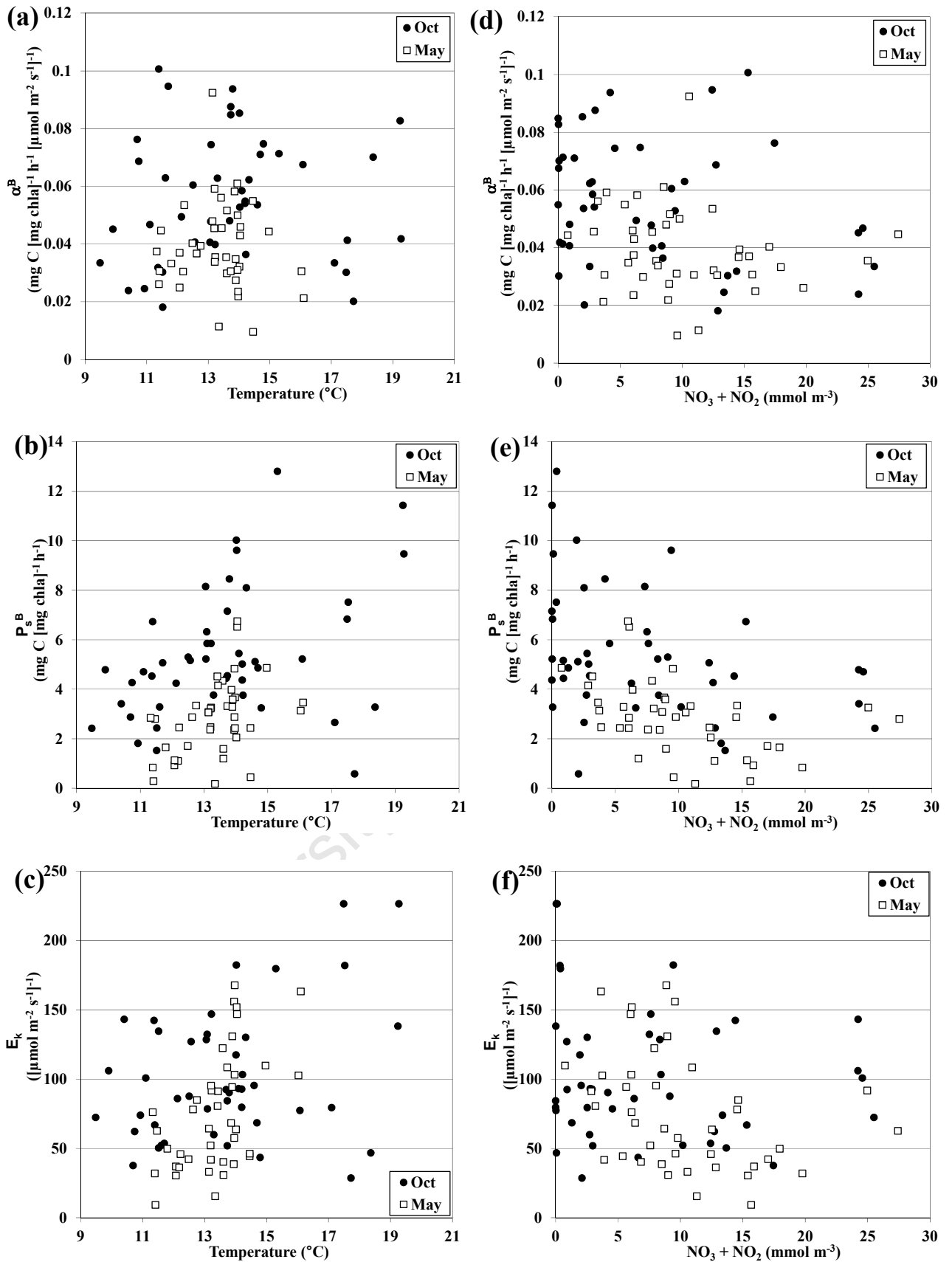


Figure 2.16. Relationships between α^B ($\text{mg C} [\text{mg chl a}]^{-1} \text{h}^{-1} [\mu\text{mol m}^{-2} \text{s}^{-1}]^{-1}$), P_s^B ($\text{mg C} [\text{mg chl a}]^{-1} \text{h}^{-1}$), E_k ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and temperature (a, b, c), and inorganic nitrogen concentrations (d, e, f) during October 2006 and May 2007.

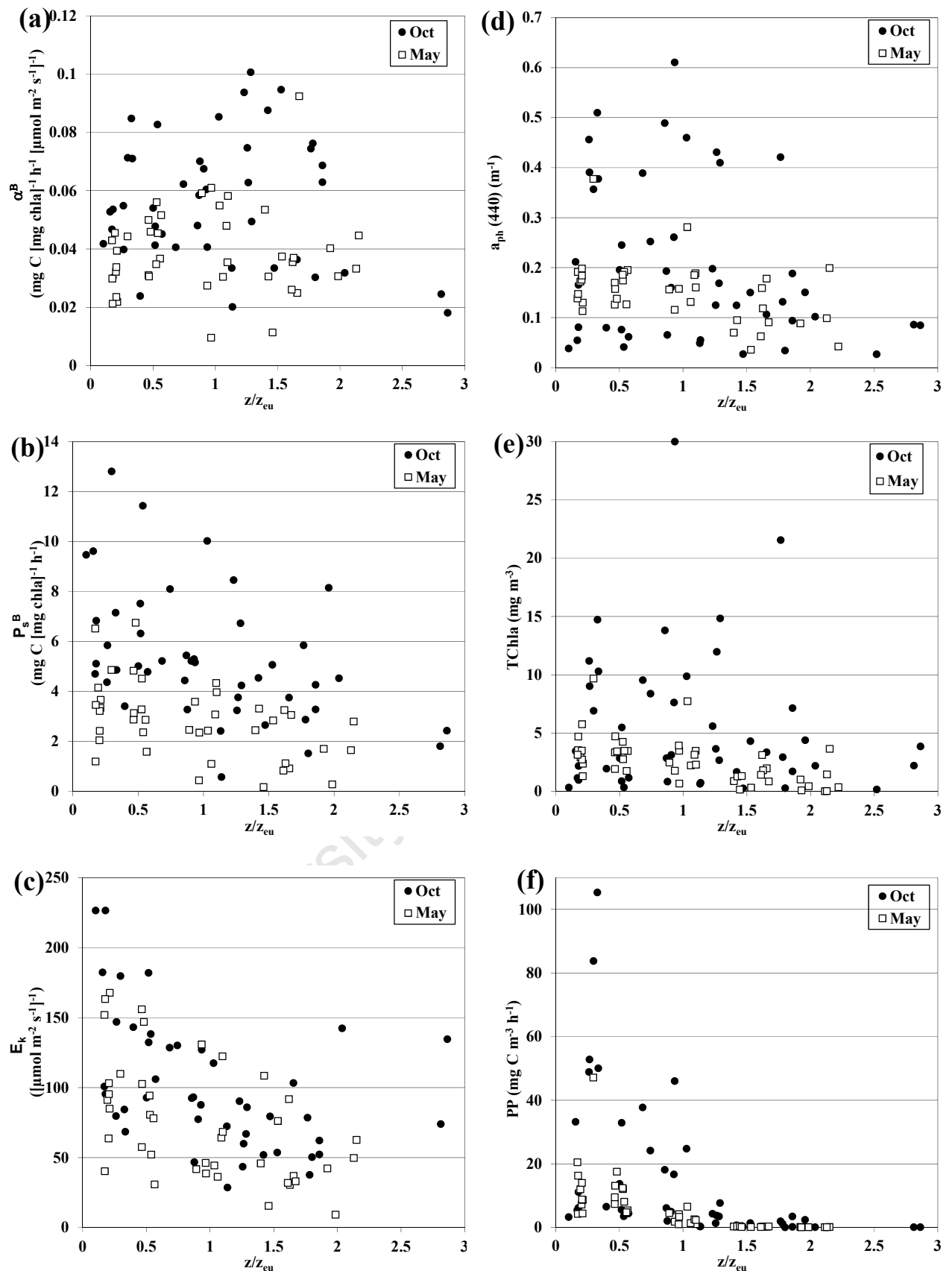


Figure 2.17. Relationships between α^B ($\text{mg C} [\text{mg chla}]^{-1} \text{h}^{-1} [\mu\text{mol m}^{-2} \text{s}^{-1}]^{-1}$), P_s^B ($\text{mg C} [\text{mg chla}]^{-1} \text{h}^{-1}$), E_k ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and z/z_{eu} (a, b, c), and between (d) $a_{ph}(440)$, (e) TChla, (f) PP and z/z_{eu} during October 2006 and May 2007.

2.3.5. Relationships between phytoplankton biomass, Primary production, and the environment

Possible relationships between phytoplankton biomass, photosynthesis (PP), temperature, nutrient concentration, and PAR were investigated. Among the regressions explored, weak but regular relationships were obtained only with temperature and nutrients (Figure 2.18.). During both cruises, TChla and PP were measured over a broad temperature range (9 – 19 °C) and there was a dramatic increase between 12 – 16 °C, suggesting that this was the optimal temperature range for primary production. Outside this temperature range, biomass and PP were generally below 2.5 mg m⁻³ and 5 mg C mg⁻³ h⁻¹, respectively. Surface temperature maps (Figure 2.4.a,b and Figure 2.5.a,b.) indicated that waters with the optimal temperature range were generally located mid-shelf, between the recently upwelled water close to the coast and the upwelling front further offshore.

Inorganic nitrogen (NO₃ + NO₂) and silicate concentrations were measured over a range of 0 – 30 mmol m⁻³. Relationships between nutrients, TChla and PP were all weak but showed similar patterns. Low nutrient levels were generally associated with the highest biomass and PP, indicating the uptake of nutrients. Conversely, high nutrient levels were related to the lowest biomass and PP. Since high nutrients are typically associated with colder, upwelled water, it is possible that low temperatures were the limiting factor responsible for lower biomass and PP.

The relationship between integrated biomass and PP is presented in Figure 2.19.a and b. Despite some scatter, a strong positive relationship was found between TChla and PP ($y = 0.0198x + 0.3013$, $R^2 = 0.71$) for pooled data from October and May (Figure 2.19.a). However, upon examining this relationship for each survey respectively (Figure 2.19.b), it was found to be stronger in October ($y = 0.0185x + 0.861$, $R^2 = 0.77$). During May, this relationship was very weak ($y = 0.0069x + 1.0269$, $R^2 = 0.072$) and integrated TChla predicted less than 1 % of PP. This indicates that while integrated TChla is a good predictor of PP for October, it fails to predict PP for May.

Plots of integrated PP as a function of surface TChla (Figure 2.19.c and d) also shows a strong linear relationship with an average of 59 % of the variance explained ($y = 0.3638x + 0.8055$, $R^2 = 0.59$) for pooled data. Similar values of R^2 were obtained for October ($y = 0.3276x + 1.6545$, $R^2 = 0.60$) and May ($y = 0.2717x + 0.5390$, $R^2 = 0.62$) and the differences in the slope and intercept probably reflected the seasonal variation in

phytoplankton biomass and PP. Despite the fact that this relationship is weaker than the one presented in Figure 2.19.b for October, surface TChla consistently predicted about 60 % of the integrated PP for both cruises. This suggests that the surface biomass contributed significantly to the integrated biomass and PP in the southern Benguela ecosystem. Surface TChla thus appeared to be a better predictor of integrated PP. This result has important implications for the estimation of PP from satellite chlorophyll *a* concentrations, and suggests that at least 60 % of the estimated PP can be attributed to surface chlorophyll concentrations. Similar investigations of the relationship between PP and chlorophyll concentrations showed good correlations off central Chile (Montecino et al. 2004) and in the southern Benguela, good relationships were found during winter, while summer comparisons showed poor correlations, with surface chlorophyll explaining more of the PP variance than integrated chlorophyll (Barlow et al. 2009).

University of Cape Town

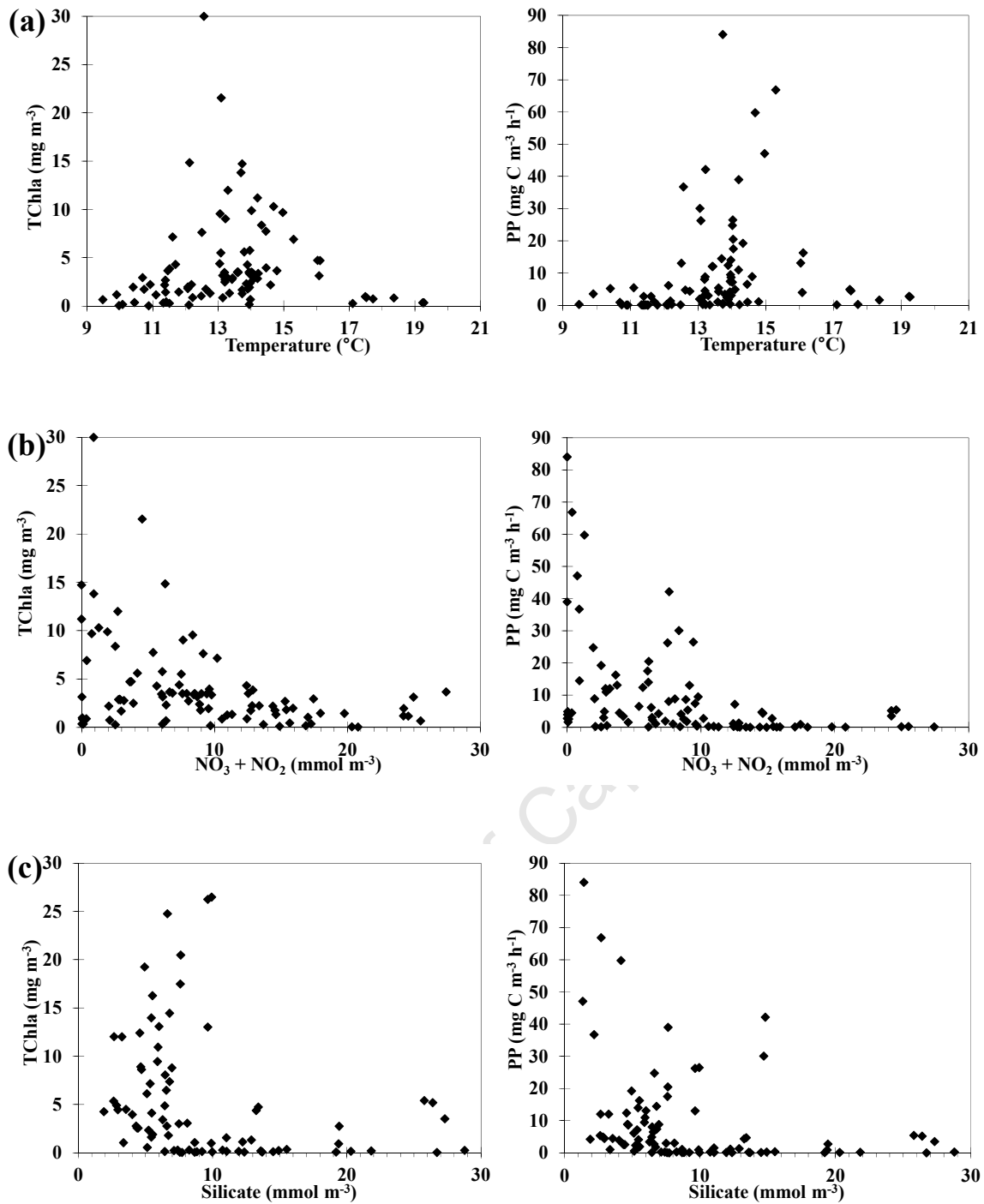


Figure 2.18. Relationship of TChla (mg m^{-3}) and photosynthesis ($\text{mg C m}^{-3} \text{h}^{-1}$) with (a) temperature ($^{\circ}\text{C}$), (b) NO_3+NO_2 (mmol m^{-3}), and (c) silicate (mmol m^{-3}).

Figure 2.20.a shows that surface TChla accounted for 75 % of the variability in integrated TChla during October ($y = 17.406x + 44.932$), and 52 % during May ($y = 9.6433x + 46.693$). A likely explanation for this may be that the phytoplankton biomass was more concentrated at the surface so as to maximise their exposure to higher irradiances. Figure 2.20.b indicates that surface PP accounted for 72 % of the variability in integrated PP ($y = 3.973x + 1.5377$) during October, and 87 % during May ($y = 5.9082x + 0.7517$). This

indicates that subsurface PP rates were considerably lower than surface rates and did not contribute significantly to the integrated values. Although subsurface TChla contributed more significantly to the integrated values during May, this did not result in elevated subsurface PP measurements. The implications are that irradiance in the water column exerts a strong control on the vertical distribution of PP.

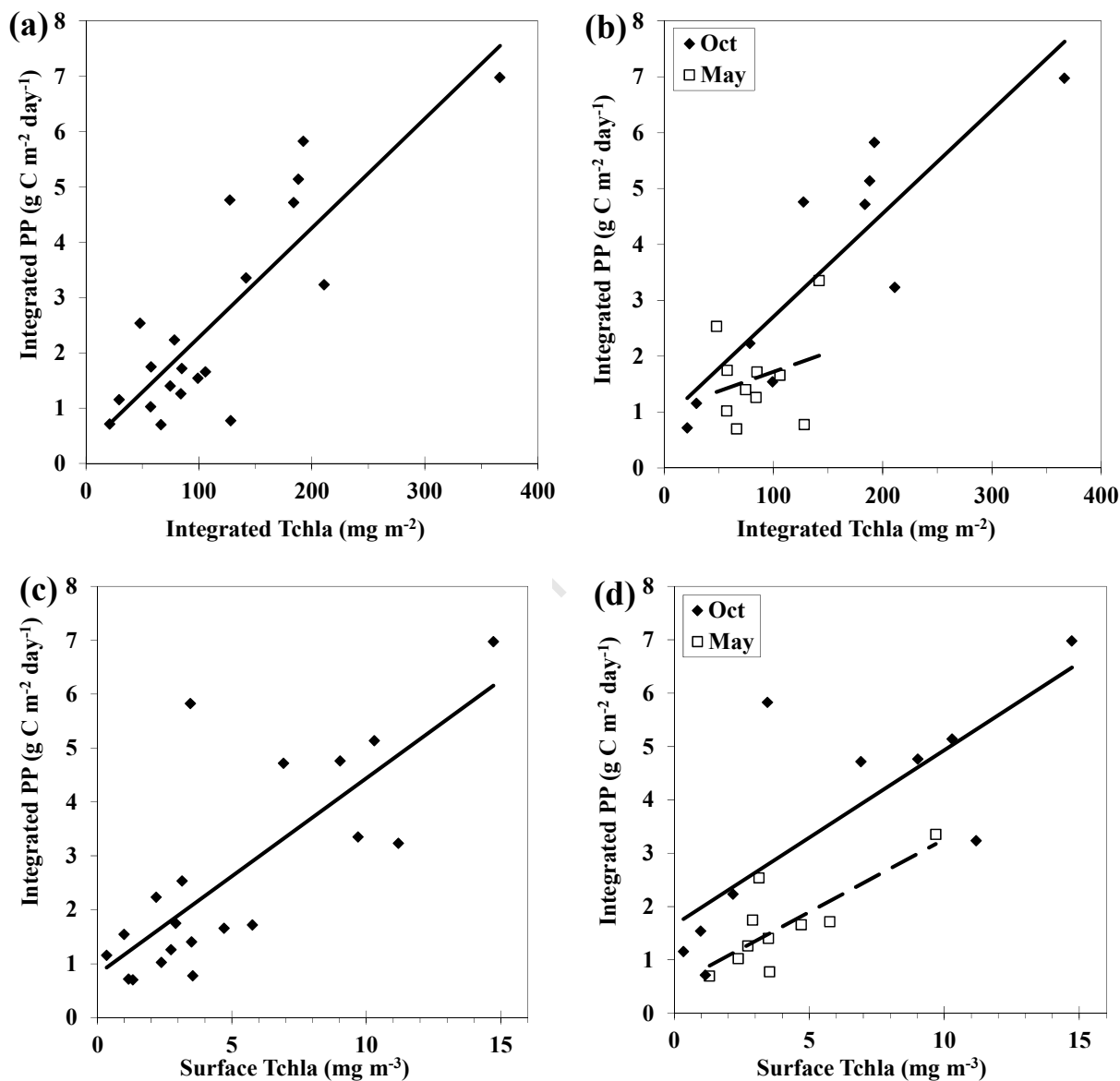


Figure 2.19. Integrated Primary Production ($\text{g C m}^{-2} \text{d}^{-1}$) plotted as a function of integrated TChla (mg m^{-2}) for (a) October and May pooled, (b) October and May separately, and as a function of surface TChla (mg m^{-3}) for (c) October and May pooled, (d) October and May separately.

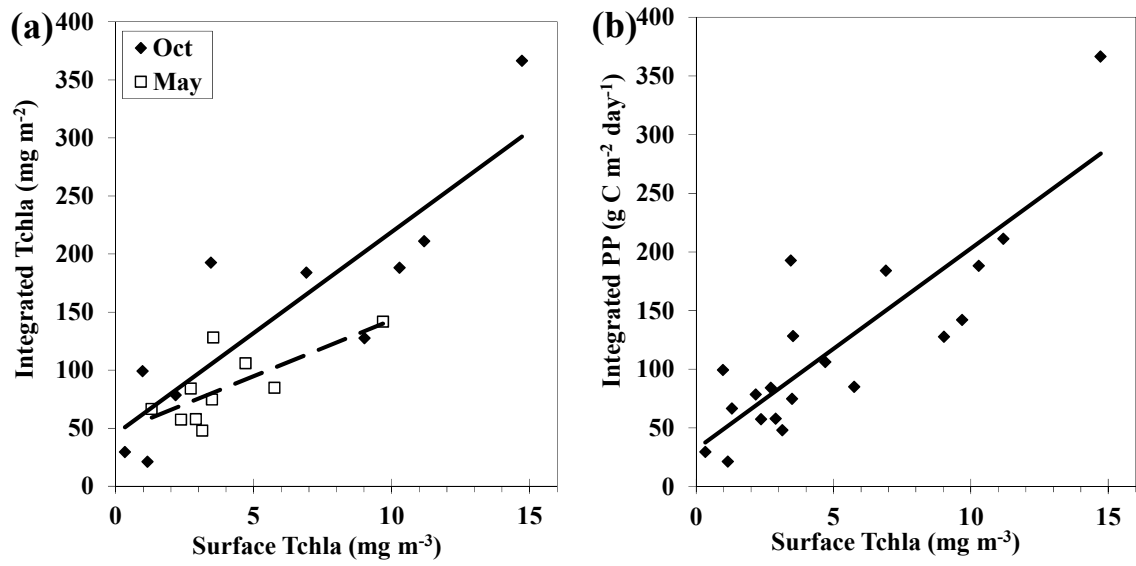


Figure 2.20. Integrated TChla (mg m^{-2}) plotted as a function of surface TChla (mg m^{-3}), for October 2006 and May 2007.

2.4. Summary and Conclusions

The biomass, bio-optical and physiological characteristics of phytoplankton in the highly productive coastal upwelling ecosystem of the southern Benguela revealed considerable seasonal variability, comparable to previous observations (Barlow et al. 2009, Brown and Field 1986, Mitchell-Innes et al. 2000). Phytoplankton communities were comprised mainly of diatoms and smaller flagellates (Barlow et al. 2001, 2005) and although differences in composition were not significant, higher PP was observed during spring, while PP in late autumn was considerably lower.

Large differences were observed across the shelf, where biomass and PP was low in recently upwelled water close to coast, elevated in the mid-shelf region and decreased again toward the shelf edge (Brown and Field 1986). Cross-shelf variations such as these have previously been used to define the limits of productive ecosystems in terms of the offshore extent of chlorophyll *a* to 1 mg m^{-3} (Demarcq et al. 2007, Nixon and Thomas 2001). In the St. Helena Bay area, the persistence of high chlorophyll *a* concentrations and PP could be attributed to the increased retention of upwelled waters on the wider shelf (Lett et al. 2006), while the considerably lower biomass and PP south of the Cape Peninsula was related to the influence of the oligotrophic Agulhas Current water.

Similar to Barlow et al. 2009 and Montecino et al. 2004, this investigation showed good correlations between surface chlorophyll and PP, supporting the estimation of PP using biomass models (Demarcq et al. 2008, Eppley et al. 1985). While surface biomass accounted for a considerable proportion of the integrated PP, and contributed substantially to the spatial variability of PP and bio-optical characteristics on a regional scale, it was not the primary variable controlling the vertical variations in photosynthesis rates. The discrepancies observed between surface biomass and PP in different seasons and vertically in the water column suggest that the use of such empirical predictions, although practical, may not be realistic for the southern Benguela region.

Since diatoms were so prominent in this study, it was difficult to relate variations in PP to changes in phytoplankton groups, and therefore it is more likely that the variability in PP was due to differences in the phytoplankton physiology in response to the underlying environmental conditions. Despite the considerable variability observed vertically and between sites, in general, low PP was associated with low photosynthetic activity, while elevated photosynthetic activity resulted in higher PP. However, exceptions to this pattern

were observed where reasonably high PP was associated with low activity, suggesting that the biomass had possibly reached a stationary phase of growth. Although there was no clear relationship between α^B and environmental variables, phytoplankton adaptation to varied environmental conditions was characterised by increased P_s^B and E_k with elevated irradiance and temperatures. Contradictory relationships between photosynthetic parameters and nutrients have previously been reported (Bouman et al. 2005, Claustre et al. 2005, Marañón and Holligan 1999, Bouman et al. 2000) and the pattern of elevated P_s^B and E_k at low nutrient concentrations observed during this study merely reflects the uptake of nutrients during photosynthesis.

Photosynthesis was greatest in the upper layers of the water column under elevated irradiance, decreasing dramatically below the euphotic zone and the response of photosynthetic parameters to changing light intensities possibly reflected photoacclimation and photoadaptation processes which are faster than the rates of vertical mixing (Cullen and Lewis 1988). Irradiance thus appeared to be the main factor influencing the productivity of phytoplankton in the southern Benguela. Grazing could be an important factor limiting PP, especially if there is selective grazing on particular phytoplankton groups. The impacts of grazing were not considered in this study and therefore future work should include investigations of the influence of selective grazing on phytoplankton species composition and PP.

Chapter 3 – Comparison of in situ and satellite-derived Primary Production

3.1. Introduction

Oceanic primary production (PP) is a key component of the global carbon cycle (Barber and Hilting 2002, Stocker et al. 2001) and may ultimately influence the trophic structure of pelagic food webs (Fréon et al. 2009). Reliable and accurate measurements of PP are thus essential for assessing the role of the oceans in regulating global climate through gas solubility and fluxes (e.g. carbon dioxide, dimethyl sulphide) (Bianchi et al. 2005, Houghton et al. 1996, Larsen 2005), and for understanding carbon cycling through food webs (Fréon et al. 2009, Ware and Thomson 2005).

