The relationship between coastal oceanographic variability and the spatial distribution of *Argyrosomus coronus* on the west coast of southern Africa

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I know the meaning of Plagiarism and declare that all of the work in the document, save for that which is properly acknowledged, is my own.

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Abstract

The northern Benguela, under the influence of the opposing forces of the poleward Angola Current and the eastern boundary Benguela upwelling regime is a highly variable environment. The impact of climate change, especially in warming water temperatures and the shifting position of the Angola Benguela Frontal Zone (ABFZ), may be compounding this variability. Biological responses such as shifts in temperate species away from the warming mid latitudes, towards the cooler poles are becoming evident. This study aimed to quantify the effects of these changes (in terms of temperature, dissolved oxygen and salinity) on the spatial distribution of an important inshore commercial, artisanal and recreational fishery species in the northern Benguela, *Argyrosomus coronus* (west coast dusky kob). The ability of MODIS Terra and Aqua sea surface temperature data to represent nearshore temperature variability with limited satellite estimation error (Terra: +0.76 ± 1.06°C; Aqua: +0.85 ± 0.85°C) overcame the paucity of *in situ* temperature data. World Ocean Atlas (WOA) data as well as Regional Ocean Model System (ROMS) BIOgeochemical model of the Benguela Upwelling System (BIOBUS) outputs were used to represent salinity, dissolved oxygen and temperature data at depth. The optimum ranges (accounting for >95% of CPUE values above 0.01fish per angler-hour) of the selected environmental variables for west coast dusky kob were estimated in terms of temperature (16-22°C), salinity (35.4-35.6) and dissolved oxygen (190-206mmol.m^{-3}). Surface Temperature (measured relatively easily throughout the region, at a high spatial resolution (2x2km) and a known accuracy) was identified as the best suited environmental variable to determine spatial variability of *A. coronus*. A warming trend of over 0.8°C.$decade^{-1}$ faster than the global mean (0.07°C.$decade^{-1}$), as well as a southerly shift (~0.9° latitude) in the 22°C isotherm were identified in the region over the last decade (2000-2010). The high rates of warming particularly in the inshore (<200m depth) regions between 15.5-17°S and 18.5-20°S indicated areas of potential warming hotspots. As a similar warming trend exists in the Pathfinder reanalysis data (25 year period) this warming may exist outside of the known decadal variability of the region. If these warming rates continue *A. coronus* is expected to undergo a southerly shift in its spatial distribution. A more accurate understanding of the nature of this distributional shift will only be possible if inshore and nearshore monitoring programmes of temperature, salinity and dissolved oxygen throughout the water column and within the identified warming hotspots are established as a matter of urgency.

Chapter 1

Introduction

1.1. Climate change impacts

According to the fourth IPCC assessment report, the fact that climate change is occurring at an unprecedented rate is unequivocal (IPCC 2007). While regional differences are evident, on average the earth's land, air and sea temperatures appear to be warming (IPCC 2007). The effects of this temperature rise on global biota are varied; however one of the most noted biological responses is a shift in distributional range. A global trend, which has become increasingly evident, is a shift in temperate species away from the rapidly warming mid latitudes and towards the cooler poles (Parmesan and Yohe 2003, Parmesan 2006, Pörtner and Knust 2007, Loarie *et al.* 2009, Burrows *et al.* 2011). This is especially true in marine environments where the effects of warming are compounded by the negative relationship between dissolved oxygen solubility and temperature. Fish, for example, experience a mismatch between a higher oxygen demand, resulting from increased rates of physiological processes in warming waters, and the amount of oxygen available for respiration (Wootton 1990, Pörtner and Knust 2007). This highlights the limiting effects of temperature on the aerobic scope of marine organisms (Pörtner and Knust 2007).

In order to ensure sustainable exploitation of marine resources in the face of global change, the scale of species specific distributional shifts will need to be determined and management plans will have to take these shifts into account (Link *et al.* 2010). Predicting an organism's response to environmental change requires an understanding of the nature and variability of its surroundings. Recent warming trends in the northern Benguela provide an opportunity for an investigation into the response of marine organisms to this change. This study explores the effects of this localised warming on the spatial distribution of *Argyrosomus coronus*. In order to undertake such an investigation, a sound understanding of the physical and biological aspects of the northern Benguela is necessary.

1.2. Oceanography:

1.2.1. The modern Benguela Current System

The Benguela Current system is highly productive, with the majority of the surface currents flowing northwards along the southern African west coast (Shillington *et al.* 2006). Along with other major eastern boundary current systems of the world (Humboldt, Canary and California) the Benguela upwelling regime is characterised by the upwelling of cold, nutrient rich, subthermocline waters to the coastal surface layer. This upwelling is thought to be the primary driver of production in the region (Hardman-Mountford 2003, Shannon 2006). The Benguela Current Large Marine Ecosystem (BCLME) has evolved over millennia into its modern form, a dynamic system which experiences seasonal and inter-annual variability in intensity and location of oceanographic features and processes (Hardman-Mountford 2003). The BCLME is set apart from other eastern boundary systems as it is bounded on both its northern and southern extremities by warm currents, the Angola Current in the north and the Agulhas Current in the south (Figure 1.1) (Shannon and Nelson 1996, Shannon 2006, Shillington *et al.* 2006). The poleward flowing Angola Current and the eastern boundary Benguela Current converge in the northern sector of the BCLME, at the Angola-Benguela Frontal Zone (ABFZ) (Figure 1.1). The convergence of these warm and cold water masses create areas of strong thermal gradients know as frontal regions. The geographic positions and intensities of these frontal regions are determined by the relative current strengths, thus controlling the influence of warm water intrusions into the cool current regime and vice versa (Veitch *et al.* 2006, Monteiro *et al.* 2008).

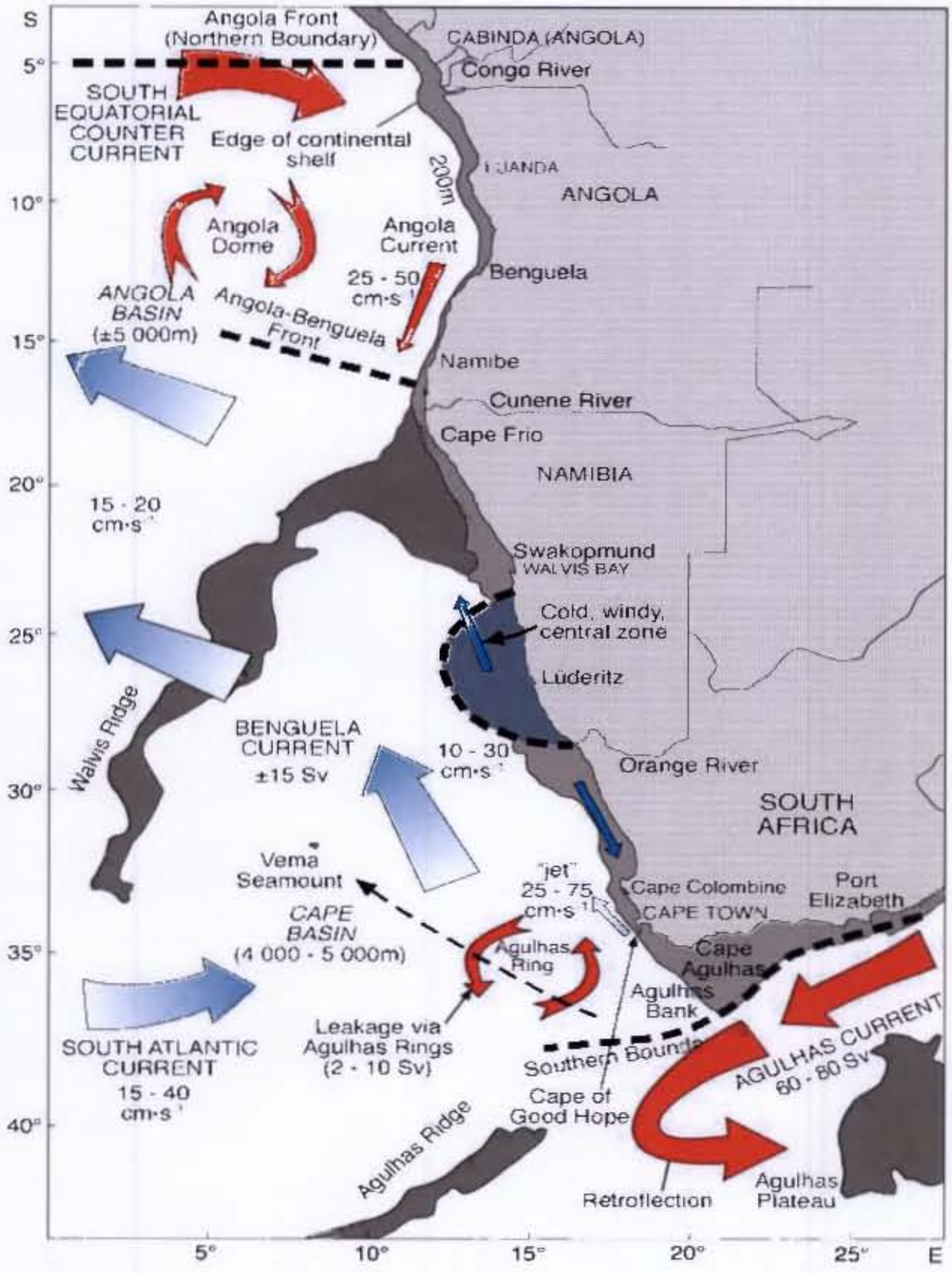


Figure 1.1 The Benguela current large marine ecosystem, and its associated boundaries, features and processes as presented by Shannon (2006).

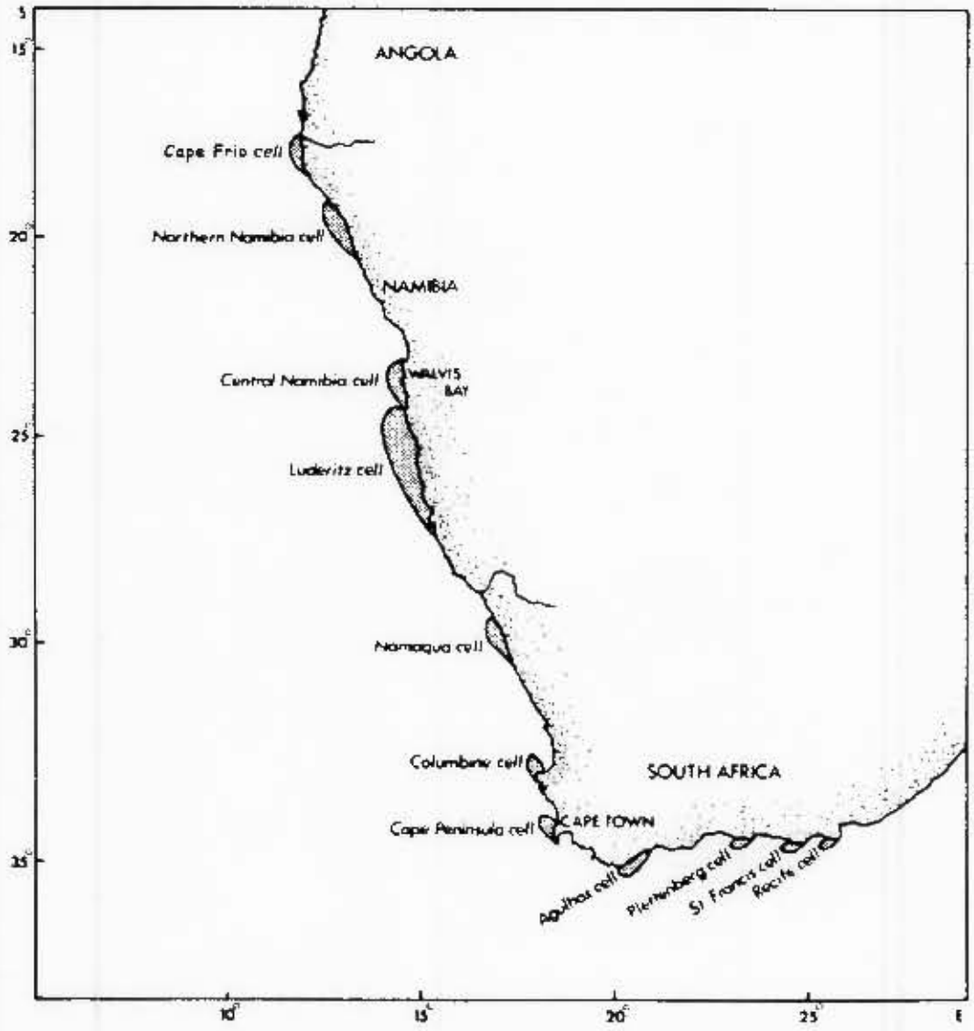


Figure 1.2 The coastal, wind-driven upwelling cells of the Benguela System. The Luderitz cell separates the northern and southern regions of the Benguela upwelling regime, and is one of the world's largest wind driven cells. (Adapted from Duncombe Rae *et al.* 1992)

The Benguela current system can be viewed as two separate branches (Veitch *et al.* 2010), an approach which has been adopted for this study.

1.2.1.1. Inshore Branch: Benguela upwelling regime

The inshore branch of the Benguela system is regarded as the coastal upwelling regime extending from 16°S to the southern tip of Africa, and incorporating a number of wind-driven upwelling cells (Shannon 1985, Veitch *et al.* 2010, Figure 1.2). The offshore boundary of the upwelling regime is defined by the edge of upwelling fronts and filaments which extend seaward with zonal orientation, downstream of the upwelling cells (Shannon and Nelson 1996, Veitch *et al.* 2010). The offshore front is well defined in the southern sector of the coastal upwelling regime along the shelf edge, however in the northern sector the upwelling front is more diffuse (Shannon and Nelson 1996). The course of the eastern boundary flow

associated with the coastal upwelling regime is known to be topographically steered (Veitch *et al.* 2010), while the Ekman pumping is driven by meridional wind stress (Colberg and Reason 2006).

In response to the equatorward surface flow of the coastal upwelling regime in the Benguela system, a poleward under current (PUC) exists following the shelf edge (Veitch *et al.* 2010). The sub surface current is the result of the balance between the Sverdrup relation and the windstress curl (Shannon 1985, Veitch *et al.* 2010), and supplies phosphate and silicate to the upwelling areas from the Angola current region (Berger and Wefer 2002). Monteiro (1996) argued that the undercurrent does not flow continuously between the northern, central and southern sectors of the Benguela Upwelling System, but rather that that it is diverted off the shelf at sites of vigorous upwelling cells which form barriers between the different sectors. Three sites of vigorous upwelling are Cape Frio (18°S), Luderitz (27°S) and Olifants/Columbine (~32°S) (Figure 1.2), all of which experience strong and constant equatorward wind stress along a narrow shelf. The majority of the undercurrent is composed of South Atlantic Central Water, which is present as part of the undercurrent throughout the Benguela Upwelling system. However each sector of the system has its own unique source of SACW (Monteiro 1996). Monteiro (1996) labelled the three sector dividers "gates" where cold, fresh SACW flows onto the shelf. This SACW is then entrained into the PUC and upwells at the relative upwelling centres of that particular sector. In turn the upwelled water is modified and becomes part of the north westerly Benguela surface flow. The cross shelf sheer at each gate site between the diverted SACW and the fresh, new SACW flowing onto the shelf results in an environmental barrier forming between the sectors. However, Monteiro (1996) noted that the environmental barriers associated with the gate sites can break down during periods of weakened upwelling, possibly caused by El Niño southern oscillation (ENSO) related events or seasonal variability. The breakdown of such barriers would allow continuous poleward transport between the sectors along the shelf edge, and possibly facilitate intrusions of low oxygen water (LOW) into the central and southern Benguela.

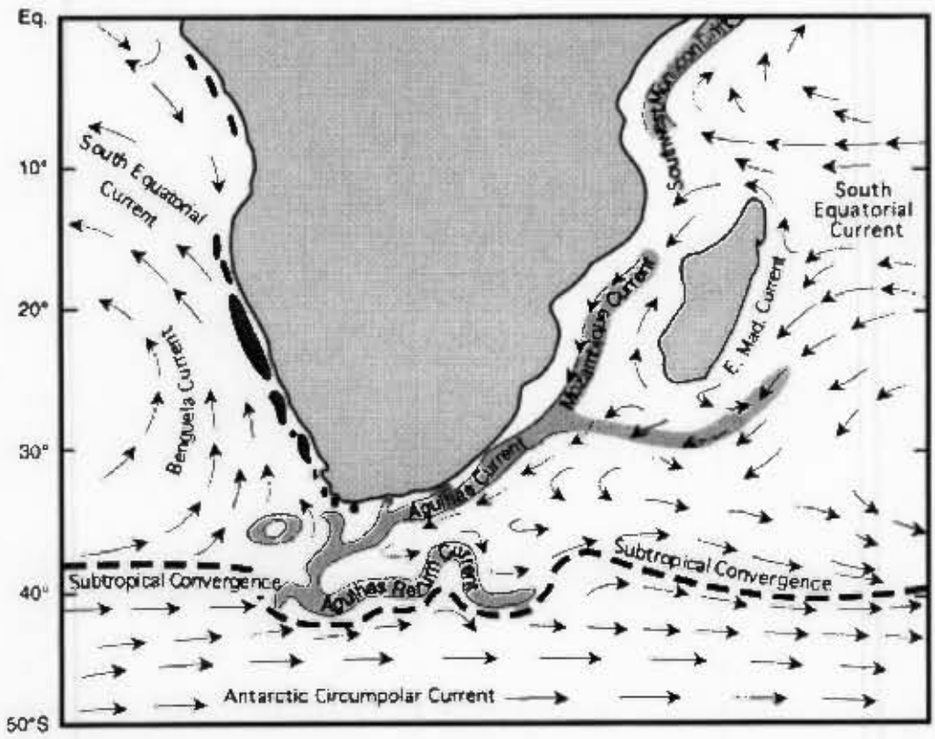


Figure 1.3 The oceanographic climate of southern Africa. The western boundary, Agulhas Current flows along the east coast of southern Africa, while the cool, eastern boundary, Benguela Current flows along the west coast, forming the eastern limb of the south Atlantic sub tropical gyre. The coastal cells of the Benguela upwelling regime are indicated by the shaded areas along the west coast. (from Lutjeharms *et al.* 2001).

1.2.1.2. Offshore Branch: Benguela Current proper

The second branch of the Benguela system is the offshore meandering flow in which Agulhas rings have been shown to interact, known as the Benguela Current (Monteiro *et al.* 2008, Veitch *et al.* 2010). This equatorward flow forms the eastern boundary of the South Atlantic Sub Tropical Gyre, veering west in an offshore direction at 20-26°S (Berger and Wefer 2002, Veitch *et al.* 2010, Figures 1.1, 1.3).

It is necessary to define the oceanographic regions and spatial scales that will be referred to throughout this study. The inshore area is considered as the region extending seaward from the high tide mark to the edge of the continental shelf (200m isobath); this area is also described as coastal waters or the coastal ocean (Molles 2005). The nearshore is considered to be the zone extending from the high tide mark in an offshore direction beyond the surfzone, and includes waters under the influence of nearshore or longshore currents (Mangor 2001, Figure 1.4). The offshore region is synonymous to the oceanic zone, the area of open

ocean, which exists beyond the continental shelf (Smith and Heemstra 2003, Molles 2005, Figure 1.4).

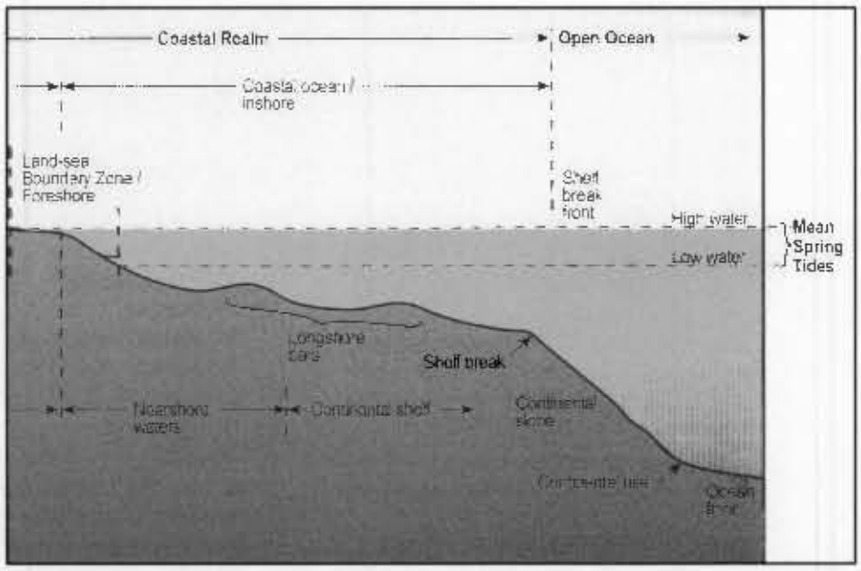
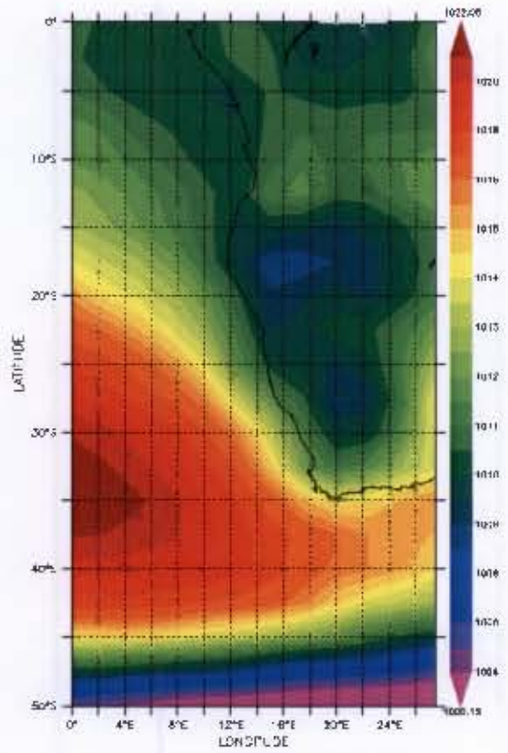


Figure 1.4 The different zones and boundaries of the coastal ocean. (Adapted from Roff and Zacharias 2011).

The cells of the Benguela upwelling regime are divided into the southern (Cape Peninsula, Cape Columbine and Namaqua upwelling cells) and northern sectors (Central Namibian, Northern Namibian and Cape Frio cells); with the Luderitz cell separating the northern and southern regimes (Monteiro 1996, Lutjeharms *et al.* 2001, Veitch *et al.* 2006, Veitch *et al.* 2010). The northern and central sectors, subjected to constant southerly windstress, experience perennial upwelling (with a slight maximum in the northern sector in austral winter) while upwelling events in the southern sector are governed by the seasonal migration of the South Atlantic Anticyclone (SAA, high pressure cell) and predominantly occur in the austral summer, when the atmospheric pressure system attains its southernmost position (Lutjeharms *et al.* 2001, Veitch *et al.* 2006). The narrow shelf at Luderitz and the constant southerly windstress makes this the strongest and possibly the most vigorous wind driven upwelling cell globally (Shannon 1985, Hardman-Mountford *et al.* 2003, Shannon 2006, Veitch *et al.* 2010, Figure 1.5).

a)



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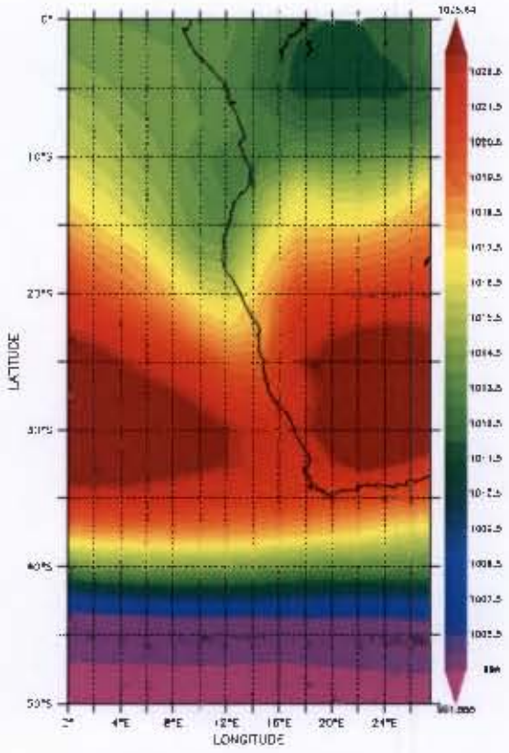


Figure 1.5 Mean sea level pressure (millibars) distribution in the Benguela system as averaged for a) summer (January) and b) winter (July) conditions. Images are constructed from the National Centre for Environmental Prediction (NCEP) reanalysis data, via the National Virtual Ocean Data System (NVODS) (NVODS 2011).

The northward transport of the Benguela Current over the Walvis ridge has been described by Garzoli and Gordon (1996) to be approximately 13Sv (1 Sv=1x106$m^3.s^{-1}$). The authors describe the water mass composition of the offshore limb of the current as comprising of roughly 50% South Atlantic Central Water (SACW), 25% Southern Indian Ocean Central Water (SICW) and 25% Tropical Central water from both the Agulhas and tropical Atlantic (Wedepohl *et al.* 2000, Shannon 1985). SACW upwells from approximately 200m below the surface with a salinity of 34.7-35.65 and temperatures between 8 and 16°C (Shannon and Nelson 1996 Mohrholz *et al.* 2001, Duncombe Rae 2005). Angola current water (24°C and salinity of 36.4) is present in the upper mixed layer of the water column in the northern Benguela, and extends southwards to 14-17°S during seasonal migrations of the Angola-Benguela Frontal Zone (Meeuwis and Lutjeharms 1990, Lass *et al.* 2000, Veitch *et al.* 2010). Agulhas rings transport heat and salt into the realm of the cold Benguela at the southern boundary where pockets of water of a salinity of 34.45, temperatures between 24 and 28°C and relatively low oxygen, travel equatorwards (Shannon and Nelson 1996, Hardman-

Mountford *et al.* 2003). Water masses form distinct boundaries on the shelf slope and are relatively easily identified however, as they become entrained into the inshore upwelling regime they are less distinguishable due to the mixing and upwelling processes (Monteiro *et al.* 2008). Seasonal hypoxia, which can have dire effects on the local taxa, is known to occur in the northern Benguela especially, and is related to the mixing of oxygen depleted water onto the continental shelf (Monteiro *et al.* 2008).