Although traditional shipboard measurements of PP remain the best and most widely accepted way to quantify and validate marine photosynthesis, they are limited to discrete locations and times and experiments are mostly conducted during the more favourable seasons of spring and summer (Aguirre-Hernández et al. 2004, Basterretxea and Arístegui 2000, Montecino et al. 2004, Tilstone et al. 2003). Although larger scale temporal and spatial patterns of PP have been investigated using discrete in situ measurements (Berger 1989), these patterns are subject to substantial extrapolation. Satellite ocean colour sensors provide synoptic measurements of phytoplankton biomass (chlorophyll *a* concentration), Sea Surface Temperature (SST) and photosynthetically available radiation (PAR) which are used in the estimation of marine PP at global scales (McClain 2009).

A broad selection of models is available for the estimation of PP from satellite data. These models vary widely in their type (chlorophyll-based or carbon-based), complexity (depth- and wavelength-resolved or integrated), and their performance. Various studies have been conducted to evaluate the complexity and performance of these models and to investigate the accuracy of the modelled PP estimates. Campbell et al. (2002) investigated 12 ocean colour models and compared their output to in situ PP estimates from 89 stations in various ecosystems. They found that the models varied substantially in performance and that the best-performing models agreed with ¹⁴C-based estimates within a factor of 2. Significant regional differences in the performance of the models were also noted. Despite differences in complexity of the models, most of the PP estimates were highly correlated with each other.

Global PP estimates from 24 ocean colour models and 7 coupled biogeochemical general ocean circulation models were compared to investigate the conditions responsible for the divergence of model estimates (Carr et al. 2006). Similar to the findings of Campbell et al. (2002), Carr et al. (2006) concluded that global estimates from ocean colour models varied over a factor of 2. It was observed that the most challenging regions in which to model PP are located poleward of 40° in all ocean basins, the equatorial region, and in the northern subtropical Indian Ocean due to high chlorophyll concentrations and extreme SST values (Carr et al. 2006).

Recently, Friedrichs et al. (2009) compared the PP estimates from 21 ocean colour and 9 biogeochemical general ocean circulation models to in situ data from about 1000 stations in the tropical Pacific Ocean. They noted that there was little significant difference in the performance of the various types of ocean colour models and that model skill was not associated with their complexity or type. While most models were observed to substantially underestimate PP variability by more than a factor of 2, their performance differed substantially in terms of their ability to reproduce the mean and median PP, with the median PP typically being overestimated. The simplest models showed considerably less bias than the more complex depth- and wavelength-resolving models. In situ data revealed a large scale shift in the tropical Pacific Ocean from low PP in the 1980s to substantially higher PP in the 1990s (Friedrichs et al. 2009). However, none of the ocean colour models were able to capture this decadal variability.

Saba et al. (2010a) assessed the ability of 36 models to estimate the mean, variability and trends of PP over multiple decades at two time series stations in the subtropical North Atlantic and Pacific oceans. Although almost all the models were found to consistently underestimate mean PP at both sites, ocean colour models performed significantly better than biogeochemical general ocean circulation models. In the most recent study by Saba et al. (2010b), output from 21 ocean colour models was compared to 1156 in situ PP measurements across ten different ecosystems in order to evaluate model skill on a region-specific basis. While model skill was found to differ significantly across the various regions, similar to Campbell et al. (2002), model type had no effect on the average model skill across the different regions. Contrary to the findings of Carr et al. (2006), the ocean colour models evaluated by Saba et al. (2010b) were not particularly challenged in extreme chlorophyll and SST conditions. A surprising result was that ocean colour model skill was

significantly lower and typically overestimated PP at water column depths shallower than 750 m, with the positive bias increasing at depths shallower than 250 m.

Although several investigations (Campbell et al. 2002, Carr et al. 2006, Friedrichs et al. 2009, Saba et al. 2010a, b) have been conducted to evaluate and compare the suitability of ocean colour models for estimating PP, the southern Benguela ecosystem was not among the regions investigated. Attempts at modelling PP in the southern Benguela using self-organising maps to predict chlorophyll profiles from satellite chlorophyll data (Demarcq et al. 2008) yielded PP estimates which were much lower than previous in situ measurements (Barlow et al. 2009, Brown and Field 1986, Mitchell-Innes and Walker 1991, Mitchell-Innes et al. 2000).

For this reason, the primary goal of this study is to compare PP estimated from various ocean colour models to measured PP in the southern Benguela, in order to identify a suitable model for PP estimation from ocean colour data. Due to the very limited in situ dataset, it must be noted that this study does not attempt a rigorous statistical assessment of individual model skill as conducted by other authors (Friedrichs et al. 2009, Saba et al. 2010a, b) but allows for the relative comparison of the selected models. The following key questions are addressed: (1) How well do ocean colour model PP estimates compare with each other? (2) How well do satellite PP estimates compare to in situ PP measurements? (3) What are the factors responsible for the differences in model PP estimates?

3.2. Methods

3.2.1. Hydrographic and Primary Production measurements

Research surveys were conducted on the continental shelf of the southern Benguela ecosystem during October 2006 and May 2007. At a total of 20 stations, sampling for primary production and physiological experiments was conducted around midday at three to five depths throughout the euphotic zone. The distribution of stations and a detailed description of the methods used to obtain PP and other hydrographic measurements are provided in Chapter 2.

3.2.2. Primary Production Modelling

Three models, namely the Eppley model, the Vertically Generalised Production Model (VGPM), and the Eppley-VGPM were selected to perform this comparison. They are all depth- and wavelength-integrated, and are among the more easily implementable production models. The choice of these models is justified in that they have been found to perform just as well as the more complex depth- and wavelength-resolving models (Friedrichs et al. 2009, Saba et al. 2010a, b). The Eppley model (Eppley et al. 1985) is by far the easiest to implement and simply estimates PP as the square root of chlorophyll *a*. The major assumptions of this model are that all biomass performs identically and that biomass is the only factor controlling the photosynthetic rate. External environmental forcing and changes in phytoplankton physiological state are ignored.

The Vertically Generalised Production Model (VGPM) was originally developed by Behrenfeld and Falkowski (1997b) and is one of the most widely known and commonly used production models. It estimates depth-integrated primary production in the euphotic zone as a function of chlorophyll *a*, available light, and the photosynthetic efficiency. The maximum observed photosynthetic rate within the water column, P_{opt}^B , required to convert the estimated biomass into a photosynthetic rate, is computed as a 7th order polynomial of SST.

The Eppley-VGPM is a variation of the original VGPM model and differs only in that P_{opt}^B is computed as an exponential function of temperature. Morel (1991) modified the original exponential temperature-dependent description of photosynthetic efficiencies (Eppley 1972) by normalising the curve to achieve a photosynthetic efficiency of 4.6 mg C [mg

$\text{chl}a]^{-1} \text{ h}^{-1}$ at a SST of 20 °C. The polynomial relationship between $\mathbf{P}_{\text{opt}}^{\text{B}}$ and SST highlights the effects of nutrient stress at higher SST's (Behrenfeld and Falkowski 1997b), while the exponential relationship gives emphasis to the effect of photoacclimation at higher SST's (Morel 1991). The model estimates primary production as:

$$\mathbf{PP} = \mathbf{chl}a * \mathbf{P}_{\text{opt}}^{\text{B}} * \mathbf{DL} * \left(0.66125 * \frac{\mathbf{I}}{\mathbf{I} + 4.1} \right) * \mathbf{z}_{\text{eu}}$$

where: \mathbf{PP} is the primary production ($\text{g C m}^{-2} \text{ d}^{-1}$), $\mathbf{chl}a$ is the chlorophyll a concentration (mg m^{-3}), $\mathbf{P}_{\text{opt}}^{\text{B}}$ is the maximum observed photosynthetic rate within the water column ($\text{mg C [mg chl}a]^{-1} \text{ h}^{-1}$), \mathbf{DL} is the number of daylight hours (decimal hours), \mathbf{I} is the photosynthetically available radiation at the surface ($\text{Einsteins m}^{-2} \text{ d}^{-1}$), and \mathbf{z}_{eu} is the euphotic zone depth (m).

Estimates of PP using the Eppley, VGPM, and Eppley-VGPM models were derived with in situ data. Chlorophyll a concentrations were derived from HPLC measurements, profiles of photosynthetically available radiation (PAR) were used to compute the euphotic zone depth to the 1 % light level, and the number of daylight hours was calculated as the difference between the times of sunrise and sunset. For stations during October 2006, an average day length of 13.10 hours was used, while an average of 10.23 hours was used for May 2007. To investigate the accuracy of PP estimated using the selected models, a comparison was made with the daily integrated PP computed in Chapter 2 according to the model of Platt et al. (1980).

PP was also estimated with the three models using ocean colour data for the same locations as the in situ stations. Daily 4km-resolution MODIS-Aqua chlorophyll a concentration and Sea Surface Temperature (SST), and SeaWiFS PAR data, processed according to the R2009.1 version, were obtained from the Ocean Biology Processing Group (OBGP) at NASA's Goddard Space Flight Center (GSFC). Detailed descriptions of the processing procedures are available at <http://oceancolor.gsfc.nasa.gov/WIKI/OCRProc.html>. Satellite-derived PP was then compared to in situ estimates.

3.3 Results and Discussion

3.3.1. PP estimated using in situ data

Utilising in situ data measured during October 2006 and May 2007, it was possible to investigate the performance of selected PP models in the southern Benguela region and Figure 3.1. illustrates a comparison between daily in situ PP and model estimates. In situ PP, showed significant differences between the two cruises, with higher PP observed in October, ranging from 0.71 – 6.98 g C m⁻² d⁻¹, and lower PP in May, ranging from 0.70 – 3.35 g C m⁻² d⁻¹. These ranges compared well with previous observations made in the southern Benguela ecosystem (Barlow et al. 2009, Brown and Field 1986, Mitchell-Innes et al. 2000). All of the models reflected this difference between the cruises, showing that October estimates were generally double the May estimates.

Overall, the differences between measured and modelled PP did not prove to be statistically significant ($P > 0.05$) for both October and May. However, when considering the PP ranges estimated by the various models and by comparing the differences on a station by station basis, it is clear that the models produced widely differing results. Estimates from the Eppley model were 0.58 – 3.84 g C m⁻² d⁻¹ in October, and 1.14 – 3.11 g C m⁻² d⁻¹ during May, while the Eppley-VGPM ranged between 0.48 and 4.41 g C m⁻² d⁻¹ in October and 0.49 – 3.32 g C m⁻² d⁻¹ in May. During October, VPGM estimates were 0.77 – 7.36 g C m⁻² d⁻¹, while May estimates ranged between 0.82 and 5.57 g C m⁻² d⁻¹. While the Eppley model and the Eppley-VGPM produced estimates that were very similar and showed the same variance, they were considerably different to the VGPM estimates and to the in situ data.

Relationships between in situ measured PP and PP modelled using the VGPM and Eppley-VGPM during October and May are shown in Figure 3.2. Although the models explained a similar proportion of the variance in measured PP for both cruises, the Eppley and Eppley-VGPM models typically underestimated PP at most stations during October ($y = 0.53x + 0.32$, $R^2 = 0.66$), while the VGPM tended to compare well to in situ estimates ($y = 0.89x + 0.48$, $R^2 = 0.66$). During May, all models tended to overestimate PP, with the VGPM yielding larger overestimates ($y = 1.28x + 0.61$, $R^2 = 0.59$) than the Eppley-VGPM ($y = 0.76x + 0.38$, $R^2 = 0.59$).

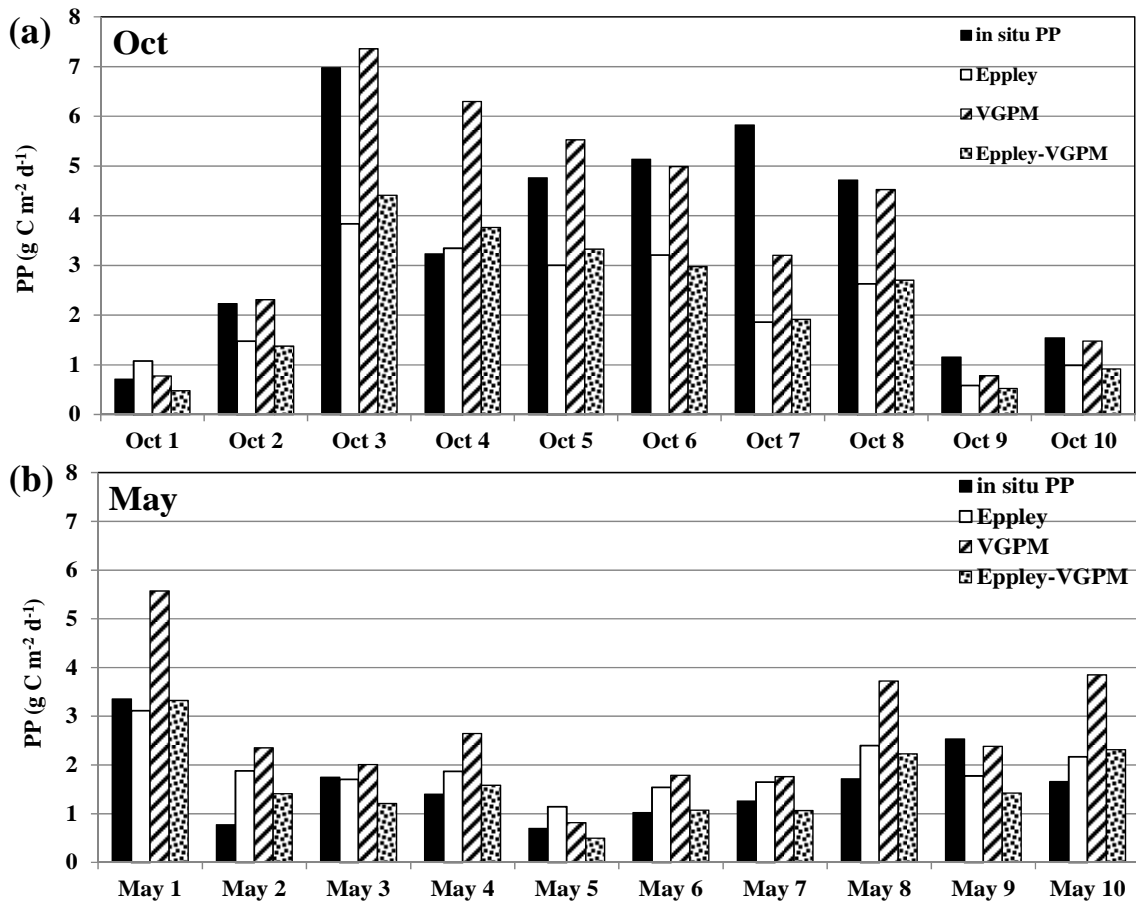


Figure 3.1. Comparison of in situ measured PP with modelled PP ($\text{g C m}^{-2} \text{d}^{-1}$) during (a) October 2006 and (b) May 2007.

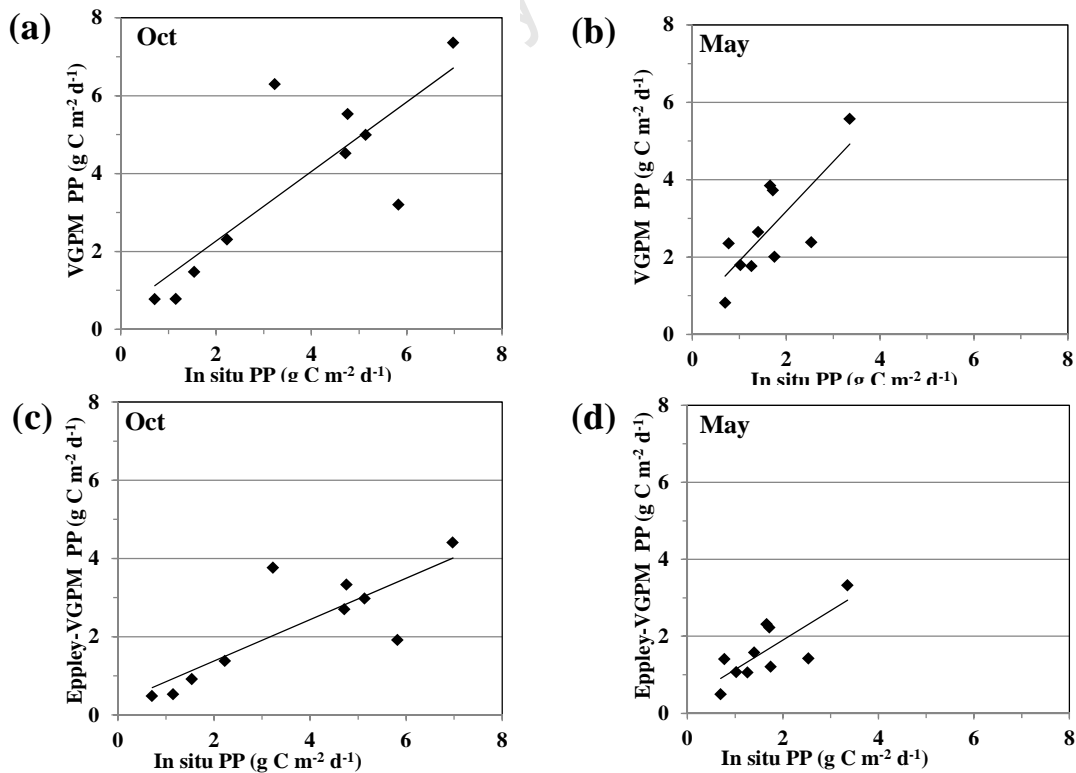


Figure 3.2. Relationships between in situ measured PP ($\text{g C m}^{-2} \text{d}^{-1}$) and PP modelled using the (a, b) VGPM and (c, d) Eppley-VGPM, during October 2006 and May 2007.

Exceptions to this pattern were noted at several stations. At Oct 4, all models overestimated PP, with the VGPM overestimating PP by nearly 50 % (Figure 3.3.) Large differences were also noted at Oct 7 and Oct 9, where all models significantly underestimated PP. During May, the VGPM consistently overestimated PP at all stations except at May 9, while the Eppley-VGPM showed the greatest variability from station to station, overestimating PP at some stations while yielding underestimates at others. Since the models were all forced by the same input data, these differences can only be explained by the construction of the models and the assumptions made.

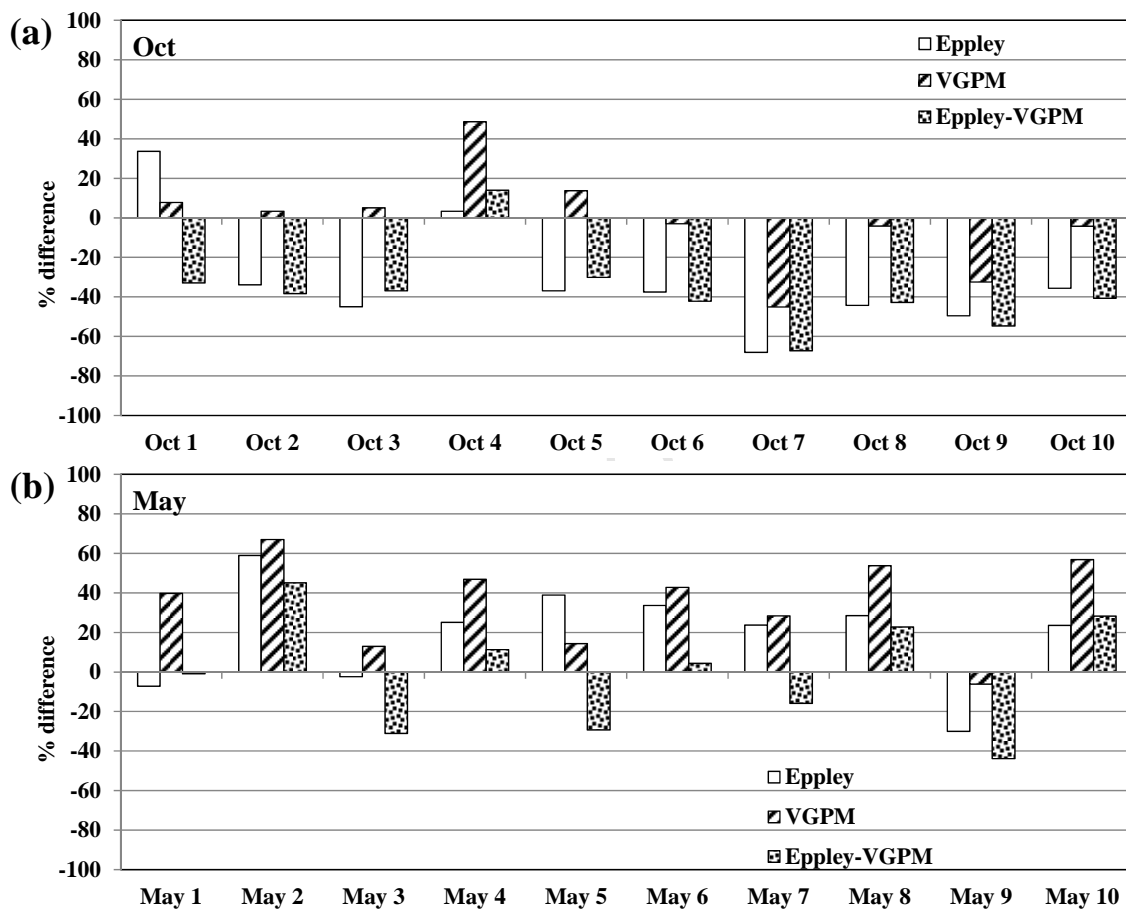


Figure 3.3. Percentage difference between in situ measured PP and modelled PP ($\text{g C m}^{-2} \text{d}^{-1}$) during (a) October 2006, and (b) May 2007.

The Eppley model is forced solely by chlorophyll *a* concentrations and does not take into consideration the influence of environmental variables or physiological state of the phytoplankton. Both variations of the VGPM model account for the influence of irradiance and provided measures of the maximum photosynthesis rates in phytoplankton. When considering the construction of the model, it appears that the relationship is not critically dependant on the surface irradiance, and the inclusion of the irradiance-dependant term has little effect on the VGPM other than the scaling factor of $(0.66125 \cdot 4.1)$. This factor has been determined empirically from numerous field measurements (Behrenfeld and

Falkowski 1997b). Since the irradiance measurements and the scaling factor was the same for both these models, it can be concluded that the observed differences between them result solely from the differences in their temperature-dependant modelling of P_{opt}^B .

Table 3.1. In situ measured P_s^B (mg C [mg chla]⁻¹ h⁻¹) and modelled P_{opt}^B (mg C [mg chla]⁻¹ h⁻¹).

Station	surface P_s^B (mg C [mg chla] ⁻¹ h ⁻¹)	VGPM P_{opt}^B (mg C [mg chla] ⁻¹ h ⁻¹)	Eppley-VGPM P_{opt}^B (mg C [mg chla] ⁻¹ h ⁻¹)
Oct-1	4.67	4.28	2.65
Oct-2	4.08	5.54	3.30
Oct-3	5.71	5.22	3.13
Oct-4	3.49	5.39	3.22
Oct-5	5.88	5.03	3.03
Oct-6	4.67	5.57	3.32
Oct-7	7.67	5.33	3.19
Oct-8	10.22	5.78	3.45
Oct-9	7.56	6.62	4.44
Oct-10	5.45	6.39	3.97
May-1	2.43	5.67	3.38
May-2	1.20	5.17	3.10
May-3	4.86	5.11	3.07
May-4	4.15	5.33	3.18
May-5	2.05	4.86	2.94
May-6	3.34	5.31	3.18
May-7	3.67	5.03	3.03
May-8	3.22	5.31	3.17
May-9	6.52	5.33	3.19
May-10	3.47	6.04	3.64

The VGPM employs a polynomial relationship between P_{opt}^B and surface temperatures (Behrenfeld and Falkowski 1997b), while the Eppley-VGPM uses an exponential relationship (Morel 1991). Table 3.1. shows the differences between the measured and modelled values of the maximum photosynthesis. It is clear that significant differences exist between the measured and modelled values for both October and May. In general, the Eppley model yielded values of P_{opt}^B which were significantly lower than those produced by the VGPM during both months. While the VGPM produces P_{opt}^B values which are very similar to the measured rates of photosynthetic efficiency during October, it appreciably overestimated the photosynthetic efficiency at most stations during May, when Eppley P_{opt}^B values appeared to be more realistic. It is notable that there was little variation in the

modelled P_{opt}^B values between stations during May, which was primarily due to the more uniform surface temperature distributions (see Figures 2.4 and 2.5., Chapter 2).

3.3.2. PP estimated using ocean colour data

Using the models described above, satellite estimates of PP at the same locations as the in situ stations were obtained by using standard daily MODIS-Aqua chlorophyll *a* concentration and Sea Surface Temperature (SST), and Photosynthetically Available Radiation (PAR) derived from the SeaWiFS sensor. Figure 3.4. illustrates the differences between the in situ and satellite-derived PP estimates. Even though the satellite data had a spatial resolution of 4 km, the lack of data due to irregular sampling resulting from cloud, incomplete coverage of the region due to the satellite zenith angle for particular swaths, and data flagging procedures, resulted in data being retrieved at only six of the sites.