1.2.2. Angola-Benguela Frontal Zone (ABFZ) Seasonality

The Benguela system as a whole undergoes extensive seasonal variability in transport velocity, upwelling intensity and productivity (Hardman-Mountford *et al.* 2003). Seasonal variability in strength and position of the system boundaries is evident (Hardman-Mountford 2003, Veitch *et al.* 2006). This is especially true at the ABFZ, where the position and intensity (thermal gradient) of the front are determined by the relative strengths of the equatorward flow associated with the upwelling regime, and the poleward flow of the Angola current (Colberg and Reason 2006). These opposing forces determine the advance or retreat of associated warm (~24°C), saline (~36.4) Angola current water in the northern Benguela (Meeuwis and Lutjeharms 1990, Colberg and reason 2006). This seasonal displacement, between 14 and 16°S affects fisheries and rainfall in the region (Meeuwis and Lutjeharms 1990). Variability in the equatorward flow of the upwelling regime is governed by seasonal fluctuations in upwelling intensity driven by southerly wind stress, while the intensity of the Angola current is driven by the strength of negative wind stress curl maxima at the coast and the resulting geostrophic flow from the north-west (Colberg and Reason 2006). The offshore Benguela current is too subject to seasonal variability, flowing faster in the winter and spring (Garzoli and Gordon 1996). During the summer the Angola-Benguela front reaches its southernmost position where it extends approximately 300km offshore in a zonal direction and exhibits a well defined thermal gradient. The front is most intense in the surface layers (50m) and decreases in definition with depth, until 200m where it is no longer distinguishable (Shannon *et al.* 1987, Hardman-Mountford 2003). Over winter the contrary is true and the front is less intense reaching its northern most position, where its zonal offshore extent is approximately 200km (Meeuwis and Lutjeharms 1990, Colberg and Reason 2006). The location of this front, however, is not only defined by seasonal variability as it has been known to be located further to the north and south of its expected seasonal position. This variability may be linked to extreme events in the coupled ocean-atmosphere system.

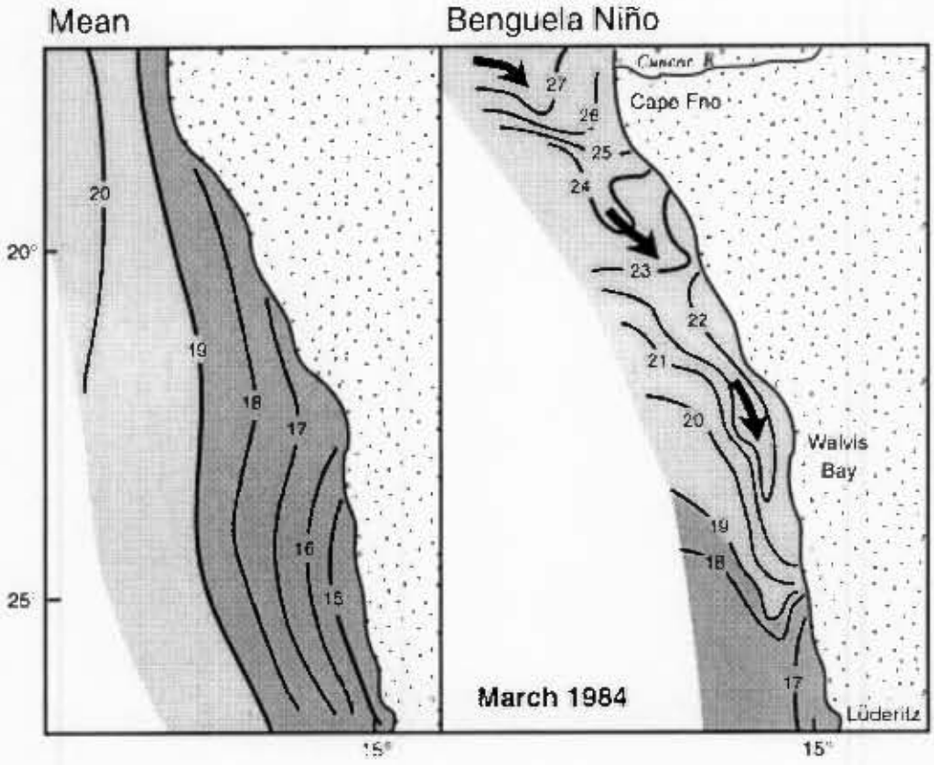


Figure 1.6 Mean surface temperature conditions off the west coast of Namibia (left) compared to those during the 1984 Benguela Niño event (right) (Image adapted from Lutjeharms *et al.* 2001).

1.2.3. Benguela Niños

The typical seasonal cycle of the ABFZ can be amplified, this occurs roughly on a decadal scale and most notably during the southerly displacement of the front, when the Angola current is strengthened and the upwelling cells of the northern sector are weakened (Mohrholz *et al.* 2001, Hardman-Mountford 2003). These amplifications are thought to be as a result of coupled ocean-atmosphere teleconnections with El Niño-Southern Oscillation (ENSO) perturbations (Colberg and Reason 2006). During such events, extreme intrusions of Angola current water enter into the northern Benguela resulting in a deepening of the thermocline and uncharacteristic warming along the Namibian coast as the frontal zone moves as far a 25°S (Mohrholz *et al.* 2001, Figure 1.6). Although the short term intra-annual mobility of the front is a result of meridional movements and seasonal weakening of the South Atlantic Anticyclone (SAA) trade wind belt (Colberg and Reason 2006), the exact mechanisms behind the inter-annual warming events are not fully understood (Florenchie *et al.* 2004, Rouault *et al.* 2007). These large scale warming events have been termed Benguela

Niños due to their likeness to their pacific counterparts (Shannon *et al.* 1986) which have a similar variability pattern, although the Pacific El Niños are stronger and more frequent (Florenchie *et al.*, 2003). Benguela Niños are seen as a chain of ocean-atmosphere coupled events occurring across the Atlantic basin which result in anomalously warm sea surface temperatures (SST) occurring along the coasts of southern Angola and Namibia (Florenchie *et al.* 2003). These warm events occur roughly two months after a sudden relaxation of zonal wind stress in the western equatorial Atlantic which, in some cases, has been linked to forcing through the El Niño Southern Oscillation (Florenchie *et al.* 2004, Figure 1.6). An equatorially trapped Kelvin wave is excited by the relaxation of the westerlies, and moves along the oceanic thermocline, also propagating in an easterly direction (Florenchie *et al.* 2004, Rouault *et al.* 2007). On hitting the west coast of Africa, the Kelvin wave becomes coastally trapped and spreads southwards (and northwards) along the coast. The extreme warm events, such as those of 1984 and 1995, took place during the late summer (February-March), early autumn (Florenchie *et al.* 2003), when the Inter-tropical convergence zone (ITCZ) over south western Africa is at its southernmost position, approx. 5°S (Reason *et al.* 2006), and the ABFZ is at its widest (Veitch *et al.* 2006). It is under these conditions that the seasonal intrusion of warm Angola current water into the northern Benguela region takes place, (Peterson and Stramma 1991) however, when combined with the influence of the coastally trapped wave and its anomalously warm water, the intrusion can be amplified. Although the southerly extent of such warming events is relatively easily identified through satellite SST imagery, when reviewing Sea surface Height (SSH) measurements over these periods it was found that pockets of anomalously warm water may have travelled along the subsurface thermocline and reached as far as 27°S where they were upwelled at the Luderitz upwelling cell, much further than the 20°S estimated using SST (Hardman-Mountford *et al.* 2003).

In contrast, during occasions when the equatorial trade winds strengthen, upwelling cells are intensified, similar to the Pacific La Niña. These events have been termed Benguela Niñas. Such events result in cool SST anomalies spreading equatorwards along the northern Namibian and Angolan coasts (Florenchie *et al.* 2003). During anomalously warm events the Kelvin wave arriving at the west African coast is in a downwelling form which suppresses the thermocline and enables warm sea surface temperature anomaly to spread along the coastline and intrude further south than the ABFZ (Hardman-Mountford *et al.* 2003). The opposite is the case during cold events where the Kelvin wave arrives at the coast as an

upwelling wave and acts to enhance upwelling. This results in a strengthening of upwelling at the ABFZ and along the Angolan coast.

During anomalous events there is a change in environmental conditions throughout the water column and the ecosystem responds in different ways. In the case of the warm events of 1984 and 1995 the economically important sardine populations found within the Namibian fishing grounds, followed their preferred oceanographic regime and food source, shifting south (Gammelsrød *et al.* 1998, , Binet *et al.* 2001, Florenchie *et al.* 2003, Shannon *et al.* 2008).The Namibian sardine fishery subsequently failed with catches falling from 1.3 million tons in the 1960s to less than 100 000 tons in the 1980s and 1990s, while the South African pelagic fishery of anchovy (1980s) and later sardine (1990s-2000s) prospered (van der Lingen *et al.* 2006a, Hutchings *et al.*2009, Figure 1.7). It is important to note that these stocks had been heavily over exploited prior to the persistence of unfavourable oceanographic conditions and were thus vulnerable to further decline. Furthermore, these unfavourable conditions may have contributed to the lack of recovery of the Namibian sardine fishery, together with continued high fishing pressure and the increase in abundance of species such as horse mackerel and jellyfish.

Both warm and cold events have been known to result in large-scale ecosystem effects which can have drastic consequences for the hugely important pelagic fisheries of Angola, Namibia and South Africa (Shillington *et al.* 2006). Although there is no information available, it is thought that the inshore linefish species in this region may show similar trends, with their southern displacement resulting in their being targeted by neighbouring fisheries. Since the 1970's extreme warm events have increased in strength and intensity (Binet *et al.* 2001). Largescale ecosystem effects relating to the increase in warm event have been observed and further change is expected if such warming continues (Binet *et al.* 2001, Shannon *et al.* 2003, Shannon *et al.* 2008). It is important to understand whether the observed fluctuations in the oceanographic conditions and the resulting biological responses have always been the case in this system, or whether they are the result of recent changes in the global climate.

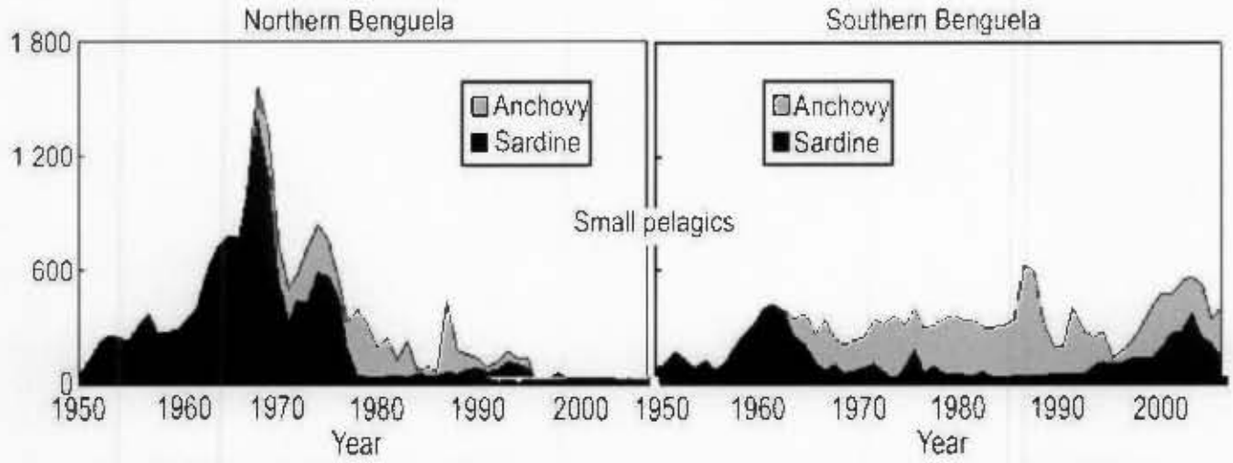


Figure 1.7 The variability in total catch per annum of sardine and anchovy in the northern Benguela (adapted from van der Lingen *et al.* 2006a, Hutchings *et al.* 2009).

1.2.4. The history of the Benguela Current System

The dynamics, variability and structure of the Benguela current as described above are very different from the oceanographic conditions off the south west coast of Africa which existed historically. A number of important events and developments have occurred during the last 130Ma (Mega annums, million years) which have shaped, what began as a 'dead' global ocean basin; into the dynamic and productive system we now call the Benguela. Understanding the formation process behind the modern Benguela current system may help to understand existing changes in the region and provide some insight into how the current may react to potential changes in the future.

The formation of the South Atlantic Basin began approximately 130Ma as Gondwana rifted and the South American and African plates separated (Shannon 1985). The basin widened with time as the continental plates drifted further apart. It was only during the early to mid tertiary (30-60Ma) (Figure 1.8) that the basin exhibited sufficient zonal extent to allow wind and ocean circulation processes similar in character to modern features (Kennet 1978). At this time warm water conditions existed throughout the water column (Shannon 1985).

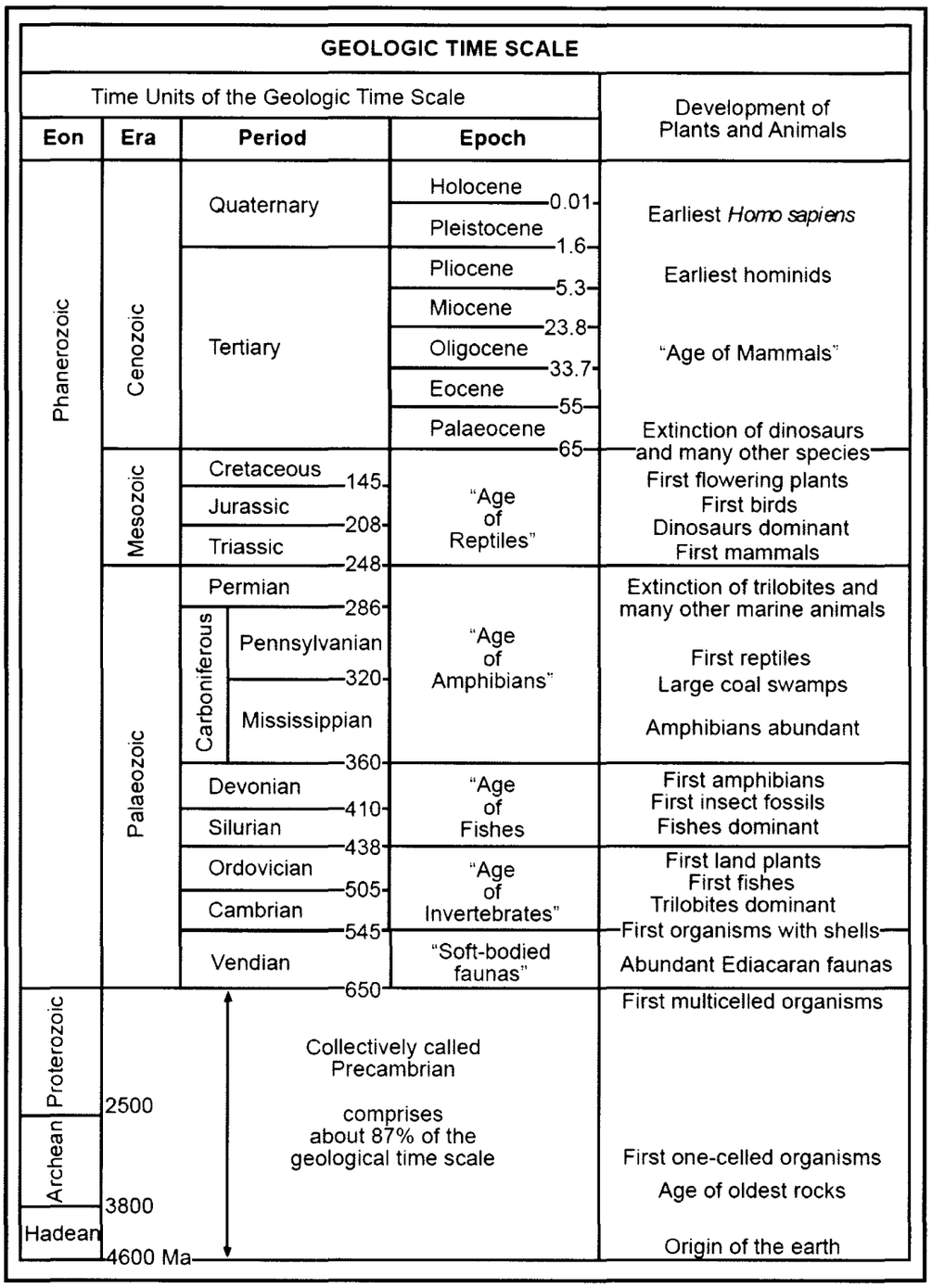


Figure 1.8 The geological time scale, units are mega annums (millions of years) (Waikato 2011).

Processes similar to those of the modern Benguela system occurred along the west African coast even during the Eocene times (Figure 1.8). As the south Atlantic gyre is believed to have been well established since the Eocene (55-36 Ma), an equatorward surface current has been present along the African coast for approximately 50 million years (Shannon 1985). This current, together with the south easterly wind stress would have resulted in a form of

upwelling along the coast, although only of warm waters (as the entire water column of the basin was still warm).

Bottom waters in the south Atlantic basin began cooling approximately 33Ma at the Eocene-Oligocene boundary, with the formation of Antarctic sea ice (Kennett 1978). This cool bottom water was then entrained into the early Benguela system and the resulting temperature differential in the water column was the basis for the beginning of modern thermohaline circulation. The next significant event in the development of the early Benguela was the establishment of modern upwelling. This meant that cool subthermocline waters were uplifted into the surface layers, rather than the simple mixing of warm water that had taken place thus far. The estimate of the initiation of upwelling in the historic Benguela region is based on the analysis of productivity indicator measurements calculated from drilled sediment cores (Siesser 1980). Much discussion exists in the literature as to the exact time period associated with the commencement of upwelling in the Benguela region; however the majority of authors agree that it coincided with the northward extension of the Benguela current to the Walvis ridge which occurred during the Miocene approximately 10 Ma (Siesser 1980 Diester-Haass *et al.* 2002). The changes in the Benguela were mirrored globally and similar increases in productivity were seen over the same period in the tropical eastern Pacific, western and northern Pacific as well as the Indian Ocean (Diester-Haass *et al.* 2002). In most cases, if not all, large biogenic blooms are suspected to have given rise to widespread increases in marine productivity as a result of global paleo-oceanographic and climate changes (Diester-Haass *et al.* 2002). The changes in paleo-climate and the cool oceanographic current are evident in the establishment of the Namib Desert between 8 and 5 Ma as the adjacent oceanographic conditions continued to cool (Ward *et al.* 1983, Krammer *et al.* 2006).

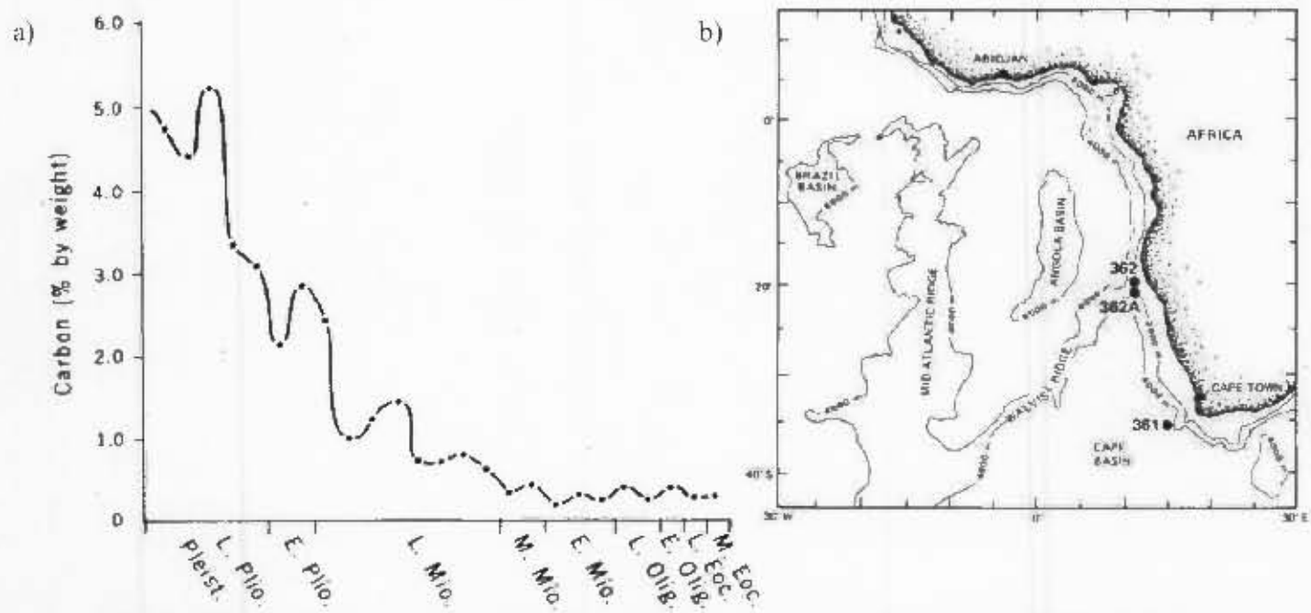


Figure 1.9 a) The percentage of organic carbon content in drilled cores from DSDP site 362/362A (~20°S, 12.3°E) leg 40 of the DSDP, b) the location of the drilling sites from Siesser *et al.* (1980) and Erdman and Schorno (1978).

After the initiation of upwelling, the intensity of this process in the region appeared to steadily increase (Siesser 1980). Modern features of the current and upwelling system migrated progressively northwards along the coast during the late Miocene and Pliocene as the oceanic and atmospheric circulation systems strengthened (Diester-Haass *et al.* 1990). As the South Atlantic Anticyclone (SAA, atmospheric high pressure) developed, during the late Pliocene (~2Ma), and south easterly wind stress on the west African coast intensified, coastal upwelling strengthened dramatically (Siesser 1980). Erdman and Schorno (1978) and Siesser *et al.* (1980) provided evidence of this significant increase in upwelling intensity through the analysis of organic content in sediment cores which showed a major increase at 2 Ma (Figure 1.9). The modern Benguela system and the associated rigorous upwelling of the inshore upwelling regime was thus established approximately 2Ma, since which time no significant changes have taken place in the processes involved in the system, although with the increase in extreme warming events such as Benguela Niños indicates an ecosystem shift may be underway (Shannon *et al.* 2003, 2008). In the past decade a number of successful environmental monitoring programmes have been initiated. One such example is the Benguela Current Large Marine Ecosystem (BCLME) programme, which has enabled investigations into environmental and biological change in the region.

1.2.5. Future changes in the BCLME

The Benguela current has an important influence on global climate through south-north heat exchange, including the transport of cool water towards the tropics and the distribution of warm Indian Ocean central water into the Atlantic through inputs via Agulhas rings (Hardman-Mountford *et al.* 2003, Shannon and Nelson 2006). Alterations to the typical behaviour of the system will therefore have an impact on global climate. When considering how the Benguela system has reacted to significant cooling or warming events in the past, one may gain insight into how the system may react under future climate change scenarios.

During past glacial events upwelling intensity increased (Diester-Haass *et al.* 1990, Berger and Wefer 2002). This is the result of a positive feedback between the intensification of atmospheric pressure gradients, increasing upwelling intensity, and the cooling of oceanic surface waters as a consequence of upwelling activity (Berger and Wefer 2002). The intensification of atmospheric pressure systems and the associated upwelling activity along the west African coast resulted in upwelling events occurring as far north as the Angolan basin (Diester-Haass *et al.* 2002). While during inter-glacial periods, the thermal gradient between the poles and the equator lessened, weakening the Benguela Current. Productivity indicators suggest that the current veered west in the Cape Basin, further south than the modern current (Krammer *et al.* 2006) (Figure 1.1, 1.3). The earth is presently experiencing an inter-glacial period however, due to anthropogenic effects on the global climate system climate related changes appear to be occurring at unprecedented rates (IPCC 2007). One of the results of the BCLME programme was the realisation that the Benguela System was currently experiencing a warming phase, as a result of weakened upwelling (Hutchings *et al.*2009). Furthermore, this warming appears to be occurring faster than expected, considering past warming phases.

Warming of temperate regions is occurring globally, and the present ecosystem response appears to be a poleward migration in temperate biota (Parmesan and Yohe 2003, Parmesan 2006, Pörtner and Knust 2007, Burrows *et al.* 2011). If the upwelling processes in the Benguela continue to weaken, the system will continue to warm and may eventually take on a form similar to that which was experienced during the last inter-glacial period. In addition to the general warming of the region an increase in extreme warming events, such as Benguela Niños would be expected. This would have significant effects on the biology of the region as the nature of habitats within the system will change considerably, and organisms may be forced to follow the global trend and track cooler temperatures by shifting to higher latitudes.

When considering the effects that oceanographic changes would have on the biology of the region it is important to consider the variable nature of the Benguela system, including the relative influences of its warm boundaries and the potential for extreme warming and cooling events. Exploring past trends in biological responses to changes in the system could provide insight into how organisms may react in the future.

1.3. Fisheries:

1.3.1. Trends in the fisheries resources of the Benguela

As the Benguela upwelling regime is one of the most productive in the world, the region supports many large fisheries (small pelagic, midwater, demersal and inshore species) (Hutchings 1992, van der Lingen *et al.* 2006a). Due to their significant economic value the offshore fisheries of the BCLME have historically dominated fishery as well as oceanographic related research. For this reason the offshore realm of the Benguela including trends in fishery yields from the system and the physical and biological drivers behind these trends are better understood than the nearshore (Figure 1.4) and shore based fisheries of the same system.

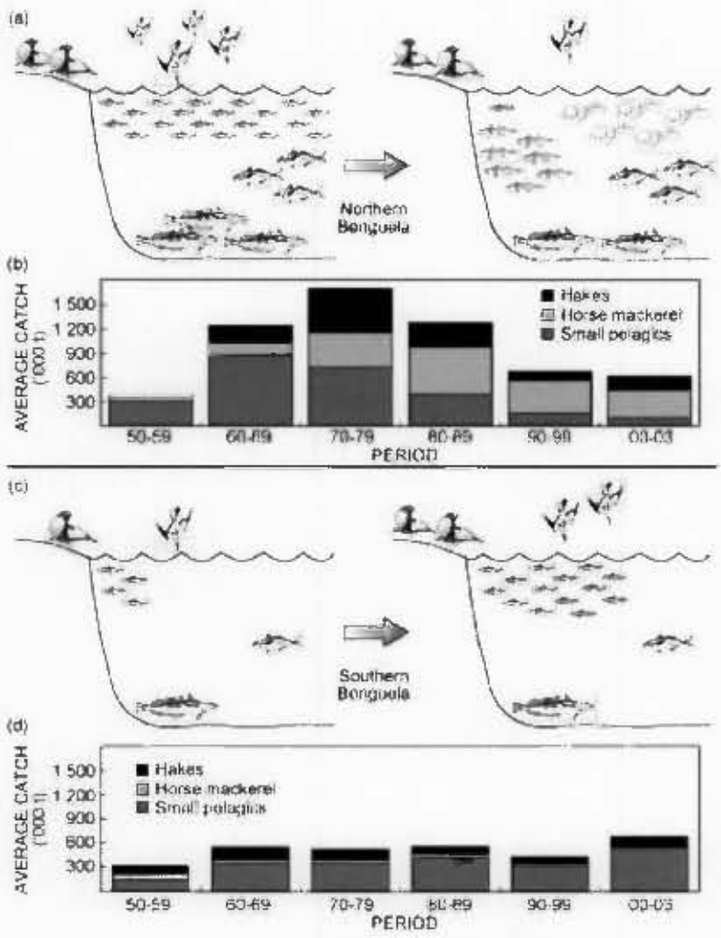


Figure 1.10 a,c) Visual schematics of the reported regime shifts in the northern and southern ecosystems of the Benguela region between the 1970's (left) and the present day (2000's). The number of living marine resources (small pelagic fish, horse mackerel, hakes, goby, jellyfish, Cape gannets and Cape fur seals) represents their relative abundance. b,d) Represent the average annual catches of three of the resources from the schematic (hakes, horse mackerel and small pelagic fish) on a decadal scale (expect for the last bar 2000-2003) for the northern (top) and southern (bottom) Benguela regions.

In recent years (Hutchings *et al.* 2002, van der Lingen *et al.* 2006a, Shannon *et al.* 2008, Hutchings *et al.* 2009) among others, have noted a shift in the distribution of catches of many of the offshore species (especially small pelagics), to the south and east of the South African coastline. Also noted is a regime shift in the northern Benguela system from an ecosystem dominated by pelagic biomass (sardine, anchovy) to one with a shorter mean trophic path which is dominated by biomass maxima in the mid-water regime (horse-mackerel, pelagic gobies), energy flows in the system are thought to have been further altered by the increase in the abundance of jellyfish (Shannon *et al.* 2003, Shannon *et al.* 2008, Hutchings *et al.* 2009, Figure 1.10). Reduction in system complexity, as described here, reduces the ecosystem's resilience to change or perturbations, which could lead to further degradation (Mora *et al.*

2007). The possible drivers behind the described regime shifts (Figure 1.10) are increases in intrusions of warm, saline Angola current water and LOW events associated with Benguela Niños. Historic over exploitation of resources, especially in the northern Benguela, is believed to have amplified the effects of these unfavourable environmental conditions (van der Lingen *et al.* 2006a). Biomass yields in the southern Benguela are now similar to those of the traditionally more productive northern sector (Figure 1.10). Regime shifts of this scale have had implications for the economies of Angola and Namibia adjacent to the northern Benguela as the fishing sector made up between 3 - 6.4% of their annual GDP (van der Lingen *et al.* 2006). The modifications of the Benguela system have been mirrored by changes in temperature, precipitation and atmospheric carbon dioxide concentrations in global systems, the exact outcomes of which are difficult to predict due to the complex interactions and feedback loops which exist between the processes involved (Barraclough *et al.* 2005). Barraclough and Davies (2005) stated that future global and local climates will differ in biologically significant ways from th

ose in which the current biota evolved. This becomes especially important when individuals of a given area are maladapted to the new conditions and their fitness is thus compromised. In the marine environment these changes can be accommodated through distribution and abundance shifts of existing populations, rather than the implementation of evolutionary responses (Tilman and Lehman 2001).

Studies conducted off the coast of Namibia suggest this may be the case as south and eastward shifting distributional ranges and local decreases in species abundances of seabirds, especially gannets and African penguins as well as the west coast rock lobster have been observed in the inshore region (Crawford 1998, Shannon *et al.* 2006, Shannon *et al.* 2008). These changes have, in some cases, been related to the offshore ecosystem changes. For example, the large increase in the number of Cape fur seals on the Namibian coast is thought to be linked to their ability to forage in deeper waters than the seabirds, thus taking advantage of the shifting trends in biomass (Shannon *et al.* 2008). In addition to the species mentioned above, recent changes in the distribution of an inshore linefish, the west coast dusky kob (*Argyrosomus coronus* (Griffiths and Heemstra 1995)) have been noted. Lamberth *et al.* (2008) describe records of *A. coronus*, caught far south of its distributional range, in the Olifants and Berg River estuaries, South Africa. It is thought that these individuals were displaced southwards after an anomalous warm event, the effects of which were exacerbated by hydrogen sulphide eruptions on the continental shelf in the northern Benguela.

Furthermore, there is evidence of a possible decline in the southern Angolan population of *A. coronus* as noted by Potts *et al.* (2010). The authors describe a decline in the catch rate of this species despite no change in the catch of other important recreational fishery species. In addition, an alarming reduction of the catch rate of adult fishes has been observed, compared with the other important species. Moreover, there appears to be an increase in the catch rate of this species further south, in northern Namibia, compared to historical data (Potts unpublished data). Taking the above mentioned evidence into account, a shift in the distribution of this inshore species may be evident, however the mechanisms behinds this distributional shift are not yet known.

1.3.2. Study species

Argyrosomus coronus, west coast dusky kob, (Figure 1.11) was selected for this study as it is spends the majority of its lifecycle in the near and inshore waters of the northern Benguela (Griffiths and Heemstra 1995, Potts *et al.* 2010). The sea surface temperatures of its distributional range have been found to have increased between 0.6 - 1°C since 1982 (Shannon *et al.* 2006, Monteiro *et al.* 2008, Shannon *et al.* 2008). As fish are poikilotherms (ectothermic), is important to understand how this species will respond to environmental change. Recent landings of *A. coronus* outside of its described distributional range (Griffiths and Heemstra 1995, Potts *et al.* 2010) may indicate aspects of this species' response.

Figure 1.11 Argyrosomus coronus, west coast dusky kob, the study species. Photograph courtesy of WM Potts.

1.3.3. Potential drivers of the distribution shift

When exploring possible physical drivers behind observed biological change it is important to understand the physical environment in which the species in question evolved, and subsequently adapted to. Recent genetic evidence describes the separation of several linefish species distributed in the northern Benguela and South Africa (Henriques *et al.* 2009).

Henriques *et al.* (2009) have determined that the populations of *Atractoscion aequidens* (geelbek) (Cuvier 1830), *Diplodus capensis* (blacktail) (Smith 1844) and *Lichia amia* (leervis) (Linnaeus 1758) in the northern Benguela are genetically separate to their respective South African populations. Genetic results from the same authors show that *A. coronus* and *A. japonicus* appear to have separated from a once continuous population of Argyrosomus spp. approximately 2Ma, with *A. coronus* now occurring in the northern Benguela and *A. japonicus* (Temmink and Schlegel 1843) on the south and east coast of South Africa (Griffiths and Heemstra 1995, Henriques *et al.*2009). Henriques *et al.* (2009) suggest the development of the Benguela upwelling regime, and specifically the Luderitz upwelling cell, which took on its modern form around 2Ma (see Oceanography section above), as the potential evolutionary mechanism driving the split of the now separated populations. If this is indeed the case, the modern distributions of *A. japonicus* and *A. coronus* may be governed by the fact that these species are only able to endure water temperatures within their evolutionary range. Physiological processes of poikilotherms evolve to function optimally within a specific environmental temperature regime; as a result these organisms are unable to function efficiently outside of their tolerable temperature range (Helfman *et al.* 2009). When a fish is exposed to temperatures above its thermal tolerance limit, it experiences an elevated metabolism and thus its oxygen demand increases. However in a warming ocean this problem is confounded as the solubility of oxygen decreases as the temperature rises, limiting the amount of oxygen available for metabolism (Pörtner and Knust 2007).

1.3.4. Influence of dispersion barriers of spatial distribution

Both *A. japonicus* and *A. coronus* have evolved in relatively warm waters, and therefore are not suited to exist in the cool waters of the Benguela upwelling regime (Griffiths and Heemstra 1995). This is especially true of the Luderitz upwelling cell, which is thought to be an evolutionary mechanism driving the relatively recent allopatric speciation event.

Major oceanographic features or processes act as potential barriers to distribution when, through differences in water mass properties, they cause discontinuities in temperature, salinity and resulting productivity (Macpherson *et al.* 2009). The development of oceanographic features or processes (such as upwelling cells, Figure 1.1, 1.2) may separate previously continuous populations of species through the formation of such barriers. The separated stocks then adapt to potentially different conditions on either side of the barrier which can ultimately result in speciation (Hemmer-Hansen *et al.* 2007). Hutchings *et al.* (2006) describe separate stocks of *Umbrina canariensis*, the canary drum, on the east coast of

South Africa. Movement between the stocks located on the Agulhas Bank and in Algoa Bay is restricted by cold water from the bottom mixed layer flowing along the narrowing continental shelf, these two stocks now show variations in life history traits as a result of adaptations to different environmental conditions (Hutchings *et al.* 2006). Dispersion barriers are not necessarily permanent and changes in climate can weaken the driving forces behind such barriers (e.g. wind stress) causing the barriers to break down (Harley *et al.*2006). This can have significant consequences for the spatial distribution of species as well as gene flows between regional fish populations (Potts and Gotz 2011).

The vigorous perennial upwelling characteristic of the Luderitz cell results in the offshore advection of pelagic eggs and larvae, exposing them to fatally low nutrient levels and turbulent conditions (Lett *et al.* 2007). This, together with the cool (12-18°C, Salat *et al.* 1992) water temperatures in the inshore region, pose a dispersion barrier to the longitudinal distribution of species between the northern and southern realms of the Benguela (Agenbag and Shannon 1988, Hardman-Mountford *et al.* 2003, Lett *et al.* 2007). The study species, which has pelagic eggs and larvae, is expected to be affected by such a barrier to pelagic dispersal. This is confirmed by the evidence presented by Henriques *et al.* (2009) who indicated that the study species and a congeneric species have been separated by this barrier for at least 2 million years. Similarly, in terms of adult distribution, *A. coronus* is restricted to regions within the range of its particular temperature tolerance. The persistent cool temperatures associated with the Luderitz upwelling cell, which extend throughout the water column at the coast, may well be below this the species' lower thermal tolerance limit and it is thought that the upwelling cell forms a barrier to range expansion even of adults.

The discovery of *A. coronus* individuals south of the Luderitz upwelling cell, in South African estuaries (Orange (28°S), Olifants (32°S) and Berg (33°S) River estuaries) suggests that the barrier is not a permanent feature, and it may experience periods of weakened upwelling, allowing adult individuals of the study species to move through it. A possible example of such an event is the seasonal intrusion of warm water from the Angola Current into the Benguela system (Hardman-Mountford *et al.* 2003). Amplifications of this seasonal event occur under Benguela Niño conditions and as a result the Luderitz upwelling cell is less effective as a barrier for the meridional interchange of pelagic species.

1.3.5. Influence of ocean variability on fish distribution

The effects of Benguela Niños and anomalous warm events have been noted throughout the ecosystem, and if their frequency continues to increase, additional changes to the Benguela ecosystems should be expected. Rising temperatures, which accompany Benguela Niño events (Figure 1.6), may be beyond the thermal tolerance level of some temperate fish species in the northern Benguela. Fish exposed to temperatures outside of their thermal tolerance limits become stressed and experience increased metabolic rates as well as changes to other physiological processes including membrane fluidity and organ function (Jensen *et al.* 1993, Helfman *et al.* 2009, Potts and Gotz 2011). The release of hormones in stressed situations enables the maintenance of normal physiological functioning, however only for a short period, after which the fish must move to a cooler environment to avoid mortality (Wootton 1990, Jensen *et al.* 1993, Helfman *et al.* 2009). Because of the thermal stability of water, warming or cooling processes are generally relatively slow and fish have time to adapt (Helfman *et al.* 2009).

Adult *A. coronus* seem to have adapted to seasonal temperature variability (Figure 1.12) by undertaking migrations in avoidance of the warm intrusions of Angola Current water into the northern reaches of its distribution (Potts *et al.* 2010). However, with the compounding effects of natural and anthropogenic induced climate change warm pulses of water into the northern Benguela where temperature changes can take place rapidly are increasing in frequency (Shannon *et al.* 2008). In order to cope with this change, fish such as *A. coronus* may respond by shifting the limits of their spatial distribution towards higher latitudes (northern Namibia), thus following cooler temperatures as has been noted in other temperate species (Parmesan 2006, Burrows *et al.* 2011). This could have significant effects on the inshore ecosystem of southern Angola, as west coast dusky kob is believed to be a key stone predator in the region (Potts *et al.*2010).

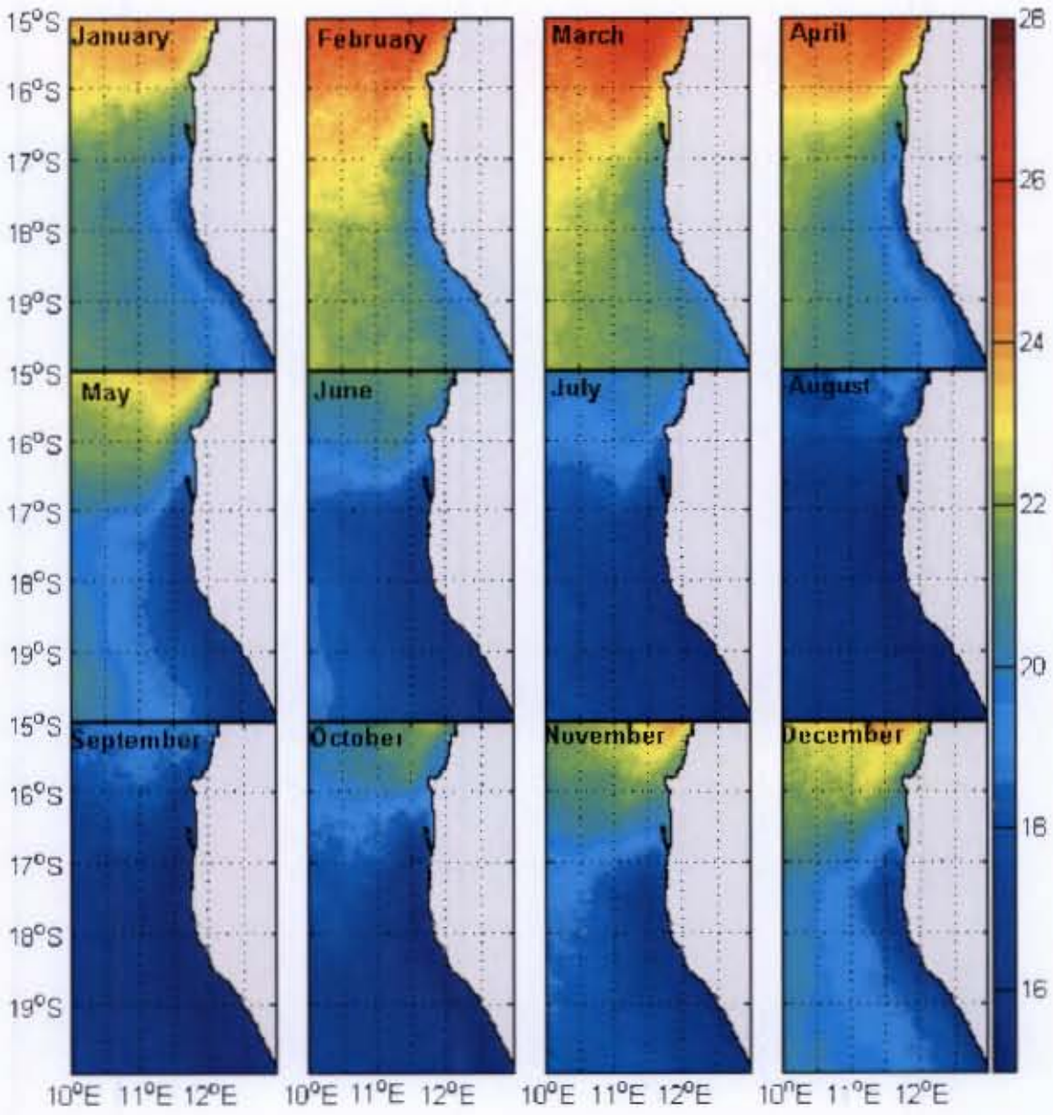


Figure 1.12 Monthly mean surface temperature variability in the vicinity of the Angola-Benguela Frontal Zone (ABFZ) (15-20°S, 10-13°E). The colour bar on the right indicates temperatures in degrees Celsius. 2x2km Resolution. Moderate Resolution Imaging Spectroradiometer (MODIS) sea surface temperature (SST) data from NASA's Terra satellite was used to create these images.

ENSO events in the eastern Pacific are known to have affected the distribution and abundance of tropical and temperate fishes (Macpherson *et al.* 2009). Tropical species specifically are noted to experience temporary range extension during El Niño events and there is evidence of changes in the composition of temperate species communities (Macpherson *et al.* 2009). van der Lingen *et al.* (2006) and Shannon *et al.* (2008) have described regime shifts in the northern and southern Benguela which they attribute to changes in the frequency and intensity of Benguela Niño events. Regime shifts of this nature are expected to become more permanent and widespread if warming events like Benguela Niños

continue their current increasing trend (Shannon *et al.* 2008). However the effects warming events have on ecosystem structure and function are only beginning to emerge and are still poorly understood. It is important to have an understanding of what changes could possibly take place in ecosystems such as the Benguela and how organisms may react to this change if we are to effectively manage marine resources.

1.3.6. Management

Many of the inhabitants of local communities situated alongside the Benguela current, as well as the economies of Angola, Namibia and South Africa, are dependent on the fisheries of the region. The most lucrative of these are the offshore small pelagic species (including anchovy, red eye round herring, sardine and sardinella), midwater species (including Cape and Cunene horse mackerel) and the demersal hake fisheries (Merluccius spp.) which support large fisheries infrastructure and employ thousands of people in Namibia and South Africa (van der Lingen *et al.* 2006a).

Local economies, however, are often dependent on inshore resources (such as linefish species); this is the case in Namibia where many coastal communities are driven by the recreational fishery, while in Angola the artisanal fishery provides much needed income in coastal regions (Stage and Kirchner 2005, Potts *et al.* 2009).These fisheries are generally of low economic value compared to those of a more commercial nature and therefore often lack scientific research and efficient managerial policies (Fidel 2005, Henriques *et al.* 2009). This can lead to a lack of understanding of local stocks, and ultimately overfishing of the resources, as has been the case in many South African and Namibian linefisheries (Brouwer and Buxton 2002).

Recreational fishers bring a large amount of foreign capital into the region from which the local communities benefit directly (Potts *et al.* 2009). In order to maintain the growth of the recreational sector of the west coast dusky kob fishery efficient and sustainable management strategies need to be implemented rapidly to avoid a decline in local stocks (Potts *et al.* 2009).

Changes in environmental limiting factors are often accommodated by shifts in the distribution or abundance of species rather than the implementation of evolutionary responses (Tilman and Lehman 2001). Pelagic life history stages, which are common in marine teleosts, enable populations to select for abundance and distributional changes ensuring the persistence of populations through range expansion or distributional shifts. Changes in the

distribution and abundance however, have species specific management implications. Increased mobility of fish stocks, especially in cases where stocks move across political borders, present resource allocation problems which may require negotiation and shared management solutions (King 1995). Management problems arise when there is a difference between the perceived stock size and location compared to the actual size and location. This is the case when a stock size apparently decreases in one area and increases in another, when in fact the stock size actually remains constant but shifts to a new location (Link *et al.* 2010). In this situation Link *et al.* (2010) advise monitoring of the newly positioned stock in order to obtain new parameters for management plans.

The west coast dusky kob fishery in southern Angola is dominated by artisanal and recreational stakeholders, and a southerly shift in the distributional range of this species would restrict the fisher's access to fishing grounds due to gear limitations or political boundaries (Potts *et al.* 2010). Besides the hypothesised decline in the artisanal and recreational catches in southern Angola, an increase in catches of west coast dusky kob in the well established recreational silver kob (*Argyrosomus inodorus*) fishery of northern Namibia are likely. The danger in increased fishing activity in the open access areas in northern Namibia is that the *A. coronus* stock would not have been assessed in this region rendering it vulnerable to rapid depletion (Link *et al.* 2010). Furthermore, the management measures in place in Namibia have been designed to preserve the fast growing and early maturing silver kob and would be not be suited to the slower growing and later maturing west coast dusky kob if they were to be found in the same waters.

If a shift in the distribution of the southern Angolan stock into Namibian waters in confirmed, an adaptive management plan will have to be developed, whereby the spatio-temporal changes in the distribution of *A. coronus* are taken into account. In the face of a changing climate on a global scale it is anticipated that regional conservation strategies will require the incorporation of climate change scenarios, and range shift predictions in order to allow effective management of threatened species through an understanding of changing ecological relationships (Link *et al.* 2010, Roff and Zacharias 2011).

In order to investigate recent warming trends in the northern Benguela and determine whether a southerly shift in the distribution of the study species may occur, it is necessary to explore water temperature variability on large temporal and spatial scales. Unfortunately *in situ* datasets of temperature are scarce in the inshore region of the northern Benguela and if

temperature changes are to be investigated on the required scales, a suitable dataset may have to be found from remotely sensed surface temperature estimates.

1.4. Remote sensing

As already discussed there is increasing evidence of the influence of natural and anthropogenic climate change acting on the Benguela current system. However the northern Benguela continues to be a data deficient region, especially in the inshore zone and the system's response to changing climatic forcing is currently not being captured by *in situ* data (Fidel 2005).

A solution to this problem could be found in the form of remotely sensed data, which enables the investigation of large spatial regions, on various time scales, with a known degree of accuracy, for offshore regions (Brown and Minnett 1999). The images received by a host of earth orbiting satellite sensors have transformed our understanding of aquatic and terrestrial environments (Grassl and Koepke 1981). Since the launch of the first earth observing satellite the capabilities and monitoring frequency of satellite sensors have increased rapidly. Scientists now have access to large datasets (often free of charge) for a wide range of parameters at varied temporal and spatial scales (Ewing 1981). The algorithms used during the processing of received data are constantly validated against *in situ* observations for land, ocean and atmospheric monitoring satellite sensors (Brown and Minnett 1999, MODIS 2011) thus ensuring an accurate end product throughout the life of the satellite sensor (Tabata 1981). If remotely sensed data is to be used with a known accuracy in the inshore region of the northern Benguela, a suitable *in situ* dataset with which to compare remotely sensed temperature estimates will have to be identified.

Despite the inhospitality of the coastline, a few nearshore temperature datasets do exist within the distribution range of *Argyrosomus coronus*. These can be used to calculate the accuracy of remotely sensed SST in the northern Benguela, after which the results can be used to explore the relationship between SST variability and the movement of the west coast dusky kob. Furthermore, once this relationship is known future distributional changes of this species may become clear.

1.5. Problem Identification

In summary, there is evidence to suggest that a spatial distribution shift of, *A. coronus*, may be taking place in southern Angola. It is thought that this species may be moving south into northern Namibia as a result of warming water temperatures in the Angola-Benguela Frontal Zone. As fish are ectothermic, and thus sensitive to temperature fluctuations, the recent warming of the region may be a reason for this response. This warming however, needs to be quantified in order to determine the extent of its possible effect on the spatial distribution of the study species as well as to identify possible future distribution changes. If the response of organisms to future environmental change is known, resource managers may be able to adapt management strategies accordingly and sustainable exploitation could be possible.

The specific aims of this study are presented in three Key Questions:

1. What is the most suitable satellite product to study surface temperature variability in the inshore zone of the northern Benguela, and what is the error associated with this product in coastal waters?
2. Explore fluctuations in catch rates of adult *A. coronus* in relation to environmental variability in southern Angola, and determine whether an environmental parameter could be used to determine the spatial distribution of the study species?
3. How rapidly are environmental conditions changing and what are the implications of these changes on the distributional patterns of adult *A. coronus* in the northern Benguela?

1.6. Structure of thesis:

This introduction is followed by Chapter Two which determines the most suitable satellite product to monitor the inshore environment of the northern Benguela and explores the accuracy of this product in the study region. The results of Chapter Two are then used in Chapter Three to examine the relationship between the catch per unit effort (CPUE) of *Argyrosomus coronus* at Flamingo Lodge in southern Angola and sea surface temperature variability. Chapter Four describes the observed oceanographic changes in the Benguela system and explores the possible effects of further environmental change on the distribution of the study species. As each of the above chapters concludes with a discussion the final chapter comprises general conclusions which summarise the findings of the study and provide recommendations for future research in the region.

Chapter 2

Assessing the accuracy of MODIS Aqua and Terra estimates of Sea Surface Temperature in the nearshore zone of the northern Benguela

2.1. Introduction to Key Question 1:

In order to explore temperature variability within the distribution range of *Argyrosomus coronus*, and the possible effects that this variability may have on the movement of the study species, a suitable inshore temperature dataset is necessary. Ideally a long term, daily temperature dataset where different depths and multiple locations are sampled is required. However, inshore oceanographic and particularly *in situ* data is largely unavailable (Fidel 2005) throughout the primary distribution of *A. coronus* (northern Namibia to southern and central Angola). This is largely due to the low (human) population density along the arid coastline. The Angolan civil war has further compounded this problem, as funding and personnel for oceanographic and biological monitoring has been scarce (Fidel 2005, Potts *et al.* 2009, 2010).

A solution may be found in the form of remotely sensed data. Cole and McGlade (1998) explained that satellite derived sea surface temperature (SST) imagery, in conjunction with chlorophyll A data, could successfully be used for the identification of oceanographic features and processes such as upwelling activity, frontal system dynamics and patterns of food abundance, which all affect the distribution of fish stocks. Recent improvements in satellite technology have lead to the development of a various satellite products which measure a host of different parameters. Each product has its own set of advantages and disadvantages in spatio-temporal coverage, resolution and accessibility, and the best suited product for measuring SST variability in terms of this particular study will have to be found. As *A. coronus* is an inshore species, the accuracy of the selected satellite product will need to be assessed in the inshore zone of the study region, especially because most validation and product calibration studies take place offshore (Tabata 1981, MODIS 2011). For this purpose an *in situ* temperature database will need to be identified. Satellite derived SST estimates can then be compared to *in situ* values in order to determine the satellite estimation error and calculate a correction factor, which would account for the calculated error of the satellite estimates. This value can be applied to the selected satellite dataset throughout the study region. In order to select the best suited satellite product for the study region, the limitations in the ability of such products to determine inshore temperature variability need to be determined.

2.1.1. Monitoring SST in inshore and nearshore environments

When investigating the accuracy of satellite SST estimations in variable environments such the Angola-Benguela frontal zone (ABFZ), it is important to test the robustness of remotely estimated SST values. Therefore a comparative study should be carried out which takes into account as many different states of this environment as possible. This includes making comparisons between satellite and *in situ* data throughout the year, during all seasons as well as during extreme warm or cold events, such as those known to occur in this region (Meeuwis and Lutjeharms 1990). Because of the high level of diurnal variability in the inshore environment of the northern Benguela (Hardman-Mountford *et al.* 2003) a comprehensive data set of *in situ* and satellite derived temperature observations measured on a daily basis throughout the year is required. More than one study site is also recommended in order to take into account any changes in the satellite's SST estimating capabilities with a change in latitude, or oceanographic conditions.