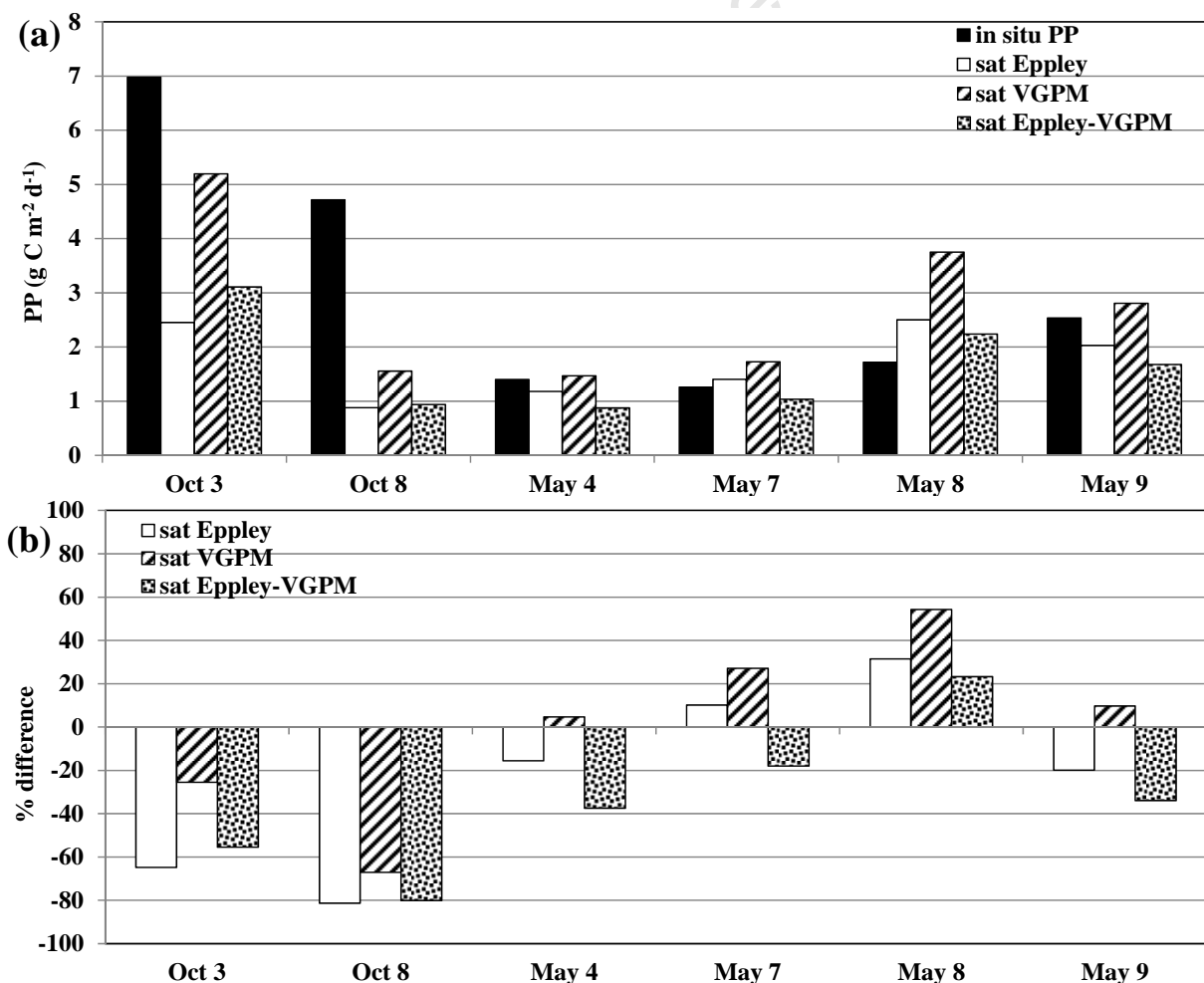


Figure 3.4. (a) Comparison, and (b) percentage difference between in situ measured PP with modelled PP ($g\ C\ m^{-2}\ d^{-1}$) during October 2006 and May 2007.

Considerable differences between satellite and in situ PP were observed at sites during October, while the differences were less significant during May. It was expected that, as observed above, the models would perform better during October than May. However, this analysis showed the reverse, with all of the models generally performing better during May, while they significantly underestimated PP during October. This could be primarily attributed to the variations in the input variables. Table 3.2. compares satellite-derived chlorophyll *a*, SST, and PAR to in situ measurements. Satellite PAR and SST compared reasonably well to those measured in situ, with satellite SST being 0.5 – 1 °C greater, as observed in other studies (McClain 2009).

Table 3.2. In situ and satellite chlorophyll *a* (mg m^{-3}), surface temperature ($^{\circ}\text{C}$), and Photosynthetically Available Radiation ($\text{E m}^{-2} \text{d}^{-1}$).

station	Chlorophyll <i>a</i> (mg m^{-3})		Surface Temperature ($^{\circ}\text{C}$)		PAR ($\text{E m}^{-2} \text{d}^{-1}$)	
	in situ	satellite	in situ	satellite	in situ	satellite
Oct-3	14.72	6.02	13.73	15.41	56.87	55.17
Oct-8	6.91	0.77	15.30	16.21	24.80	55.58
May-4	3.49	1.40	14.02	14.69	29.17	28.81
May-7	2.73	1.97	13.21	14.09	38.74	26.74
May-8	5.76	6.27	13.97	14.95	37.48	26.45
May-9	3.14	4.11	14.04	14.	36.87	25.64

However, the differences between satellite and in situ chlorophyll *a* were significant, with considerably larger variations observed in October, clearly indicating that chlorophyll *a* concentrations were responsible for the large differences in satellite PP. The differences in chlorophyll *a* are likely due to the differences in spatial resolution between satellite and in situ data, and to the patchiness of phytoplankton distributions in the southern Benguela. Furthermore, in upwelling ecosystems such as the southern Benguela, traditional ocean colour chlorophyll algorithms are challenged by optically complex waters close to coastlines (Weeks et al. 2006).

The results of this study showed that the performance of the selected models was significantly hampered by the accuracy of the input variables, with PAR and SST having a relatively small influence, while chlorophyll *a* significantly influenced the accuracy of PP estimates. Similar observations were reported by Friedrichs et al. (2009) and Saba et al.

(2010b). In contrast to Saba et al. (2010b), the models examined here were not particularly challenged at locations with a shallow water column depth (< 200 m).

3.4. Summary and Conclusions

This study examined the performance of selected PP models in the southern Benguela ecosystem, and investigated the factors causing differences between models. The results obtained indicated that although the models produced different results during the two months investigated, they captured the seasonal difference between October (mid-spring) and May (late autumn). During October, the VGPM model was found to be the most accurate, producing PP estimates that differed from in situ measurements by less than 10 % at most stations. The temperature-dependant modelling of P_{opt}^B was a key factor that caused differences between model estimates, indicating that modelling this parameter from temperature does not fully account for the variations observed in measured rates of maximum photosynthesis. Further research is required to achieve better modelling of this parameter.

Satellite estimates of PP were found to be significantly hampered by the accuracy of remotely-sensed chlorophyll *a* concentrations. By improving chlorophyll estimates, and bearing in mind the limitations of P_{opt}^B modelled by the VGPM, it appears that this model may be suitable for application to satellite data for investigations of PP at seasonal and interannual time scales in the southern Benguela.

Chapter 4 – Long-term patterns of remotely-sensed Primary Production

4.1. Introduction

The southern Benguela upwelling system is a highly dynamic environment with significant seasonal variability in oceanography and meteorology which drives the variability in primary production (PP). This environment supports a rich pelagic ecosystem, including top predators such as seals, Cape gannets and penguins (Coetzee et al. 2008, Hutchings et al. 2009, van der Lingen et al. 2006). Although the pelagic yield in the southern Benguela has remained relatively constant (Hutchings et al. 2009), there has been a pronounced eastward shift in pelagic resources during the past decade (Roy et al. 2007), and no-fishing areas have been created around certain colonies in an attempt to circumvent any further decline in these populations (Crawford et al. 2008).

Understanding the spatial and temporal patterns and trends in PP in the southern Benguela is important for the effective management of the economically and ecologically significant pelagic ecosystem. Warming trends observed in most Large Marine Ecosystems of the world (Belkin 2009) have resulted in large spatial changes in phytoplankton distributions and a reduction of global PP since the early 1980s (Behrenfeld et al. 2006). The predicted decrease in global PP has important consequences for the sustainability of fisheries ecosystems like the southern Benguela, and for future climate change impacts on these systems.

Micro-scale investigations conducted previously (Barlow et al. 2009, Brown et al. 1991, Mitchell-Innes et al. 2000, Shannon and Field 1985) and in Chapter 2 have demonstrated considerable variability of biomass and PP in relation to physiology and environmental conditions. Although these types of studies provide important information on the small-scale physical processes and biological responses which essentially underpins the variability at larger scales, they are extremely limited in space and time, rendering their use to quantify variability at regional scales and over longer time periods unrealistic due to the substantial extrapolation required. This necessitates the use of remotely-sensed data, which is the only way to achieve synoptic mesoscale coverage of the ecosystem.

Ocean colour data have been used extensively in studies of global and regional phytoplankton biomass distribution and variability (Behrenfeld et al. 2001, Carr and Kearns 2003, Demarcq et al. 2003, 2007, Thomas et al. 2001, 2003), relationships between physical and biological variables (Wilson and Coles 2005), long-term trends (Antoine et al. 2005, Demarcq 2009, Djavidnia et al. 2010, Gregg et al. 2005, Vantrepotte and Mélin 2009), and to validate biogeochemical model output (Gregg et al. 2003b). Using high-resolution (1 km) satellite data, Weeks et al. (2006) examined detailed changes in the frequency and extent of upwelling and the phytoplankton response on intra-seasonal time scales in the southern Benguela. However, these studies have primarily focussed on the interpretation of chlorophyll *a* (chl_a) as an index of phytoplankton production, without considering the variability in production rates.

The primary aim of this study is to investigate the large scale spatial and temporal variability in phytoplankton biomass and production rates in the southern Benguela at seasonal and interannual time scales. Although lower resolution (4 and 9 km) satellite data prohibits the description of most of the finer-scale spatial and temporal changes observed by Weeks et al. (2006), especially in the inshore coastal regions, it is useful for examining patterns over larger scales. Despite the limitations identified, Chapter 3 suggested that the Vertically Generalised Production Model (VGPM) is useful for estimating PP over larger scales in the southern Benguela ecosystem.

The VGPM model is applied to monthly SeaWiFS and MODIS-Aqua data over a 13 year time period and the spatial and temporal components of variability are addressed by examining the mean biomass and PP in the southern Benguela, and by comparing the differences between zones within the ecosystem. Three zones (Cape Peninsula, St Helena Bay, Namaqua), which have previously been identified as key biogeographic regions in the southern Benguela (Demarcq et al. 2003, 2007, Huggett et al. 2009, Weeks et al. 2006), were selected for this comparison.

4.2. Methods

Standard monthly-averaged ocean colour data from the SeaWiFS and MODIS-Aqua sensors, with a spatial resolution of 9.26 km, was provided by the Ocean Biology Processing Group (OBGP) at NASA's Goddard Space Flight Center (GSFC). The data was processed according to the R2009.1 processing version, and detailed descriptions of the processing are available at <http://oceancolor.gsfc.nasa.gov/WIKI/OCRproc.html>. SeaWiFS data used in this study covered the time period from September 1997 to June 2002, while MODIS-Aqua covered the period from July 2002 to May 2010.

Primary production data estimated using the VGPM model (Behrenfeld and Falkowski 1997a) was obtained from the Ocean Productivity Site (<http://www.science.oregonstate.edu/ocean.productivity/>). The VGPM estimates PP from chlorophyll *a* concentrations using a temperature-dependant relationship of the chlorophyll-specific photosynthetic efficiency. Temperature is a good indicator of the physical environment to which phytoplankton are exposed (Carr 2002). Co-sampled satellite Sea Surface Temperatures (SST) are available for the MODIS-Aqua period, but not for the SeaWiFS period. To provide a long term data set of satellite temperatures common to both periods, the Advanced Very High Resolution Radiometer (AVHRR) Pathfinder SST (version 5), with a spatial resolution of 4 km, for the period from September 1997 to December 2009 was obtained from the National Oceanographic Data Centre (NODC) (<http://www.nodc.noaa.gov/sog/pathfinder4km/>) and used to explore the relationship between PP and environmental variability.

The Niño 3.4 Index is the mean SST anomaly in the NINO3.4 region of the tropical Pacific Ocean (5 °S - 5 °N; 170 °W - 120 °W) and is used to identify and monitor El Niño and La Niña conditions. A major mode of variance in the South Atlantic Ocean is located over the South Atlantic anticyclone and is strongly linked to El Niño/Southern Oscillation (ENSO) events (Colberg and Reason 2007, Reason et al. 2006). Monthly values of the Niño 3.4 Index for the period September 1997 to December 2010 were obtained from the NOAA Climate Prediction Center (<http://www.cpc.ncep.noaa.gov/data/indices/soi/>) and used to investigate the relationship between basin scale forcing and PP variability in the southern Benguela.

Monthly time series of SST, chlorophyll *a* and PP were constructed by computing the mean over an area, approximately 200 km wide, along the coast between 29°S and 34.3°S

(Figure 4.1.), and used to investigate the temporal patterns in the whole southern Benguela upwelling ecosystem. Anomalies were computed by subtracting the monthly climatic mean from each month in the time series. Latitudinal differences were investigated by plotting the latitudinal mean and anomalies against latitude for the entire coast between 29°S and 34.3°S, while cross-shelf differences were examined along three latitudinal transects, namely, Cape Peninsula (34.1°S), St Helena Bay (32.6°S), and Namaqua (29.9°S).

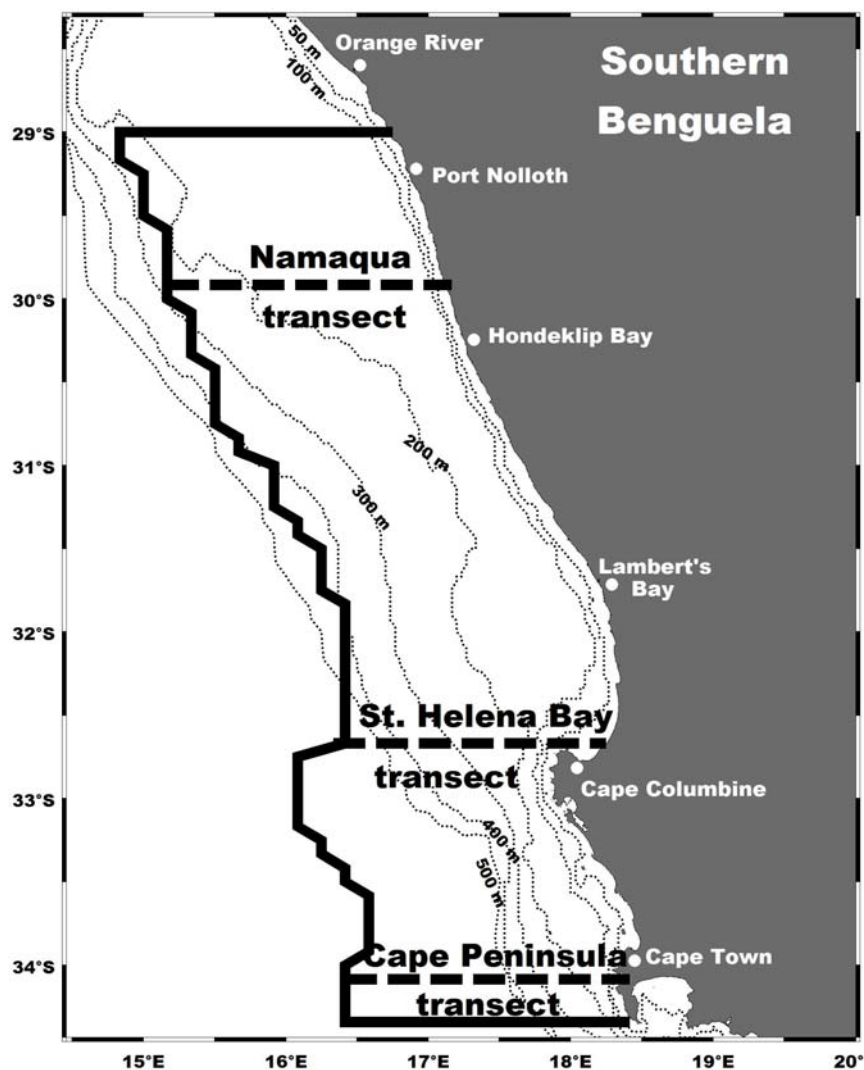


Figure 4.1. Bathymetric map of the Southern Benguela. The dark solid line indicates a 200 km wide area, while the dashed lines indicate the three latitudinal transects.

4.3. Results

The means and anomalies in chl_a, PP and SST, averaged over an approximately 200 km wide area along the southern Benguela coast, are presented in Figure 4.2. and were used to investigate temporal patterns in the ecosystem. The Hovmöller plots comprising the latitudinal mean and anomalies of these variables over time, presented in Figures 4.3. and 4.5., were used describe the latitudinal variations in these variables.

Sea Surface Temperature

Time series of monthly mean SST (Figure 4.2a.) showed the expected seasonal pattern, with elevated SST's observed during spring and summer, while autumn and winter were characterised by lower temperatures. This pattern was evident throughout the southern Benguela ecosystem, as seen in Figure 4.3., with notably higher spring and summer SSTs observed south of Cape Columbine (Demarcq et al. 2003, Hardman-Mountford et al. 2003). The abrupt change in the seasonal pattern south of Cape Columbine, also noted by Weeks et al. (2006), was primarily due to the much narrower shelf (Figure 4.1.).

Consequently, mean SSTs in this region were influenced by warmer Agulhas current water located beyond the boundary of the upwelling zone, which is strongly confined to the shelf. Throughout the time series, mean SST's ranged between 14 – 21 °C, with the highest summer temperatures found during 2002 and 2003 (Figure 4.21, Demarcq et al. 2007) and the lowest observed during 2006. A clear decreasing trend in the summer maxima is evident for the period from 2003 to 2006, and corresponded to the cooling trend described by Rouault (2007). While the highest winter SST's were noted during 1999 and over the last three years of the time series, the lowest was observed in 1998, 2002, 2003, and 2006.

Figure 4.2b. showed that although notable positive anomalies of 0.5 °C and 1 °C were observed during February 1998 and December 1999, respectively, SST anomalies across the ecosystem were typically small but negative until 2000, when a considerable negative anomaly, peaking at -1.9 °C, was observed during autumn. Subsequently, an abrupt change to mainly positive anomalies occurred and continued until mid-2003. The largest and most prolonged positive anomalies, averaging around 1 °C, occurred during the summer and autumn seasons of 2001/2002 and 2002/2003, with the largest positive anomaly of 2.5 °C observed in March 2002. While most of 2004 was dominated by small negative anomalies, the last three months were notably positive.

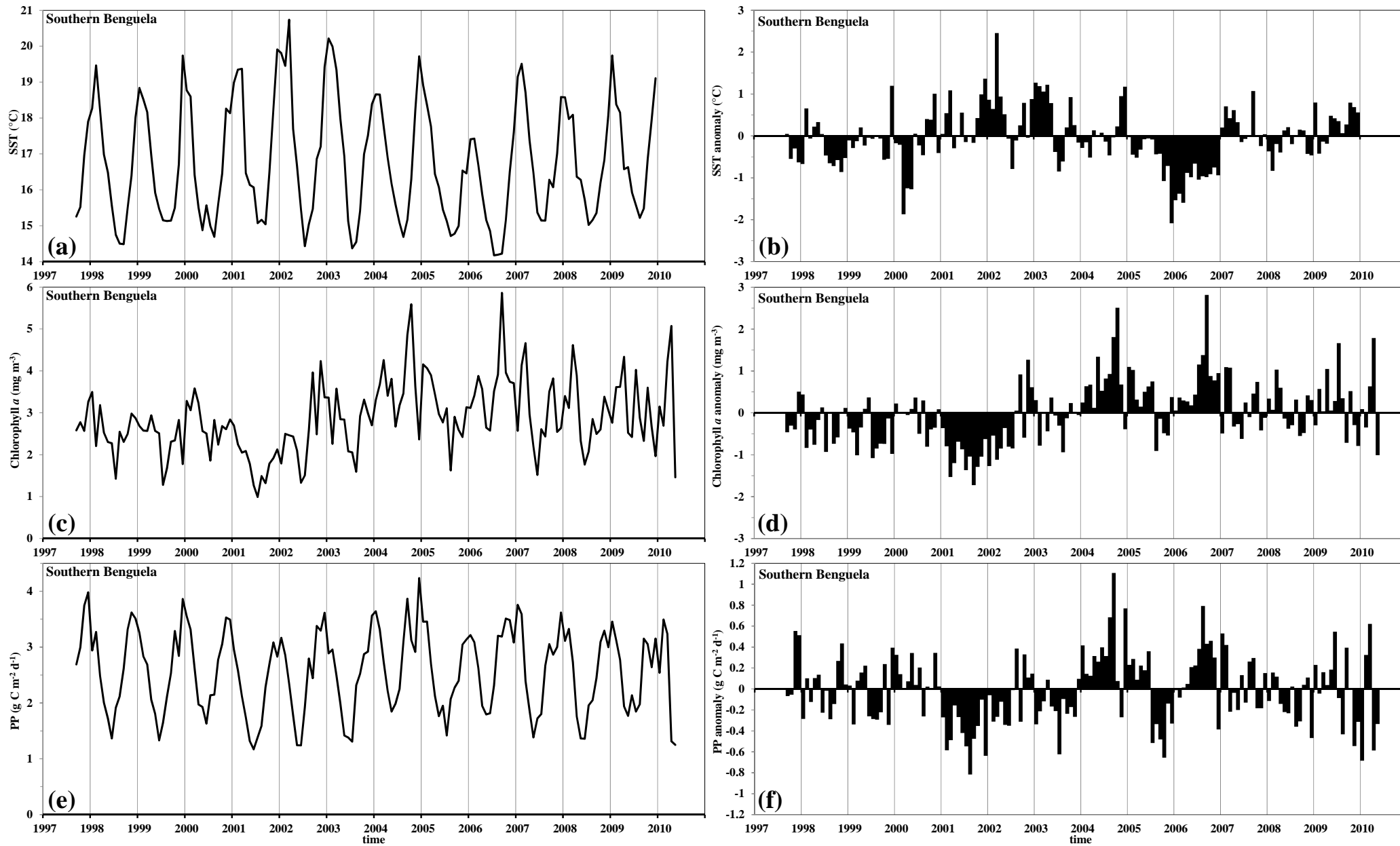


Figure 4.2. Monthly means (a, c, e), and anomalies (b, d, f) of SST (°C), chlorophyll *a* (mg m⁻³), and PP (g C m⁻² d⁻¹) averaged over a 200 km wide area along the southern Benguela coast.

During February 1998, the warming was most evident in the northern part of the region, off the Namaqua shelf, with slight warming notable south of Cape Columbine, while the St. Helena Bay area appeared to be less affected (Figure 4.3b.). The warming in December 1999 (Roy et al. 2001), the summer/autumn seasons of 2001/2002 and 2002/2003 (Weeks et al. 2006), and during the latter part of 2004, was more apparent throughout the region. A 2-year period of prolonged negative SST anomalies were observed throughout the system during 2005 and 2006, with the most negative anomaly occurring in the summer of 2005/2006 (Figure 4.3b). Anomalies in the last three years of the time series were relatively smaller and appeared to oscillate from positive in 2007 to slightly negative in 2008 and positive again in 2009 and 2010.

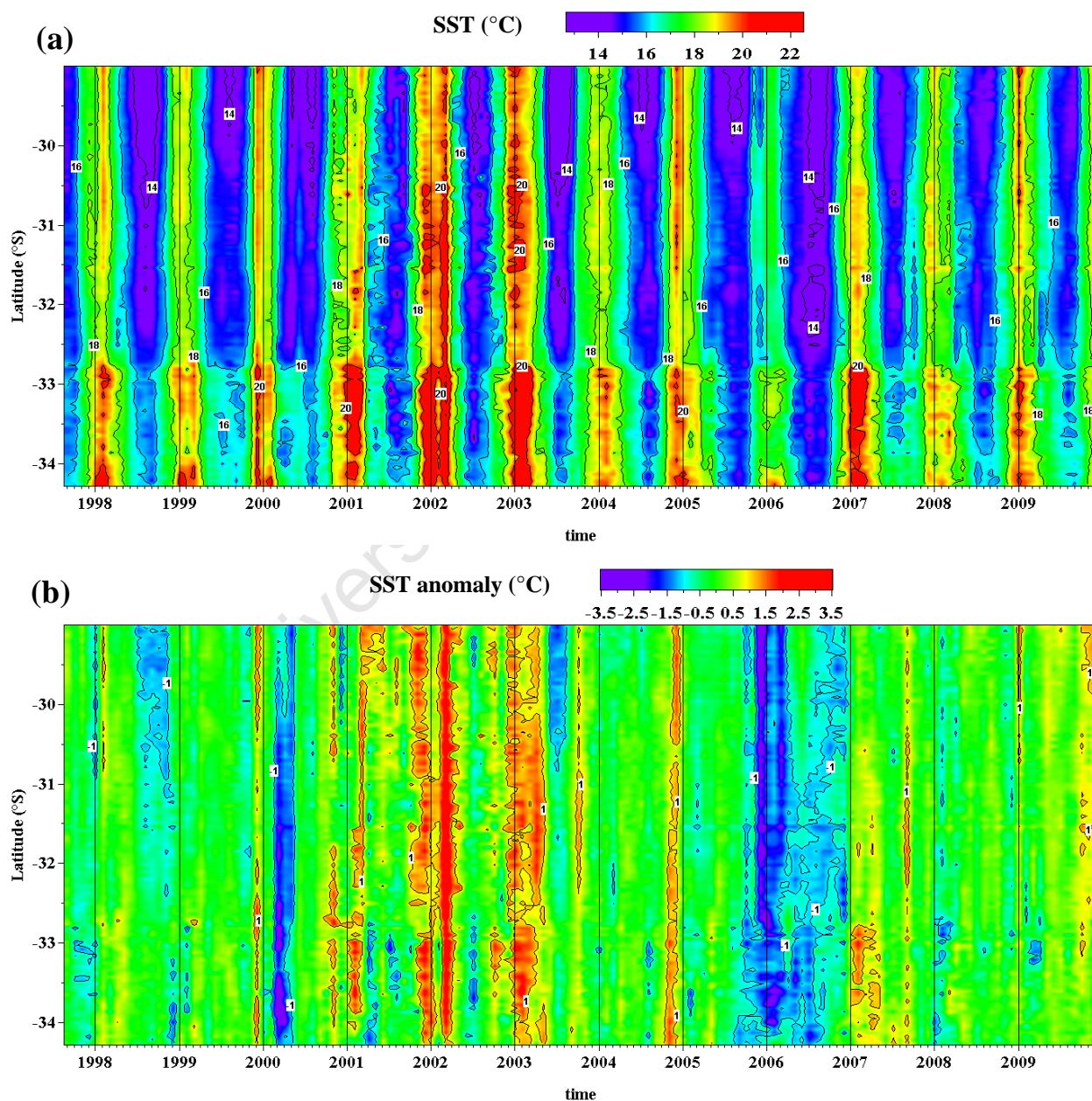


Figure 4.3. Hovmöller plots of the latitudinal (a) mean SST (°C) and (b) SST anomalies (°C) for the southern Benguela ecosystem between 29 °S and 34.3 °S, averaged over 200 km.