A range of satellite products that estimate SST of the inshore environment are available (Minnett *et al.* 2002, Ricciardulli and Wentz 2004). However, one historical short coming of marine monitoring satellites is that the algorithms used to calculate the parameter values as well as the poor resolution of available products result in inaccurate SST estimates in the nearshore regions (Ricciardulli and Wentz 2004). Various characteristics of the nearshore environment, which include steep temperature gradients, shallow water and close proximity to adjacent land, can result in interference with infrared and microwave measurements.

One reason for the decrease in accuracy can be attributed to scan angle effects (Pearce and Pattiaratchi 1997, Ricciardulli and Wentz 2004) where higher scan angles at the edges of the satellite swath, which is generally where coastal pixels are situated in this case and which can result in pixels becoming contaminated by atmospheric aerosols and water vapour. The close proximity to adjacent land masses also plays a role in decreasing the accuracy of satellite readings (Tanner and Volkman 2009). This is because infrared sensors measure infrared radiance emitted from the ocean surface, which is easily contaminated by heat from the adjacent land in nearshore waters (Tanner and Volkman 2009). The greatest influence of satellite SST accuracy however, is the atmospheric attenuation of outgoing radiance, where radiance is absorbed by water vapour and atmospheric aerosols before it reaches the satellite sensors (Tanner and Volkman 2009). In order to determine, and account for the relative influences of atmospheric attenuation, an estimate of the amount of atmospheric water vapour present in a particular swath area is made. This is done by calculating the difference in

temperature estimates in two different spectral bands with varying rates of water vapour absorption (Anding and Kauth 1970, Ricciardulli and Wentz 2004, Tanner and Volkman 2009). Therefore the technical constraints of each satellite product should be considered and accounted for when studying the coastal environment (Ricciardulli and Wentz 2004). Furthermore, as is the case with all environmental monitoring equipment, the satellite sensors need to be validated against ground truths in order to correct for any satellite estimation error.

2.2. Materials and Methods

2.2.1. Study sites

2.2.1.1. Flamingo Lodge, southern Angola

An area where *in situ* surface water temperatures have been recorded for a number of years on a daily basis is Flamingo Lodge, Namibe, in southern Angola (Figure 2.1). Flamingo Lodge is ideally situated in the centre of the distribution of *Argyrosomus coronus* and has a good catch record for this species (Potts *et al.* 2009, 2010). For this reason the site is an important monitoring area for the west coast dusky kob and the data collected at this location forms an invaluable part of this study. Temperature data has been collected concomitantly with catch per unit effort (CPUE) data for *Argyrosomus coronus* at Flamingo Lodge between 2005 and 2009, which ensures the applicability of this dataset to the broader aims of the study.

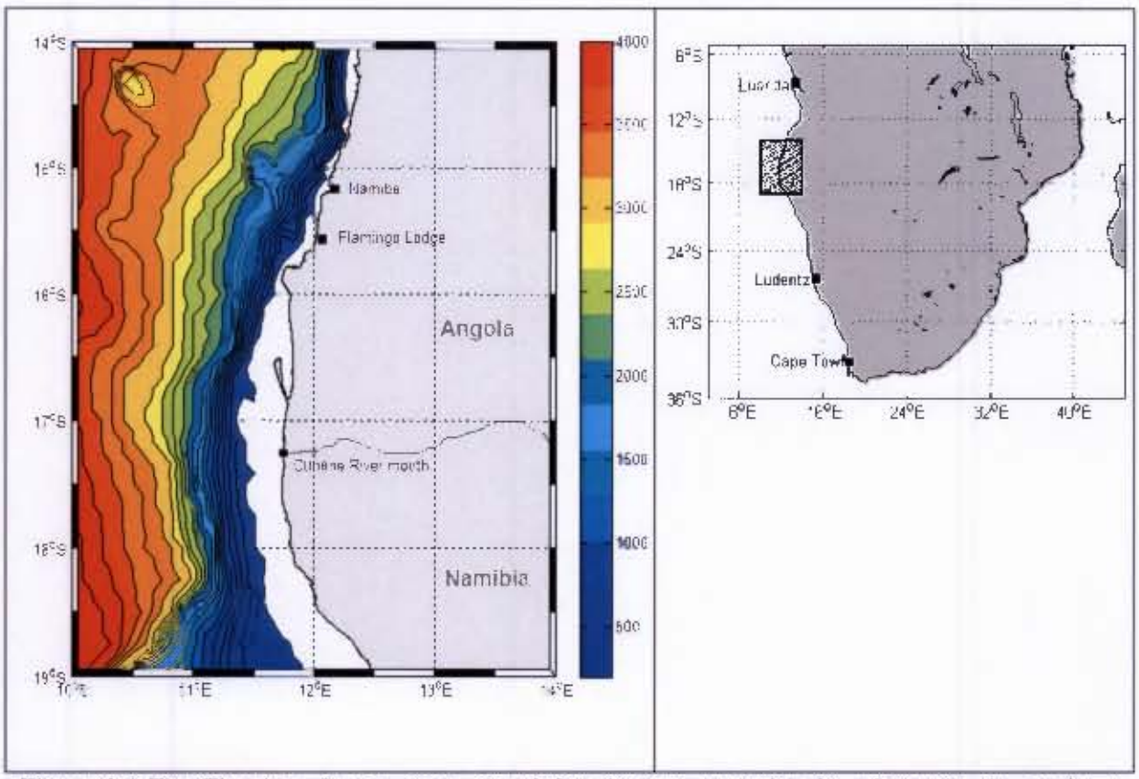


Figure 2.1 The Flamingo Lodge study site (left), situated near the city of Namibe in southern Angola. The shaded block of the insert represents the enlarged map area. Colour bar represents depth (m).

Water temperature data was collected daily from the shoreline at the lodge (15.57°S, 12.02°E) at around 8am (local time) between May 2005 and December 2009. A water sample was collected and recorded from immediately below the surface, in the surf zone, measured using a standard hand held thermometer, to an accuracy of 0.20°C. *In situ* water temperature was sampled on a total of 596 days during the study period. Gaps in the data set were a result of equipment failure or lack of personnel.

2.2.1.2. Luderitz Harbour, Namibia

A second study site was situated at the Luderitz harbour (26.62°S, 15.10°E) in central Namibia (Figure 2.2), adjacent to the Luderitz upwelling cell, identified in the first chapter as a potential distribution barrier for the study species. The daily temperature dataset (2008-2011) in this area is unfortunately not as comprehensive (22 sampling days recorded) as that collected in the Flamingo region. The dataset is still important however, as the oceanographic conditions between the two study sites are very different and the satellite SST estimation error should be calculated at each, in order to determine its accuracy throughout the study region.

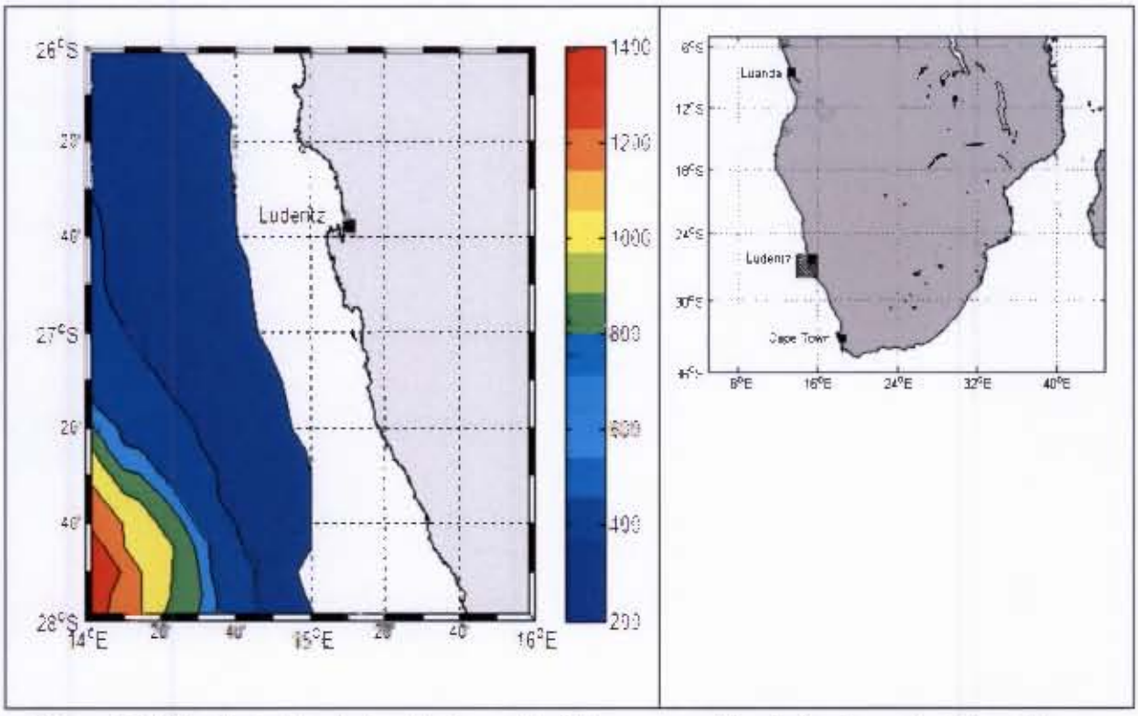


Figure 2.2 The Luderitz study site, located off the coast of Luderitz in central Namibia. The shaded area of the insert represents the enlarged study area. Colour bar represents depth (m).

Temperature sampling was carried out in the Luderitz harbour and bay areas as part of a monitoring programme run by the Namibian Ministry of Fisheries and Marine Resources (MFMR) (K Grobler *pers. comm.* 2010). Temperature, dissolved oxygen and wind data were made available from the monitoring programme over the period between April 2008 and March 2011. Measuring of temperature and dissolved oxygen was carried out via conductivity, temperature and dissolved oxygen meter (CTD) which was lowered into the water column from a hatch on board a stationary research vessel. Wind data was measured at an automatic weather station located at Diaz Point, Luderitz.

2.2.2. Selection of the best suited satellite dataset

It was important to select the best suited satellite product to estimate sea surface temperatures in the inshore zone of the two study areas. For this particular region and within the confines of this study, the ideal product had to have data available over the period of *in situ* data collection (2005-2011) as well as data before this time, to allow trends in temperature variability to be explored in the next phases of the project. The SST retrievals also needed to have high levels of accuracy as close to the shoreline as possible and therefore a fine resolution of ~2x2 Km was required. As the inshore zone of the northern Benguela is a highly variable environment (Hardman-Mountford *et al.* 2003) it was necessary to find a product

which retrieved daily SST estimates in order to capture this variability. Daily satellite SST retrievals would also enable direct comparisons with the *in situ* datasets which were both collected on a daily basis.

Careful consideration had to be given to the choice of satellite product; especially as remote sensing products are known to decrease in accuracy as measurements are made closer inshore (Tanner and Volkman 2009). Thus a comparison between the different satellite products which estimate SST was carried out. Seven aspects of the available satellite sensors and products were rated according to Table 2.1. The sensor or product with the highest mean score was deemed the most suitable for the constraints of this particular study.

Table 2.1 The methodology used to rate the different features of satellite sensors or products in the inshore region of the study area. The score of a sensor or product was determined for each of the 7 aspects (rows) out of 5, according to the description in the columns. The sensor or product with the highest average score was deemed the most suitable for this particular study.

	1	2	3	4	5
Beginning of active period	2006-2011	2001-2005	1996-2000	1991-1995	<1990
Temporal resolution	>10days	7-10days	4-6days	1.1-3days	Daily
Spatial resolution	>15km	11-15km	6-10km	1-5km	0-1km
Ease of access to data	Not available to public.	Payment required.	Delivery by post.	Freely available via internet.	Freely available via internet, with adequate online and user support.
Proximity to the coast of nearest accurate data	>35km	21-35km	11-20km	6-10km	0-5km
Ability to determine SST in variable environment	Poor (<50%)	-	Average (51-79%)	-	Good (>80%)
SST estimates available in over cast conditions?	No (Infrared sensors)	-	At times (Infrared and microwave sensors)	-	Yes (Microwave sensors)

2.2.3. *In situ* validation

In situ data collected from each study site was directly compared to satellite derived sea surface temperature estimates from the corresponding location and for the same day. In order to ensure satellite estimates were not influenced by radiant emittance from adjacent land masses, three different pixels were selected for comparison with *in situ* data at Flamingo Lodge (Figure 2.1) and two at Luderitz (Figure 2.2). The pixel with the most consistently accurate estimate of the observational data was selected for the remainder of the study. The MODIS Aqua and Terra data derived from this pixel during the study period (2005-2011) were then compared directly to the available *in situ* data. The average difference between the satellite derived estimate and the *in situ* observation was calculated and was used as the standard correction factor each product.

2.2.4. Satellite data retrieval and analysis

The MODIS instrument, on board the Terra and Aqua satellites observes every point on the earth's surface every 1-2 days in 36 discrete spectral bands and has been collecting data since 2000 (Terra), 2002 (Aqua) (Minnett *et al.* 2002, MODIS 2011). Level-2 MODIS data, consisting of irradiance values which are corrected for instrumentation and radiometric error, was downloaded from the Ocean Color website (http://oceancolor.gsfc.nasa.gov) (Minnett *et al.* 2002, MODIS 2011). This data was then processed at a 2x2km or 4x4km resolution using the SeaWiFS Data Analysis System (SeaDAS – http://seadas.gsfc.nasa.gov). Only the daytime, long wave (11μm), passes were processed as this allows the use of the cloud flag (CLDICE), determined from the ocean colour images. Several other SeaDAS flags were then applied to the extracted MODIS data (ATMFAIL, LAND, HILT, CLDICE, HISOLZEN, LOWLW, MAXAERITER, ATMWARN, NAVFAIL and FILTER). In terms of this particular study, the Terra satellite passes over the Flamingo study site in southern Angola between 10:00 and 11:00am while Aqua passes over the same site between 13:30 and 14:30pm. As the *in situ* data from Flamingo Lodge was collected at 8am, this results in a ~3 hour delay before the Terra overpass, and a ~6 hour delay before the Aqua satellite passes the study area.

The MODIS sensor measures the infrared radiance emitted from the top 10 μm of the ocean surface (Brown and Minnett 1999, Minnett *et al.* 2002), this measurement is termed the skin temperature, which is known to be susceptible to diurnal warming. The potential influence of the diurnal warming signal on satellite derived SST estimates was therefore explored. This was done by determining the partial diurnal signal through a comparison between MODIS Aqua and Terra SST estimates as they were determined approximately 3 hours apart.

2.2.5. Comparison between *in situ* and satellite derived SST

MODIS Aqua and Terra daily sea surface temperature estimates were compared to the observed temperature values recorded at both study sites. Due to the influence of cloud cover on satellite SST estimates or gaps in the *in situ* datasets, daily "match-ups" between the datasets were relatively limited.

Once the match-ups days between the *in situ* and satellite derived datasets had been selected using MATLAB 2009a, the accuracy of each pixel from both the Aqua and Terra MODIS sensors were investigated. The pixel with the lowest average satellite estimation error and standard deviation as well as the highest correlation coefficient in each case was considered as the best representative of the shoreline temperature. This pixel then became the location from which to determine the MODIS derived SST for the remainder of the study. In the case of the Flamingo Lodge study site three separate pixels (Figure 2.3) were used for comparison with *in situ* data in order to determine which pixel from each product best described the observed *in situ* temperature dataset. While at the Luderitz study site, two MODIS pixels one in the vicinity of each of the sampling sites, were used to determine which pixel best described the *in situ* data (Figure 2.4).

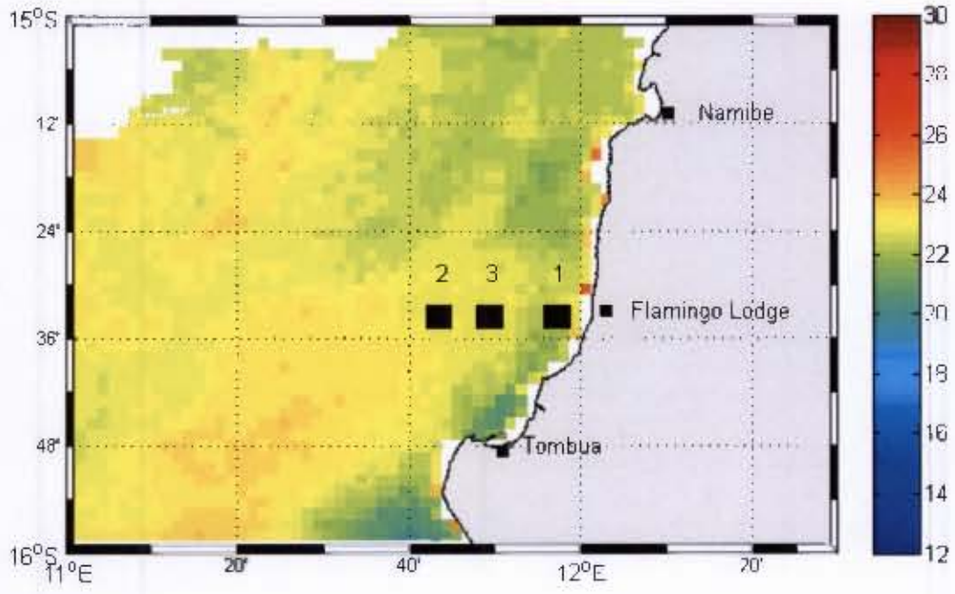


Figure 2.3 MODIS AQUA SST image (14 August 2008, 2x2km resolution) of the location of the three different pixels (1, 2 & 3) adjacent to Flamingo Lodge, southern Angola. The colour bar depicts the SST values in degrees Celsius. (pixel 1: 15.54 - 15.58°S, 11.93 - 11.98°E; pixel 2: 15.54 - 15.58°S, 11.70 - 11.75°E; pixel 3: 15.54 - 15.58°S, 11.80 - 11.85°E).

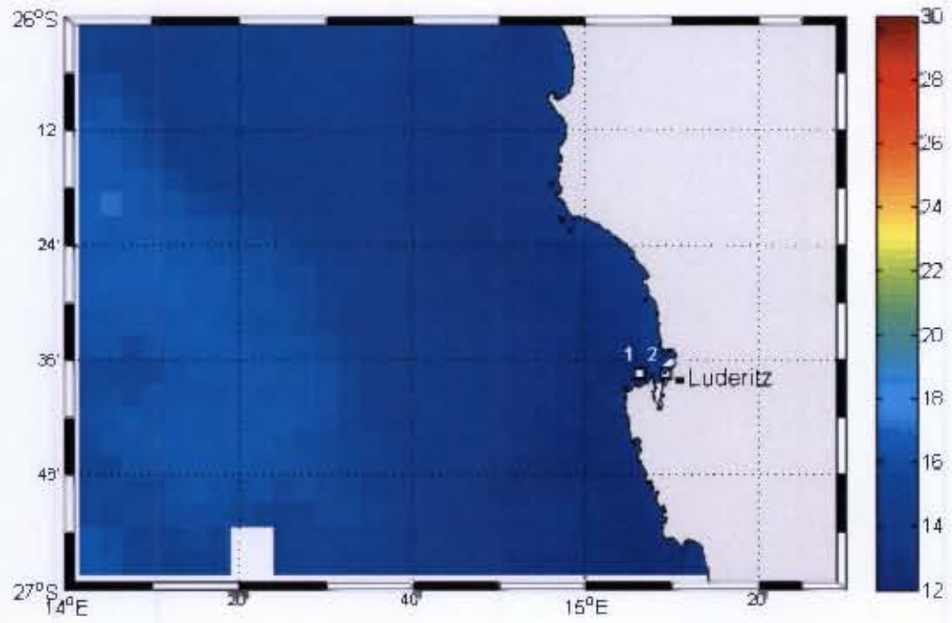


Figure 2.4 MODIS TERRA SST image (4 October 2010, 4x4km resolution) of the positions of the two sampling areas within the Luderitz study site, Namibia. Sampling site 1 represents, Shearwater Bay, while 2 represents the Lagoon adjacent to Luderitz harbour. 1: 26.60-26.64°S, 15.09-15.14°E; 2: 26.60-26.64°S, 15.15-15.17°E. The colour bar represents the SST values in degrees Celsius. For ease of comparison, the colour scale is the same for both figures.

An investigation into the spread of the daily satellite estimation error calculations was undertaken where the distribution of the satellite estimation error was analysed through a description of its skewness, or asymmetry:

$$skewness = \frac{\sum (x(i)-xbar)3}{(n)\,\sigma 3}$$

as well as its kurtosis, or the amplitude of the curve around the mode:

$$kurtosis = \frac{\sum (x(i)-xbar)4}{(n)\,\sigma 4}$$

where x are the individual satellite estimation error calculations, $xbar$ is the average satellite estimation error, n is the sample size and σ is the standard deviation of x. These parameters can be compared to a normal distribution, which has a skewness of zero and a kurtosis of 3 (Mathworks 2011).

The divergence of the satellite data from *in situ* values was considered as the satellite estimation error. A seasonal investigation into the satellite estimation error evident in both

MODIS sensors was carried out. This calculation determined whether a separate correction factor for MODIS Aqua and Terra data was needed for each season. Unfortunately the small number of match up days at the Luderitz study site meant that a seasonal satellite estimation error investigation was only possible for the Flamingo Lodge region. For the purposes of the seasonal investigation, an average satellite estimation error was calculated for each season (summer = December, January, February; autumn = March, April, May; winter = June, July, August and spring = September, October, November) from the average of daily error values within each seasonal grouping. The significance of seasonal differences in satellite estimation errors were calculated at the 95% level using a non parametric one-way ANOVA Kruskalwallis test (MatlabR2009a) as well as a multiple comparison test (MatlabR2009a) (Mathworks 2009) to verify which pairs were significantly different from each other.

After consideration of the above mentioned results, a correction factor was calculated as the average satellite estimation error, on a seasonal and year round scale. This enabled the derivation of inshore temperatures in the northern Benguela from MODIS AQUA or TERRA data.

2.2.6. Diurnal Warming cycle at Flamingo Lodge

An investigation into the amplitude of the diurnal cycle was necessary in order to assess its effect on satellite estimation error throughout the year. This was carried out through a comparison between the difference between the SST estimations derived from the MODIS sensor onboard Terra and those derived ~3-4.5hrs later from the MODIS sensor on Aqua. Unfortunately as Aqua passed over Flamingo Lodge around midday it was not be possible to explore the complete diurnal cycle, however the seasonality of the partial cycle was useful in explaining the seasonal variation in satellite estimation error. The comparison was based on match up days, where both an Aqua and Terra derived SST estimate was available from study area. The direct comparisons were then grouped into seasons (summer = Dec, Jan, Feb; autumn = Mar, Apr, May; winter = Jun, Jul, Aug, spring = Sep, Oct, Nov) allowing the investigation of seasonal variability. It should be noted that these calculations do not represent the full extent of the diurnal cycle, but rather the extent of warming (or cooling in some cases), occurring between ~10am and ~13.30pm at the Flamingo Lodge, as well as the Luderitz study site.

2.2.7. Seasonal variability of wind stress in the study regions

Wind stress affects the amplitude of the diurnal warming cycle, as high levels of wind stress (>3m.s^{-1}) cause mixing of the water column and thus destroy any diurnal warming signal (Gentemann *et al.* 2003). Alternatively low wind regimes (<3m.s^{-1}) in tropical and temperate regions can result in stratification of the surface layers, and high diurnal warming signals. Wind stress variability was thus expected to be related to the variability in the magnitude of satellite estimation error. Therefore together with the results of the investigation into the extent of the partial diurnal warming signal, an investigation into the wind stress of both stud regions was undertaken at both study sites.

In situ wind data was available on a daily scale from January 2008 until December 2009 for the Luderitz study site, and this data was used to determine the seasonal variability of wind stress in the area. Unfortunately no wind data was available from the Flamingo Lodge study site, and data derived from the Climate Forecast System Reanalysis (CFSR) dataset (1979-2009), was used to explore the wind stress seasonality in the region. The CFSR dataset, a National Centre for Environmental Protection (NCEP) project, is a partially coupled ocean and atmosphere data assimilation system, which is used for the reanalysis of ocean, atmosphere, sea ice and land variables (Xue *et al.* 2010, Ebisuzaki and Zhang 2011). One major advantage of the CFSR dataset is that it incorporates all available *in situ*, satellite and model output data in order to determine a "best guess" of the environmental variables, in this case wind components, acting on a particular area (Xue *et al.* 2010). The CFSR wind data has been found to be better correlated (by up to 15%) to *in situ* datasets worldwide than many of its predecessors, NCEP R1, R2 and R3 as well as ERA40 (Liléo and Petrik 2010, Xue *et al.* 2010), and was therefore considered to provide a good estimate of wind stress variability in the Flamingo region. A short coming in the application of CFSR data to a regional scale study is that it is a global dataset and will provide a generalised wind stress pattern for the region, without the ability to take into account localised wind patterns.

The U and V wind components available at the Luderitz study site and those from the CFSR dataset for the Flamingo Lodge region were used to calculate a monthly climatology of direction and speed vectors. Wind rose plots of the climatology from each site were created in MATLABR2009a (Mathworks 2009), in order to view seasonal variability.

2.3. Results

NASA's MODIS infrared spectro-radiometer, which is currently in use aboard the NASA EOS AQUA (launched May 2002) and TERRA (December 1999) was considered the most appropriate product for use in this study. The data collected from the MODIS sensors is better suited for nearshore oceanographic studies than all alternative sensors or products investigated as it records data at a very high resolution on a daily scale and is relatively accurate in the inshore and nearshore regions (Table 2.2, Minnett *et al.* 2002, MODIS 2011).

Table 2.2 Comparison of the satellite products considered to monitor inshore SST in southern Angola and central Namibia. Overall ranking (column 8) shows the suitability of the product for this study, 5 being the most suitable and 1 the least. GHRSST-OSTIA = GODEA High Resolution Sea Surface Temperature – Operational sea Surface Temperature and sea Ice Analysis; ODYSSEA = Ocean Data analYsis System for merSEA; NIRST = New Infra Red Scanner Technology; AMSR-E = Advanced Microwave Scanning Radiometer; TRMM = Tropical Rainfall Measuring Mission; AASTR = Advanced Along-Track Scanning Radiometer; AVHRR = Advanced Very High Resolution Radiometer; MODIS = Moderate Resolution Imaging Spectro-radiometer.

Satellite Product	Beginning of active period	Temporal resolution	Spatial resolution	Ease of access to data	Proximity to the coast of nearest accurate data	Ability to determine SST in variable environment	Affected by clouds	**Overall ranking (average score)**	References
GHRSST-OSTIA (interpolation)	1	5	4	5	4	5	3	**2 (3.86)**	(PODAAC 2011), GHRSST 2011)
ODYSSEA (interpolation)	1	5	3	5	4	5	3	**3 (3.71)**	(Autret and Piolle 2007)
NIRST	1	2	5	5	3	3	1	**6 (2.86)**	(Largerloef *et al.* 2008)
AMSR-E	2	5	1	5	1	3	5	**5 (3.14)**	(RSS 2011)
TRMM	3	4	1	5	1	3	5	**5 (3.14)**	(ESA 2011, PODAAC 2011 , RSS 2011)
AATSR	2	5	5	5	3	1	1	**5 (3.14)**	(PODAAC 2011 , ESA 2007)
AVHRR	5	5	4	5	4	1	1	**4 (3.57)**	(ESA 2011, PODAAC 2011)
MODIS	2	5	5	5	5	5	1	**1 (4)**	(PODAAC 2011)

2.3.1. Flamingo Lodge:

2.3.1.1. Determination of satellite estimation error

At the Flamingo lodge study site both the Aqua and Terra MODIS data best represented the *in situ* dataset at pixel 1 (15.54 -15.58°S, 11.93-11.98°E) (Table 2.3). In both cases this pixel exhibited the lowest mean satellite estimation error, the highest R^2 value and the lowest standard deviation compared to pixels 2 and 3 (Table 2.3). Of the 596 *in situ* observations carried out between 2005 and 2009 a total of 161 daily match ups with MODIS TERRA SST estimations were found, while 193 match ups with MODIS Aqua data were determined.

Table 2.3 Differences between the MODS Aqua and Terra SST estimates and in situ data from three different locations: pixel 1: 15.54 - 15.58°S, 11.93 - 11.98°E; pixel 2: 15.54 - 15.58°S, 11.80 - 11.85°E; pixel 3: 15.54 - 15.58°S, 11.70 - 11.75°E off Flamingo Lodge, southern Angola (2005-2009). (C.I. – confidence interval).

	Aqua			Terra		
	Pixel (1)	Pixel (2)	Pixel (3)	Pixel (1)	Pixel (2)	Pixel (3)
Mean:	0.84	1.98	1.33	0.74	1.22	1.98
Max:	3.70	7.58	5.47	4.93	8.20	7.09
Min:	-1.49	-2.29	-2.23	-1.40	-4.73	-2.95
Standard deviation:	0.97	1.53	1.21	1.05	1.33	1.32
Correlation coefficient (R2):	0.92	0.83	0.88	0.89	0.83	0.84
C.I. plus (95%):	0.97	2.20	1.50	0.90	1.43	2.20
C.I. minus (95%):	0.70	1.76	1.17	0.58	1.01	1.74
Number of matches:	193	185	207	161	158	125

MODIS Aqua and Terra data from pixel 1 at the Flamingo Lodge study site (Figure 2.3) were extracted for the study period (2005-2009) and averaged for each month. These values were then compared to the monthly averaged *in situ* SST values from the Flamingo Lodge dataset (Figure 2.5).

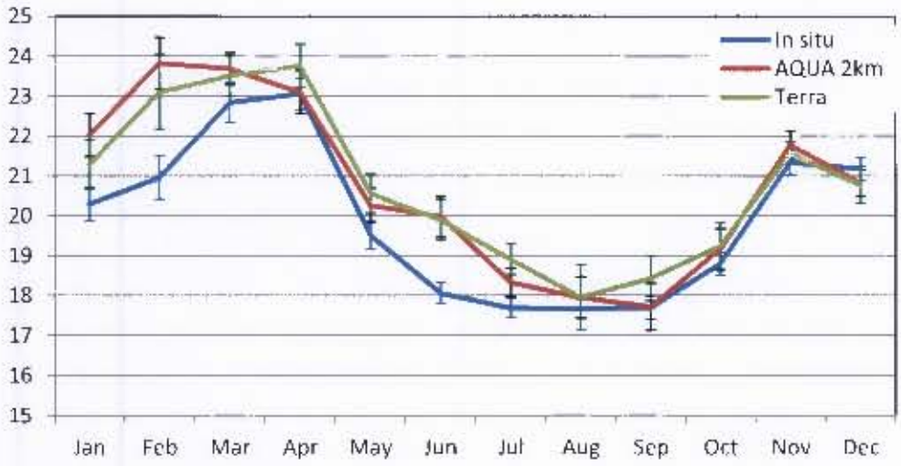


Figure 2.5 Comparison of the average monthly in situ, MODIS 2x2km resolution Aqua and Terra satellite sea surface temperature (SST) estimates at Flamingo Lodge, southern Angola, for the period 2005-2009 (error bars showing 95% confidence interval). n=596 (in situ), n=463 (Aqua), n=322 (Terra).

The mean difference between the MODIS SST estimates and *in situ* temperature values was 0.84 ± 0.97°C for the qua dataset and 0.74 ± 1.05 for Terra derived estimates (Table 2.3). Generally both MODIS sensors over estimated the *in situ* data (Table 2.3, Figure 2.5). It is interesting to note that the difference between the observed and satellite estimated SST values is neither consistent throughout the study period nor are the calculated differences normally distributed, (Kolmogorov-Smirnov ($P<0.05$, h=1, P=1.6841x10-40).

The distribution of the differences can be further described through the calculation of their skewness, 0.39 (n=193), and its kurtosis, or amplitude of the curve relative to normal around the mode, 3.42 (n=193) (Figure 2.6). These values can be compared to the normal distribution which has a skewness of zero and a kurtosis value of 3, and in both cases indicate the over estimation of *in situ* SST. The skewness values emphasise MODIS overestimation of *in situ* values, while the positive kurtosis indicates that the mean estimation error occurs frequently.

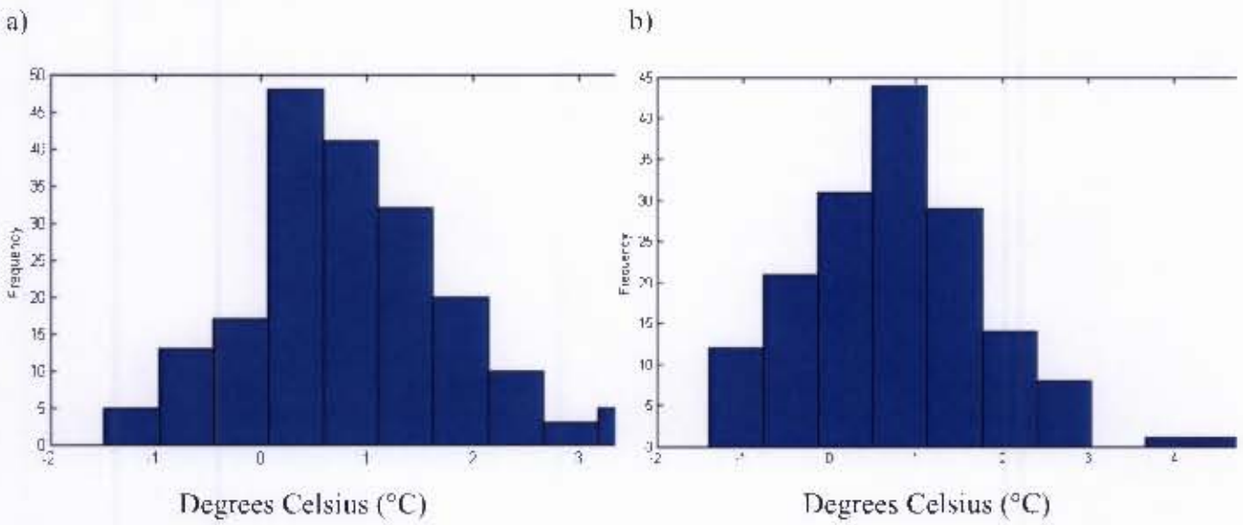


Figure 2.6 Histograms representing the distribution of the satellite estimation error for both the MODIS Aqua (a) and Terra (b) sensors when estimating in situ data collected at Flamingo Lodge, southern Angola between 2005 and 2009. The satellite estimations were retrieved from Pixel 1 (15.54-15.58°S; 11.90-11.95°E), a total of 193 comparison days are shown here for the Aqua sensor and 161 from the Terra dataset.

2.3.1.2. Seasonal variability in satellite estimation error

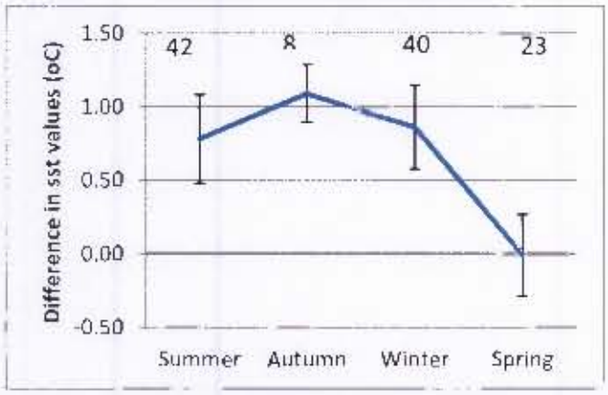
As the mean deviation from the observations (by both the MODIS sensors) is not constant, it is important to determine whether the differences are related to a time period (such as a seasonal cycle) or whether they occur at random.

A seasonal comparison showed a significant difference in averaged satellite estimation error was evident between the four seasons when using Aqua (Kruskalwallis: $p<0.05$, $h=1$, $p=1.33\text{x}10\text{-}6$) as well as Terra (Kruskalwallis: $p<0.05$, $h=1$, $1.83\text{x}10\text{-}5$) MODIS data (Table 2.4, Figure 2.7). The greatest overestimation of *in situ* temperatures by both MODIS sensors occurred in autumn, while during the spring the satellite SST estimations show little error (Table 2.4, Figure 2.7). Therefore the presented correction factors (Table 2.4) should be subtracted from original satellite SST retrievals in the northern Benguela, except during the months of spring where they should be added.

Table 2.4 The seasonal correction factors determined from the satellite estimation error of MODIS Aqua and TERRA data when determining in situ SST in the Flamingo study region, southern Angola (2005-2009). Presented error is standard deviation and numbers in brackets represent sample size.

	Summer	Autumn	Winter	Spring
MODIS AQUA	0.78 ± 1.00 (42)	1.09 ± 0.93 (88)	0.86 ± 0.92 (40)	-0.01 ± 0.68 (23)
MODIS TERRA	0.78 ± 1.25 (30)	1.05 ± 0.91 (74)	0.93 ± 0.87 (27)	-0.22 ± 0.70 (30)

a)



b)

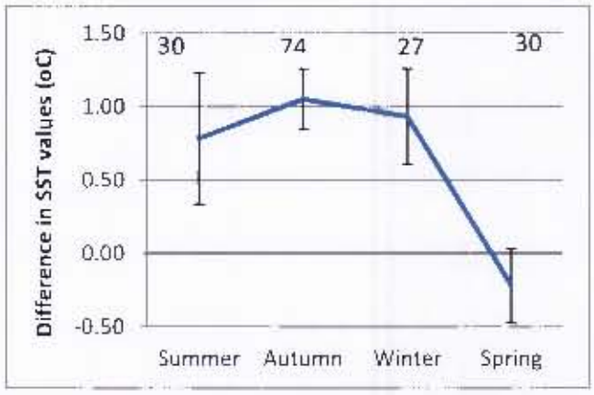


Figure 2.7 The mean seasonal differences between the satellite estimation error of in situ temperatures at Flamingo Lodge, southern Angola, for a) Modis Aqua data and b) MODIS Terra data. The seasons comprise of three months each, summer (DJF), autumn (MAM), winter (JJA), and spring (SON). Numbers above each seasonal mean denote sample size, error bars represent the 95% confidence intervals.

2.3.1.3. Seasonal variability of the partial diurnal cycle:

The partial diurnal cycle was calculated by comparing satellite derived SST estimates in the morning (Terra) and in the early afternoon (Aqua) and was averaged according to seasons in order to assess seasonal variability (Figure 2.8). The warming signal was found to be greatest during summer and least during spring (Figure 2.8).

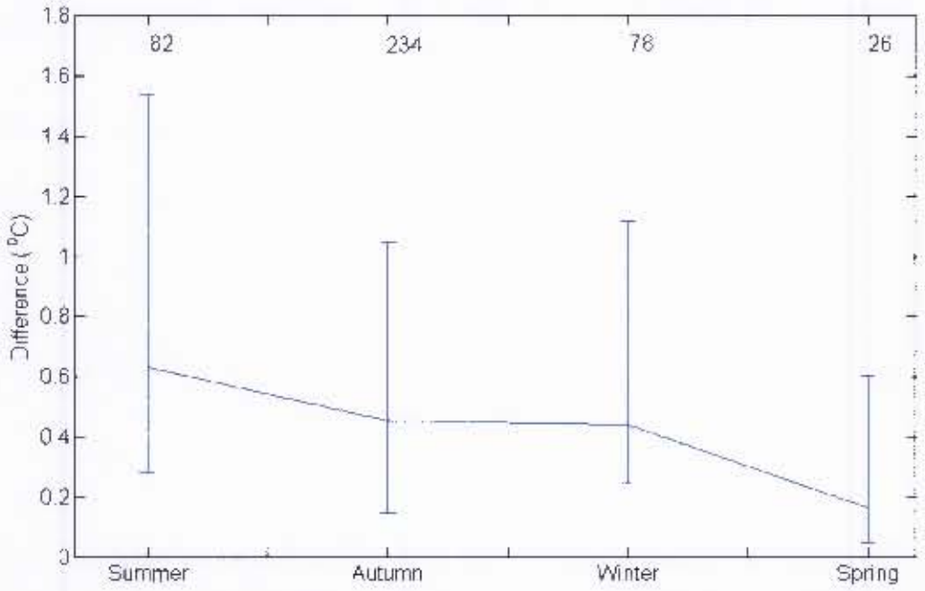


Figure 2.8 The seasonal variability of the partial diurnal warming signal (~10:00am-14:00pm) calculated for the Flamingo Lodge study site in southern Angola shown as the difference between MODIS TERRA and AQUA SST (2002-2011) estimates. The number above each seasonal estimate represents the sample size of match-up days for that season; the error bars represent the upper and lower 95% confidence intervals.

2.3.1.4. Seasonal Wind stress at Flamingo Lodge:

The climatology of wind speeds for the Flamingo Lodge study site (Figure 2.9) indicated that monthly average wind speeds throughout the year were below $3m.s^{-1}$ with a seasonal range of $0.65m.s^{-1}$. Wind speeds at Flamingo Lodge were lower (~2.30-$2.50m.s^{-1}$) during winter and early spring (June-September), with higher wind speeds (~2.70-$2.98m.s^{-1}$) observed during the rest of the year. South easterly winds dominated at the Flamingo Lodge study site, except for the months of May, June and July where the wind swung to a more south-south-easterly direction (Figure 2.10).

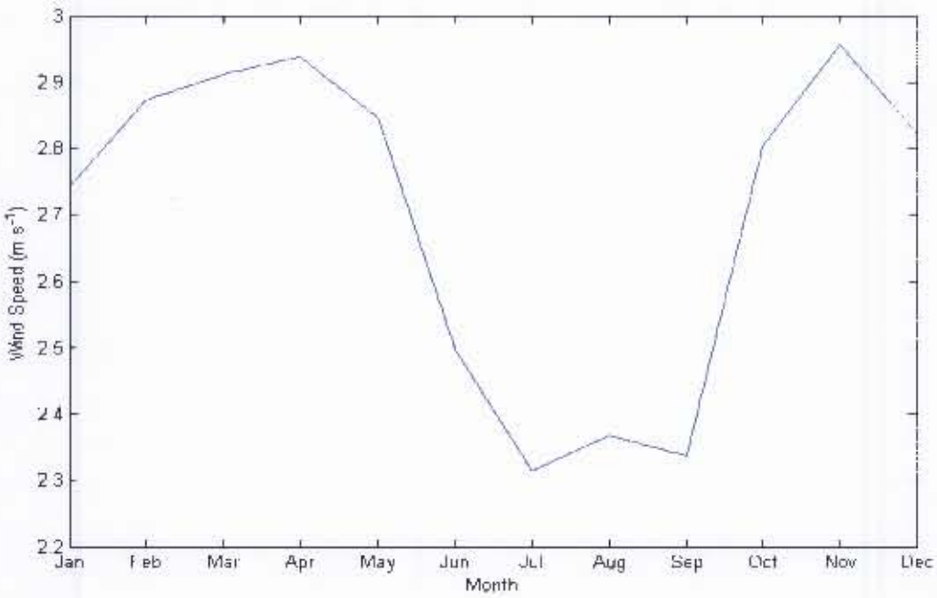


Figure 2.9 Average monthly wind speeds derived from Climate Forecast System Reanalysis (CFSR) data (1979-2009) at Flamingo Lodge, southern Angola area (15.5°S, 12°E).

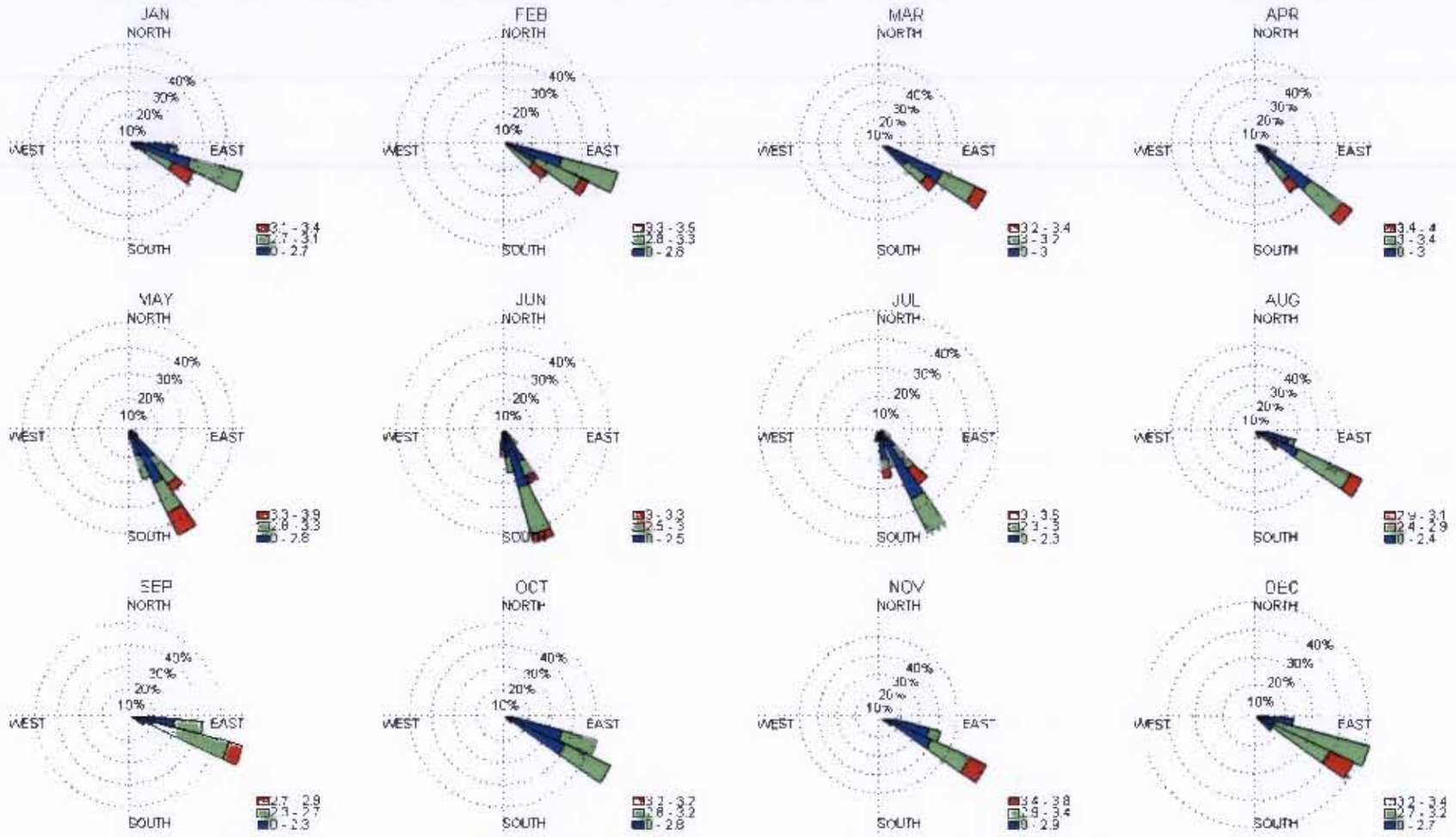


Figure 2.10 Monthly wind patterns derived from the average Climate Forecast System Reanalysis (CFSR) wind speed ($m.s^{-1}$) estimates between January 1979 and December 2009 from the Flamingo Lodge study region. The data represents the seasonal cycle for one pixel of the dataset, 15.5°S, 12°E and the wind speed values have been separated by the 50th and 90th percentiles.

2.3.2. Luderitz Case Study

Satellite data was only available for eight of the 22 sampling days using the MODIS Terra database and only four days using the Aqua data. The average estimation error by the MODIS Terra product was 1.97 ± 1.51°C and 1.05 ± 1.33°C for the Lagoon and Shearwater Bay sampling sites, respectively (Figure 2.11). While MODIS Aqua over estimated the *in situ* data at the Lagoon site by 0.46 ± 1.28°C and by 1.48 ± 0.79°C at the Shearwater Bay site. However, due to the low sample size of these comparisons, especially the MODIS Aqua values, further sampling is required in order to accurately determine the satellite estimation error in the Luderitz area.

The Shearwater Bay site was expected to be less affected by any diurnal warming cycle in the region as it is located outside of the harbour area in deeper water. It was also situated further from the influence of radiance interference from the adjacent land. Thus the Shearwater Bay site was chosen as the best location to estimate *in situ* SST using the MODIS Terra sensor. An approximate correction factor for MODIS Terra SST data at the Luderitz site was estimated to be ~1.05°C, and ~1.48°C for the MODIS Aqua SST retrievals.

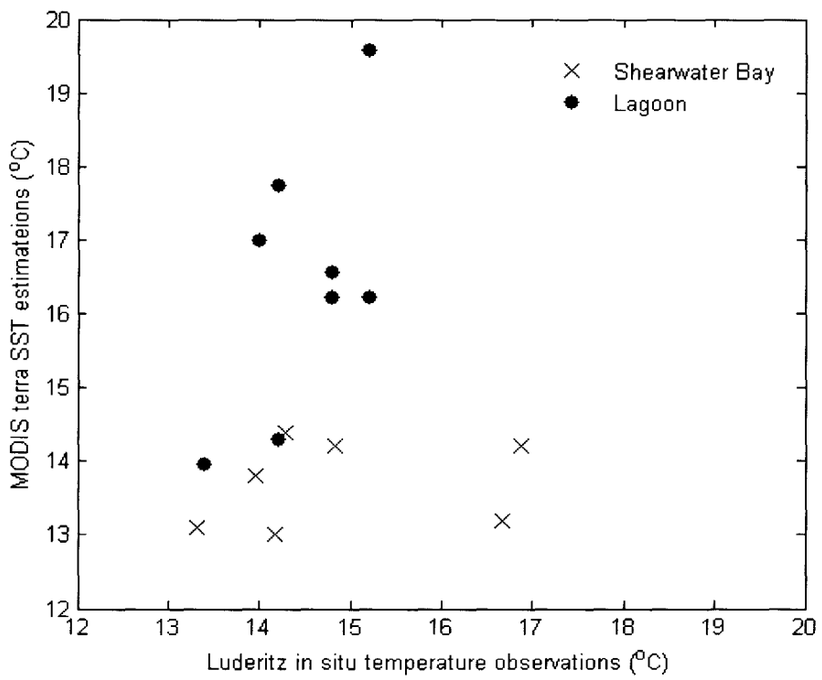


Figure 2.11 The correlation between *in situ* data collected at two sampling sites (the Lagoon and Shearwater Bay) in the Luderitz study area between April 2008 and December 2009 and MODIS Terra SST estimations.

The potential effects of a diurnal signal on satellite derived SST values in the Luderitz area were estimated through a comparison of seasonal averages of the difference between MODIS Aqua and Terra estimates retrieved at ~14:45 pm and ~9.45am respectively (Figure 2.12). An average diurnal warming signal of 0.76 ± 1.18°C was identified in the Shearwater Bay study site, with a slight increase in the winter (JJA) (Figure 2.12).

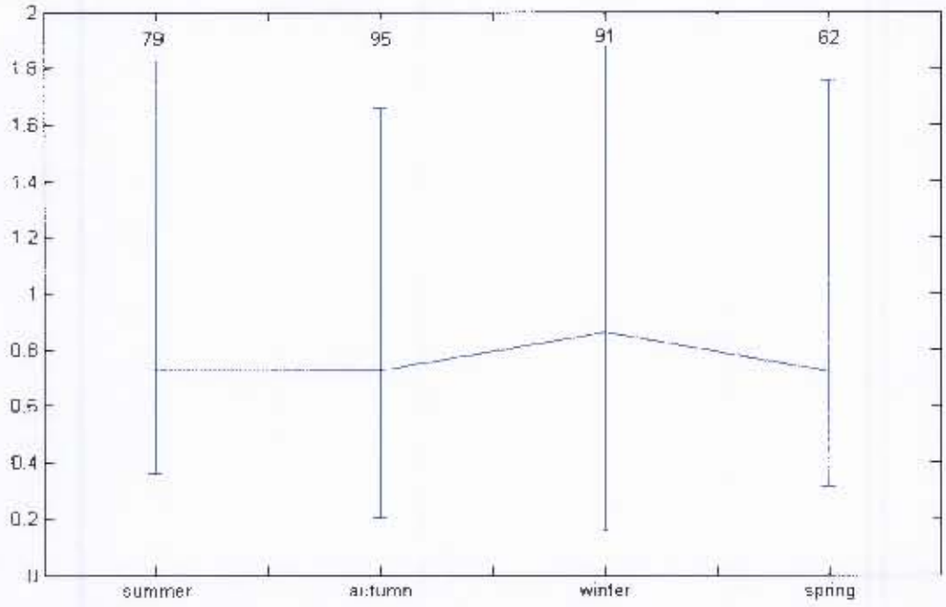


Figure 2.12 The extent of the partial diurnal signal (°C) evident from the divergence of MODIS Aqua 4x4km resolution SST estimates from MODIS Terra values at the Shearwater Bay study site (26.60-26.64°S, 15.09-15.14°E) in the vicinity of Luderitz, Namibia. All match up values from 2002 until 2010 were used in this comparison and the numbers above each data point represent sample size for each season.

2.3.2.1. Seasonal wind stress at the Luderitz study site

The average monthly wind speeds at Luderitz ranged between 3 and 8m.s^{-1} and were lower (~3.5 – 4.5m.s^{-1}) during early winter (May, June, July), with higher wind speeds (~6.8 - 8m.s^{-1}) observed during spring and early summer (September – December) (Figure 2.13).