There appeared to be a good agreement between SST anomalies in the southern Benguela and the Niño 3.4 index shown in Figure 4.4. Positive deviations of the Niño 3.4 index are consistent with abnormally warm water in the eastern tropical Pacific Ocean and El Niño conditions, while negative deviations correspond to unusually cold water and are indicative of La Niña conditions. The index showed large positive anomalies, indicative of El Niño conditions during the spring and summer of 1997/1998, for a prolonged period between 2002 to late 2005, and during spring/summer of 2006/2007 and 2009/2010. La Niña conditions were observed from mid-1998 to mid-2001, during summer 2005/2006, from 2007 to 2009, and again in the latter part of 2010 (Figure 4.4.).

Typical La Niña conditions include increased southeasterly winds along the west coast of South Africa, resulting from a strengthening of high-pressure systems in the Atlantic and Indian oceans, and a southward displacement of the Atlantic high-pressure associated with a low-pressure anomaly to the east, while the converse is true during El Niño conditions (Hutchings et al. 2009). Although the exact timing did not always coincide on a month to month basis, above-average SSTs in the southern Benguela generally corresponded to the El Niño events, while negative SST anomalies were generally associated with La Niña events. The warm period between 2001 and 2003, and during the latter part of 2009, corresponded to a shift from La Niña to strong El Niño conditions

Some exceptions to this pattern were observed during the El Niño of 1997/1998 when SST anomalies were negative. The warm event observed in the southern Benguela during December 1999 (Roy et al. 2001) was unusual since it occurred during a period of prolonged La Niña conditions, and only the most negative SST anomalies in the 2005-2007 period coincided with negative deviations of the Niño 3.4 index.

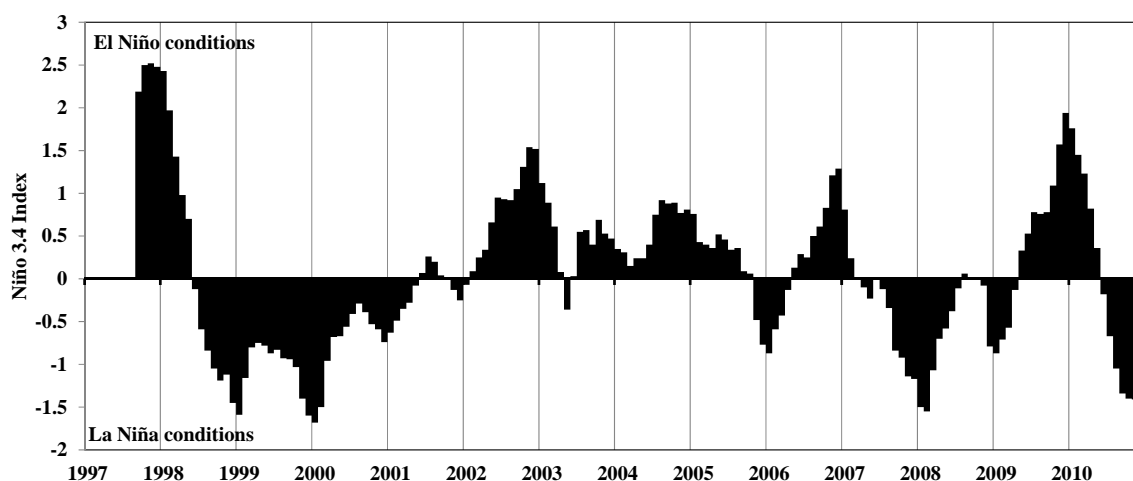


Figure 4.4. The Niño 3.4 Index.

Chlorophyll *a*

Chla concentrations during the first 5 years of the time series (Figure 4.2c.) were generally low and showed a steady decline until 2002. Thereafter, chla increased until 2005 and maintained higher levels for the remainder of the time series. 2001 and 2002 exhibited the lowest concentrations, while the highest were observed during spring of 2004 and 2006. Figure 4.5a indicates that this pattern was evident throughout the southern Benguela ecosystem. The seasonal cycle of chla (Figure 4.2c.) was fairly complex, with minima typically observed during winter, and two or more maxima occurring mainly from spring, through summer, to autumn.

When considering the latitudinal differences (Figure 4.5a) it was apparent that the seasonal signal shown by the ecosystem-wide mean chla was complicated by the fact that the timing of the main seasonal peak in chla changed from south to north. In the southern part of the ecosystem, south of Cape Columbine, chla was typically low and exhibited a very clear seasonal signal with elevated concentrations observed from spring through summer to early/mid-autumn and minima occurring in winter.

Further north, in the St. Helena Bay region, chla was considerably higher throughout the year, and instead of a distinct spring peak, chla increased progressively from September to November, maintaining these levels until a peak was reached during autumn. Although concentrations in the northernmost part of the region, off the Namaqua shelf, were more moderate than in St. Helena Bay, the highest occurred during spring, with a smaller peak notable in autumn. The sudden change in the seasonal chla signal south of Cape Columbine matched the change in the SST pattern described earlier and distinct regions of persistently lower chla are evident around 33 °S and south of 34 °S. This pattern was also observed by Weeks et al. (2006).

Negative chla anomalies dominated the first 5 years of the time series (Figure 4.2d.), with anomalies becoming progressively more negative and reaching a peak of almost -2 mg m^{-3} during 2001/2002, corresponding to the latter part of a prolonged period characterised by La Niña conditions (Figure 4.4.). Much of the period from late 2002 to early 2007, characterised by El Niño conditions (Figure 4.4.), was dominated by persistent positive chla anomalies, with peaks of 2.5 mg m^{-3} and 2.8 mg m^{-3} occurring in October 2004 and September 2006, respectively. Throughout the rest of 2007 and 2008, anomalies were relatively small, while they tended to increase in 2009 and 2010.

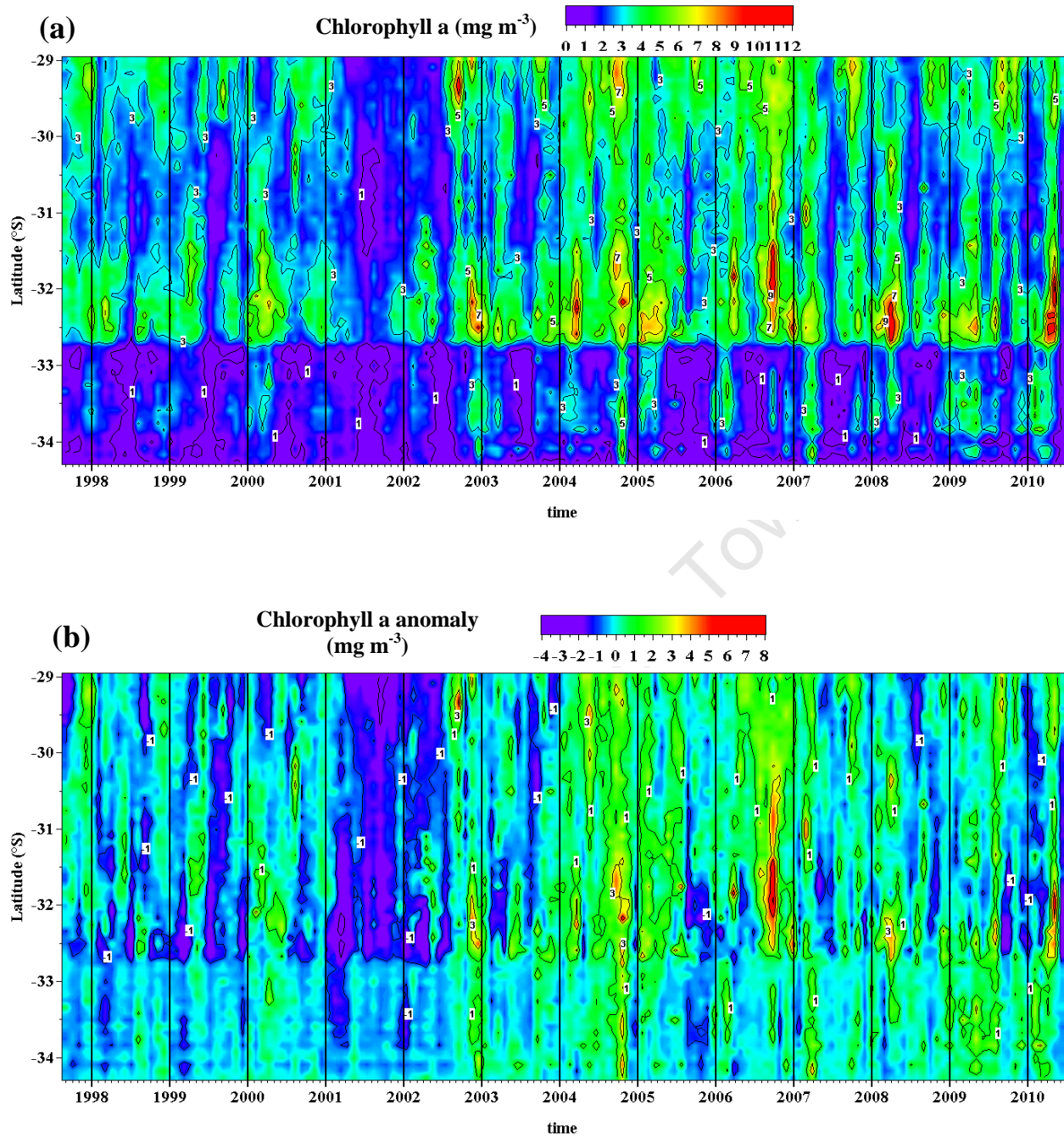


Figure 4.5. Hovmöller plots of the latitudinal mean (a) and anomalies (b) of chlorophyll *a* (mg m^{-3}) in the southern Benguela ecosystem between 29 °S and 34.3 °S, averaged over 200 km.

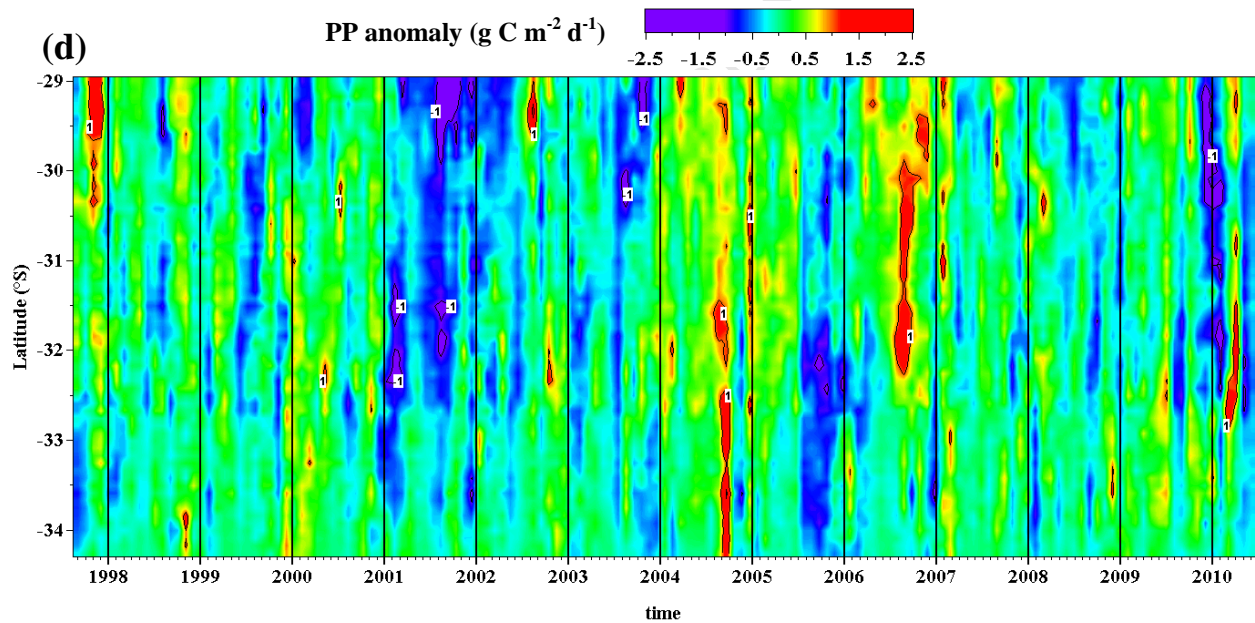
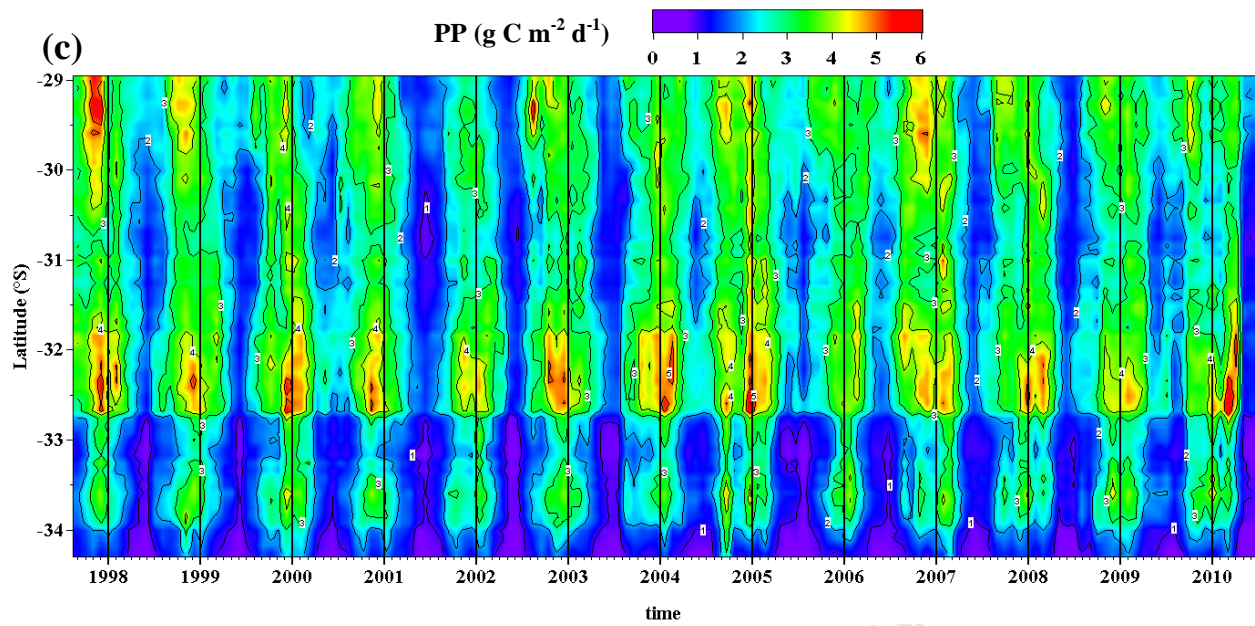


Figure 4.5. (continued) Hovmöller plots of the latitudinal mean (c) and anomalies (d) of PP ($g\ C\ m^{-2}\ d^{-1}$) in the southern Benguela ecosystem between $29^{\circ}S$ and $34.3^{\circ}S$, averaged over 200 km.

Primary Production

PP estimates across the southern Benguela region (Figure 4.2e.) typically ranged between about $1 - 4 \text{ g C m}^{-2} \text{ d}^{-1}$ throughout the time series, and the seasonal signal was notably clear, with higher PP observed during spring and summer, while lower PP was evident during autumn and winter. The highest summer PP was found in 1997/1998, 1999/2000 and 2004/2005, while the lowest summer PP occurred during 2000/2001, 2001/2002, and again in 2005/2006. A clear decreasing trend in the maximum summer PP is observed from 1997 to 2003 and again from 2007 to 2010, while PP during 2004 and 2005 was typically above-average.

Generally, above-average PP (Figure 4.2f) was noted from 1997 to 2000, with the positive anomalies decreasing progressively toward the end of 2000. During this period, the largest positive PP anomaly, up to $0.6 \text{ g C m}^{-2} \text{ d}^{-1}$, was observed during El Niño conditions (Figure 4.4.) in the summer of 1997/1998, corresponding to above-average chl_a and negative SST anomalies (Figure 4.2b,d). The period from 2001 to the end of 2003 was generally characterised by prolonged negative PP anomalies reaching peaks of $-1 \text{ g C m}^{-2} \text{ d}^{-1}$ and $-0.8 \text{ g C m}^{-2} \text{ d}^{-1}$ during early spring of 2001 and 2003, respectively. The exception was the latter months of 2002 where positive anomalies were observed.

Below-average PP during this period was related to negative chl_a anomalies and above-average SSTs. Although PP was generally above-average over the following three years, reaching peaks of $1 \text{ g C m}^{-2} \text{ d}^{-1}$ in September 2004 and $0.8 \text{ g C m}^{-2} \text{ d}^{-1}$ in August 2006, this pattern was interrupted by a series of negative anomalies during the spring/summer season of 2005/2006, corresponding to below-average chl_a and large negative SST anomalies during La Niña conditions. PP anomalies were relatively small during 2007 and 2008, similar to the chl_a pattern, but they tended to increase in the last two years.

Latitudinal variability in PP (Figure 4.5c.) was evident throughout the ecosystem, and in general, the patterns of PP were similar to those observed for chl_a. The highest PP was observed in the St. Helena Bay region, while PP was more moderate further north along the Namaqua shelf. In the southern part of the system, PP was typically lower than in the north, with elevated PP between Cape Columbine and the Cape Peninsula bounded by regions of persistently lower PP around 33°S and south of 34°S . The above-average PP observed during the summer of 1997/1998 was most significant off the Namaqua shelf,

while the positive PP anomaly in spring 1998 was most notable off the Cape Peninsula (Figure 4.5d).

During the latter part of 2002, positive PP anomalies peaking in August and October, were most significant in the northern part of the region and in St Helena Bay, respectively. Above-average PP during 2004 was evident across the entire system, while it was more limited to the region north of 33 °S during 2006, and to the St. Helena Bay region during the early part of 2010. Although below-average PP was observed throughout the system from 2001 – 2003 and during the 2009/2010 summer, they were most significant from St. Helena Bay northward, while the converse was true for the negative PP anomalies during spring/summer of 2005/2006 when anomalies were more pronounced in the southern part of the region.

Variations in the mean and anomalies of PP across the shelf were examined along three key transects, namely, the Cape Peninsula, St. Helena Bay, and Namaqua (Figures 4.6. and 4.7.). For each of the transects, the highest PP was observed adjacent to the coast, while offshore rates were typically below 1 g C m⁻² d⁻¹. Although it was less obvious along the Cape Peninsula transect, a common feature was the decreasing trend in maximum PP from 1997 to 2002, followed by four years of higher summer PP (2003 – 2007), while an increasing trend was observed along the Cape Peninsula and St. Helena Bay transects during the latter part of the timeseries.

Along the Cape Peninsula transect, higher PP, typically above 3 g C m⁻² d⁻¹, was observed mainly during spring and summer, with minima evident during winter (Figure 4.6a.). Above-average PP (greater than 5 g C m⁻² d⁻¹) occurred during summers of 1998, 1999, 2002, 2007 and 2009 (Figure 4.7a.), with the most significant occurring in spring 2004, extending over 100 km offshore. Below-average PP was found during spring/summer of 1997, 2000, 2003, and 2005.

The Cape Peninsula transect was located on the boundary between elevated PP to the north and considerably lower PP to the south (Figure 4.5c.), and since the response of phytoplankton to upwelling off the Cape Peninsula typically occurs upstream of the area directly influenced by the upwelling cell (Weeks et al. 2006), a better representation of the variations in PP may be obtained north of 34°S. However, careful examination of the latitudinal variations (Figure 4.5c.) indicated that seasonal and interannual signals to the north of the transect were very similar to those along the transect.

PP along the St. Helena Bay transect (Figure 4.6b.) was generally two to three times greater than that observed along the Cape Peninsula transect, with winter minima being short-lived and high values occurring for most of the year. Peak PP typically occurred during summer, with a secondary peak sometimes found in autumn. Although PP was generally high, the numerous anomalies observed here indicated the high variability of PP in the region (Figure 4.7b.). Of note was the above-average PP observed during the 1997 summer, throughout most of the year in 2000 and 2004, and in the early part of 2010. The greatest offshore extent of elevated PP was attained during these years, while the 2005/2006 spring/summer period was characterised by prolonged below-average PP.

Along the Namaqua transect, PP was more moderate and, owing to the significant width of the shelf in this area, fewer low values were observed offshore. The most significant PP was found during 1997, 2000, for much of 2004 to 2008, and in the early part of 2010. A clear pattern of decreasing PP was noted from 1997 to 2003, with negative anomalies increasing progressively and reaching a peak in 2003 (Figure 4.7c.), followed by mainly positive PP anomalies during 2004 to 2007, and a subsequent decreasing trend.

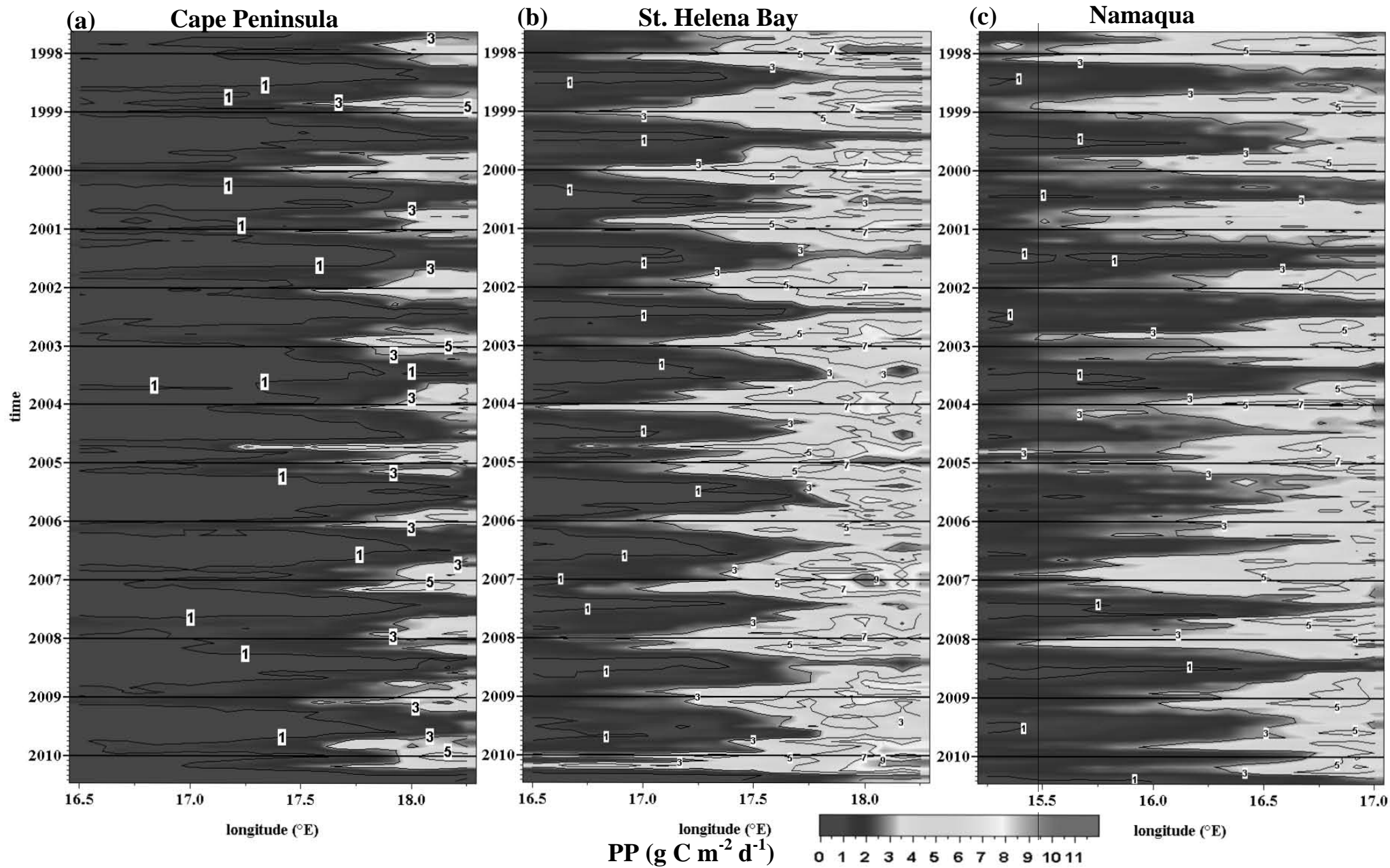


Figure 4.6. Hovmöller plots of PP ($\text{g C m}^{-2} \text{d}^{-1}$) for the 200 km wide (a) Cape Peninsula, (b) St Helena Bay, and (c) Namaqua transects.

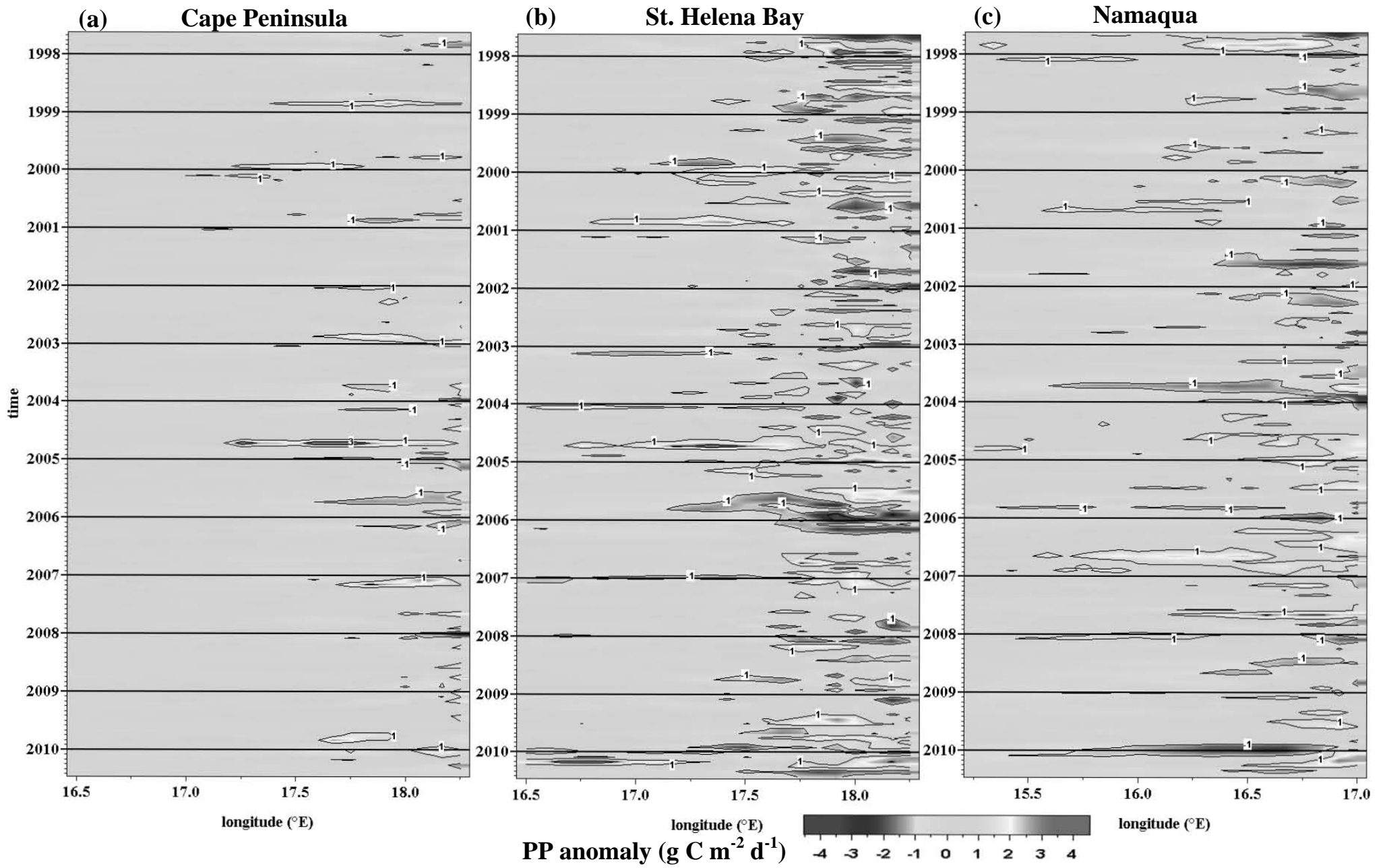


Figure 4.7. Hovmöller plots of PP anomalies ($\text{g C m}^{-2} \text{d}^{-1}$) for the 200 km wide (a) Cape Peninsula, (b) St Helena Bay, and (c) Namaqua transects.