South easterly winds dominated the Luderitz study site with slight deviations in the form of a westerly wind which is common in winter (Figure 2. 14).

Figure 2.13 Average monthly wind speeds (2008-2009) from anemometer data at the Dias Point weather station, Luderitz.

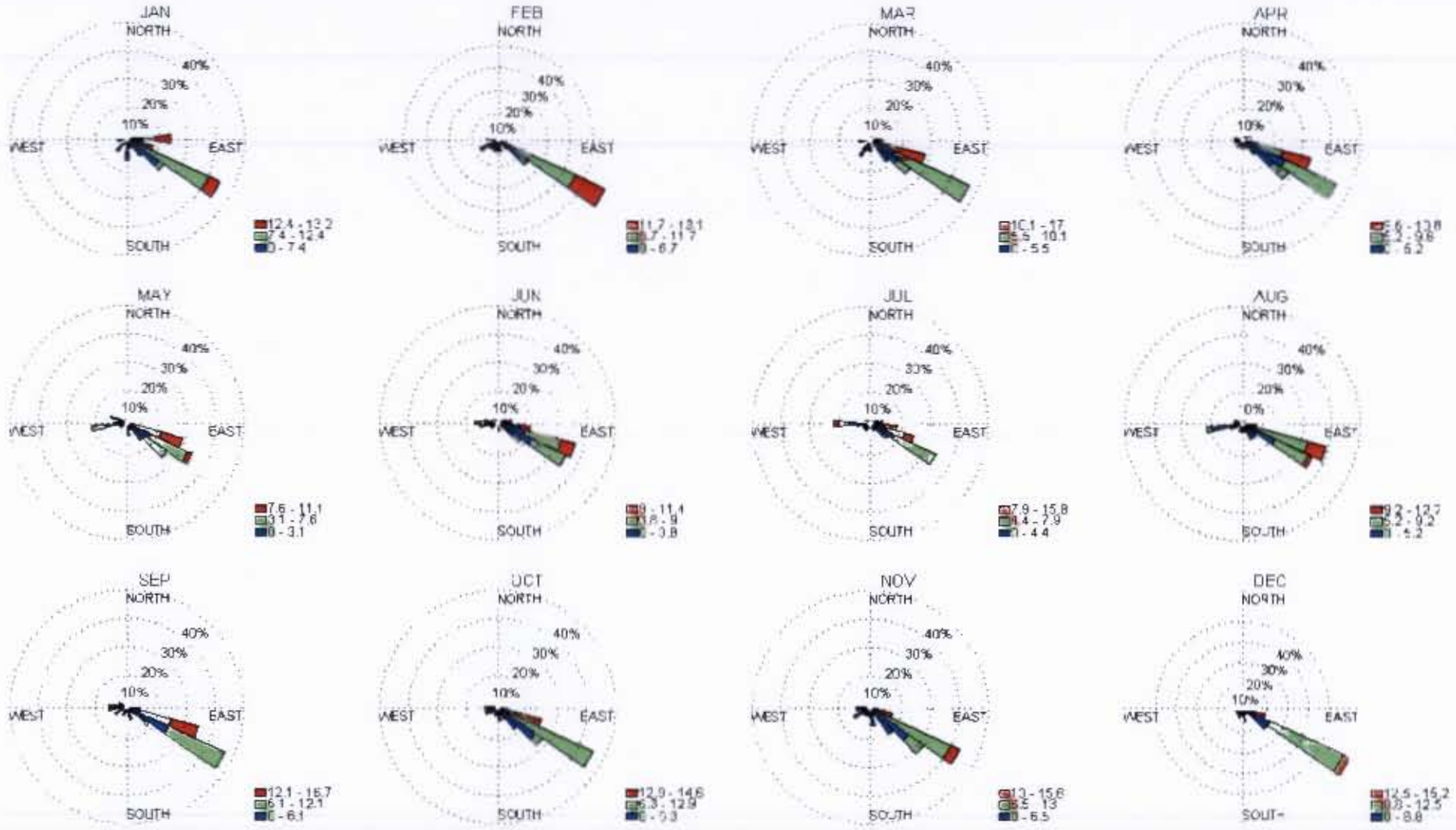


Figure 2.14 The monthly averaged wind speed ($m.s^{-1}$) and direction values collected at Dias Point, Luderitz between January 2008 and December 2009. The wind spe divisions of the wind rose represent the 50th and 90th percentiles.

2.3.3. Determining a generalised correction factor for MODIS data in the northern Benguela

It is not always necessary and sometimes not possible to incorporate a seasonal correction factor into studies utilising satellite derived surface temperature data. Therefore a generalised correction factor was determined which is applicable to both Terra and Aqua derived MODIS data throughout the northern Benguela region (Table 2.5).

Table 2.5 Determining an all purpose correction factor for the northern Benguela region for use with both Aqua and Terra derived MODIS SST estimates. The satellite estimation error form both of the sampling sites (Flamingo Lodge, southern Angola and Luderitz, Namibia) was taken into account. The weighted average for each sensor (column 4) can be applied to MODIS data throughout the year in the northern Benguela. If a greater temporal resolution is required the seasonal correction factors presented in Table 2.5 should be applied instead.

	Flamingo Lodge	Luderitz	Weighted average
MODIS Terra	+0.74 ± 1.05°C (161)	+1.05 ± 1.32°C (8)	+0.76 ± 1.06°C
MODIS Aqua	+0.84 ± 0.97°C (193)	+1.48 ± 0.78°C (4)	+0.85 ± 0.85°C

2.4. Discussion

2.4.1. Choosing the correct satellite product

NASA's Moderate Resolution Imaging Spectro-radiometer (MODIS) sensor was considered the best suited satellite product for this study (Table 2.2). Although the more recently developed interpolation products such as GHRSST-OSTIA and ODYSSEA, which combine all available forms of data for each region, would have been well suited these products were not available over the required time period.

Whether to use infrared or microwave sensor SST estimates in the inshore zone was also an important consideration. The great advantage of microwave sensing is that data retrievals are not affected by cloud or atmospheric water vapour, ensuring constant data availability (Minnett *et al.* 2002, Ricciardulli and Wentz 2004). Microwave sensors, however are negatively influenced by the effects of shallow water depths and suspended particles, as well as sea surface roughness which, in combination, render their temperature estimates inaccurate until at least 35km offshore (Ricciardulli and Wentz 2004). Infrared sensors on the other hand, are able to accurately measure radiance levels on a fine spatial scale, allowing accurate SST measurements in the coastal zone, as well as in regions of high temperature gradients

(Ricciardulli and Wentz 2004). A major limitation of infrared sensing is that infrared radiance is absorbed by atmospheric water vapour, and therefore infrared sensors are unable to collect radiance data during cloudy or over-cast conditions (Minnett *et al.* 2002). MODIS is an infrared sensor and in order to overcome the data gaps caused by overcast days, monthly averaged data were used for the remainder of the study.

The MODIS sensors currently in orbit are carried on board two of NASA's satellite platforms, namely Terra and Aqua (MODIS 2011). These satellites orbit the earth in a sun synchronous fashion and in opposite directions, thus producing two separate sea surface temperature estimates at different times of the day (Brown and Minnett 1999, MODIS 2011). The Terra satellite (ascending track) crosses the equator at approximately 10:30am, while the MODIS sensor on board the Aqua satellite (descending track) crosses at around 1:30pm. It is important to include SST estimates from both flyover times in order to assess any diurnal cycles of surface warming which may be present in the study region.

2.4.2. Satellite estimation error in the northern Benguela

The MODIS sensors on board both the NASA satellites, Aqua and Terra, were able to capture monthly (Figure 2.5) temperature variability relatively well at both study sites. However MODIS SST retrievals generally overestimated the SST when compared with *in situ* observations (Tables 2.3, Figure 2.7). Therefore, while the MODIS sensor adequately captures the variability of the nearshore environment it is recommended that a correction factor be applied to satellite SST estimates in this region to improve their accuracy. Based on these results, generalised correction factors were determined which are applicable throughout the study area and at any time of the year, for both of the MODIS sensors (Table 2.5). These were calculated as 0.76°C and 0.85°C for the MODIS Terra and Aqua sensors respectively. However, for studies that require higher temporal resolution, the seasonal correction factors presented in Table 2.4 should be applied to the relative MODIS sensor data for the applicable season.

Satellite estimation error in the Luderitz area was relatively high (MODIS Aqua: +1.48°C and MODIS Terra: +1.05°C) compared to that calculated for the Flamingo Lodge region (MODIS Aqua: +0.85°C and MODIS Terra: +0.76°C). The use of 4x4km resolution data at the Luderitz study site as opposed to the 2x2km resolution data used at Flamingo Lodge, did not significantly alter the satellite estimation error (MODIS Aqua (2x2km vs. 4x4km) Two

sample t-test P>0.05; MODIS Terra (2x2km vs. 4x4km) Two sample t-test P>0.05) and therefore the higher estimation error at Luderitz was not expected to be a result of the use of lower resolution data. Instead it is thought that the high satellite estimation error in the region can be attributed to the low number of 'match-up' days between satellite and *in situ* data sources. For this reason it is imperative that routine sea surface temperature monitoring continues in the Luderitz area.

2.4.3. Reasons for the observed satellite estimation error

The observed estimation error by the MODIS Aqua and Terra sensors may have been caused by a number of factors. These include equipment restrictions, variability of regional wind stress and the existence diurnal warming cycles, explained below in the context of this study.

2.4.3.1. Equipment restrictions

One of the most common causes of satellite infrared sensor estimation error is the infrared retrieval methodology itself. This is especially true in coastal regions, which are often located on the edge of the satellite swath and in waters adjacent to land masses.

The SST estimates retrieved from the MODIS sensors on board the Terra and Aqua satellites are most accurate when the water mass being measured is located directly below the sensor (Brown and Minnett 1999, MODIS 2011). However in order to ensure global coverage of the sensor, the width and length of the sensor's swath are extended to include as large an area as possible. The accuracy of SST estimates however, decreases towards the edges of the swaths (often where coastal regions are located) as a result of atmospheric contamination (Tabata 1981). The erroneous values are removed from the dataset through the application of error flags, which are user-specified (see methods) but are originally applied by the OBPG group. It is possible for pixels to be incorrectly flagged (especially those located very close to the shoreline), which can lead to over or underestimations of the true surface temperature at that location. For this reason the areas selected for comparison to *in situ* datasets in this study are located further offshore (Figures 2.3, 2.4).

A number of physical variables are also expected to have an influence on the ability of the MODIS sensors to estimate SST of the extreme inshore region.

2.4.3.2. The influence of the diurnal warming cycle and wind stress on satellite estimation error

The use of infrared sensors, such as those used by MODIS are particularly sensitive to diurnal warming, as they measure the skin temperature, or upper 1μm of the surface layer, which is where the highest rates of diurnal warming occur (Gentemann *et al.* 2003, Ricciardulli and Wentz 2004). A Further compounding factor is that the conditions under which MODIS performs best (clear sky) is when the surface layer of the ocean, exposed to full sunlight, is most susceptible to diurnal warming (Silio-Calzada *et al.* 2008). The difference in SST estimates between the MODIS Aqua and MODIS Terra (Figure 2.8, 2.12) illustrate the effects of a partial diurnal warming signal in both study regions.

The amplitude of the diurnal warming cycle has been found to be as much as 2.8°C in regions which experience low wind stress (1-3m.s^{-1}) (Gentemann *et al.* 2003, Ricciardulli and Wentz 2004). In the case of Flamingo Lodge, the low wind speed (average 2.70m.s^{-1}) and temperate location (15.5°S) of the study site indicate the potential importance of the diurnal cycle as a source of satellite estimation error in the region. In support of this, the seasonality of the partial diurnal warming signal (mean=0.63°C, Figure 2.8) was closely related to the seasonal variability of the estimation error (Table 2.4, Figure 2.7). However, an exception occurred during late winter, early spring (July - September) where the wind speed dropped to between 2.3-2.4 (Figure 2.9) and the partial diurnal warming signal did not increase as was expected (Figure 2.8). Spring is known to be a season of strengthened upwelling in the northern Benguela (Hardman-Mountford *et al.* 2003, Hutchings *et al.* 2009) and it is thought that the development of local upwelling favourable winds during the day would mix the water column and bring cool water to the surface, breaking down any diurnal warming cycle. These localised winds are however, not well represented in the global CFSR dataset (Figure 2.10) and investigations into the variability of localised wind stress are needed before their effects on surface temperatures in the region can be quantified.

Furthermore, the low number of 'match up' days in the Flamingo Lodge region during the months of spring indicates a high frequency of cloud cover. This would have resulted in lower insolation and therefore also played a part in weakening the diurnal cycle in the region.

Under wind stress conditions of greater than 10m.s^{-1}, the diurnal warming signal is thought to be negligible (Gentemann *et al.* 2003). Furthermore in areas of high winds stress (>3m.s^{-1})

(Gentemann *et al.* 2003), such as that observed at the Luderitz site (Figure 2.13), the diurnal warming signal was expected to be less pronounced than that determined in the Flamingo region. This was not the case however, as the average partial diurnal signal in the Luderitz region was found to be 0.76°C (Figure 2.12). This may be because of the sheltered nature of the Shearwater Bay study site, which is protected from the strong winds common in the Luderitz region (Figure 2.4). The slight increase in the partial diurnal warming signal in winter (Figure 2.12) could be related to the drop in wind speed in the region (Figure 2.13) and an increase in stratification of the surface layers in the region.

The application of the correction factors calculated in this study should account for the effects of these influences on the satellite estimation error in the northern Benguela. To investigate the origin of estimation error from satellite derived data in the inshore zone, future studies should consider both the amplitude of the regional diurnal warming cycle, the variability and intensity of wind stress as well as the influence of radiant emittance from adjacent land masses.

Chapter 3

Could an environmental parameter be used to estimate the spatial distribution of *Argyrosomus coronus*?

3.1. Introduction to Key Question 2:

Many fisheries management strategies are dependent on at least a rough estimation of the extent and variability of the spatial distribution of a target species. Knowledge of the changes in spatial distribution of migratory species are particularly important as the targeted stock moves to different locations during different times of the year, where they may become more or less vulnerable to fishing effort (Link *et al.* 2010). Low oxygen water (LOW), seasonal temperature variability, salinity changes and other factors such as lack of food leading to unfavourable local conditions can force species out of their traditional distribution ranges (Jensen *et al.* 1993, Parmesan and Yohe 2003, Parmesan 2006, Helfman *et al.* 2009, Link *et al.* 2010).). Future management strategies will be ineffective unless they incorporate accurate data on the variability of the spatial distribution of the study species in relation to changes in oceanographic conditions, especially in the face of global change (Link *et al.* 2010).

The response of a species in the northern Benguela, *Argyrosomus coronus*, in the northern Benguela, to changes in environmental parameters may be greater than those in relation to changes in prey distributions or abundance as this fish is a generalist feeder (Griffiths and Heemstra 1995, Potts *et al.* 2010) and is not reliant of one source of prey. Furthermore, the high seasonal variability in oceanographic conditions in the area associated with the seasonal migration of the Angola Benguela Frontal Zone (ABFZ) (Shannon 1985, Hardman-Mountford *et al.* 2003), the northern periphery of this species' distribution, suggests that west coast dusky kob individuals may regularly be exposed to conditions which fall outside of the range in which it evolved. Therefore despite considerable tolerance, extremes of very warm or very cold water may affect the spatial distribution of the study species. However, the exact optimum environmental ranges of this species and how it will respond to anticipated climatic changes are still unknown.

When the optimum environmental ranges for a particular species are known, the most influential environmental variable could be used as a proxy for fish distribution, provided the variable could be measured relatively easily and on appropriate spatial and temporal scales (Pörtner and Knust 2007, Nye *et al.* 2009, Link *et al.* 2010). Management strategies could be dramatically improved if it is possible to estimate species distribution, even predicting future changes in this distribution, based on the variability of the selected parameter.

This chapter therefore addresses the second key question of the study by exploring fluctuations in relative abundance of *A. coronus* in relation to temperature variability, as well as assessing the relative importance of temperature in determining this species' spatial distribution.

3.1.1. Identifying environmental parameters which could determine spatial distribution of *A. coronus*

A host of environmental variables which potentially indicate environmental change are available to be measured. These are water temperature, dissolved oxygen and salinity (Wootton 1990, Pörtner and Knust 2007, Helfman *et al.*2009). The availability of accurate, long term datasets of these variables however, is limited. This is especially true in the northern Benguela and the application of a variety of different datasets in this study was necessary to overcome the paucity of data.

Although the individual influence of temperature, oxygen and salinity on the spatial distribution of *A. coronus* will be explored in this chapter, it is important to note that fish are not exposed to any of these environmental parameters in isolation, and that it is frequently the combined influence of several interacting parameters which affect species distributions (Wootton 1990, Jensen *et al.* 1993). If the inter-relationships between the selected variables are known, one indicator variable (e.g. temperature) may be selected to determine changes in spatial distribution of fish populations. For this purpose, three environmental variables are considered the most influential while also being relatively easy to measure.

3.1.1.1. Temperature

Temperature has successfully been used to track or explain the spatial distribution shifts of a number of fish species (Pörtner and Knust 2007, Nye *et al.* 2009, Link *et al.* 2010). As ocean temperatures are expected to rise globally (Parmesan and Yohe 2003, Parmesan 2006, IPCC 2007, Link et al 2010) in the near future, and are currently rising at a rate of 0.07°C per decade (Burrows *et al.* 2011), a latitudinal shift in the distribution of species towards the cooler poles is probable (Parmesan and Yohe 2003, Pörtner and Knust 2007, Nye *et al.* 2009, Potts and Gotz 2011).

Fish have evolved to function optimally within a certain temperature range, and when exposed to temperatures out of this range their physiological processes (governing

metabolism, reproduction and osmoregulation) are affected. Even small fluctuations in temperature affect species spatial distributions as fish will move to a better suited environment in the face of adverse conditions (Pörtner and Knust 2007, Potts and Gotz 2011). Due to the high heat capacity of water however, temperature change often takes place at a relatively slow rate (Sturtevant 1977) allowing fish to move into better suited conditions.

Although there is a paucity of environmental data in the study region, MODIS Terra and Aqua SST estimates have been evaluated in the study region and can therefore provide information on surface temperature variability (Chapter 2). Alternatives to *in situ* subsurface monitoring can be found in global databases of sampling station data devolved from international and local research cruises. One such database is the World Ocean Atlas 2009 (WOA) (Locarnini *et al.* 2009, Garcia *et al.* 2009, Antonov *et al.* 2010), a global database of research cruise sampling stations, which is freely available and incorporates data quality flags, invaluable use in oceanographic studies. Outputs from regional ocean model simulations may also prove useful in indicating temperature variability with depth, especially where the abundance of WOA sampling stations are limited. In the northern Benguela the regional ocean model system (ROMS) has successfully resolved major oceanographic features and processes of the area (including upwelling cells and surface currents) and is believed to provide an accurate representation of the variability of temperature (as well as other variables) with depth (Penven *et al.* 2001, Veitch *et al.* 2010). Through the employment of a combination of datasets, a good understanding of the variability of temperature in the inshore environment of the northern Benguela is possible.

3.1.1.2. Dissolved Oxygen

Oxygen too plays a part in determining the spatial distribution of ectothermic species as the amount of dissolved oxygen in the water column determines the maximum rate of aerobic respiration in fish at a given temperature (Jensen *et al.* 1993, Pörtner and Knust 2007, Helfman *et al.* 2009). However the effects of temperature and oxygen variability are strongly coupled, as oxygen solubility decreases with an increase in water temperature (Wootton 1990, Jensen *et al.* 1993, Pörtner and Knust 2007). A fish's aerobic scope is thus limited outside of its thermal tolerance range (Pörtner and Knust 2007). This is the case in a warming ocean, where the increase in oxygen demand of fish caused by an elevated metabolism is mismatched by the lowered amount of dissolved oxygen available in the water column (Pörtner and Knust 2007). Therefore changes in either variable can greatly affect species

distribution, as fish will move to more favourable environments (where dissolved oxygen concentrations are >5mg.m-3 or >156.26mmol.m^{-3}) when faced with adverse temperature and dissolved oxygen levels.

Obtaining dissolved oxygen data is more challenging than retrieving SST values in the study region, as satellite sensors are unable to make surface or subsurface estimations of oxygen saturation. The WOA dataset can be used in this case to derive dissolved oxygen variables from regionally extracted datasets, as described above. Dissolved oxygen data is, however, recorded less frequently than water temperature, which may limit the applicability of this dataset. A solution may be available in model outputs. ROMS which is based purely on physical relationships and hydrodynamic equations has been coupled with a biological model (BIOgeochemical model of the Benguela Upwelling System, BIOBUS) where a variety of biological parameters are represented (le Vu *et al.* in press, Gutknecht *et al.* in press). The model simulates each month of a typical year, and dissolved oxygen variability can be explored in the Benguela system at different depths.

3.1.1.3. Salinity

Oceanic fishes have evolved to cope with relatively narrow salinity ranges, as opposed to euryhaline, estuarine dwelling species which can withstand salinity ranges from freshwater (<0.5) to brackish water (0.5-17) as well as ocean water salinities (>35). As a result, dramatic changes in salinity levels affect osmoregulatory processes and can result in the loss of ionic balance within the tissues of a fish (Wootton 1990, Helfman *et al.* 2009). Salinities outside of a fish's tolerance limits require an increased rate of osmoregulation in order to maintain normal functioning. As greater amounts of energy are required to osmoregulate, additional oxygen uptake is required (Wootton 1990). Oxygen solubility is also lowered at high salinities (Wootton 1990, Jensen *et al.* 1993), which means that in a situation where salinity and temperature are elevated, dissolved oxygen levels will be significantly lowered and fish will become stressed if they do not move into more favourable conditions.

A. coronus spends the majority of its life history in coastal waters and is thus exposed to the natural variability of salinity in the region (35.3-35.9) (Salat *et al.* 1992) as well as the fresh water conditions associated with river outflow at the Cunene River mouth. This species is thus thought to have an optimum salinity range of ~1.7–35.9. Its allopatric species *A. japonicus,* occurring on the south and east coasts of southern Africa however, is estuarine

dependent and has therefore evolved to cope with a relatively large range of salinities (3-66) (Whitfield 1998). The west coast dusky kob may therefore exhibit a higher tolerance range of salinity than is expected for an oceanic species. If this is indeed the case, salinity would not act as an effective proxy for this species' distribution.

Salinity data is becoming increasingly accessible after the launch of the first microwave/infrared surface salinity sensor on board the NASA's Aquarius in August 2011 (Aquarius 2011). Sea surface salinity (SSS) will soon be available at various spatial scales from this monitoring platform, and where salinity can be used as a predictive variable, managers should take advantage of this advancement. Alternatives for measuring salinity are similar to those for the measurement of dissolved oxygen.

3.1.2. Measuring relative abundance of a species

If changes in relative abundance estimates can be predicted by variability of one of the above mentioned environmental parameters, this parameter could be used as a proxy for the spatial distribution of the species. Studying exact range boundaries can be difficult for marine species, and an alternative to this is to investigate relative abundance of a species at one location and use this as an estimate of distributional variability (Harley *et al.* 2006). Catch per unit effort (CPUE) monitoring provides an estimate of the relative abundance of a population over time, in a specified region, on condition that the method of catching fish remains constant and does not improve in efficiency.

Problems associated with using CPUE as an indicator of relative abundance do exist however, the most important of which arise from the assumption that the 'catchability' of a species (the proportionality constant for the relationship between CPUE and abundance) remains constant over time (Harley *et al.* 2001, Maunder *et al.* 2006). This is not necessarily the case as the catchability in many fisheries increases as the fishery increases in efficiency over time (e.g. through gear changes/adaptations), is subject to fluctuations in environmental conditions (e.g. effects of El Niños on fish populations) and is affected by population dynamics within the target species (Maunder *et al.* 2006). The problems associated with variable catchability were limited in the CPUE dataset recorded at Flamingo Lodge through the use of a fixed study site and the use of standardised gear and fishing method (Rod and Line cast from the beach) ensuring the fishing efficiency remained constant. Additionally, any changes in bait or hook type were factored into the standardisation process. The

recording of *in situ* temperature data together with CPUE accounted for environmental variability and as the *A. coronus* population in the Flamingo Lodge study region was thought to be at near pristine levels before the study period (2005-2009) (Potts *et al.* 2010) historic population dynamics shifts were not expected to have influenced to ability of CPUE to represent the relative abundance of the study species in this region.

3.1.3. Specific aims:

The combined use of four different datasets namely, *in situ* temperature and CPUE monitoring, MODIS Terra SST estimates, the World Ocean Atlas (WOA) dataset as well as model outputs from the ROMS BIOBUS simulation provide sufficient information on the oceanographic variability of the northern Benguela (focusing on two study sites namely Flamingo Lodge and the Cape Frio upwelling cell). This study therefore aims to determine whether Temperature, salinity and dissolved oxygen values from these datasets could be utilised to estimate the spatial distribution of the study species.

3.2. Materials and methods

In order to address this aim, the following methodology was carried out:

3.2.1. Study region

The study region was selected to encompass the region under the influence of the southerly extent of the seasonal migration of the Angola-Benguela Frontal Zone (ABFZ) (see Chapter 1) as well as the southerly extent of the migration undertaken by the study species as described by Potts *et al.* (2010). The study region extended offshore to 10°E, beyond the boundaries of the continental slope (~200m depth), in order to include the regional variability of offshore oceanographic conditions. This allowed for the investigation of possible offshore movements of *A. coronus* when adverse conditions prevailed in the inshore zone. The domain of the study region was thus 15-19°S and 10-12.5°E (Figure 3.1(A)). In order to investigate environmental variability with depth, two smaller study sites were included in the study. One of these (Figure 3.1(B)) was directly off the coast of Flamingo Lodge, southern Angola, while the second was located further south at the Cape Frio upwelling cell, south of the Cunene River mouth (Figure 3.1(C)).