4.4. Discussion and Conclusions

The variations in seasonal and interannual signals of SST, chl_a and PP in the southern Benguela ecosystem during the period September 1997 to May 2010 were examined and latitudinal differences were compared in this study. Shelf-averaged plots allowed the identification of regions of elevated phytoplankton biomass and PP along the length of the coast, and cross-shelf transects enabled comparisons of the variability in these variables in certain key biogeographic regions.

Seasonal and Latitudinal Variability

The seasonal variations in SST (Figures 4.2a and 4.3a.), where higher temperatures were observed during spring and summer and lower temperatures in autumn and winter, have previously been described by several authors (e.g. Demarcq et al. 2003, 2007, Hardman-Mountford et al. 2003) and follows the pattern of solar insolation. Using annual climatologies, Demarcq et al. (2003) noted major upwelling areas off the Namaqua shelf, Cape Columbine, and off the Cape Peninsula, and through the use of high resolution (1 km) data, Weeks et al. (2006) investigated the extent and frequency of upwelling at these locations on intra-seasonal time scales.

Notably, during this study, the cycles of upwelling were not apparent and this may be attributed to the combined effect of the spatial and temporal averaging and to the coarse resolution of the data used. Also, the use of SST as an index of upwelling strength does not take into consideration the influence of solar heating, which almost completely masks the upwelling signals. However, the intended use of SST in this study was not to identify upwelling cycles, but rather to describe the long-term SST variability within the region.

The seasonal signal shown by the ecosystem-wide mean chl_a (Figure 4.2c) was obscured by the change in the timing of the main seasonal peaks from south to north. Typically elevated concentrations were observed from spring to autumn off the Cape Peninsula, while peak concentrations were noted during autumn in the St. Helena Bay region, and during spring and autumn off the Namaqua shelf (Figure 4.5). The seasonality in chlorophyll concentrations and PP was generally in phase with periods of maximum upwelling during spring and summer (Hardman-Mountford et al. 2003, Thomas et al. 2001).

Although latitudinal variations in PP compared well with chl_a, the seasonal variations in PP were different to those in chl_a, with PP generally peaking during spring and summer throughout the system. This suggests that, although influenced by peaks in phytoplankton biomass, the seasonal peaks in PP are more closely related to the seasonal patterns in available light, which are maximum during spring and summer and lower during autumn and winter.

In the vicinity of the Cape Columbine and Cape Peninsula upwelling cells clear regions of decreased chlorophyll concentrations and primary production were visible (Figure 4.5). Similar decreases in the region of the Namaqua upwelling cell were not observed, and this is most likely due to the phytoplankton response to upwelling in this region occurring over a much broader latitudinal range (Weeks et al. 2006). The influence of bathymetry was notable in the southernmost part of the region, where a sharp discontinuity in the seasonal patterns was observed. This was primarily due to the influence of warmer Agulhas current water located beyond the boundary of the upwelling zone, which is strongly confined to the shelf (Shannon and Nelson 1996, Shillington 1998).

Using 9 km resolution data, Carr and Kearns (2003) observed the largest offshore Ekman transport during spring and summer, and noted that upwelling decreased with increasing latitude in the Benguela ecosystem. They also found that while winter minima were typical, seasonal variations were weak, and that minimum chlorophyll concentrations occurred off the Namaqua shelf, while maximum chlorophyll was observed off Cape Columbine. Other investigations also showed clear minima in chlorophyll concentration during winter, with no significant seasonality (Thomas et al. 2001, Weeks and Shillington 1994).

Mean chlorophyll computed for the first 100 km from the coast, using 4.5 km resolution monthly SeaWiFS data, showed that seasonal maximum in chlorophyll coincided with the seasonal maximum in upwelling, both temporally and spatially along the coast (Thomas et al. 2003). Off the Namaqua shelf, elevated chlorophyll was observed throughout the year, while south of 30 °S, the variations in chlorophyll were in phase with seasonal variations in wind forcing. Thomas et al. (2003) concluded that the significant differences observed in chlorophyll seasonality during previous studies (Hill et al. 1998) were the result of insufficient coverage of the Coastal Zone Colour Scanner (CZCS) data that was used in those studies (Mackas et al. 2006).

Demarcq et al. (2007) described the spatial and temporal variability in phytoplankton biomass over a period of eight years, using a chlorophyll index derived from low resolution SeaWiFS data. They observed that the seasonal signal was the dominant pattern of variability in the southern Benguela and that no clear long-term trend was evident. Weeks et al. (2006) observed that the response of phytoplankton biomass to upwelling primarily occurred downstream of the upwelling centres.

Interannual Variability

Considerable interannual variability was observed in SST, chl_a, and PP in the southern Benguela, with considerably higher values observed in some years, while other years were characterised by significantly lower values. Djavidnia et al. (2010) concluded that the global chlorophyll frequency distributions provided by SeaWiFS and MODIS-Aqua were extremely similar and yielded relatively consistent monthly time series with similar levels of variance, high correlation coefficients, and an average log root mean square difference of 0.137. Thus, the understanding is that the decline in chlorophyll concentrations from 1997 to 2002, followed by a steady increase until 2005, with higher levels maintained for the rest of the time series, was not due to inconsistencies between the products from various sensors, but was a true reflection of the variations in chl_a over the time period.

In general, above-average temperatures and phytoplankton biomass and PP that were typically lower than the mean were associated with El Niño events (Figure. 4.4.). In contrast, below-average temperatures were generally associated with positive anomalies of biomass and PP, and tended to coincide with La Niña events. This agreement is most likely due to the fact that atmospheric sea level pressure anomalies, associated with the South Atlantic anticyclone along the west coast of South Africa, have been found to be strongly linked to ENSO events (Colberg and Reason 2007, Reason 2006). Such links have been reported to significantly impact ecosystems on a variety of trophic levels from phytoplankton (Behrenfeld et al. 2001, Barber and Chavez 1983) to fisheries and top predators (Boyd and Doney 2002, Chavez et al. 2003).

The interactions between the South Atlantic and South Indian atmospheric anticyclonic pressure systems and the continental low drives variations in equatorward winds along the west coast. This, in turn, drives the variations in upwelling (Hutchings et al. 2009). The

ultimate result of these interactions is to yield stronger upwelling-favourable winds during La Niña periods, while the converse is true during periods of El Niño conditions. Less consistent correlations between ENSO events and SST, chl_a, and PP in the southern Benguela may be related to the reported shift in the nature of El Niño events from the classically described warm event in the eastern Pacific to a warm event in the central Pacific Ocean (Ashok and Yamagata 2009).

Of note was the considerable El Niño event of 1997/1998 that corresponded to negative temperature anomalies and above-average phytoplankton biomass and PP in the southern Benguela, with maximum biomass and PP observed off the Namaqua shelf. The distinct warm event that occurred throughout the region in December 1999 (Figure 4.2b and 4.3b.) was unusual since it occurred during a period of prolonged La Niña conditions, and was followed by a period of intense upwelling during late summer (Roy et al. 2001). This significant warming was associated with anomalously lower biomass and PP throughout the region. The prolonged upwelling that followed was associated with elevated PP, even though phytoplankton biomass did not appear to be significantly above average, and led to the enhanced retention of eggs and larvae within the coastal domain (Hutchings et al. 1998, Penven et al. 2000), resulting in a peak in anchovy recruitment during that season.

Huggett et al. (2009) showed that from 1997 to 2000, total copepod biomass and production was significantly greater off the St. Helena Bay region and the Namaqua shelf, in comparison to further south, and there was a shift from high biomass and production to significantly lower values during 2001 - 2003. They also observed an overall shift in the size composition of the copepod population from elevated biomass of medium and large copepods to a dominance of smaller copepods over their study period. This pattern corresponded well to the interannual changes in phytoplankton production observed in this study for those years.

A clear decreasing trend in the maximum summer PP was observed from 1997 to 2003 and again from 2007 to 2010 (Figure 4.2.e), while PP during 2004 and 2005 was typically above-average (Figure 4.2.f and Figure 4.5.d) and was associated with higher than normal biomass (Figure 4.2.d and Figure 4.5.b) and SST (Figure 4.2.b and Figure 4.3.b), and also corresponded to a prolonged period of El Niño conditions (Figure 4.4.). Similarly, the findings of Behrenfeld et al. (2006) showed a strong correspondence between primary production and the variations in ENSO cycles.

In the St. Helena Bay region, Weeks et al. (2006) observed a trend toward increased chlorophyll concentrations in 2002 and 2003. Using Reynolds SST for the period 1985 to 2005, Rouault (2007) observed significant warming in the northern and southern boundary regions of the Benguela, but noted a cooling trend close inshore in the southern Benguela. Exploring the trends in meridional wind, SST and chlorophyll in the major eastern boundary upwelling systems, Demarcq (2009) observed that in the southern Benguela, SST increased by $0.1\text{ }^{\circ}\text{C decade}^{-1}$, while upwelling-favourable winds showed an increase of $0.36\text{ m s}^{-1}\text{ decade}^{-1}$, and chlorophyll decreased by $0.47\text{ mg m}^{-3}\text{ decade}^{-1}$. Although no significant cooling trend was observed in the southern Benguela during this study, Belkin (2009) predicted that cooling of upwelling systems may likely occur as a result of increased upwelling-favourable winds due to enhanced land-ocean pressure gradients developing from increased atmospheric CO_2 over the land.

Demarcq (2009) noted that trends in chlorophyll *a* were more significantly related to trends in upwelling-favourable winds, than to the trends observed in SST. It has also been noted that PP estimates from biomass-based models, such as the VGPM, produced extremely similar trends to those observed in chlorophyll. It was thus expected that the time series of PP in the southern Benguela region would reveal patterns of variability which closely matched those observed in chlorophyll concentrations, with higher PP correlated with higher chla, and vice versa. While higher PP coincided with higher chla during most months of the timeseries, there were months where a poor correlation was observed, but there was no regular pattern to this mismatch (Figure 4.2d,f and Figure 4.5b,d).

In conclusion, the seasonal variability in SST, chla, and PP, is inconsistent with observations in some investigations (e.g. Carr and Kearns 2003), but compares well to the findings of Demarcq et al. (2007), Thomas et al. (2003) and Weeks et al. (2006). Although significant changes in phytoplankton may have occurred in recent decades (Reid et al. 1998), the seasonal and spatial patterns of primary production have been shown to be consistent at global scales (Conkright and Gregg 2003), as was the case in this study. Over the long term, temporal variations in primary production were observed to be larger than the spatial differences. This was opposite to the findings of Chassot et al. (2010), who showed that spatial variations were generally greater.

Interannual variations in SST described here correspond well to those noted by Demarcq (2009) and Hardman-Mountford et al. (2003). Similar to the findings of Behrenfeld et al. 2006, the long term variations in SST, chlorophyll *a*, and PP were linked to variations in

climate, with increasing temperatures related to a decrease in phytoplankton biomass and PP, and vice versa. These variations are likely to have a significant impact on ecosystem functioning by driving changes in the physiological state of phytoplankton (Behrenfeld et al. 2006), taxonomic composition of zooplankton populations (Huggett et al. 2009), and ultimately influencing the trophic structure of pelagic food webs (Boyd and Doney 2002, Fréon et al. 2009, Roy et al. 2007) by limiting the average and maximum fisheries catches over short and long time scales (Chassot et al. 2010). However, this pattern is not straightforward for the southern Benguela and may be complicated by regionally-driven events, as was observed during the summer of 1999/2000 (Roy et al. 2001).

University of Cape Town

Chapter 5 – Discussion

Phytoplankton Production in the Southern Benguela

Spatio-temporal variability in the major eastern boundary upwelling ecosystems is primarily driven by alongshore equatorward winds which result in the upwelling of cold, nutrient-rich water into the euphotic zone. Average upwelling-favourable winds are weakest in the Humboldt, while the strongest winds are observed in the California, Northwest Africa, and Benguela upwelling systems. Despite the prevailing wind regimes, upwelling is strongest in the Humboldt, while slightly less upwelling is observed off NW Africa and in the Benguela, and the lowest occurs off California (Aristegui et al. 2009, Checkley and Barth 2009, Hutchings et al. 2009, Montecino and Lange 2009).

Subsurface mean nitrate concentrations are greatest off NW Africa, while slightly lower concentrations are found in the Benguela and California systems, and the lowest occurs in the Humboldt. However, nitrate supply to the euphotic zone is highest in the Humboldt, with lower values observed off NW Africa and in the Benguela, while nitrate supply off California is significantly lower (Chavez and Messié 2009, Messié et al. 2009). This continual supply of nitrate to the euphotic zone fuels biological productivity and results in elevated levels of phytoplankton biomass and primary production in coastal upwelling ecosystems.

Satellite-derived estimates of phytoplankton biomass and PP are highest off NW Africa, slightly lower in the Benguela and the Humboldt, and significantly lower off California (Carr 2002, Chavez and Messié 2009). In situ ^{14}C -based estimates suggest that the highest rates of PP occur in the Benguela (up to $12.3 \text{ g C m}^{-2} \text{ d}^{-1}$), with slightly lower rates observed in the Humboldt (up to $9.3 \text{ g C m}^{-2} \text{ d}^{-1}$) and NW Africa (up to $5.3 \text{ g C m}^{-2} \text{ d}^{-1}$), while the lowest rates (up to $3 \text{ g C m}^{-2} \text{ d}^{-1}$) are found off California (Aguirre-Hernández et al. 2004, Daneri et al. 2000, Montecino et al. 2004, Tilstone et al. 2003). The discrepancy between satellite and in situ biomass and PP off NW Africa is probably due to satellite estimates being biased by the inability of the atmospheric correction algorithm to compensate for the occurrence of aeolian dust from the Sahara (Carr 2002).

Relatively infrequent measurements of PP have been made in the Benguela and the majority of these have been estimated through traditional on-deck incubations. These studies have shown that PP typically ranges between $0.14 - 8.83 \text{ g C m}^{-2} \text{ d}^{-1}$ throughout the northern and southern Benguela ecosystems (Barlow et al. 2009, Brown and Field 1986, Brown et al. 1991, Tilstone et al. 2009). Photosynthesis-Irradiance experiments have been conducted in a very localised area off Lambert's Bay in order to assess PP estimates made from natural fluorescence and show PP rates as high as $12.3 \text{ g C m}^{-2} \text{ d}^{-1}$ during a red tide event (Mitchell-Innes et al. 2000).

The current study presents the first shelf-wide investigation of the spatial and temporal variations in PP and physiology across the continental shelf of the southern Benguela using photosynthesis-irradiance experiments. The physiological mechanisms governing these changes and the effects of environmental variables on phytoplankton photosynthesis were also explored. Seasonal variability was evident, with higher PP observed during mid-spring, ranging from $0.71 - 6.98 \text{ g C m}^{-2} \text{ d}^{-1}$, and lower in late autumn, varying from $0.70 - 3.35 \text{ g C m}^{-2} \text{ d}^{-1}$ (Figure 2.10.).

Cross-shelf differences were observed, with low biomass and PP in newly upwelled water close to the coast, elevated biomass and PP in the mid-shelf region, and lower values found at and beyond the shelf edge (Figures 2.4.a,b; 2.5.a,b, and 2.10). Similar differences were described by Brown and Field (1986) and Brown et al. (1991). Latitudinal variations indicated higher biomass and PP within the St. Helena Bay region, most likely due to the enhanced retention of upwelled water in this region (Lett et al. 2006). South of the Cape Peninsula, the lower biomass and PP were related to the influence of oligotrophic Agulhas current water (Figure 2.6; 2.7.a. and 2.10.).

In general, lower PP was associated with low photosynthetic activity, while elevated activity resulted in higher PP. Exceptions to this pattern were noted where reasonably high PP was associated with low activity, suggesting that the biomass had possibly reached a stationary phase of growth (Figures 2.14. and 2.15.). It has been suggested that variations in photosynthesis can be explained by environmental influences such as nutrient availability (Platt et al. 1992, Sathyendranath et al. 1996) and the intensity and spectral quality of light (Falkowski et al. 1981, Kyewalyanga et al. 1998). Although subsurface chlorophyll maxima were observed at numerous stations, the highest photosynthesis rates were always observed at the surface and declined sharply with depth.

The general correspondence between integrated biomass and PP (Figure 2.10.) indicated that phytoplankton biomass levels contributed to the spatial variability in PP. However, the mismatch between chlorophyll *a* and photosynthesis profiles suggested that phytoplankton biomass levels were not responsible for the vertical variations in PP (Figure 2.14.). The pattern of decreasing P_s^B and E_k with increasing z/z_{eu} (Figure 2.17.) indicated that these photosynthetic parameters were the most important in determining the integrated PP, and that irradiance was the primary environmental variable controlling the vertical variations in PP. Since diatoms were so prominent in this study (Figure 2.11.), it was difficult to relate variations in PP to changes in the taxonomic composition of phytoplankton, and thus it was concluded that the variations were due to differences in phytoplankton physiology in response to the prevailing environmental conditions. However, revealing the environmental forcing responsible for the variations in biological processes is very challenging.

No clear relationship was observed between α^B and environmental variables (Figures 2.16.a,d. and 2.17.a.). This was in contrast to previous studies that reported a significant increase in α^B with a decrease in available light (Barlow et al. 2010, Uitz et al. 2008). Phytoplankton adaptation to varied environmental conditions was characterised by increased P_s^B and E_k under elevated temperatures and irradiance (Figures 2.16.b,c. and 2.17.b,c.). It was noted that the highest biomass and PP was observed within a temperature range of 12 – 16 °C. The pattern of elevated P_s^B and E_k at low nutrient concentrations simply reflected the uptake of nutrients by the phytoplankton. Similar patterns have been reported by other authors (Barlow et al. 2010, Bouman et al. 2005, Claustre et al. 2005).

Due to the scarcity of in situ PP measurements, interannual differences and longer term changes in the southern Benguela can only be assessed through the use of ocean colour data. Several comprehensive global and regional comparison and validation studies of numerous satellite PP model estimates have been conducted. While earlier investigations concluded that model estimates varied substantially in terms of complexity, performance and accuracy, more recent studies have shown that there is no significant improvement of PP with an increase in model complexity. The simplest models produced similar results to some of the most complex models and the models that showed the greatest skill varied depending on the method of skill assessment used (Campbell et al. 2002, Carr et al. 2006, Friedrichs et al. 2009, Saba et al. 2010a, b).

In order to address how well ocean colour model estimates compared with each other and with in situ PP, this study compared the output from three satellite algorithms to in situ PP measurements in the southern Benguela ecosystem, and examined the factors responsible for the differences in PP estimates. The models were all forced with in situ data to test their performance and accuracy within the region and it was concluded that the differences between measured and modelled PP were not statistically significant, and that the models were able to capture the seasonal differences in PP between October and May (Figures 3.1 and 3.2). However, it is possible that the insignificant difference observed between measured and modelled PP may be a consequence of the relatively small dataset used.

The Eppley and Eppley-VGPM produced similar results, while the PP estimates obtained from the VGPM were substantially different. Since the Eppley model is based solely on chlorophyll concentration, it is interesting that it produced comparable results to the Eppley-VGPM, which incorporates a measure of physiological status. Results obtained in Chapter 2 indicated that similar values of chlorophyll concentration can yield different PP values depending on the dominant phytoplankton group, physiological state of the phytoplankton, as well as prevailing light and nutrient conditions, as observed in other studies (Bouman et al. 2005, Tilstone et al. 2003).

It was also noted that model accuracy varied between October and May, with the Eppley and Eppley-VGPM models generally underestimating PP during October, while the VGPM compared well to in situ measurements. During May, all the models overestimated PP, with the VGPM yielding the largest overestimates (Figure 3.3.). The parameterisation of P_{opt}^B was found to be a primary cause of the differences between measured and modelled PP. Other authors have previously attributed the variability in PP in the Atlantic Ocean to changes in the chlorophyll specific maximum photosynthetic rate (Behrenfeld et al. 2002, Marañón et al. 2000, Marañón and Holligan 1999).

The exponential temperature-dependent description of P_{opt}^B used in the Eppley-VGPM yielded photosynthesis rates that were significantly lower than those produced by the VGPM polynomial relationship (Table 3.1.). VGPM P_{opt}^B values were generally more similar to the measured P_s^B during October, while the Eppley-VGPM P_{opt}^B was significantly lower than the measured values. A likely reason for this difference may be that most of the data used to construct the polynomial temperature relationship originated from eutrophic regions in the Northwest Atlantic Ocean where phytoplankton photo-physiology depends

strongly on temperature (Behrenfeld and Falkowski 1997b). However, during May, the reverse was true, with the Eppley-VGPM producing more realistic P_{opt}^B values.

The exponential parameterisation of P_{opt}^B (Eppley et al. 1985) has previously been shown to perform well in eutrophic regions (Bouman et al. 2005). The results obtained in Chapter 3 suggest that the relationship between P_{opt}^B and temperature may be regionally specific and may vary seasonally in the southern Benguela. Although attempts have been made to improve the estimation of P_{opt}^B (Behrenfeld et al. 2002), it is not possible to routinely apply these improvements to satellite data since appropriate spatial and temporal distributions of mixed-layer depth and nutrients are not readily available.

Since differences between the measured and modelled PP were primarily due to the construction and the assumptions made by the models, it could be expected that the models would perform in a similar manner when applied to satellite data. The models were expected to perform better during October than May, but the comparison of satellite with in situ PP (Figure 3.4.) showed the opposite pattern, with smaller differences being observed during May.

A comparison of the input variables (chlorophyll *a*, SST, PAR) revealed that differences between satellite and in situ chlorophyll concentrations were responsible for large disparities observed between satellite and in situ PP (Table 3.2.). This discrepancy may be due to the lower spatial resolution of satellite data and the patchiness of phytoplankton distributions in the southern Benguela. The observed differences may also result from the standard atmospheric corrections, bio-optical algorithms and processing parameters not being optimal for application in the highly productive waters of the Benguela ecosystem (Weeks et al. 2006).

Despite the limitations identified in Chapter 3, the VGPM was found to be useful for investigating seasonal and interannual variations over larger scales. Chapter 4 examined the seasonal and interannual signals of SST, chlorophyll, and PP in the southern Benguela over a 13-year period and the variations were observed to be consistent with the findings of other authors (Demarcq et al. 2007, Thomas et al. 2003, Weeks et al. 2006). Summer temperatures were highest throughout the system from 2001 to 2003, followed by a clear decreasing trend until 2006 when a prolonged cool period was observed throughout the

region, after which higher temperatures were evident (Figures 4.2a and 4.3a). The observed cooling corresponded to the trend described by Rouault (2007).

The seasonality in chlorophyll concentrations and PP was found to be generally in phase with the maximum upwelling periods during spring and summer (Hardman-Mountford et al. 2003, Thomas et al. 2001). The seasonal peak in chlorophyll levels varied from south to north, with elevated levels observed off the Cape Peninsula from spring to autumn, during autumn in the St. Helena Bay region, and during spring and autumn off the Namaqua shelf. Maximum PP was observed during spring and summer throughout the region, suggesting that although PP levels are influenced by peaks in chlorophyll, they appear to be more closely related to the seasonal variations in available irradiance, which are maximum during spring and summer and lower during autumn and winter.

Throughout the time series, PP typically ranged from $0.5 - 6 \text{ g C m}^{-2} \text{ d}^{-1}$ with the highest rates consistently found in the St. Helena Bay region due to the enhanced retention in that area, while the lowest rates were observed off the Cape Peninsula, related to the narrow shelf and influence of less productive, warmer water beyond the boundary of the upwelling zone (Shannon and Nelson 1996, Shillington 1998, Weeks et al. 2006). Considerable interannual variations were evident, with chlorophyll concentrations decreasing steadily from 1997 to 2002, followed by a steady increase until 2005, after which higher levels were maintained for the remainder of the time series. A clear decreasing trend in the summer maximum PP was observed from 1997 to 2003 and again from 2007 to 2010, while summer maximum PP was higher during 2004 and 2005.

In general, above-average biomass and PP corresponded to negative SST anomalies that tended to be associated with La Niña conditions. In contrast, positive SST anomalies associated with El Niño conditions generally coincided with below-average biomass and PP. Some exceptions to this pattern occurred during the considerable El Niño event of 1997/1998 when SST anomalies were negative, and phytoplankton biomass and PP were above-average throughout the southern Benguela, with the maximum observed off the Namaqua shelf (Roy et al. 2001). The warm event during December 1999 unusually occurred during a period of prolonged La Niña conditions, and was followed by a period of intense upwelling during late summer (Roy et al. 2001). This warming was associated with anomalously lower biomass and PP throughout the region, followed by elevated PP related to the subsequent prolonged upwelling activity (Hutchings et al. 1998, Penven et al. 2000).

The longer term variations in SST, chlorophyll, and PP appear to be linked to variations in climate, with an increase in temperature related to a decrease in phytoplankton biomass and PP, and vice versa. Similar variations were described by Behrenfeld et al. (2006) and seem to be generally related to ENSO events. However, this correlation is not straightforward in the southern Benguela, and may result from the Benguela ecosystem being less affected by basin-scale variations and more strongly influenced by smaller scale local physical forcing (Chavez & Messié 2009, Roy et al. 2001). It may also be related to the phase shift in the nature of El Niño events reported by Ashok and Yamagata (2009).

Overall, the seasonal, interannual and latitudinal patterns of phytoplankton biomass and PP described in this study corresponded well to previous observations (Chavez & Messié 2009, Demarcq et al. 2007, Thomas et al. 2003, Tilstone et al. 2009). Unlike previous investigations, which described these variations over much larger areas, the current study focussed solely on the southern Benguela ecosystem, and illustrated sub-regional variability that appeared to correspond to variations in zooplankton biomass distributions (Huggett et al. 2009) and variations in pelagic fish recruitment (Hutchings et al. 1998, Penven et al. 2000). However, due to the limited length of the time series, no conclusions could be made regarding decadal scale variations.

The results presented here are in contrast to the findings of Sarmiento et al. (2004) who concluded that increasing temperatures would lead to increased chlorophyll concentrations and PP, and Aiken et al. (2008) who found no significant trend in a decadal assessment of in situ chlorophyll in the Atlantic Ocean. Aiken et al. (2008) also concluded that small variations in chlorophyll may be related to multi-variate ENSO events. However, as shown by Behrenfeld et al. (2006), changes in the temperature and stratification in the upper ocean influences the availability of nutrients in the surface layer, leading the changes in PP, with increasing temperatures related to decreasing PP. These changes are likely to have significant impacts on the functioning of ecosystems by driving variations in the physiological state of phytoplankton, taxonomic composition of zooplankton populations, and ultimately influencing the trophic structure of pelagic food webs (Behrenfeld et al. 2006, Chassot et al. 2010, Huggett et al. 2009, Roy et al. 2007).

Throughout the past few decades, significant improvements in the understanding of the variations in phytoplankton biomass and primary production have taken place globally. Increasing interest in quantifying the role of the oceans in regulating global climate has led to the formulation and development of numerous models to estimate photosynthetic carbon

fixation by marine phytoplankton. Due to the drawbacks in modelling the values of $\mathbf{P}_{\text{opt}}^{\text{B}}$, the VGPM may not be the most accurate model, but it is widely used to estimate PP from satellite data because it can be easily implemented and, as shown in this study, provides useful details on seasonal and interannual changes (Chavez and Messié 2009, Kahru and Mitchell 2002). Tilstone et al. (2009) suggested that semi- and fully analytical models provide better estimates of PP as they are not affected by regional biases, while other authors have shown that correctly parameterised non-spectral models are able to produce similarly accurate PP estimates (Bouman et al. 2005, Kyewalyanga et al. 1992, 2007).

Further research to determine a more optimal parameterisation of $\mathbf{P}_{\text{opt}}^{\text{B}}$ in the southern Benguela, as well as regional optimisation of the atmospheric corrections applied to ocean colour data, bio-optical algorithms and processing parameters, would improve satellite biomass and PP estimates. As more data becomes available it is essential to conduct further regional and sub-regional comparison and validation exercises in order to further improve satellite estimates and understand the variability of phytoplankton biomass and PP in the Benguela ecosystem.

Bibliography

- Aiken J, Hardman-Mountford NJ, Barlow R, Fishwick J, Hirata T, Smyth T (2008) Functional links between bioenergetics and bio-optical traits of phytoplankton taxonomic groups: an overarching hypothesis with application for ocean colour remote sensing. *Journal of Plankton Research* 30: 165 – 181
- Aiken J, Woodward MS, Robinson C, Rees A, Serret P, Bowie A, Woodd-Walker R, Pilgrim D, Holligan P, Suggett D, Hooker S, Dempsey C, Brown J, Maritorea S, Barlow R, Lucas M, Tilstone G, Teira E (1998) Atlantic Meridional Transect (AMT) 6 cruise report, Cape Town to Grimsby, 14 May to 16 June 1998
- Aguirre-Hernández E, Gaxiola-Castro G, Nájera-Martínez S, Baumgartner T, Kahru M, Mitchell BG (2004) Phytoplankton absorption, photosynthetic parameters, and primary production off Baja California: summer and autumn 1998. *Deep-Sea Research II* 51: 799 - 816
- Anderson D, Glibert P, Burkholder J (2002) Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. *Estuaries* 25: 704 – 726
- Andre JM (1992) Ocean colour remote sensing and the subsurface vertical structure of phytoplankton pigments. *Deep-Sea Research* 39: 763 – 779
- Andrews WRH and Hutchings L (1980) Upwelling in the Southern Benguela Current. *Progress in Oceanography* 9(1): 1 – 81
- Anning T, MacIntyre HL, Pratt SM, Sammes PJ, Gibb S, Geider RJ (2000) Photoacclimation in the marine diatom *Skeletonema costatum*. *Limnology and Oceanography* 45(8): 1807 – 1817
- Antoine D, Andre JM, Morel A (1996) Oceanic primary production. 2. Estimation at global scale from satellite (coastal zone color scanner) chlorophyll. *Global Biogeochemical Cycles* 10: 57 – 69
- Antoine D, Morel A, Gordon HR, Banzon VF, Evans RH (2005) Bridging ocean colour observations of the 1980s and 2000s in search of long-term trends. *Journal of Geophysical Research* 110: C06009, doi:10.1029/2004JC002620
- Arbones B, Figueiras FG, Varela R (2000) Action spectrum and maximum quantum yield of carbon fixation in natural phytoplankton populations: implications for primary production estimates in the ocean. *Journal of Marine Systems* 26: 97 – 114
- Arístegui J, Barton ED, Álvarez-Salgado XA, Santos AMP, Figueiras FG, Kifani S, Hernández-León S, Mason A, Machú E, Demarcq H (2009) Sub-regional ecosystem variability in the Canary Current upwelling. *Progress in Oceanography* 83: 33 – 48
- Ashok K, Yamagata T (2009) Climate Change: The El Niño with a difference. *Nature* 461: 481 – 484
- Babin M, Morel A, Claustre H, Bricaud A, Kolber Z, Falkowski PG (1996) Nitrogen- and irradiance-dependant variations of maximum quantum yield of carbon fixation in eutrophic, mesotrophic and oligotrophic marine systems. *Deep-Sea Research* 43: 1241 – 1272
- Babin M, Morel A, Gagnon R (1994) An incubator designed for extensive and sensitive measurements of phytoplankton photosynthetic parameters. *Limnology and Oceanography* 39(3): 694 – 702
- Bailey GW and Chapman P (1991) Short-term variability during an anchor study in the southern Benguela upwelling system: Chemical and physical oceanography. *Progress in Oceanography* 28: 1 – 37
- Baker KS, Smith RC, Bidigare RR, Prézelin BB, Lewis MR (1990) A bio-optical model for the prediction of phytoplankton productivity during Fronts '85 and Watercolors '88. *Eos* 71: 147
- Balkanski Y, Monfray P, Battle M, Heimann M (1999) Ocean primary production derived from satellite data: An evaluation with atmospheric oxygen measurements. *Global Biogeochemical Cycles* 13: 257 – 271
- Baltar F, Arístegui J, Montero MF, Espino M, Gasol JM, Herndl GJ (2009) Mesoscale variability modulates seasonal changes in the trophic structure of nano- and pico-plankton communities across the NW Africa-Canary Islands transition zone. *Progress in Oceanography* 83 (1-4): 180 – 188

- Banase K (1976) Rates of growth, respiration and photosynthesis of unicellular algae as related to cell size – a review. *Journal of Phycology* 12: 135 – 140
- Banase K (1982) Cell volumes, maximum growth rates of unicellular algae and ciliates, the role of ciliates in the marine pelagial. *Limnology and Oceanography* 27: 1059 – 1071
- Banase K (1992) Grazing, temporal changes of phytoplankton concentrations, and the microbial loop in the open sea. In: Falkowski PG, Woodhead AD (eds) *Primary productivity and biogeochemical cycles in the sea*. Plenum, New York, p 409 – 440
- Barber RT, Chavez FP (1983) Biological consequences of El Niño. *Science* 222: 1203 – 1210
- Barber RT, Hilting AK (2002) History of the study of plankton productivity. In: Williams P, LeB, Thomas DN, Reynolds C (eds) *Phytoplankton productivity: Carbon assimilation in marine and freshwater ecosystems*. Blackwell Science, Oxford, pp. 16 – 43
- Barber RT and Smith WO Jr (1980) The role of circulation, sinking and vertical migration in physical sorting of phytoplankton in the upwelling center at 15°S. In: FA Richards (ed) *Coastal upwelling*. American Geophysical Union, Washington DC, p 366 – 371
- Barlow RG (1982a) Phytoplankton ecology in the southern Benguela current. I. Biogeochemical composition. *Journal of Experimental Marine Biology and Ecology* 63(3): 209 – 227
- Barlow RG (1982b) Phytoplankton ecology in the southern Benguela current. II. Carbon assimilation patterns. *Journal of Experimental Marine Biology and Ecology* 63(3): 229 – 237
- Barlow RG (1982c) Phytoplankton ecology in the southern Benguela current. III. Dynamics of a bloom. *Journal of Experimental Marine Biology and Ecology* 63(3): 239 – 248
- Barlow RG (1984a) Dynamics of the decline of a phytoplankton bloom after an upwelling event. *Marine Ecology Progress Series* 16: 121 – 126
- Barlow RG (1984b) Physiological responses of phytoplankton to turbulent and stable environments in an upwelling region. *Journal of Plankton Research* 6: 385 – 397
- Barlow RG, Aiken J, Sessions HE, Lavender S, Mantel J (2001) Phytoplankton pigment, absorption and ocean colour characteristics in the southern Benguela ecosystem. *South African Journal of Science* 97: 230 – 238
- Barlow RG, Cummings DG, Gibb SW (1997) Improved resolution of mono- and divinyl chlorophylls a and b and zeaxanthin and lutein in phytoplankton extracts using reverse-phase C-8 HPLC. *Marine Ecology Progress Series* 161: 303 – 307
- Barlow RG, Kyewalyanga M, Sessions H, van den Berg M, Morris T (2008) Phytoplankton pigments, functional types, and absorption properties in the Delagoa and Natal Bights of the Agulhas ecosystem. *Estuarine, Coastal and Shelf Science* 80: 201 – 211
- Barlow RG, Lamont T, Kyewalyanga M, Sessions H, Morris T (2010) Phytoplankton production and physiological adaptation on the southeastern shelf of the Agulhas ecosystem. *Continental Shelf Research* 30: 1472 – 1486
- Barlow RG, Lamont T, Mitchell-Innes B, Lucas M, Thomalla S (2009) Primary Production in the Benguela ecosystem, 1999 – 2002. *African Journal of Marine Science* 31(1): 97 – 101
- Barlow RG, Louw D, Balarin M, Alheit J (2006) Pigment signatures of phytoplankton composition in the northern Benguela ecosystem during spring. *African Journal of Marine Science* 28: 479 – 491
- Barlow RG, Sessions H, Balarin M, Weeks S, Whittle C, Hutchings L (2005) Seasonal variation in phytoplankton in the southern Benguela: pigment indices and ocean colour. *African Journal of Marine Science* 27 (1): 275 – 287
- Barlow RG, Stuart V, Lutz V, Sessions H, Sathyendranath S, Platt T, Kyewalyanga M, Clementson L, Fukasawa M, Watanabe S, Devred E (2007) Seasonal pigment patterns of surface phytoplankton in the subtropical southern hemisphere. *Deep-Sea Research I* 54: 1687 – 1703

- Basterretxea G, Arístegui J (2000) Mesoscale variability in phytoplankton biomass distribution and photosynthetic parameters in the Canary – NW African coastal transition zone. *Marine Ecology Progress Series* 197: 27 – 40
- Behrenfeld MJ, Falkowski PG (1997a) A consumer's guide to phytoplankton primary productivity models. *Limnology and Oceanography* 42: 1479 – 1491
- Behrenfeld MJ, Falkowski PG (1997b) Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and Oceanography* 42: 1 – 20
- Behrenfeld MJ, O'Malley RT, Siegal DA, McClain CR, Sarmiento JL, Feldman GC, Milligan AJ, Falkowski PG, Letelier RM, Boss ES (2006) Climate-driven trends in contemporary ocean productivity. *Nature* 444: 752 – 755
- Behrenfeld MJ, Randerson JT, McClain CR, Feldman GC, Los SO, Compton JT, Falkowski PG, Field CB, Frouin R, Esaias WE, Kolber DD, Pollack NH (2001) Biospheric primary production during an ENSO transition. *Science* 291: 2594 – 2597
- Belkin IM (2009) Rapid warming of Large Marine Ecosystems. *Progress in Oceanography* 81: 207 – 213
- Bender M, Sowers T, Labeyrie L (1994) The Dole effect and its variations during the last 130 000 years as measured in the VOSTOK ice core. *Global Biogeochemical Cycles* 8: 363 – 376
- Berger WH, Smetacek VS, Wefer G (1989) Ocean Productivity and Paleoproductivity – An Overview. In: Berger WH, Smetacek V, Wefer G (eds) *Productivity of the Ocean: Present and Past*. John Wiley and Sons, Chichester, p 1 – 34
- Berger WH (1989) Global maps of primary productivity. In: Berger WH, Smetacek VS, Wefer G (eds.), *Productivity of the Ocean: Present and Past*. John Wiley and Sons, Chichester, pp. 429 – 455
- Bianchi AA, Bianucci L, Piola AR, Pino DR, Schloss I, Poisson A, Balestrini CF (2005) Vertical stratification and air-sea CO₂ fluxes in the Patagonian shelf. *Journal of Geophysical Research* 110, C07003. doi: 10.1029/2004JC002488
- Bidigare RR, Smith RC, Baker KS, Marra J (1987) Oceanic pigment production estimates from measurements of spectral irradiance and pigment concentrations. *Global Biogeochemical Cycles* 1: 171 – 186
- Blasco D, Estrada M, Jones B (1980) Relations between the phytoplankton distribution and composition and the hydrography in the upwelling region near Cabo Corbeiro. *Deep-Sea Research* 27: 799 – 821
- Blasco D, Packard TT, Garfield PC (1982) Size dependence of growth rate, respiratory electron transport system activity, and chemical composition in marine diatoms in the laboratory. *Journal of Phycology* 18: 58 – 63
- Botes L, Sym SD, Pitcher GC (2003) *Karenia cristata* sp. Nov. and *Karenia bicuneiformis* sp. Nov. (Gymnodiniales, Dinophyceae): two new *Karenia* species from the South African coast. *Phycologia* 42: 563 – 571
- Boyd PW, Doney SC (2002) Modelling regional responses by marine pelagic ecosystems to global climate change. *Geophysical Research Letters* 29, 1806, doi:10.1029/2001GLO14130
- Bouman HA, Platt T, Kraay GW, Sathyendranath S, Irwin BD (2000) Bio-optical properties of the subtropical North Atlantic. I. Vertical Variability. *Marine Ecology Progress Series* 200: 3 – 18
- Bouman HA, Platt T, Sathyendranath S, Stuart V (2005) Dependence of light-saturated photosynthesis on temperature and community structure. *Deep-Sea Research I* 52: 1248 – 1299
- Bricaud A, Claustre H, Ras J, Oubelkheir K (2004) Natural variability of phytoplankton absorption in oceanic waters: influence of the size structure of algal populations. *Journal of Geophysical Research* 109: C11010
- Bricaud A and Stramski D (1990) Spectral absorption coefficients of living phytoplankton and nonalgal biogenous matter: a comparison between the Peru upwelling area and the Sargasso Sea. *Limnology and Oceanography* 35: 562 – 582

- Brink KH, Jones BH, Van Leer JC, Mooers CNK, Stuart DW, Stevenson MR, Dugdale RC, Heburn GW (1980) Physical and biological structure and variability in an upwelling center off Peru near 15°S during March 1977. In: FA Richards (ed) Coastal upwelling. American Geophysical Union, Washington DC, p 473 – 495
- Brown PC (1984) Primary productivity at two contrasting nearshore sites in the southern Benguela upwelling region. *South African Journal of Marine Science* 2: 205 – 215
- Brown PC and Field JG (1985) Diel variation in production rates of natural phytoplankton populations in the southern Benguela upwelling region. *Botanica Marina* 28: 201 – 208
- Brown PC and Field JG (1986) Factors limiting phytoplankton production in a nearshore upwelling area. *Journal of Plankton Research* 8(1): 55 – 68
- Brown PC and Henry JL (1985) Phytoplankton production, chlorophyll a and light penetration in the southern Benguela region during the period between 1977 and 1980. In: LV Shannon (ed) South African Ocean Colour and Upwelling Experiment. Sea Fisheries Research Institute, Cape Town, p 211 – 218
- Brown PC and Hutchings L (1987a) The development and decline of phytoplankton blooms in the southern Benguela upwelling system. 1. Drogue movements, hydrography and bloom development. In: The Benguela and Comparable Ecosystems. Payne AIL, Gulland JA, Brink KH (eds) *South African Journal of Marine Science* 5: 357 – 391
- Brown PC and Hutchings L (1987b) The development and decline of phytoplankton blooms in the southern Benguela upwelling system. 2. Nutrient relationships. In: The Benguela and Comparable Ecosystems. Payne AIL, Gulland JA, Brink KH (eds) *South African Journal of Marine Science* 5: 393 – 409
- Brown PC, Painting SJ, Cochrane KL (1991) Estimates of phytoplankton and bacterial biomass and production in the northern and southern Benguela ecosystems. *South African Journal of Marine Science* 11: 537 – 564
- Brundrit GB, Shannon LV (1989) Storms & the Agulhas Current: a glimpse of the future. *South African Journal of Marine Science* 84: 584 – 586
- Caddy JF, Cochrane KL (2001) A review of fisheries management: past and present and some future perspectives for the third millennium. *Ocean Coastal Management* 44 (9-10): 653 – 682
- Campbell J, Antoine D, Armstrong R, Arrigo K, Balch W, Barber R, Behrenfeld M, Bidigare R, Bishop J, Carr M-E, Esaias W, Falkowski P, Hoepffner N, Iverson R, Kiefer D, Lohrenz S, Marra J, Morel A, Ryan J, Vedernikov V, Waters K, Yentsch C, Yoder J (2002) Comparison of algorithms for estimating ocean primary production from surface chlorophyll, temperature, and irradiance. *Global Biogeochemical Cycles* 16 (3), doi: 10.1029/2001GB001444
- Carr M-E (2002) Estimation of potential productivity in Eastern Boundary Currents using remote sensing. *Deep-Sea Research II* 49: 58 – 80
- Carr M-E, Friedrichs MAM, Schmeltz M, Aita MN, Antoine D, Arrigo KR, Asanuma I, Aumont O, Barber R, Behrenfeld M, Bidigare R, Buitenhuis ET, Campbell J, Ciotti A, Dierssen H, Dowell M, Dunne J, Esaias W, Gentili B, Gregg W, Groom S, Hoepffner N, Ishizaka J, Kameda T, Le Quéré C, Lohrenz S, Marra J, Mélin F, Moore K, Morel A, Reddy TE, Ryan J, Scardi M, Smyth T, Turpie K, Tilstone G, Waters K, Yamanaka Y (2006) A comparison of global estimates of marine primary production from ocean colour. *Deep-Sea Research II* 53: 741 – 770
- Carr M-E and Kearns EJ (2003) Production regimes in four Eastern Boundary Current systems. *Deep-Sea Research II* 50: 3199 – 3221
- Cermeño P, Marañón E, Pérez V, Serret P, Fernández E, Castro CG (2006) Phytoplankton size structure and primary production in a highly dynamic coastal ecosystem (Ría de Vigo, NW-Spain): Seasonal and short-time scale variability. *Estuarine Coastal and Shelf Science* 67: 251 – 266
- Cermeño P, Estévez-Blanco P, Marañón E, Fernández E (2005a) Maximum photosynthetic efficiency of size-fractionated phytoplankton assessed by ¹⁴C uptake and fast repetition rate fluorometry. *Limnology and Oceanography* 50: 1438 – 1446

- Cermeño P, Maraño E, Rodríguez J, Fernández E (2005b) Large-sized phytoplankton sustain higher carbon-specific photosynthesis than smaller cells in a coastal eutrophic system. *Marine Ecology Progress Series* 297: 51 – 60
- Chaigneau A, Eldin G, Dewitte B (2009) Eddy activity in the four major upwelling systems from satellite altimetry (1992 – 2007). *Progress in Oceanography* 83 (1-4): 117 – 123
- Chapman P, Shannon LV (1985) The Benguela Ecosystem. Part 2. Chemistry and related processes. *Oceanography and Marine Biology: An Annual Review* 23: 183 – 251
- Chassot E, Bonhommeau S, Dulvy NK, Mélin F, Watson R, Gascuel D, Le Pape O (2010) Global marine primary production constrains fisheries catches. *Ecology Letters* 13(4): 495 – 505
- Chavez FP, Messié M (2009) A comparison of Eastern Boundary Upwelling Ecosystems. *Progress in Oceanography* 83 (1-4): 80 – 96
- Chavez FP, Ryan J, Lluch-Cota SE, Niquen MC (2003) From anchovies to sardines and back: Multidecadal change in the Pacific ocean. *Science* 299: 217 – 221
- Checkley DM and Barth JA (2009) Patterns and processes in the California Current System. *Progress in Oceanography* 83: 49 – 64
- Chisholm SW (1992) Phytoplankton size. In: PG Falkowski, AD Woodhead (eds) *Primary productivity and biogeochemical cycles in the sea*. Plenum, New York, p 213 – 237
- Claustre H, Babin M, Merien D, Ras J, Prieur L (2005) Toward a taxon-specific parameterisation of bio-optical models of primary production: A case study in the North Atlantic. *Journal of Geophysical Research* 110, C07S12
- Coetzee J, van der Lingen CD, Hutchings L, Fairweather T (2008) Has the fishery contributed to a major shift in the distribution of South African Sardine? *ICES Journal of Marine Science* 65: 1676 – 1688
- Colberg F, Reason CJC (2007) Diagnosis of large scale South Atlantic modes that impact on the transboundary Benguela Current large marine ecosystem: investigating the potential for improved predictability and sustainable management. Final Report, BCLME project EV/LS/02/06
- Conkright M, Gregg W (2003) Comparison of global chlorophyll climatologies: In situ, CZCS, Blended in situ-CZCS and SeaWiFS. *International Journal of Remote Sensing* 24: 969 – 991
- Côté B and Platt T (1984) Utility of the light-saturation curve as an operational model for quantifying the effects of environmental conditions on phytoplankton photosynthesis. *Marine Ecology Progress Series* 18: 57 – 66
- Crawford RJM, Sabaros PS, Fairweather T, Underhill LG, Wolfaardt AC (2008) Implications for seabirds off South Africa of a long-term change in the distribution of sardine. *African Journal of Marine Science* 30(1): 177 – 184
- Crosbie ND, Furnas MJ (2001) Net growth rates of pico-cyanobacteria and nano-/microphytoplankton inhabiting shelf waters of the central (17°S) and southern (20°S) Great Barrier Reef. *Aquatic Microbial Ecology* 24: 209 – 224
- Cullen JJ and Lewis MR (1988) The kinetics of algal photoadaptation in the context of vertical mixing. *Journal of Plankton Research* 10: 1039 – 1063
- Cullen JJ, Yang X, MacIntyre HL (1992) Nutrient limitation in marine photosynthesis. In: Falkowski PG and Woodhead AD (Eds.) *Primary Productivity and Biogeochemical Cycles in the Sea*. Plenum Press, New York, pp. 69 – 88
- Demarcq H (2009) Trends in primary production, sea surface temperature and wind in upwelling systems (1998-2007). *Progress in Oceanography* 83: 376 – 385
- Demarcq H, Barlow RG, Hutchings L (2007) Application of a chlorophyll index derived from satellite data to investigate the variability of phytoplankton in the Benguela ecosystem. *African Journal of Marine Science* 29(2): 271 – 282

- Demarcq H, Barlow RG, Shillington FA (2003) Climatology and variability of sea surface temperature and surface chlorophyll in the Benguela and Agulhas ecosystems as observed by satellite imagery. *African Journal of Marine Science* 25: 363 – 372
- Demarcq H, Richardson AJ, Field JG (2008) Generalised model of primary production in the southern Benguela upwelling system. *Marine Ecology Progress Series* 354: 59 – 74
- Djavidnia S, Mélin F, Hoepffner N (2010) Comparison of global ocean colour data records. *Ocean Science* 6: 61 – 71
- Drapeau L, Pecquerie L, Fréon P, Shannon LJ (2004) Quantification and representation of potential spatial interactions in the southern Benguela ecosystem. *African Journal of Marine Science* 26: 141 – 159
- Dubinsky Z, Falkowski PG, Wyman K (1986) Light harvesting and utilisation by phytoplankton. *Plant and Cell Physiology* 27 (7): 1335 – 1349
- Duncombe Rae CM (1991) Agulhas retroreflection rings in the South Atlantic: an overview. *South African Journal of Marine Science* 11: 327 – 344
- Duncombe Rae CM, Shillington F, Agenbag J, Taunton-Clark J, Grundlingh M (1992) An Agulhas ring in the south Atlantic ocean and its interaction with the Benguela upwelling frontal system. *Deep-Sea Research* 39 (11-12): 2009 – 2027
- Duncombe Rae CM (2005) A demonstration of the hydrographic partition of the Benguela upwelling ecosystem at 26°40'S. *African Journal of Marine Science* 27(3): 617 – 628
- Eppley RW (1972) Temperature and phytoplankton growth in the sea. *Fishery Bulletin* 70(4): 1063 – 1085
- Eppley RW and Peterson BW (1979) Particulate organic matter flux and phytoplanktonic new production in the deep ocean. *Nature* 285: 677 – 680
- Eppley RW, Stewart E, Abbott MR, Heyman U (1985) Estimating ocean primary production from satellite chlorophyll. Introduction to regional differences and statistics for the Southern California Bight. *Journal of Plankton Research* 7: 57 – 70
- Falkowski PG (1980) Light-shade adaptation in marine phytoplankton. In: Falkowski PG and Woodhead AD (Eds.) *Primary Productivity in the Sea*. Plenum Press, New York, pp 99 – 120
- Falkowski PG (1981) Light-shade adaptation and assimilation numbers. *Journal of Plankton Research* 3: 203 – 216
- Falkowski PG, Barber RT, Smetacek V (1998) Biochemical controls and feedbacks on ocean primary production. *Science* 281: 200 – 206
- Falkowski PG, Raven JA (1997) *Aquatic Photosynthesis*. 1st Edition. Blackwell Science
- Falkowski PG and Wirick CD (1981) A simulation model of the effects of vertical mixing on primary productivity. *Marine Biology* 65: 69 – 75
- FAO Marine Resources Service, FRD (2005) *Review of the State of the World Marine Fishery Resources*. Rome. Fisheries Technical Paper 457
- Fasham MJR, Ducklow HW, McKelvie SM (1990) A nitrogen-based model of plankton dynamics in the oceanic mixed layer. *Journal of Marine Research* 48: 591 – 639
- Fawcett A, Pitcher GC, Bernard S, Cembella AD, Kudela RM (2007) Contrasting wind patterns and toxigenic phytoplankton in the southern Benguela upwelling system. *Marine Ecology Progress Series* 348: 19 – 31
- Fenchel T (1974) Intrinsic rates of natural increase: the relationship to body size. *Oecologia* 14: 317 – 326
- Fernández C, Fariás L, Alcaman ME (2009) Primary production and nitrogen regeneration processes in surface waters of the Peruvian upwelling system. *Progress in Oceanography* 83 (1-4): 159 – 168