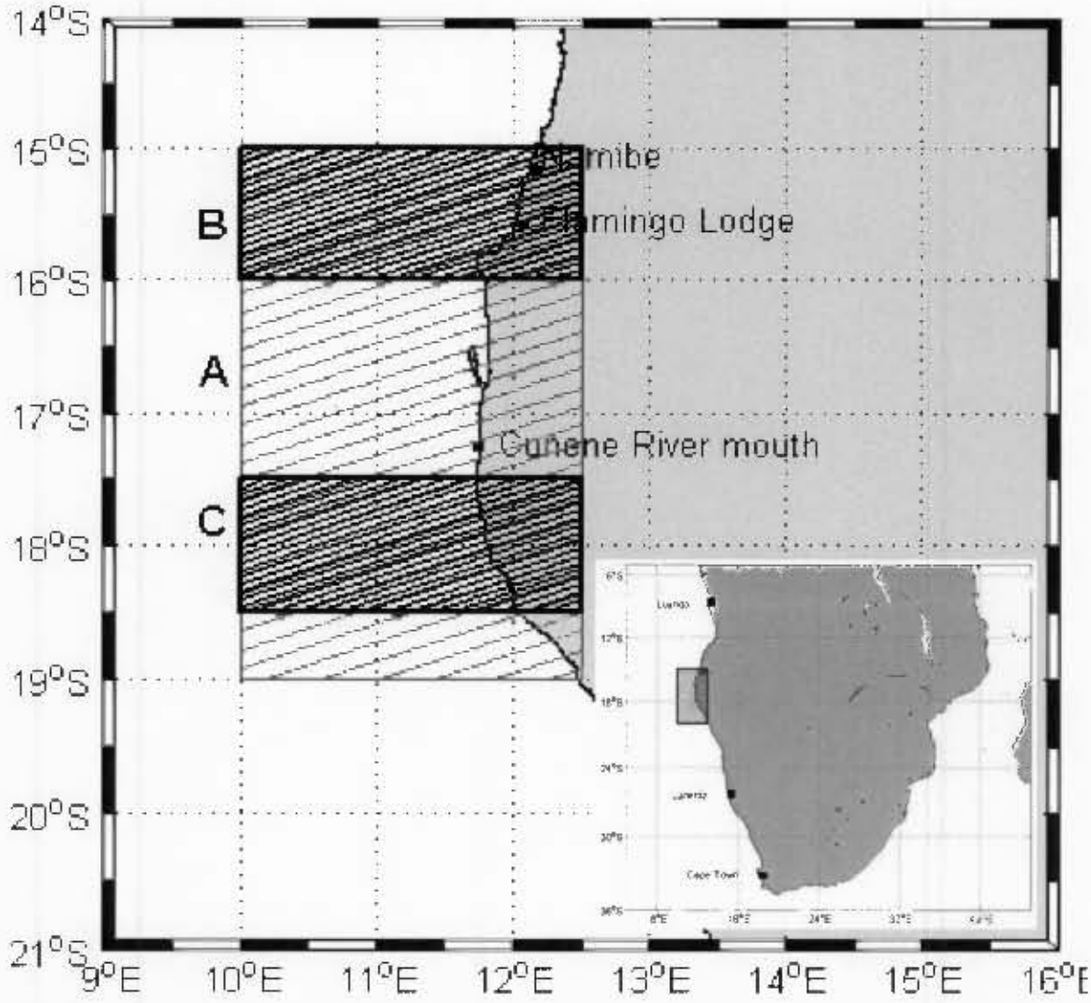


Figure 3.1 The study region in the northern Benguela. A: The whole study region (grey box) (15-19°S, 10-12.5°E), B: The Flamingo Lodge study region (15-16°S, 10-12.5°E). C: The southern study region, at the Cape Frio upwelling cell (17.5-18.5°S, 10-12.5°E).

3.2.2. Catch per unit effort (CPUE)

Catch per unit effort (CPUE) data was used in this study as an estimate of population abundance for *A. coronus*. CPUE was recorded at Flamingo Lodge in Southern Angola (see Chapter 2) on a daily basis between May 2005 and June 2009 for a total of 545 days. The fishing method used was rod and line and all fishing activity took place in the surf, from the beach. All landed catches of *A. coronus* from the recreational fishery were recorded, whether they were released or kept for biological sampling. The recreational fishery consisted of research, tourist and local fishers. After every angling outing, the total number of angler

hours and the lure or bait type used was recorded. This provided an accurate and standardised estimation of fishing effort. The total amount of fish caught was then divided by the standardised fishing effort in order to calculate the CPUE. Daily CPUE was averaged by month in order to determine a climatology of CPUE variability which could then be compared to similarly averaged environmental variables.

3.2.3. Environmental variable data collection

As a result of the paucity of oceanographic monitoring in the study area temperature, dissolved oxygen and salinity datasets from four different sources (listed below) were used and compared in this study.

3.2.3.1. *In situ*

The first method of data collection considered was the *in situ* water temperature dataset, collected daily at Flamingo Lodge, southern Angola between May 2005 and June 2009 (see Chapter 2). The daily temperature values were averaged into a monthly climatology for comparison to CPUE, which was collected in conjunction with this dataset. The *in situ* temperature values recorded at Flamingo Lodge were regarded as representative of local surface temperatures.

3.2.3.2. Satellite derived estimates

Satellite derived estimates of sea surface temperature (SST) were available over the study time period (2005-2009) from the MODIS sensor aboard NASA's Terra polar orbiting satellite (see Chapter 2). MODIS Terra data was used here as Terra was launched in 2000 whereas Aqua was only launched in 2002; the longer dataset of the Terra MODIS sensor gives a more accurate climatology of the annual variability of SST than the Aqua version. MODIS Terra daily SST estimates of 2x2km resolution data were extracted for the region between 15-19°S and 12.5°E (Figure 3.1(A)). The SST values were averaged monthly to develop a climatology for the region. These values were then corrected according to Table 2.4 (Chapter 2), in order to ensure their accuracy in the inshore region at all times of the year.

3.2.3.3. World Ocean Atlas 2009

World Ocean Atlas (2009) (Garcia *et al.* 2009, Locarnini *et al.* 2009, Antonov *et al.* 2010), data for the study region was extracted using Ocean Data View (ODV) (Schlitzer 2011). This dataset is a compilation of oceanographic profiles and surface data collected during scientific research cruises from 1955 until 2009. Data was extracted according to the seasons, summer

(DJF), autumn (MAM), winter (JJA) and spring (SON) to allow investigation into the seasonal subsurface variability for the selected environmental parameters. Seasonal instead of monthly averaged data was used here due to the low number of research stations in the study region. ODV was used to create seasonally averaged temperature, dissolved oxygen and salinity profiles of the region in the proximity of the Flamingo Lodge as well as the Cape Frio study sites (Figure 3.1 (B, C)).

3.2.3.4. Regional Ocean Model Simulation (ROMS) and BIOgeochemical model of the Benguela Upwelling System (BIOBUS) model outputs

ROMS is topographical following sigma coordinate model which has been regionally resolved in the northern Benguela through the use of a child model forced with parent boundaries (Vietch *et al.* 2010). The child model has been fitted with biological data (BIOBUS) at an 8x8km resolution (le Vu *et al.* in press, Gutknecht *et al.* in press). A ROMS BIOBUS simulation was run to output the environmental parameters for an average year. The climatologies of dissolved oxygen, temperature and salinity were extracted from the surface level (Sigma level 32) (or from a depth of -10m for dissolved oxygen) for the northern Benguela study region (15-19°S, 10-12.5°S, Figure 3.1(A)).

3.2.4. Extent of the seasonal cycle in the study region

As the effects of the seasonal cycle on the spatial distribution of *A. coronus* were under investigation, it was important to determine whether any other mode of variability could have had a significant influence on the oceanographic conditions of the region. The influence of the seasonal cycle on local temperature variability (Figure 3.1(A)) was thus explored through a correlation, where the total amount of variance in daily SST estimates (MODIS Terra) explained by the monthly SST climatology (MODIS Terra) was calculated (MATLAB R2009a).

3.2.5. Determining the optimum environmental ranges

The optimum range for *A. coronus* in terms of each of the selected environmental parameters (temperature, dissolved oxygen and salinity) was defined as the range of a particular parameter which accounted for >95% of the total number of instances of CPUE >0.01fish.per angler-hour. To calculate this, the frequency of temperature, salinity and dissolved oxygen values where CPUE was above 0.01fish.per angler-hour was determined and the range in parameter values which included >95% of the CPUE values >0.01fish.per angler-hour was considered to be the optimum range. Daily *in situ* temperature values were compared with

daily CPUE values from Flamingo Lodge to determine the optimum temperature range of *A. coronus*. While Monthly averaged salinity and dissolved oxygen values extracted from the ROMS BIOBUS simulation outputs at 15.5°S and 11.58°E, where used to determine the optimum ranges of salinity and dissolved oxygen.

Furthermore, the maximum thermal range of *A. coronus* was established by determining the lowest and highest *in situ* temperatures where >0.01fish.per angler-hour CPUE was recorded.

Hovmöller plots of each environmental variable were constructed in order to investigate their regional variability. ROMS BIOBUS simulation outputs were extracted to display regional variability in salinity and dissolved oxygen, while MODIS Terra data (corrected according to Chapter 2) was used to represent sea surface temperature (SST) variability. The optimum ranges of each variable were then applied to these plots, to estimate the potential spatial distribution of *A. coronus* as described by each variable. All three of these ranges were then overlaid on the same Hovmöller plot to determine the potential spatial distribution of the study species according to the combined optimum ranges of salinity, dissolved oxygen and temperature.

3.2.6. Variability of spatial distribution in terms of avoidance limits at depth

As adult west coast dusky kob individuals have been observed offshore (Potts *et al.* 2010) it was important to assess the environmental conditions at various depths in the water column, and to determine the seasonal changes at these depths. Cross sections of temperature, dissolved oxygen and salinity data were extracted from the WOA dataset and ROMS BIOBUS outputs for the same region (15-16°S and 10-12.5°E). This allowed a comparison of the seasonal changes in oceanographic conditions in the water column, as well as a comparison between the WOA data and the model outputs.

As the Cape Frio region is expected to be the southernmost point of the seasonal migration undertaken by the study species as described by Potts *et al.* (2010), seasonal cross sections were also extracted from the region (17.5-18.5°S and 10-12.5°E) (Figure 3.1(C)). This allowed the exploration of the suitability of the region for west coast dusky kob at different times of the year in terms of the defined optimum environmental ranges.

The optimum environmental ranges (defined above) were then applied to these cross sections to determine whether the conditions were suited to an offshore movement for the study

species, during periods when the nearshore conditions deteriorated. The oceanographic conditions in the water column, to a depth of 200m were viewed in terms of all three environmental parameters simultaneously, by overlaying the different cross-sections. The oceanographic conditions were deemed suitable if they were within the defined optimum ranges of at least two of the selected environmental variables.

3.3. Results

3.3.1. Seasonal signal in the study region:

An average of 79.0% of the total variability in SST (MODIS Terra) was explained by the seasonal climatology of SST (Figure 3.2a). The extent of the seasonal variability is further highlighted by the amplitude of the seasonal cycle which had a regional average of 2.85 (Figure 3.2b).

The seasonal cycle of temperature is evident in the MODIS Terra SST data (Figure 3.3a) which was corrected according to Table 2.4 (Chapter 2). Temperatures were found to increase in the summer and autumn, in the vicinity of Flamingo Lodge (15.5°S), while decreasing in the winter and spring. A similar cycle was observed in the salinity dataset (Figure 3.3b). Dissolved oxygen showed less seasonal variability with a high concentration north of 15.5°S (>200mmol.m^{-3}) and lower concentrations (140-200mmol.m^{-3}) south of this location for the majority of the annual cycle (Figure 3.3c).

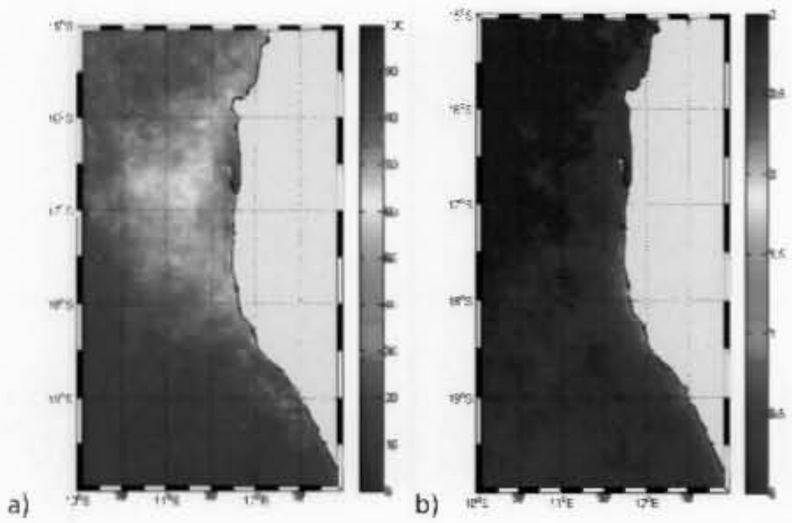


Figure 3.2 a) The amount of variance in MODIS Terra derived SST estimates, explained by the seasonal SST climatology per pixel. The colour bar represents the correlation coefficient (R^2) x100. b) The amplitude of the annual period emphasising the magnitude of the seasonal signal in the region.

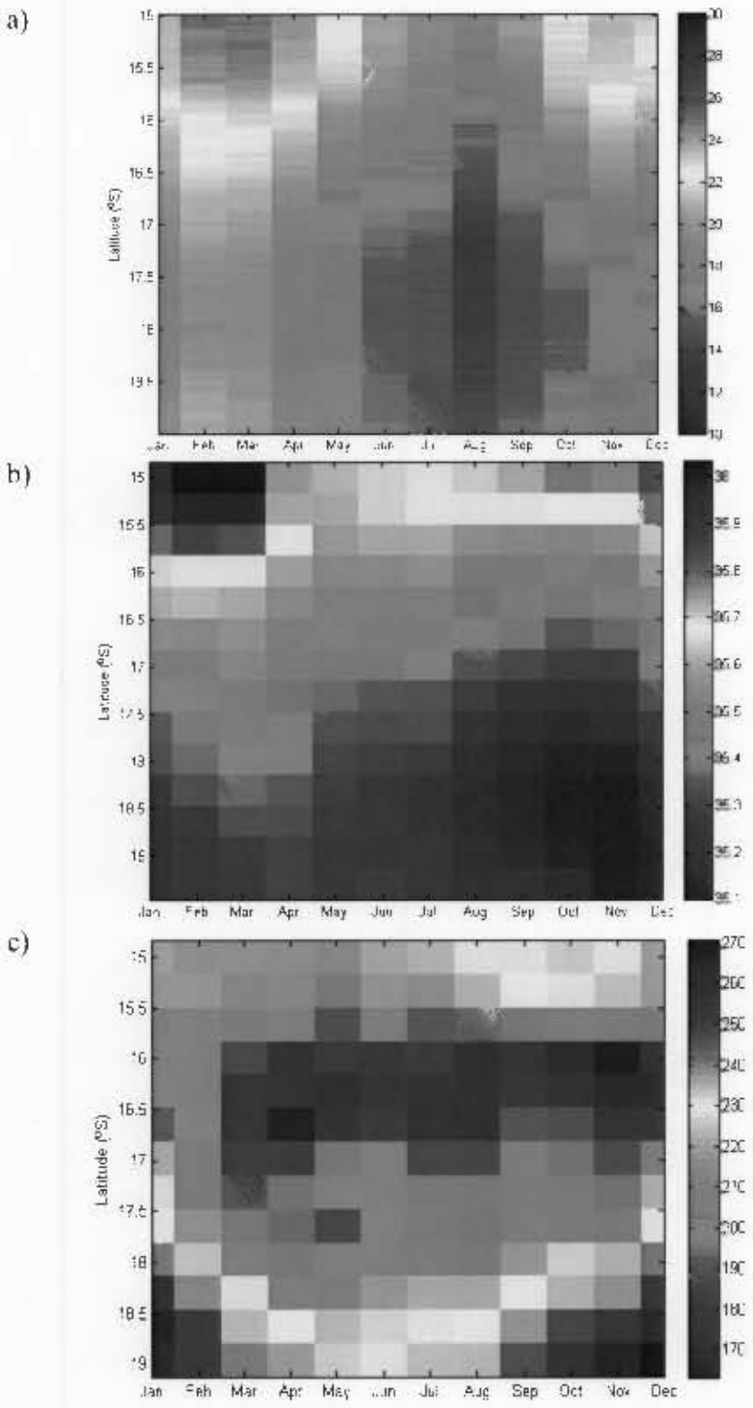


Figure 3.3 Hovmöller (latitude-time) plots of (a) MODIS Terra SST estimates (corrected according to Table 2.4 (Chapter 2)) , (b) ROMS BIOBUS surface salinity and (c) ROMS BIOBUS dissolved oxygen (mmol.m-3) (10m below the surface) data extracted from the region between 15-19°S along 11.58°E.

3.3.2. Determining the optimum environmental ranges for *A. coronus* in the southern Benguela

An initial relationship between MODIS Terra SST as well as *in situ* temperature estimates and monthly averaged CPUE (Figure 3.4) suggested that CPUE declined rapidly when monthly averaged sea surface temperatures (SST) rose above 20°C, while increasing when temperatures were below 20°C. Although the CPUE appeared to decrease when temperatures reached 18°C, no monthly average temperatures below 18°C were recorded and it was therefore not possible to determine whether west coast dusky kob avoided temperatures below this value.

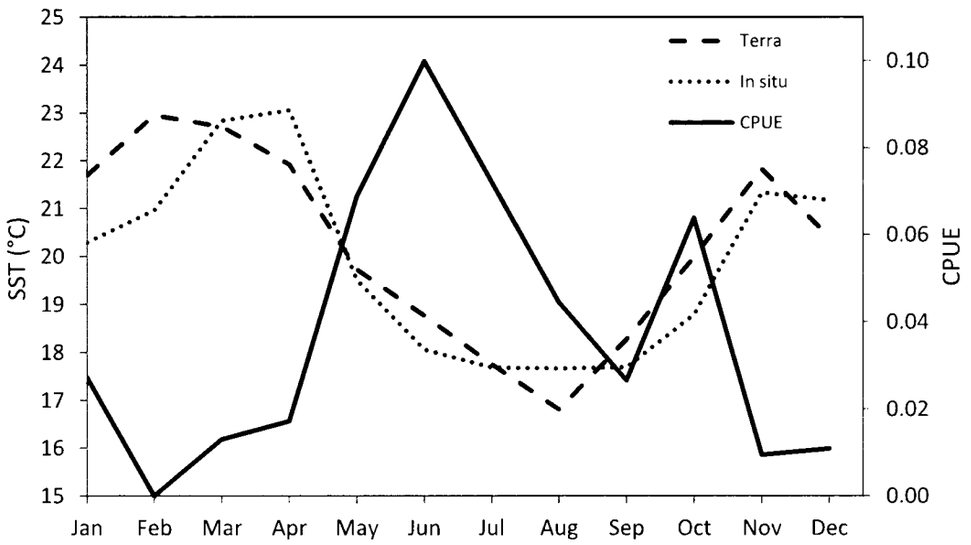
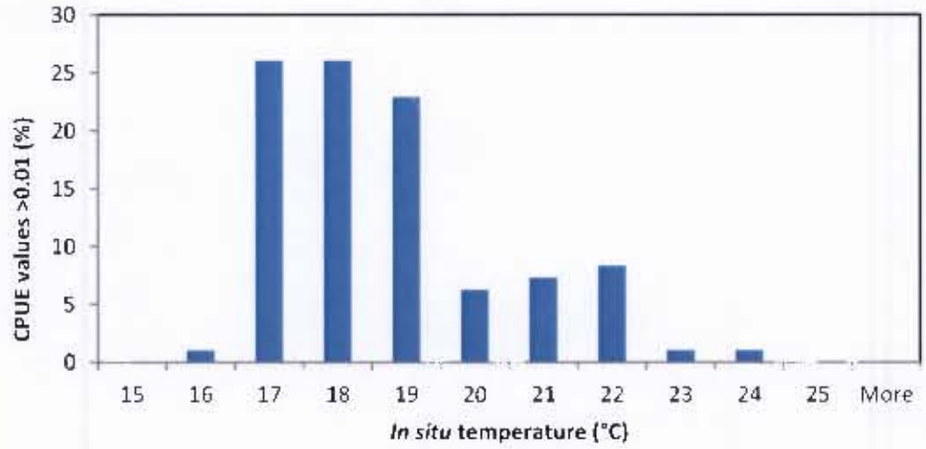


Figure 3.4 Climatology of sea surface temperatures (SST) (in situ: 2005-2009, MODIS Terra: 2000-2010) measured at Flamingo Lodge southern Angola compared with the monthly average catch per unit effort (CPUE) of Argyrosomus coronus for the same location (2005-2009).

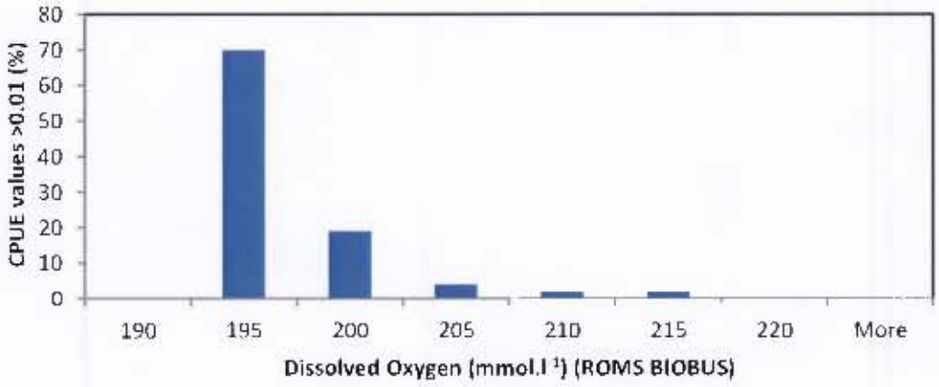
When considering daily CPUE and *in situ* SST measurements, the maximum temperature where CPUE was above 0.01fish per angler-hour was 24.8°C, while the minimum was 16°C. Although 24.8°C can thus be identified as the upper avoidance limit of *A. coronus*, 16°C cannot be considered the lower avoidance limit as no temperatures lower than this value were recorded in the *in situ* dataset. The range of temperatures which accounted for 96.9% of CPUE values greater than 0.01fish per angler-hour was between 16-22°C (Figure 3.5a) and this temperature range was considered the optimum thermal range for west coast dusky kob in southern Angola.

The optimum range of dissolved oxygen (monthly averaged ROMS BIOUBUS outputs) was determined as 190-206mmol.m^{-3} as this range included 95.8% of CPUE values greater than 0.01fish per angler-hour (Figure 3.5b). However it should be noted that an upper limit to oxygen concentrations tolerable to the study species is probably unlikely in reality. In terms of salinity, the optimum range for west coast dusky kob was established as 35.4-35.6 which accounted for 97.9% of CPUE values >0.01fish per angler-hour (Figure 3.5c).

a)



b)



c)

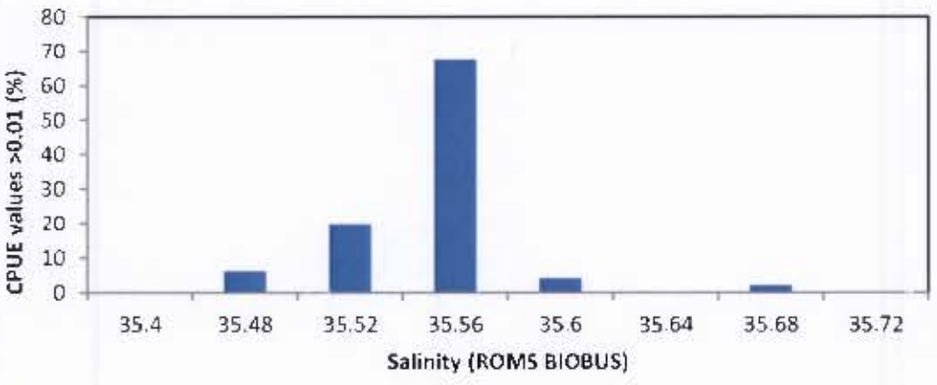


Figure 3.5 Frequency of daily CPUE (A. coronus) values greater than 0.01 (recorded at Flamingo Lodge, southern Angola) displayed in terms of (a) the associated in situ daily temperature values, (b) ROMS BIOBUS monthly averaged oxygen values and (c) ROMS BIOBUS monthly averaged salinity values. In situ temperature data and CPUE were recorded

at 15.57°S, 12.02°E, while dissolved oxygen and salinity data were extracted at 15.5°S and 11.58°E.

The combination of the optimum ranges of the three environmental parameters (temperature, salinity and dissolved oxygen) (Figure 3.6 a,b,c) indicated that west coast dusky kob were potentially situated south of Flamingo Lodge (~15.75-16.65°S, 11.80°E) during summer, the range narrowing and moving further northwards (~15-16°S) in autumn (March-May), widening again in winter (June-August) and becoming extremely narrow (~15.65-15.75°E) in spring (September-November) (Figure 3.6). All three environmental parameters suggest that west coast dusky kob are not found in the Flamingo Lodge region (15.57°S, 12.01°E) during summer and autumn, while both salinity and temperature optimum ranges indicate that this species would avoid regions south of Flamingo Lodge during late winter and early spring (Figure 3.6a,b).

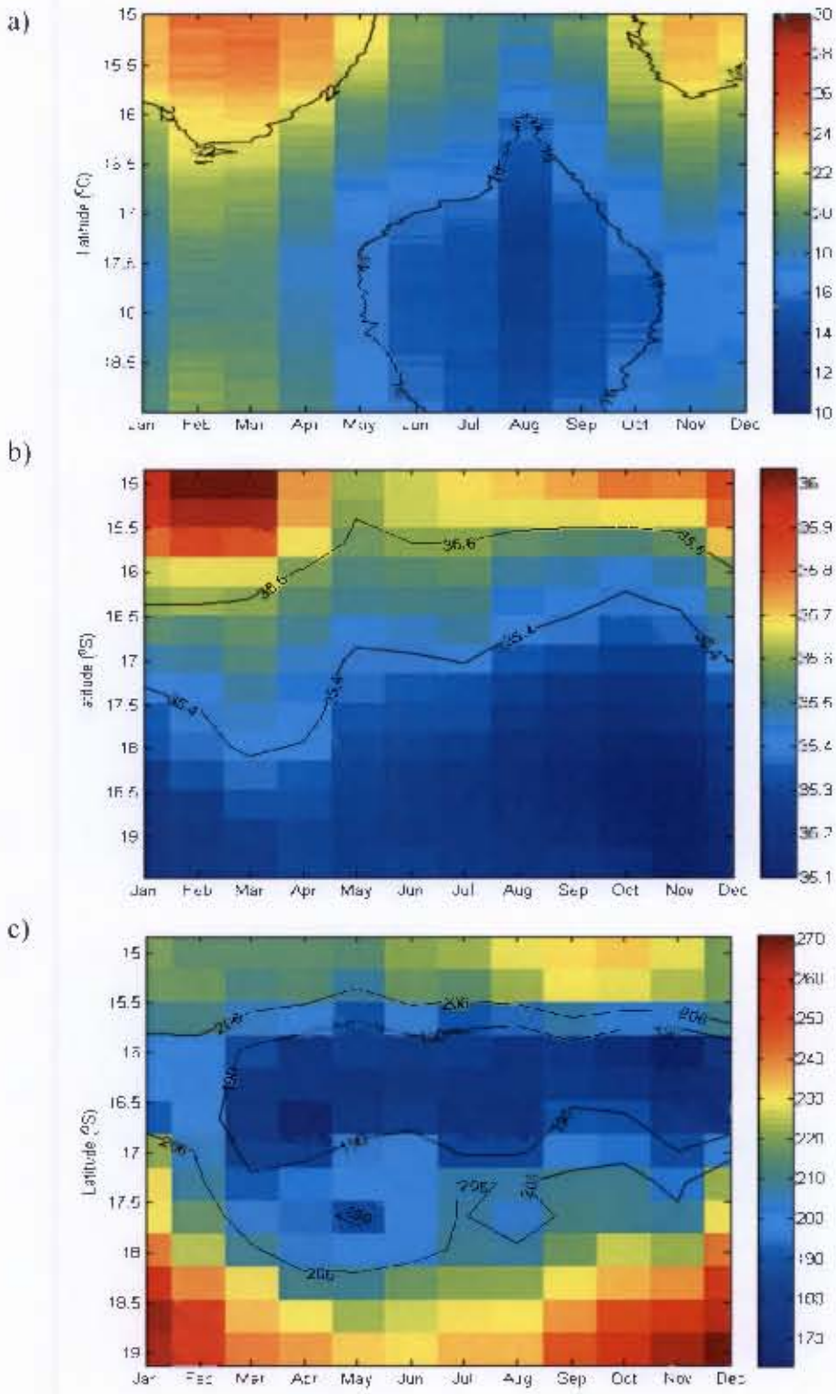


Figure 3.6 Hovmoller plots of the three environmental variables a) temperature, b) salinity and c) dissolved oxygen with the optimum range of *A.coronus* for each variable superimposed. *A. coronus* are expected to be located between the displayed upper and lower levels of the identified optimum ranges.