- Field CB, Behrenfeld MJ, Randerson JT, Falkowski P (1998) Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science* 281: 237 – 240
- Field JG, Shillington FA (2006) Variability of the Benguela Current System. In: Robinson AR, Brink KH (eds) *The global coastal ocean, Interdisciplinary regional studies and syntheses. The Sea, Vol. 14, Part B.* Harvard University Press, p 833 – 860
- Figueiras FG, Arbones B, Estrada M (1999) Implications of bio-optical modelling of phytoplankton photosynthesis in Antarctic waters: Further evidence of no light limitation in the Bransfield Strait. *Limnology and Oceanography* 44 (7): 1599 – 1608
- Figueiras FG, Pitcher GC, Estrada M (2006) Harmful Algal Bloom dynamics in relation to physical processes. In: Graneli E, Turner JT (eds) *Ecology of Harmful Algae. Ecological Studies* 189. Springer-Verlag, Berlin, p 127 – 138
- Finkel ZV, Irwin AJ, Schofield O (2004) Resource limitation alters the $\frac{3}{4}$ size scaling of metabolic rates in phytoplankton. *Marine Ecology Progress Series* 273: 269 – 279
- Fischer G, Reuter C, Karakaş G, Nowald N, Wefer G (2009) Offshore advection of particles within the Cape Blanc filament, Mauritania: results from observational and modelling studies. *Progress in Oceanography* 83 (1-4): 322 – 330
- Frenette J-J, Demers S, Legendre L, Dodson J (1993) Lack of agreement among models for estimating the photosynthetic parameters. *Limnology and Oceanography* 38 (3): 679 – 687
- Frenette J-J, Vincent W, Legendre L, Nagata L (1996) Size dependent phytoplankton responses to atmospheric forcing in Lake Biwa. *Journal of Plankton Research* 18: 371 – 391
- Fréon P, Barange M, Aristegui J (2009) Eastern boundary upwelling ecosystems: integrative and comparative approaches. *Progress in Oceanography* 83: 1 – 14
- Fréon P, Drapeau L, David JHM, Morena AF, Leslie RW, Oosthuizen WH, Shannon LV, van der Lingen CD (2005) Spatialized ecosystem indicators in the southern Benguela. *ICES Journal of Marine Science* 62: 459 – 468
- Friedrichs MAM, Carr M-E, Barber RT, Scardi M, Antoine D, Armstrong RA, Asanuma I, Behrenfeld MJ, Buitenhuis ET, Chai F, Christian JR, Ciotti AM, Doney SC, Dowell M, Dunne J, Gentili B, Gregg W, Hoepffner N, Ishizaka J, Kameda T, Lima I, Marra J, Mélin F, Moore JK, Morel A, O'Malley RT, O'Reilly J, Saba VS, Schmeltz M, Smyth TJ, Tjiputra J, Waters K, Westberry TK, Winguth A (2009) Assessing the uncertainties of model estimates of primary productivity in the tropical Pacific Ocean. *Journal of Marine Systems* 76: 113 – 133
- Furnas ML (1991) Net in situ growth rates of phytoplankton in an oligotrophic, tropical shelf ecosystem. *Limnology and Oceanography* 36: 13 – 29
- Gallegos CL (1992) Phytoplankton photosynthesis, productivity and species composition in a eutrophic estuary: comparison of bloom and non-bloom assemblages. *Marine Ecology Progress Series* 81: 257 – 267
- Gallegos CL, Platt T, Harrison WG, Irwin B (1983) Photosynthetic parameters of arctic marine phytoplankton: vertical variations and time scales of adaptation. *Limnology and Oceanography* 28: 698 – 708
- Garzoli SL, Richardson PL, Dumcombe Rae CM, Fratantoni DM, Goni GJ, Roubicek AJ (1999) Three Agulhas rings observed during the Benguela Current Experiment. *Journal of Geophysical Research* 104: 20971 – 20985
- Geider RJ and MacIntyre HL (2002) Physiology and Biochemistry of Photosynthesis and Algal Carbon Acquisition. In: Williams PJ le B, Thomas DN, and Reynolds CS (Eds.) *Phytoplankton Productivity: Carbon assimilation in marine and freshwater systems*, Blackwell Science, Oxford, pp. 44 – 77
- Geider RJ, MacIntyre HL, Kana TM (1996) A dynamic model of photoadaptation in phytoplankton. *Limnology and Oceanography* 41: 1 – 15
- Geider RJ, Platt T, Raven JA (1986) Size dependence of growth and photosynthesis in diatoms: a synthesis. *Marine Ecology Progress Series* 30: 93 – 104

- Glibert PM, Anderson DM, Gentien P, Granéli E, Sellner KG (2005) The global, complex phenomena of harmful algal blooms. *Oceanography* 18: 136 – 147
- Glibert P, Harrison J, Heil C, Seitzinger S (2006) Escalating worldwide use of urea – a global change contributing to coastal eutrophication. *Biogeochemistry* 77: 441 – 463
- González HE, Daneri G, Iriarte JL, Yannicelli B, Menschel E, Barria C, Pantoja S, Lizárraga L (2009) Carbon fluxes within the epipelagic zone of the Humboldt current system off Chile: the significance of euphausiids and diatoms as key functional groups for the biological pump. *Progress in Oceanography* 83 (1-4): 217 – 227
- González-Dávila M, Santana-Casiano JM, Ucha IR (2009) Seasonal variability of fCO₂ in the Angola-Benguela region. *Progress in Oceanography* 83 (1-4): 124 – 133
- Gregg WW, Casey NW, McClain CR (2005) Recent trends in global ocean chlorophyll. *Geophysical Research Letters* 32: doi:10.1029/2004GL021808
- Gregg WW, Conkright ME, Ginoux P, O'Reilly JE, Casey NW (2003a) Ocean Primary Production and Climate: Global Decadal Changes. *Geophysical Research Letters* 30(15): 1809
- Gregg WW, Ginoux P, Schopf PS, Casey NW (2003b) Phytoplankton and iron: Validation of a global three-dimensional ocean biogeochemical model. *Deep-Sea Research II* 50: 3143 – 3169
- Hardman-Mountford NJ, Richardson AJ, Agenbag JJ, Hagen E, Nykjaer L, Shillington FA, Villacastin C (2003) Ocean climate of the South East Atlantic observed from satellite data and wind models. *Progress in Oceanography* 59: 181 – 221
- Harris GP (1980) The relationship between chlorophyll a fluorescence, diffuse attenuation changes and photosynthesis in natural phytoplankton populations. *Journal of Plankton Research* 2: 109 – 127
- Harrison W and Platt T (1980) Variations in the assimilation number of coastal marine phytoplankton: Effects of environmental covariates. *Journal of Plankton Research* 2 (4): 249 – 260
- Harrison WG, Platt T, Irwin B (1987) f-ratio and its relationship to ambient nitrate concentration in coastal waters. *Journal of Plankton Research* 9: 235 – 248
- Hashimoto S, Shiomoto A (2002) Light utilization efficiency of size-fractionated phytoplankton in the subarctic Pacific, spring and summer 1999: high efficiency of large-size diatoms. *Journal of Plankton Research* 24: 83 – 87
- Henley WJ (1993) Measurement and interpretation of photosynthetic light-response curves in algae in the context of photoinhibition and diel changes. *Journal of Phycology* 29: 729 – 745
- Hill AE, Hickey BM, Shillington FA, Strub PT, Brink KH, Barton ED, Thomas AC (1998) Eastern Ocean Boundaries. In: Robinson AR, Brink KH (eds) *The Global Coastal Ocean, Regional Studies and Syntheses. The Sea, Vol. 11*. John Wiley and Sons, New York, p 29 – 68
- Hirata T, Hardman-Mountford NJ, Barlow R, Lamont T, Brewin R, Smyth T, Aiken J (2009) An inherent optical property approach to the estimation of size-specific photosynthetic rates in eastern boundary upwelling zones from satellite ocean colour: An initial assessment. *Progress in Oceanography* 83 (1-4): 393 – 397
- Hitchcock GL (1980) Influence of temperature on the growth rate of *Skeletonema costatum* in response to variations in daily light intensity. *Marine Biology* 57: 261 – 269
- Hood RR, Neuer S, Cower TJ (1992) Autotrophic production, biomass and species composition at two stations across an upwelling front. *Marine Ecology Progress Series* 83: 221 – 232
- Houghton JT, Jenkins GJ, Ephraums JJ (1990) *Climate Change: The IPCC Scientific Assessment*. Cambridge University Press, Cambridge.
- Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K (1996) *Climate Change 1995: The Science of Climate Change. Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge

- Huggett J, Fréon P, Mullon C, Penven P (2003) Modelling the transport success of anchovy *Engraulis encrasicolus* eggs and larvae in the southern Benguela: The effect of spatio-temporal spawning patterns. *Marine Ecology Progress Series* 250: 247 – 262
- Huggett J, Verheye H, Escribano R, Fairweather T (2009) Copepod biomass, size composition and production in the Southern Benguela: Spatio-temporal patterns of variation, and comparison with other eastern boundary upwelling systems. *Progress in Oceanography* 83 (1-4): 197 – 207
- Huntley ME, Lópes MD, Karl DM (1991) Top predators in the Southern Ocean: a major leak in the biological carbon pump. *Science* 253: 64 – 66
- Hutchings L (1992) Fish harvesting in a variable, productive environment – searching for rules or searching for exceptions? In: Payne AIL, Brink KH, Mann KH, Hilborn R (eds) *Benguela Trophic Functioning*. South African Journal of Marine Science 12: 297 – 318
- Hutchings L, Barange M, Bloomer SF, Boyd AJ, Crawford RJM, Huggett JA, Kerstan M, Korrùble JL, De Oliveira JAA, Painting SJ, Richardson AJ, Shannon LJ, Schülein FH, van der Lingen CD, Verheye HM (1998) Multiple factors affecting South African anchovy recruitment in the spawning, transport and nursery area. In: Pillar SC, Moloney CL, Payne AIL, Shillington FA (eds) *Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources*. South African Journal of Marine Science 19: 211 – 225
- Hutchings L, Pitcher GC, Probyn TA, Bailey GW (1995) The chemical and biological consequences of coastal upwelling. In: Summerhayes CP, Emeis K-C, Angel MV, Smith RL, Zeitzschel B (eds) *Upwelling in the Ocean: Modern Processes and Ancient Records*. John Wiley and Sons, p 65 – 81
- Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM, Verheye HMS, Bartholomae CH, van der Plas AK, Louw D, Kreiner A, Ostrowski M, Fidel Q, Barlow RG, Lamont T, Coetzee J, Shillington F, Veitch J, Currie JC, Monteiro PMS (2009) The Benguela Current: An ecosystem in four components. *Progress in Oceanography* 83 (1-4): 15 – 32
- Iriarte JL, Pizarro G, Trancoso VA, Sobarzo M (2000) Primary production and biomass of size-fractionated phytoplankton off Antofagasta, Chile (23 - 24°S) during pre-El Niño and El Niño 1997. *Journal of Marine Systems* 26 (1): 37 – 51
- Jassby AD, Platt T (1976) Mathematical formulation for the relationship between photosynthesis and light for phytoplankton. *Limnology and Oceanography* 21: 540 – 547
- Jeffrey SW, Vesik M (1997) Introduction to marine phytoplankton and their pigment signatures. In: Jeffrey SW, Mantoura RFC, Wright SW (eds) *Phytoplankton pigments in Oceanography: Guidelines to Modern Methods*. Paris, UNESCO Publishing, Paris, p 37 – 84
- Jochem FJ (2003) Photo- and heterotrophic pico- and nanoplankton in the Mississippi River plume: distribution and grazing activity. *Journal of Plankton Research* 25: 1201 – 1214
- Joint I, Groom SB, Wollast R, Chou L, Tilstone GH, Figueiras FG, Liojens M, Smyth TJ (2002) The response of phytoplankton production to periodic upwelling and relaxation events at the Iberian shelf break: estimates by the ¹⁴C method and by satellite remote sensing. *Journal of Marine Systems* 32: 219 – 238
- Joint IR and Pomroy AJ (1983) Production of picoplankton and small nanoplankton in the Celtic Sea. *Marine Biology* 77: 19 – 27
- Joint IR and Pomroy AJ (1986) Photosynthetic characteristics of nanoplankton and picoplankton from the surface mixed layer. *Marine Biology* 92: 465 – 474
- Joint I, Rees AP, Woodward EMS (2001) Primary production and nutrient assimilation in the Iberian upwelling in August 1998. *Progress in Oceanography* 51: 303 – 320
- Jones BH and Halpern D (1981) Biological and physical aspects of a coastal upwelling event observed during March-April 1974 off northwest Africa. *Deep-Sea Research* 28: 71 – 81
- Kirk JTO (1994) *Light and photosynthesis in Aquatic Ecosystems*, 2nd Edition. Cambridge University Press, Cambridge

- Kjørboe T (1993) Turbulence, phytoplankton cell size and the structure of the pelagic food webs. *Advances in Marine Biology* 29: 1 – 72
- Koné V, Machu E, Penven P, Anderson V, Garçon V, Fréon P, Demarcq H (2005) Modelling the primary and secondary productions of the southern Benguela upwelling system: A comparative study through two biogeochemical models. *Global Biogeochemical Cycles* 19 (4): GB4021
- Kudela RM (2008) Silicon: Nitrogen interactions in the marine environment. In: Capone D, Bronk D, Mulholland M, Carpenter E (eds) *Nitrogen in the Marine Environment*, second ed. Elsevier, New York, p 1589 – 1626
- Kywalyanga MN, Platt T, Sathyendranath S (1992) Ocean primary production calculated by spectral and broad-band models. *Marine Ecology Progress Series* 85: 171 – 185
- Kywalyanga MN, Platt T, Sathyendranath S (1997) Estimation of the photosynthetic action spectrum: implication for primary production models. *Marine Ecology Progress Series* 146: 207 – 223
- Kywalyanga MN, Platt T, Sathyendranath S, Lutz VA, Stuart V (1998) Seasonal variations in physiological parameters of phytoplankton across the North Atlantic. *Journal of Plankton Research* 20: 17 – 42
- Landry MR, Ohman MD, Goericke R, Stukel MR, Tsyrklevich K (2009) Lagrangian studies of phytoplankton growth and grazing relationships in a coastal upwelling ecosystem off Southern California. *Progress in Oceanography* 53 (1-4): 208 – 216
- Larsen SH (2005) Solar variability, dimethyl sulphide, clouds, and climate. *Global Biogeochemical Cycles* 19, GB1014. doi: 10.1029/2004GB002333
- Laws E and Bannister TT (1980) Nutrient and light-limited growth of *Thalassiosira fluviatilis* in continuous culture, with implications for phytoplankton growth in the oceans. *Limnology and Oceanography* 25: 457 – 473
- Laws E, Sakshaug E, Babin M, Dandonneau Y, Falkowski PG, Geider R, Legendre L, Morel A, Sondergaard M, Takahashi M, Williams PJ le B (2002) *Photosynthesis and Primary Productivity in Marine Ecosystems: Practical Aspects and Application of Techniques*. JGOFS Report 36
- Lee ZP, Carder KL, Marra J, Steward RG, Perry MJ (1996) Estimating primary production at depth from remote sensing. *Applied Optics* 35: 463 – 474
- Legendre L (1981) Hydrodynamic control of marine phytoplankton production: the paradox of stability. In: Nihoul JCJ (ed) *Ecohydrodynamics*. Proceedings of the 12th International Liège Colloquium on Ocean Hydrodynamics. Amsterdam, Elsevier, Elsevier Oceanography Series 32: 191 – 208
- Legendre L (1990) The significance of microalgal blooms for fisheries and for the export of particulate organic carbon in oceans. *Journal of Plankton Research* 12: 681 – 699
- Legendre L, Gosselin M, Hirsche HJ, Kattner G, Rosenberg G (1993) Environmental control and potential fate of size fractionated phytoplankton in the Greenland Sea (75°N). *Marine Ecology Progress Series* 98: 297 – 313
- Legendre L and Le Fèvre J (1989) Hydrodynamical singularities as controls of recycled versus export production in oceans. In: Berger WH, Smetacek VS, Wefer G (eds) *Productivity in the Oceans: Past and Present*. John Wiley and Sons, p 46 – 63
- Legendre L, Rassoulzadegan F (1996) Food-web mediated export of biogenic carbon in oceans: environmental control. *Marine Ecology Progress Series* 145: 179 – 193
- Lett C, Roy C, Levasseur A, van der Lingen C, Mullan C (2006) Simulation and quantification of enrichment and retention processes in the southern Benguela upwelling ecosystem. *Fisheries Oceanography* 15(5): 363 – 372
- Lett C, Veitch J, van der Lingen C, Hutchings L (2007) Assessment of an environmental barrier to transport of ichthyoplankton from the southern to the northern Benguela ecosystem. *Marine Ecology Progress Series* 347: 247 – 259

- Lewis MR, Horne EPW, Cullen JJ, Oakey NS, Platt T (1984) Turbulent motions may control phytoplankton photosynthesis in the upper ocean. *Nature* 311: 49 – 50
- Lewis MR and Smith JC (1983) A small volume, short-incubation-time method for measurement of photosynthesis as a function of incident irradiance. *Marine Ecology Progress Series* 13: 99 – 102
- Lewis MR, Warnock RE, Platt T (1985) Absorption and photosynthetic action spectra for natural phytoplankton populations: implications for production in the open ocean. *Limnology and Oceanography* 30: 394 – 806
- Li WKW (2002) Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean. *Nature* 419: 154 – 157
- Li WKW, Subba Rao DW, Harrison WG, Smith JC, Cullen JJ, Irwin B, Platt T (1983) Autotrophic picoplankton in the tropical Ocean. *Science* 219: 292 – 295
- Liu K-K, Atkinson L, Chen C-TA, Gao S, Hall J, Macdonald RW, Talaue McManus L, Quinones R (2000) Exploring continental margin carbon fluxes on a global scale. *EOS, Transactions of the American Geophysical Union* 81: 641 – 644
- Lohrenz SE, Fahnenstiel GL, Redalje DG (1994) Spatial and temporal variations of photosynthetic parameters in relation to environmental conditions in coastal waters of the Northern Gulf of Mexico. *Estuaries* 17: 779 – 795
- Longhurst AR (1991) Role of the marine biosphere in the global carbon cycle. *Limnology and Oceanography* 36: 1507 – 1526
- Longhurst AR, Sathyendranath S, Platt T, Caverhill C (1995) An estimate of global primary production in the ocean from satellite radiometer data. *Journal of Plankton Research* 17(6): 1245 – 1271
- Lorenzo LM, Arbones B, Figueiras FG, Tilstone GH, Figueroa FL (2002) Photosynthesis, primary production and phytoplankton growth rates in Gerlache and Bransfield Straits during austral summer: cruise FRUELA 95. *Deep-Sea Research II* 49: 707 – 721
- Lorenzo LM, Arbones B, Tilstone GH, Figueiras FG (2005) Across-shelf variability of phytoplankton composition, photosynthetic parameters and primary production in the NW Iberian upwelling system. *Journal of Marine Systems* 54: 157 – 173
- Lorenzo LM, Figueiras FG, Tilstone GH, Arbones B, Mirón I (2004) Photosynthesis and light regime in the Azores Front region during summer: are light-saturated computations of primary production sufficient? *Deep-Sea Research I* 51: 1229 – 1244
- Lucas MI, Probyn TA, Painting SJ (1987) An experimental study of dinoflagellate bacterivory: further evidence for the importance and complexity of microplanktonic interactions. In: Payne AIL, Gulland JA, Brink KH (eds) *The Benguela and Comparable Frontal Ecosystems*. *South African Journal of Marine Science* 5: 791 – 810
- Lutjeharms JRE (2006) *The Agulhas Current*. Springer, Berlin
- Lutjeharms JRE, Meeuwis JM (1987) The extent and variability of South-east Atlantic upwelling. In: Payne AIL, Gulland JA, Brink KH (eds) *The Benguela and Comparable Frontal Ecosystems*. *South African Journal of Marine Science* 5: 51 – 62
- Lutjeharms JRE, Monteiro PMS, Tyson PD, Obura D (2001) The oceans around Southern Africa and regional effects of climate change. *South African Journal of Science* 97: 119 – 130
- Lutjeharms JRE, Shillington FA, Duncombe Rae CM (1991) Observations of extreme upwelling filaments in the South East Atlantic Ocean. *Science* 253: 774 – 776
- Lutjeharms JRE and Stockton PL (1987) Kinematics of the upwelling front off Southern Africa. In: Payne AIL, Gulland JA, Brink KH (eds) *The Benguela and Comparable Frontal Ecosystems*. *South African Journal of Marine Science* 5: 35 – 49
- Lutjeharms JRE, van Ballegooyen RC (1988) The retroflexion of the Agulhas Current. *Journal of Physical Oceanography* 18(11): 1570 – 1583

- Mackas DL, Strub PT, Thomas A, Montecino V (2006) Eastern regional ocean boundaries pan-regional overview. In: Robinson AR, Brink KH (eds) *The global coastal ocean, Interdisciplinary regional studies and syntheses*. The Sea, Vol. 14, Part A. Harvard University Press, p 441 – 501
- Malone TC (1977) Light-saturated photosynthesis by phytoplankton size fractions in the New York Bight, USA. *Marine Biology* 42: 281 – 292
- Malone TC (1980) Size fractionated primary productivity of marine phytoplankton. In: Falkowski PG (ed) *Primary productivity in the sea*. Plenum Press, New York, p 301 – 319
- Mann KH (1992) Physical influences on biological processes: how important are they? In: Payne AIL, Brink KH, Hilborn RS (eds) *Benguela Trophic Functioning*. *African Journal of Marine Science* 12: 107 – 121
- Mann KH (1993) Physical oceanography, food chains, and fish stocks: a review. *ICES Journal of Marine Science* 50: 105 – 119
- Marañón E, Holligan PM (1999) Photosynthetic parameters of phytoplankton from 50°N to 50°S in the Atlantic Ocean. *Marine Ecology Progress Series* 176: 191 – 203
- Margalef R (1958) Temporal succession and spatial heterogeneity in phytoplankton. In: Buzzati-Traverso AA (ed) *Perspectives in marine biology*. University of California Press, Berkeley, p 323 – 348
- Marra J (1980a) The time course of light intensity adaptation in a marine diatom. *Marine Biology Letters* 1: 175 – 183
- Marra J (1980b) Phytoplankton photosynthetic response to vertical movement in a mixed layer. *Marine Biology* 46: 203 – 208
- Marra J, Trees CC, O'Reilly JE (2007) Phytoplankton pigment absorption: A strong predictor of primary productivity in the surface ocean. *Deep-Sea Research I* 54: 155 – 163
- Matthews SG and Pitcher GC (1996) Worst recorded marine mortality on the South African coast. In: Yasumoto T, Oshima Y, Fukuyo Y (eds) *Harmful and Toxic Algal Blooms*. Intergovernmental Oceanographic Commission of UNESCO, Paris, p 89 – 92
- McClain CR (2009) A decade of satellite ocean colour observations. *Annual Review of Marine Science* 1: 19 – 42
- Meeuwis JM, Lutjeharms JRE (1990) Surface thermal characteristics of the Angola-Benguela Front. *South African Journal of Marine Science* 9: 261 – 279
- Messié M, Ledesma J, Kolber DD, Michisaki RP, Foley DG, Chavez FP (2009) Potential new production estimates in four eastern boundary upwelling systems. *Progress in Oceanography* 83 (1-4): 151 – 158
- Michaels AF, Silver MW (1988) Primary production, sinking fluxes and the microbial food web. *Deep-Sea Research* 35: 473 – 490
- Mitchell-Innes BA, Pitcher GC, Probyn TA (2000) Productivity of dinoflagellate blooms on the west coast of South Africa, as measured by natural fluorescence. *South African Journal of Marine Science* 22(1): 273 – 284
- Mitchell-Innes BA and Walker DR (1991) Short-term variability during an Anchor Station study in the southern Benguela upwelling system. Phytoplankton production and biomass in relation to species changes. *Progress in Oceanography* 28 (1&2): 65 – 89
- Montecino V, Astoreca R, Alarcón G, Retamal L, Pizarro G (2004) Bio-optical characteristics and primary productivity during upwelling and non-upwelling conditions in a highly productive coastal ecosystem off central Chile (~ 36°S). *Deep-Sea Research II* 51: 2413 – 2426
- Montecino V and Lange CB (2009) The Humboldt Current System: Ecosystem components and processes, fisheries, and sediment studies. *Progress in Oceanography* 83: 65 – 79
- Monteiro PMS and van der Plas AK (2006) Low oxygen water (LOW) variability in the Benguela ecosystem: key processes and forcing scales relevant to forecasting. In: Shannon V, Hempel G, Malanotte-Rizzoli P,

- Moloney CL, Woods J (eds) Benguela: Predicting a Large Marine Ecosystem. Large Marine Ecosystems 14, Elsevier, Amsterdam, p 71 – 90
- Moore III B, Gates WL, Mata LJ, Underdal A (2001) Advancing Our Understanding. In: Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA (eds) Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, p 771 – 785
- Moore LR, Goericke R, Chisholm SW (1995) Comparative physiology of *Synechococcus* and *Prochlorococcus*: influence of light and temperature on growth, pigments, fluorescence and absorptive properties. Marine Ecology Progress Series 116: 259 – 275
- Morán XAG, Estrada M (2001) Short-term variability of photosynthetic parameters and particulate and dissolved primary production in the Alboran Sea (SW Mediterranean). Marine Ecology Progress Series 212: 53 – 67
- Morán XAG, Estrada M (2005) Winter pelagic photosynthesis in the NW Mediterranean. Deep-Sea Research I 52: 1806 – 1822
- Morel A (1988) Optical modelling of the upper ocean in relation to its biogenous matter content (case 1 waters). Journal of Geophysical Research 93: 10749 – 10768
- Morel A (1991) Light and marine photosynthesis: A spectral model with geochemical and climatological implications. Progress in Oceanography 26: 263 – 306
- Morel A and Berthon JF (1989) Surface pigments, algal biomass and potential production of the euphotic layer: relationships reinvestigated in view of remote sensing applications. Limnology and Oceanography 34: 1545 – 1562
- Mostert SA (1983) Procedures used in South Africa for the automatic photometric determination of macronutrients in seawater. South African Journal of Marine Science 1: 189 – 198
- Nelson G (1992) Equatorward wind and atmospheric pressure spectra as metrics for Primary Productivity in the Benguela System. In: Payne AIL, Brink KH, Mann KH, Hilborn R (eds) Benguela Trophic Functioning. South African Journal of Marine Science 12: 19 – 28
- Nelson G, Boyd AJ, Agenbag JJ, Duncombe Rae CM (1998) An upwelling filament north-west of Cape Town, South Africa. In: Pillar SC, Moloney CL, Payne AIL, Shillington FA (eds) Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources. South African Journal of Marine Science 19: 75 – 88
- Nelson G and Hutchings L (1983) The Benguela Upwelling Area. Progress in Oceanography 12(3): 333 – 356
- Nixon S and Thomas A (2001) On the size of the Peru upwelling ecosystem. Deep-Sea Research I 48: 2521 – 2528
- Painting SJ, Lucas MI, Mur DG (1989) Fluctuations in heterotrophic bacterial community structure, activity and production in response to development and decay of phytoplankton in a microcosm. Marine Ecology Progress Series 53: 129 – 141
- Parada C, Mullon C, Roy C, Fréon P, Hutchings L, van der Lingen CD (2008) Does vertical migratory behaviour retain fish larvae onshore in upwelling ecosystems? A modelling study of anchovy in the southern Benguela. African Journal of Marine Science 30 (3): 437 – 452
- Parada C, van der Lingen CD, Mullon C, Penven P (2003) The effect of buoyancy on the transport of anchovy (*Engraulis capensis*) eggs from spawning to nursery grounds in the southern Benguela: An IBM approach. Fisheries Oceanography 12: 1 – 15
- Parsons TR, Maita Y, Lalli CM (1984) A manual of chemical and biological methods for seawater analysis. New York. Pergamon
- Penven P, Roy C, Colin de Verdière A, Largier J (2000) Simulation of a coastal jet retention process using a barotropic model. Oceanologica Acta 23: 615 – 634

Pitcher GC, Agenbag JJ, Calder D, Horstman DA, Jury MR, Taunton-Clark J (1995) Red tide in relation to the meteorology of the southern Benguela upwelling system. In: Lassus P, Arzul G, Erard E, Gentien P, Marcaillou C (eds) Harmful Marine Algal Blooms. Paris, Technique et Documentation – Lavoisier, p 657 – 662

Pitcher GC, Bernard S, Ntuli J (2008) Contrasting bays and red tides in the southern Benguela upwelling system. *Oceanography* 21: 82 – 91

Pitcher GC and Boyd AJ (1996) Cross-shelf and alongshore dinoflagellate distributions and the mechanisms of red tide formation within the southern Benguela upwelling system. In: Yasumoto T, Oshima Y, Fukuya Y (eds) Harmful and Toxic Algal Blooms. Paris, Intergovernmental Oceanographic Commission of UNESCO: 243 – 246

Pitcher GC, Boyd AJ, Horstman DA, Mitchell-Innes BA (1998) Subsurface dinoflagellate populations, frontal blooms and the formation of red tide in the southern Benguela upwelling system. *Marine Ecology Progress Series* 172: 253 – 264

Pitcher GC, Brown PC, Mitchell-Innes BA (1992) Spatio-temporal variability of phytoplankton in the southern Benguela upwelling system. In: Payne AIL, Brink KH, Mann KH, Hilborn R (eds) Benguela Trophic Functioning. *South African Journal of Marine Science* 12: 439 – 456

Pitcher GC and Calder D (2000) Harmful algal blooms in the southern Benguela Current: a review and appraisal of monitoring from 1989 to 1997. *South African Journal of Marine Science* 22: 255 – 271

Pitcher GC and Cockcroft AC (1998) Low oxygen, rock lobster strandings and PSP. In: Wyatt T (ed) Harmful Algae News No. 17. Intergovernmental Oceanographic Commission of UNESCO, Paris, p 1 – 3

Pitcher GC, Figueiras FG, Hickey BM, Moita MT (2010) The physical oceanography of upwelling systems and the development of harmful algal blooms. *Progress in Oceanography* 85: 5 – 32

Pitcher GC, Horstman DA, Calder D (1993) Formation and decay of red tide blooms in the southern Benguela upwelling system during the summer of 1990/91. In: Smayda TJ, Shimizu Y (eds) Toxic Phytoplankton Blooms in the Sea. New York, Elsevier: 317 – 322.

Pitcher GC and Nelson G (2006) Characteristics of the surface boundary layer important to the development of red tide on the southern Namaqua shelf of the Benguela upwelling system. *Limnology and Oceanography* 51(6): 2660 – 2674

Pitcher GC and Pillar S (2010) Harmful algal blooms in eastern boundary upwelling systems. *Progress in Oceanography* 85: 1 – 4

Pitcher GC and Weeks SJ (2006) The variability and potential for prediction of Harmful Algal Blooms in the southern Benguela ecosystem. In: Shannon V, Hempel G, Malanotte-Rizzoli P, Moloney C, Woods J (eds) Benguela: Predicting a Large Marine Ecosystem. Large Marine Ecosystems 14. Elsevier, Amsterdam, p 125 – 146

Platt T, Gallegos CL, Harrison WG (1980) Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *Journal of Marine Research* 38: 687 – 701

Platt T and Harrison WG (1985) Biogenic fluxes of carbon and oxygen in the ocean. *Nature* 318: 55 – 58

Platt T and Jassby AD (1976) The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. *Journal of Phycology* 12: 421 – 430

Platt T and Sathyendranath S (1988) Ocean primary production: estimation by remote sensing at local and regional scales. *Science* 241: 1613 – 1620

Platt T and Sathyendranath S (1991) Biological production models as elements of coupled atmosphere-ocean models for climate research. *Journal of Geophysical Research* 96: 2585 – 2592

Platt T, Sathyendranath S, Joint I, Fasham MJR (1993) Photosynthetic characteristics of the phytoplankton in the Celtic Sea during late spring. *Fisheries Oceanography* 2: 191 – 201

Platt T, Sathyendranath S, Ulloa O, Harrison WG, Hoepffner N, Goes J (1992) Nutrient control of phytoplankton photosynthesis in the western North Atlantic. *Nature* 356: 229 – 331

- Platt T, Subba Rao DW, Irwin B (1983) Photosynthesis of picoplankton in the oligotrophic ocean. *Nature* 301: 702 – 704
- Pecquerie L, Drapeau L, Fréon P, Coetzee JC, Leslie RW, Griffiths MH (2004) Distribution patterns of key fish species of the southern Benguela ecosystem: an approach combining fishery-dependent and fishery-independent data. *African Journal of Marine Science* 26: 115 – 139
- Prentice IC, Farquhar GD, Fasham MJR, Goulden ML, Heimann M, Jaramillo VJ, Kheshgi HS, Le Quéré C, Scholes RJ, Wallace DWR (2001) The Carbon Cycle and Atmospheric Carbon Dioxide. In: Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA (eds) *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, p 185 – 237
- Preston-Whyte RA, Tyson PD (1988) *The Atmospheric and Weather of Southern Africa*. Oxford University Press, Cape Town, South Africa
- Prézelin BB, Bidigare RR, Matlick HA, Ver Hoven B (1987) Diurnal patterns of size-fractionated primary productivity across a coastal front. *Marine Biology* 96: 563 – 574
- Prézelin BB and Glover HE (1991) Variability in time/space estimates of phytoplankton, biomass and productivity in the Sargasso Sea. *Journal of Plankton Research* 13: 45 – 67
- Prézelin BB and Matlick HA (1980) Time-course of photoadaptation in the photosynthesis-irradiance relationship of a dinoflagellate exhibiting photosynthetic periodicity. *Marine Biology* 58: 85 – 96
- Probyn TA (1985) Nitrogen uptake by size-fractionated phytoplankton populations in the southern Benguela upwelling system. *Marine Ecology Progress Series* 22(3): 249 – 258
- Probyn TA (1992) The inorganic nitrogen nutrition of phytoplankton in the southern Benguela: new production, phytoplankton size and implications for pelagic foodwebs. In: Payne AIL, Brink KH, Mann KH, Hilborn R (eds) *Benguela Trophic Functioning*. South African Journal of Marine Science 12: 411 – 420
- Probyn TA, Pitcher GC, Monteiro PMS, Boyd AJ, Nelson G (2000) Physical processes contributing to harmful algal blooms in Saldanha Bay, South Africa. *South African Journal of Marine Science* 22: 285 – 297
- Reason CJC, Florenchie P, Rouault M, Veitch J (2006) Influences of large scale climate modes and agulhas system variability on the BCLME region. In: Shannon V, Hempel G, Malanotte-Rizzoli P, Moloney CL, Woods J (eds) *Benguela: Predicting a Large Marine Ecosystem*. Large Marine Ecosystems 14, Elsevier, Amsterdam, pp. 223 – 238
- Reid PC, Edwards M, Hunt HG, Warner AJ (1998) Phytoplankton change in the North Atlantic. *Nature* 391: 546
- Richardson AJ, Pfaff MC, Field JG, Siluwane NF, Shillington FA (2002) Identifying characteristics chlorophyll a profiles in the coastal domain using an artificial neural network. *Journal of Plankton Research* 24 (12): 1289 – 1303
- Rodríguez J (1994) Some comments on the size-based structural analysis of the pelagic ecosystem. *Scientia Marina* 58: 1 – 10
- Roesler CS (1998) Theoretical and experimental approaches to improve the accuracy of particulate absorption coefficients derived from the quantitative filter technique. *Limnology and Oceanography* 43: 1649 – 1660
- Rossi V, Lopez C, Sudre J, Hernandez-Garcia E, Garçon V (2008) Comparative study of mixing and biological activity of the Benguela and Canary upwelling systems. *Geophysical Research Letters* 35: L11602. doi:10.1029/2008GLO33610
- Rouault M (2007) Observed trends in the ocean and atmosphere around southern Africa over the past 50 years. In: Veitch J (Compiler) *The changing state of the Benguela Current Large Marine Ecosystem: Expert Workshop on Climate Change and Variability and Impacts Thereof in the BCLME region*, 15 – 16th May 2007. Climate Change Workshop Report.

- Roy C, van der Lingen CD, Coetzee JC, Lutjeharms JRE (2007) Abrupt environmental shift associated with changes in distribution of Cape anchovy *Engraulis encrasicolus* spawners in the southern Benguela. *African Journal of Marine Science* 29(3): 309 – 319
- Roy C, Weeks S, Rouault M, Nelson G, Barlow R, van der Lingen C (2001) Extreme oceanographic events recorded in the southern Benguela during the 1999-2000 summer season. *South African Journal of Science* 97: 1 – 7
- Rubio A, Blanke B, Speich S, Grima N, Roy C (2009) Mesoscale activity in the southern Benguela upwelling system from satellite altimetry and model data. *Progress in Oceanography* 83 (1-4): 288 – 295
- Rykaczewski RR, Checkley DM (2008) Influence of ocean winds on the pelagic ecosystem in upwelling regions. *Proceedings of the National Academy of Sciences* 105 (6): 1965 – 1970
- Saba VS, Friedrichs MAM, Carr M-E, Antoine D, Armstrong RA, Asanuma I, Aumont O, Bates NR, Behrenfeld MJ, Bennington V, Bopp L, Bruggeman J, Buitenhuis ET, Church MJ, Ciotti AM, Doney SC, Dowell M, Dunne J, Dutkiewicz S, Gregg W, Hoepffner N, Hyde KJW, Ishizaka J, Kameda T, Karl DM, Lima I, Lomas MW, Marra J, McKinley GA, Mélin F, Moore JK, Morel A, O'Reilly J, Salihoglu B, Scardi M, Smyth TJ, Tang S, Tjiputra J, Uitz J, Vichi M, Waters K, Westberry TK, Yool A (2010a) Challenges of modelling depth-integrated marine primary productivity over multiple decades: A case study at BATS and HOT. *Global Biogeochemical Cycles* 24, GB3020, doi:10.1029/2009GB003655
- Saba VS, Friedrichs MAM, Antoine D, Armstrong RA, Asanuma I, Behrenfeld MJ, Ciotti AM, Dowell M, Hoepffner N, Hyde KJW, Ishizaka J, Kameda T, Marra J, Mélin F, Morel A, O'Reilly J, Scardi M, Smith Jr. WO, Smyth TJ, Tang S, Uitz J, Waters K, Westberry TK (2010b) An evaluation of ocean colour model estimates of marine primary productivity in coastal and pelagic regions across the globe. *Biogeosciences Discuss* 7: 6749 – 6788
- Sakshaug E, Bricaud A, Dandonneau Y, Falkowski PG, Kiefer KA, Legendre L, Morel A, Parslow J, Takahashi M (1997) Parameters of photosynthesis: definitions, theory and interpretation of results. *Journal of Plankton Research* 19 (11): 1637 – 1670
- Sathyendranath S, Longhurst AR, Caverhill CM, Platt T (1995) Regionally and seasonally differentiated primary production in the North Atlantic. *Deep-Sea Research I* 42: 1773 – 1802
- Sathyendranath S, Platt T, Caverhill CM, Warnock RE, Lewis MR (1989) Remote sensing of oceanic primary production: Computations using a spectral model. *Deep-Sea Research* 36: 341 – 453
- Sathyendranath S, Platt T, Horne EPW, Harrison WG, Ulloa O, Outerbridge R, Hoepffner N (1991) Estimation of new production in the ocean by compound remote sensing. *Nature* 353: 129 – 133
- Schofield O, Bidigare RR, Prézelin BB (1990) Spectral photosynthesis, quantum yield and blue-green light enhancement of productivity rate in the diatom *Chaetoceros gracile* and the prymnesiophyte *Emiliania huxleyi*. *Marine Ecology Progress Series* 64: 175 – 186
- Shannon LV (1985) The Benguela Ecosystem Part 1. Evolution of the Benguela, physical features and processes. *Oceanography and Marine Biology: An annual review* 23: 105 – 182
- Shannon LV (2006) A plan comes together. In: Shannon V, Hempel G, Malanotte-Rizzoli P, Moloney C, Woods J (eds) *Benguela: Predicting a Large Marine Ecosystem*. Large Marine Ecosystems 14, Elsevier, Amsterdam, p 3 – 10
- Shannon LV, Agenbag JJ, Buys MEL (1987) Large- and mesoscale feature of the Angola-Benguela Front. In: Payne AIL, Gulland JA, Brink KH (eds) *The Benguela and Comparable Ecosystems*. *South African Journal of Marine Science* 5: 11 – 34
- Shannon LV, Agenbag JJ, Walker ND, Lutjeharms JRE (1990) A major perturbation in the Agulhas Retroflection area in 1986. *Deep-Sea Research* 37(3): 493 – 512
- Shannon LV and Field JG (1985) Are fish stocks food-limited in the southern Benguela pelagic ecosystem? *Marine Ecology Progress Series* 22(1): 7 – 19
- Shannon LV, Moloney CL, Jarre A, Field JG (2003) Trophic flows in the southern Benguela during the 1980's and the 1990's. *Journal of Marine Systems* 39: 83 – 116

- Shannon LV and Nelson G (1996) The Benguela: large scale features and processes and system variability. In: Wefer G, Berger H, Siedler G, Webb DJ (eds) *The South Atlantic: Past and Present Circulation*. Springer Verlag, Berlin, p 163 – 210
- Shannon LV and Pillar SC (1986) The Benguela ecosystem. Part III. Plankton. *Oceanography and Marine Biology: An Annual Review* 24: 65 – 170
- Shillington FA (1998) The Benguela Upwelling System off Southwest Africa. In: Ronbinson AR, Brink KH (eds) *The Global Coastal Ocean, Regional Studies and Syntheses, The Sea*, vol. 11. John Wiley and Sons, New York, p 538 – 604
- Shillington FA, Reason CJC, Dumcombe Rae CM, Florenchie P, Penven P (2006) Large scale Physical Variability of the Benguela Current Large Marine Ecosystem (BCLME). In: Shannon V, Hempel G, Malanotte-Rizzoli P, Moloney C, Woods J (eds) *Benguela: Predicting a Large Marine Ecosystem*. Large Marine Ecosystems 14, Elsevier, Amsterdam, p 49 – 70
- Siegenthaler U, Sarmiento JL (1993) Atmospheric carbon dioxide and the ocean. *Nature* 365: 119 – 125
- Smayda TJ (2010a) Adaptations and selection of harmful and other dinoflagellate species in upwelling systems. 1. Morphology and adaptive polymorphism. *Progress in Oceanography* 55: 53 – 70
- Smayda TJ (2010b) Adaptations and selection of harmful and other dinoflagellate species in upwelling systems. 2. Motility and migratory behaviour. *Progress in Oceanography* 55: 71 – 91
- Smayda TJ, Trainer VL (2010) Dinoflagellate blooms in upwelling systems: Seeding, variability, and contrasts with diatom bloom behaviour. *Progress in Oceanography* 55: 92 – 107
- Smith RC, Heburn GW, Barber RT, O'Brien JJ (1983) Regulation of phytoplankton communities by physical processes in upwelling systems. *Journal of Marine Research* 41: 539 – 556
- Smith RC, Prézelin BB, Bidigare RR, Baker KS (1989) Bio-optical modelling of photosynthetic production in coastal waters. *Limnology and Oceanography* 34: 1524 – 1544
- Stæhr PA, Markager S, Sand-Jensen K (2004) Pigment specific *in vivo* light absorption of phytoplankton from estuarine, coastal and oceanic waters. *Marine Ecology Progress Series* 275: 115 – 128
- Stocker TF, Clarke GKC, Le Treut H, Lindzen RS, Meleshko VP, Mugara RK, Palmer TN, Pierrehumbert RT, Sellers PJ, Trenberth KE, Willebrand J (2001) Physical Climate Processes and Feedbacks. In: Houghton JT, Ding Y, Griggs DJ, Noguera M, van der Linden PJ, Dai X, Maskell K, Johnson CA (eds) *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, pp. 419 – 470
- Swart S, Waldron HN, Hutchings L (2007) Evidence of carbon transport between shelf and slope waters in the Benguela upwelling system. *African Journal of Marine Science* 29 (1): 137 – 139
- Talling JF (1984) Past and contemporary trends and attitudes in work on primary production. *Journal of Plankton Research* 6: 203 – 217
- Takahashi M and Bienfang PK (1983) Size structure of phytoplankton biomass and photosynthesis in subtropical Hawaiian water. *Marine Biology* 76: 203 – 211
- Tamigneaux E, Legendre L, Klein B, Mingelbier M (1999) Seasonal dynamics and potential fate of size-fractionated phytoplankton in a temperate nearshore environment (western Gulf of St. Lawrence, Canada) *Estuarine Coastal and Shelf Science* 48: 253 – 269
- Tang EPY (1995) The allometry of algal growth rates. *Journal of Plankton Research* 17: 1325 – 1335
- Tassan S, Ferrari GM (1995) An alternative approach to absorption measurements of aquatic particles retained on filters. *Limnology and Oceanography* 40: 1358 – 1368
- Taylor AH, Geider RJ, Gilbert F (1997) Seasonal and latitudinal dependencies of phytoplankton carbon-to-chlorophyll *a* ratios: a modelling study. *Marine Ecology Progress Series* 152: 51 – 66
- Thomas AC, Carr M-E, Strub PT (2001) Chlorophyll variability in Eastern Boundary Currents. *Geophysical Research Letters* 28(18): 3421 – 3424

- Thomas AC, Strub PT, Carr M-E, Weatherbee R (2003) Comparison of chlorophyll variability between the four major eastern boundary currents. *International Journal of Remote Sensing* 24: 1 – 5
- Thompson PA, Harrison PJ, Parlow JS (1991) Influence of irradiance on cell volume and carbon quota for ten species of marine phytoplankton. *Journal of Phycology* 27: 351 – 360
- Tilstone GH, Figueiras FG, Fermin EG, Arbones B (1999) Significance of nanophytoplankton photosynthesis and primary production in a coastal upwelling system (Ría de Vigo, NW Spain). *Marine Ecology Progress Series* 183: 13 – 27
- Tilstone GH, Figueiras FG, Lorenzo LM, Arbones B (2003) Phytoplankton composition, photosynthesis and primary production during different hydrographic conditions at the Northwest Iberian upwelling system. *Marine Ecology Progress Series* 252: 89 – 104
- Tilstone GH, Miguez BM, Figueiras FG, Fermin EG (2000) Diatom dynamics in a coastal ecosystem affected by upwelling: coupling between species succession, circulation and biogeochemical processes. *Marine Ecology Progress Series* 205: 23 – 41
- Tilstone GH, Smyth TJ, Gowen RJ, Martinez-Vicente V, Groom SB (2005) Inherent optical properties of the Irish Sea and their effect on satellite primary production algorithms. *Journal of Plankton Research* 27: 1127 – 1148
- Trainer VL, Pitcher GC, Reguera B, Smayda TJ (2010) The distribution and impacts of harmful algal bloom species in eastern boundary upwelling systems. *Progress in Oceanography* 85: 33 – 52
- Tremblay J-E, Legendre L (1994) A model for the size-fractionated biomass and production of marine phytoplankton. *Limnology and Oceanography* 39: 2004 – 2014
- Uitz J, Huot Y, Bruyant F, Babin M, Claustre H (2008) Relating phytoplankton photophysiological properties to community structure on large scales. *Limnology and Oceanography* 53: 614 – 630
- Varela M, Prego R, Pazos Y, Moróño Á (2005) Influence of upwelling and river runoff interaction on phytoplankton assemblages in a Middle Galician Ria and comparison with northern and southern rias (NW Iberian Peninsula). *Estuarine, Coastal and Shelf Science* 64: 721 – 737
- van der Lingen CD, Shannon LJ, Cury P, Kreiner A, Moloney CL, Roux J-P, Vaz-Velho F (2006) Resource and ecosystem variability, including regime shifts in the Benguela Current System. In: Shannon V, Hempel G, Malanotte-Rizzoli P, Moloney CL, Woods J (eds) *Benguela: Predicting a Large Marine Ecosystem*. Large Marine Ecosystems 14, Elsevier, Amsterdam, p 147 – 185
- van Straten G, Herodeck S (1982) Estimation of algal growth parameters from vertical primary production profiles. *Ecological Modelling* 15: 287 – 311
- Vantrepotte V, Mélin F (2009) Temporal variability of 10-year global SeaWiFS time-series of phytoplankton chlorophyll-a concentration. *ICES Journal of Marine Science* 66: 1547 – 1556
- Veitch JA, Florenchie P, Shillington FA (2006) Seasonal and interannual fluctuations of the Angola-Benguela Frontal Zone (ABFZ) using 4.5km resolution satellite imagery from 1982 to 1999. *International Journal of Remote Sensing* 27(5): 987 – 998
- Veitch J, Penven P, Shillington F (2009) The Benguela: a laboratory for comparative modelling studies. *Progress in Oceanography* 83 (1-4): 296 – 302
- Verheye-Dua F and Lucas MI (1988) Southern Benguela frontal region: I. Hydrology, phytoplankton and bacterioplankton. *Marine Ecology Progress Series* 47: 271 – 280
- Vollenweider RA (1974) *A manual on Methods for Measuring Primary Production in Aquatic Environment*. IBP Handbook No. 12. Blackwell Scientific. Oxford
- Waldron HN and Probyn TA (1992) Nitrate supply and potential new production in the Benguela upwelling system. In: Payne AIL, Brink KH, Mann KH, Hilborn R (eds) *Benguela Trophic Functioning*. South African Journal of Marine Science 12: 29 – 39

- Waldron HN, Probyn TA, Brundrit GB (1998) Carbon pathways and export associated with the southern Benguela upwelling system: a re-appraisal. In: Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources. South African Journal of Marine Science 19: 113 – 118
- Ware D (1992) Production characteristics of upwelling systems and the trophodynamic role of hake. In: Payne AIL, Brink KH, Mann KH, Hilborn R (eds) Benguela Trophic Functioning. South African Journal of Marine Science 12: 501 – 513
- Ware DW, Thomson RE (2005) Bottom-up ecosystem trophic dynamics determine fish production in the northeast Pacific. Science 308: 1280 – 1284
- Webb WL, Newton M, Starr D (1974) Carbon dioxide exchange of *Alnus Rubra*: A mathematical model. Oecologia 17: 281 – 291
- Weeks SJ, Barlow R, Roy C, Shillington FA (2006) Remotely sensed variability of temperature and chlorophyll in the southern Benguela: upwelling frequency and phytoplankton response. African Journal of Marine Science 28(3&4): 493 – 509
- Weeks SJ, Currie B, Bakun A (2002) Satellite imaging: massive emissions of toxic gas in the Atlantic. Nature 415: 493 – 494
- Weeks SJ, Currie B, Bakun A, Peard KR (2004) Hydrogen sulphide eruptions in the Atlantic Ocean off southern Africa: implications of a new view based on SeaWiFS satellite imagery. Deep-Sea Research I 51: 153 – 172
- Weeks SJ and Shillington FA (1994) Interannual scales of variation of pigment concentrations from CZCS data in the Benguela upwelling system and the subtropical convergence zone south of Africa. Journal of Geophysical Research 99: 7385 – 7400
- Wefer G, Fischer G (1991) Annual primary production and export flux in the Southern Ocean from sediment trap data. Marine Chemistry 35: 597 – 613
- Wilkerson F, Dugdale R (2008) Coastal upwelling. In: Capone D, Bronk D, Mulholland M, Carpenter E (eds) Nitrogen in the Marine Environment, second ed. Elsevier, New York, p 771 – 807
- Wilson C, Coles VJ (2005) Global climatological relationships between satellite biological and physical observations and upper ocean properties. Journal of Geophysical Research, 110, C10001, doi:10.1029/2004JC002724
- Zahn R (2010) Investigating the Global Impacts of the Agulhas Current. Eos, Transactions, American Geophysical Union 91(12): 109 – 116