3.3.3. Subsurface variability in the northern Benguela

3.3.3.1. Flamingo Lodge

Oceanographic conditions were found to be well suited to west coast dusky kob at the Flamingo Lodge study region during winter and spring, at depths of up to 60m (Figures 3.7c,d;3.8c,d). In the case of WOA data these suitable conditions, in terms of temperature, salinity and dissolved oxygen extended as far as 200km offshore (Figure 3.8c,d). ROMS BIOBUS simulation outputs showed an increase in area of suitable temperature conditions in the winter (Figure 3.7c) while this area decreased in the spring as the 16°C isotherm swallowed (Figure 3.7d).

Although the thermal conditions of the ROMS BIOBUS outputs appear to be well suited to *A. coronus* individuals during the summer and autumn months (Figure 3.7a,b), the WOA data suggest that only deeper waters (10-20m in summer and 20-40m in autumn) fall within the defined optimum ranges of temperature, salinity and oxygen (Figure 3.8c,d).

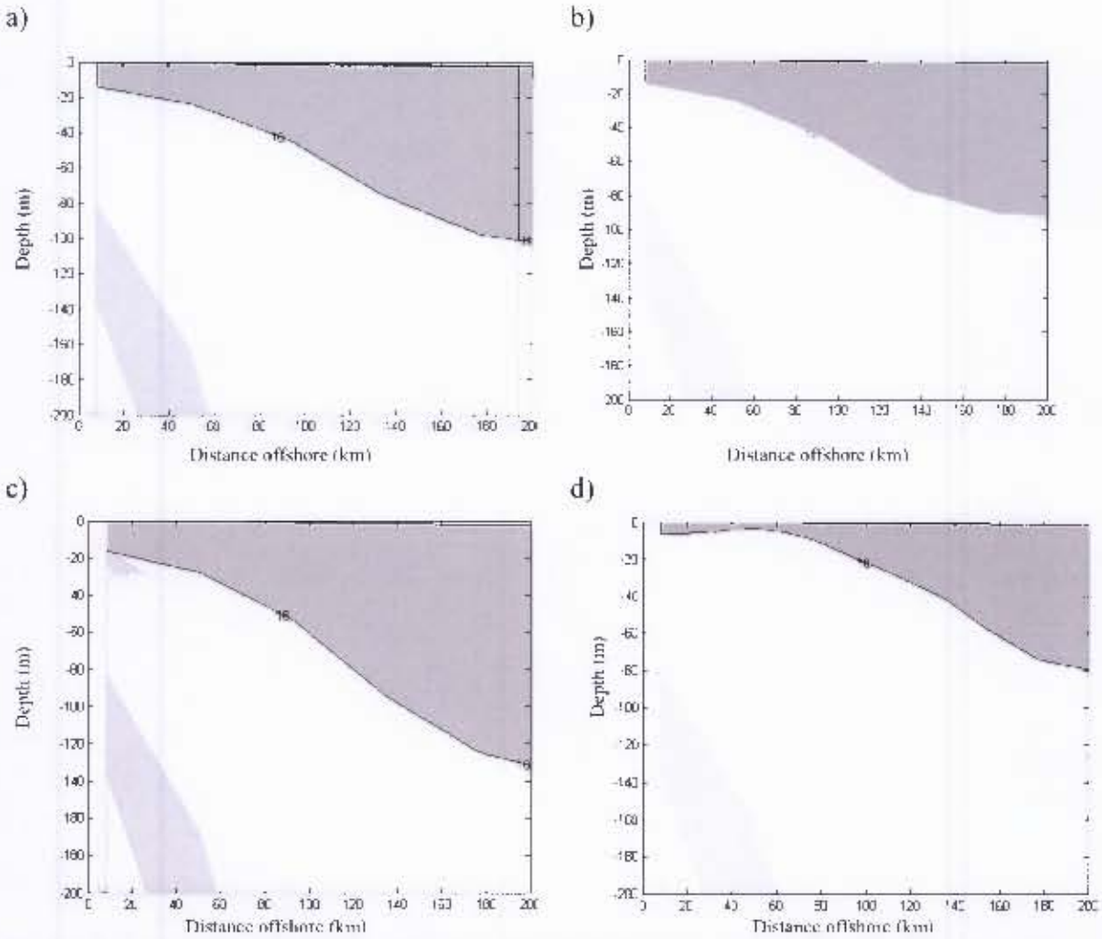


Figure 3.7 Seasonal variability (with depth) of optimum environmental parameters for A. coronus in terms of temperature (16-22°C) (dark grey) and dissolved oxygen (190-206 mmol.m^{-3}) (light grey) at the Flamingo Lodge study site, southern Angola (15-16°S, 10-12.5°E) for a) summer, b) autumn, c) winter and d) spring. Data was extracted from ROMS BIOBUS simulations.

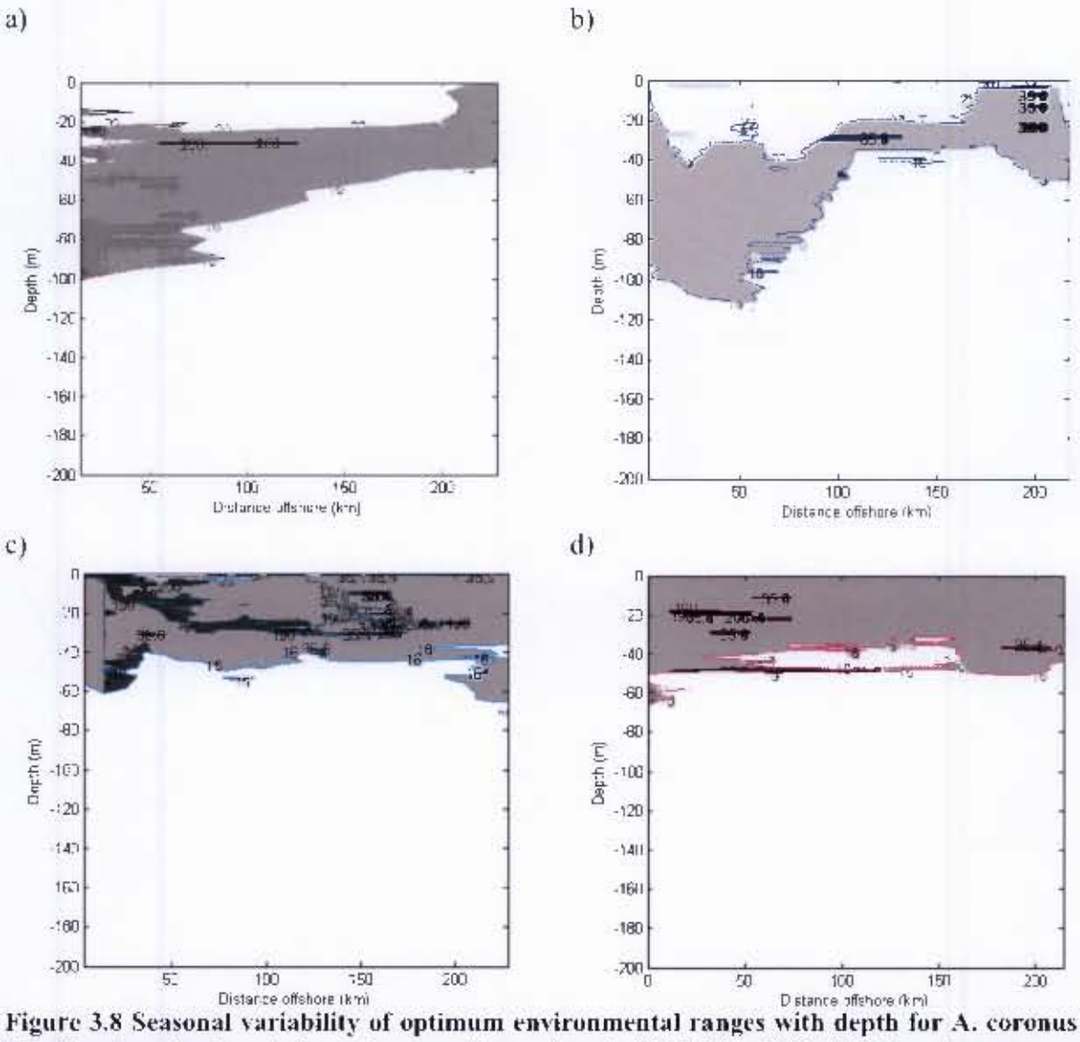


Figure 3.8 Seasonal variability of optimum environmental ranges with depth for A. coronus in the Flamingo Lodge study region, southern Angola (15-16°S, 10-12.5°E) for a) summer, b) autumn, c) winter, d) spring. Data was extracted from the WOA database.

3.3.3.2. Cape Frio

In contrast to the Flamingo Lodge region, the conditions at the Cape Frio study region appear to be well suited to west coast dusk kob during the summer and autumn months (Figures 3.9,3.10).The WOA data suggests that conditions within the defined optimum ranges of temperature, salinity and dissolved oxygen persist to depths of between 40-60m until at least 200km offshore (Figure 3.10a,b). The ROMS BIOBUS outputs indicate that suitable temperatures exist in the upper 10m until between 20 and 40km offshore, and extend to 20m only in excess of 90km offshore (Figure 3.9a,b).

Winter and spring exhibit poor conditions for west coast dusky kob in the Cape Frio region (Figures 3.9c, d; 3.10c, d). Suitable conditions in terms of salinity and dissolved oxygen from the WOA dataset are evident between 40 and 60km offshore, while conditions within the thermal optimum range are only found between 70 and 150km offshore (Figures 3.10c, d). The ROMS BIOBUS data supports these findings as winter temperatures within the defined optimum range are only located ~160km offshore (Figure 3.9c), while no autumn temperatures within the range of 16-22°C were identified (Figure 3.9d).

No salinity data within the defined optimum range (35.4-35.6) from the ROMS BIOBUS outputs was identified at either of the study sites. Although seasonal variability of salinity values below 35.4 was evident (Annex 2).

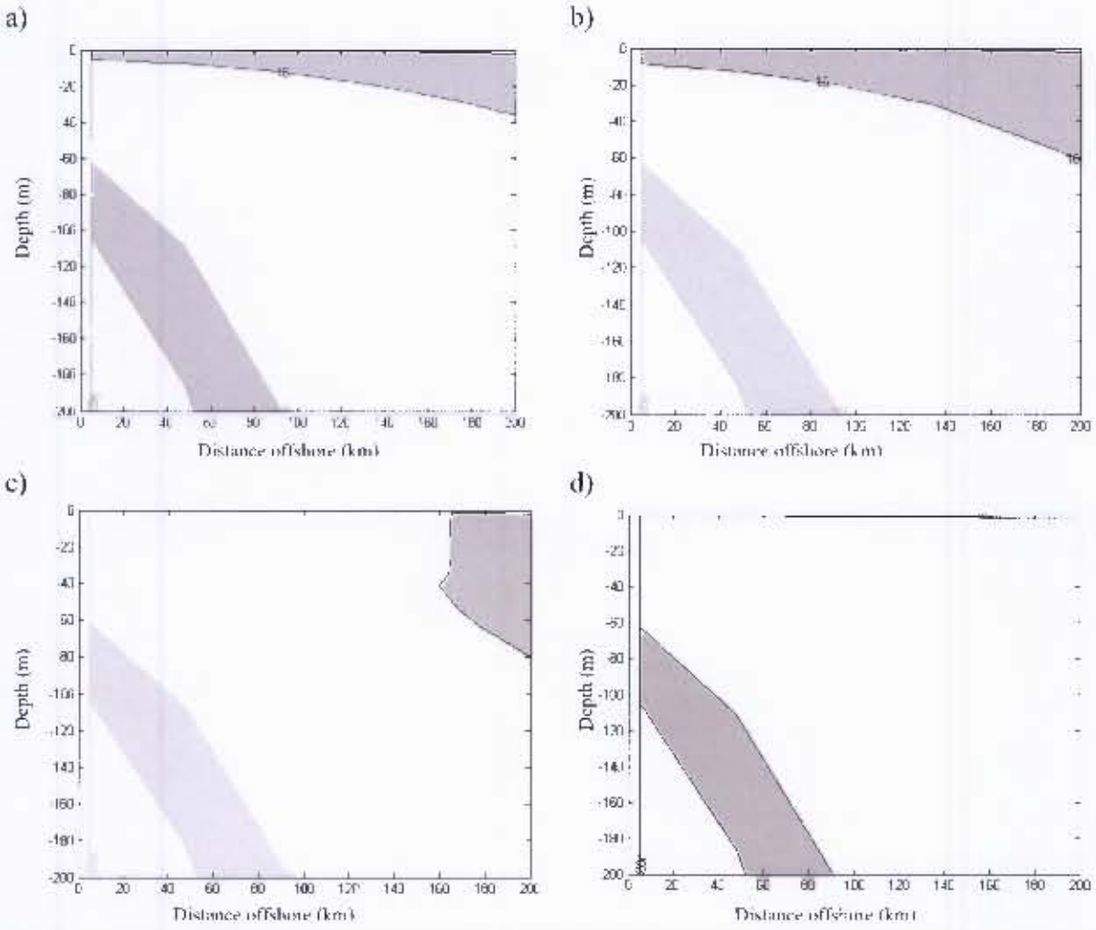


Figure 3.9 Seasonal variability of optimum environmental parameters (temperature 16-22°C, dissolved oxygen 190-206mmol.m^{-3}) for *A. coronus* at the Cape Frio study site (17.5-18.5°S, 10-12.5°E) in a) summer, b) autumn, c)winter and d) spring. Data extracted from ROMS BIOBUS simulations.

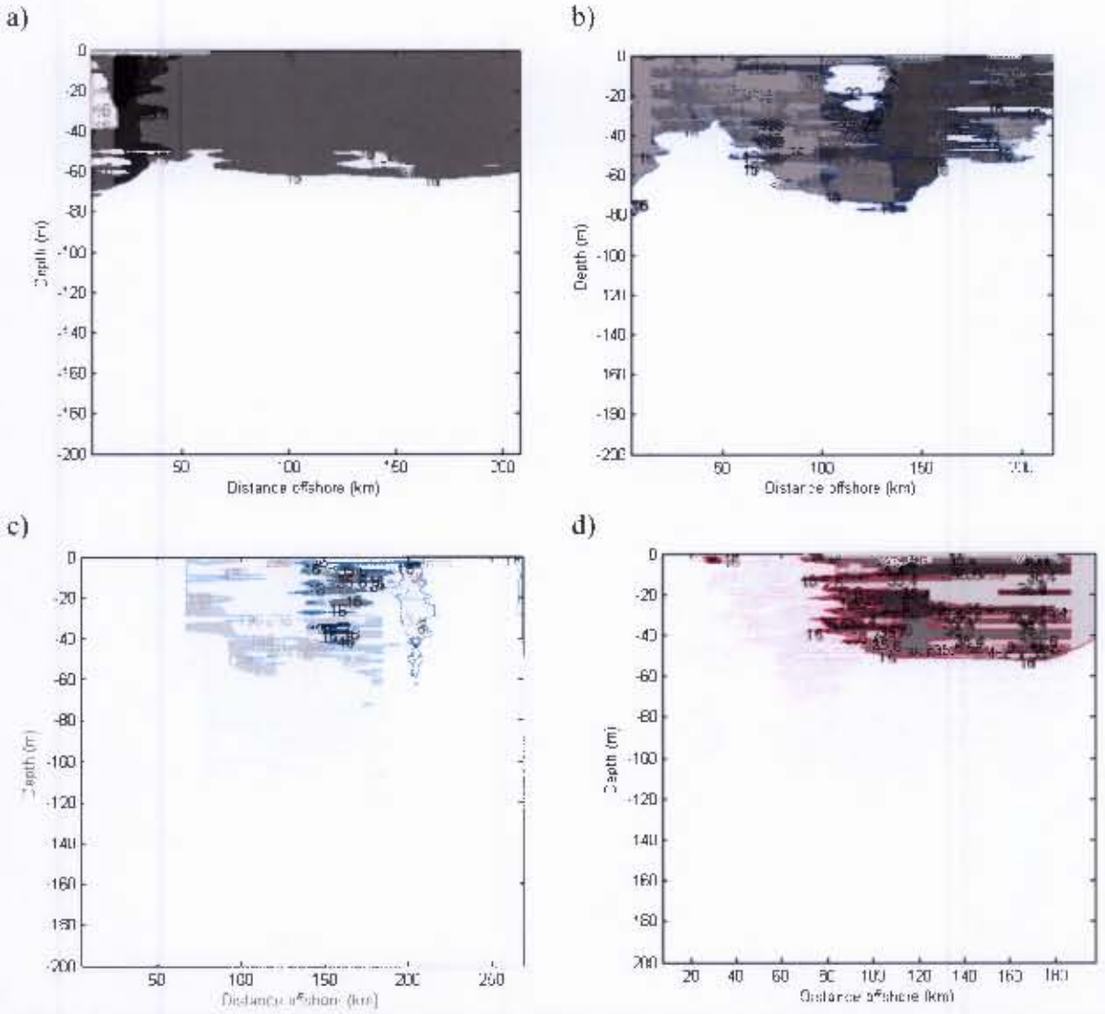


Figure 3.10 Seasonal variability in optimum environmental ranges with depth for *A. coronus* at the Cape Frio study region (17.5-18.5°S,10-12.5°E), (a) summer, (b) autumn, (c) winter and (d) spring conditions. Data extracted from the WOA database.

3.4. Discussion

The seasonal cycle of SST (MODIS Terra SST, 2x2km resolution) in the region having explained an average of 79.0% of the annual regional variability, is expected to have the greatest influence on the dominant oceanographic conditions of the study area (Figure 3.2a). Furthermore, regional temperature variability (Figure 3.3a) provided an accurate description of the spatial extent of the late summer intrusion of the Angola Current into the northern Benguela and the expected behaviour of the Angola-Benguela Frontal Zone (ABFZ) as described in the literature (Meeuwis and Lutjeharms 1990, Hardman-Mountford *et al.* 2003, Veitch *et al.* 2006, Colberg and Reason 2006) (Figure 1.1). This is because of the very different temperature signatures of the two dominant water masses in the region, South Atlantic Central water (12-18°C), and Angola Current water (17-24°C) (Salat *et al.*1992).

The optimum thermal ranges defined for *A. coronus* are thus expected to encompass the majority of the variability in the region as they are calculated according to temperature changes. Additionally, this thermal range (16-22°C) (Figure 3.5a) is within the natural range limit of the closely related *A. japonicus* (12-28°C) (Whitfield 1998, Collett *et al.* 2008).The optimum tolerance range of farmed *A. japonicus* individuals however, is 24-26°C (Bernatzeder and Britz 2007, Collett *et al.* 2008), perhaps indicating the ability of A, coronus to cope more effectively with cooler water temperatures (~16°C) than the allopatric *A. japonicus*. This is supported by evidence indicating 76% of Flamingo Lodge CPUE records greater than 0.01fish per angler-hour occurred in temperatures between 16 and 19°C (Figure 3.5a).

The optimum salinity range of 35.4-35.6 (Figure 3.5c) was slightly higher than the optimum functioning range of 35 indicated for farmed dusky kob individuals, potentially a result of an adaption to the high salinities of the northern Benguela. While the optimum range for dissolved oxygen of 190-206mmol.m^{-3} (Figure3.5b) is similar to normoxic conditions (~212mmol.m^{-3}) and could suggest (as would be expected) that the study species avoids low oxygen conditions (<100mmol.m^{-3}). It should be noted, however, that the salinity and dissolved oxygen optimum ranges were calculated using monthly averaged data extracted from the ROMS BIOBUS model outputs and do not necessarily accurately represent *in situ* variability. This is probably a result of the limited amount of *in situ* data available for the validation of such models.

The establishment of optimum environmental ranges are important in terms of fisheries management as such measures can be used to determine the spatial distribution of a species. This is because fish exposed to adverse conditions will move out of the unfavourable area if possible (Pörtner and Knust 2007). Additionally this movement is expected to take place before the negative impacts of exposure to such conditions affect the physiological functioning of fish (Pörtner and Knust 2007). The optimum ranges presented here are therefore not necessarily representative of the critical values for this species in the open ocean, but rather their optimal functioning limits, where growth and reproduction are maximised (Smith 1985, Wootton 1990, Helfman *et al.* 2009). Environmentally controlled laboratory experiments will need to be carried out in the future in order to accurately define the perceived tolerance ranges of *A. coronus* and to determine the relative critical environmental values.

3.4.1. The potential spatial distribution of *A. coronus* at different times of the year

The seasonal variability of the defined optimum ranges of surface temperature, salinity and dissolved oxygen, highlighted potential areas within the study region which would be suited to west coast dusky kob individuals (Figure 3.6). The surface conditions were not within the range of any of the selected environmental parameters in the vicinity of Flamingo Lodge (~15.7°S) during the summer and autumn months. The contrary was true for the Cape Frio study region (~18°C) where conditions were well suited to *A. coronus* during the summer and autumn months, but were deemed unsuitable during winter and the beginning of spring (Figure 3.6). The regional shift in the optimum environmental ranges suggests that west coast dusky kob would be situated south of Flamingo Lodge during summer and early autumn, and in the vicinity of the lodge in the winter and spring. These movements are similar to those described by the proposed seasonal migration of *A. coronus* in the northern Benguela (Potts *et al.* 2010). As the seasonal distributional shifts described here only represent surface movements, the possibility of offshore movements during adverse nearshore conditions was explored.

3.4.2. Exploring subsurface variability

Subsurface variability is especially important in this study as the CPUE measure was recorded from beach based fishing activity, and fish that potentially moved into deeper waters during the study period would be out of range of the fishers. This highlights the fact that periods of decreased CPUE did not necessarily indicate a southerly migration of west coast dusky kob, but could have been a result of their movement into deeper waters further offshore.

Summer and autumn subsurface conditions in the Flamingo Lodge study region did appear to be suited to the study species in terms of WOA data, as conditions within the defined optimum ranges existed 30-40m below the surface (Figures 3.8a,b). It should be noted that the limited number of sampling stations in the study region may mean that the data does not represent the true variability of the subsurface region at Flamingo Lodge. It is not certain that the study species would move offshore at the Flamingo Lodge study site during summer and autumn as Nye *et al.* (2009) stated that spatial distributional changes of fishes in response to environmental variability are strongly dependent on their biogeography. The fact that *Argyrosomus coronus* is an inshore species (Griffiths and Heemstra 1995) suggests it more than likely evolved in an inshore environment. Thus the possibility of offshore movement in response to adverse nearshore conditions is reduced. This is also suggested by the seasonal migration of the study species described by Potts *et al.* (2010). *In situ* temperature datasets at various depths in the water column would help to accurately determine whether or not, and the extent to which fish are able to move offshore when faced with adverse nearshore conditions.

The prevailing summer and autumn conditions further south towards the Cape Frio upwelling cell (17.5-18.5°S, 10-12.5°E) (Figure 3.1(C)) however, appeared well suited for *A. coronus* individuals (Figure 3.9a,b; 3.10a,b). This indicated that the study species would be able to move into these areas when warm water dominated the inshore zone of the northern study area. This is possibly a more likely response than an offshore movement into deeper waters at ~15.57S. This in agreement with the southerly migration of the study species described by Potts *et al.* (2010), based on the results of a tagging study and CPUE monitoring at the Cunene River mouth during the summer and autumn. These authors suggest a southerly migration takes place during late spring, which is when the 22°C surface isotherm moves south of Flamingo Lodge (15.57°S) (Figure 3.3a). The results of this study further

corroborate these findings and suggest that surface temperature variability is an adequate indicator of the spatial extent of the seasonal migration undertaken by the study species.

The return migration (northwards) of this species described by Potts *et al.* (2010) during winter, further supports these findings as west coast dusky kob follow the retreating ABFZ and associated warm, saline Angola current water towards the Flamingo Lodge region once again (Figures 3.3a). Temperatures well suited to the presence of west coast dusky kob, may extend further northwards than Flamingo Lodge especially in spring as upwelling at the Cape Frio upwelling cell strengthens (Monteiro *et al.* 2008). This would allow the study species to move into such regions. Indeed, several anglers have reported catches of *A. coronus* in late August as far north as Cabo Ledo, Angola (9.4°S) (WM Potts *pers. comm.* 2011).

A limitation of identifying suitable subsurface environs for west coast dusky kob using optimum ranges determined from surface (ROMS BIOBUS) or near-surface (*in situ*) data is that subsurface conditions change with depth. Although estimates of suitable subsurface regions for the study species are presented (Figures 3.7, 3.8, 3.9, 3.10), in order to accurately determine offshore spatial variability of west coast dusky kob, monitoring programmes including the installation of *in situ* stations at various depths as well as boat based CPUE measures need to be established.

The relationship between CPUE and the selected environmental variables is based on the assumption that CPUE accurately describes the seasonal changes in relative abundance of the study species in the vicinity of Flamingo Lodge, southern Angola. However, an important point to consider when utilising CPUE data as a population abundance estimate, is that it is a measure of the abundance of feeding fish in the region, and does not indicate the absolute presence or absence of individuals. This is not expected to have affected the use of CPUE as a relative abundance estimate in the study area, as during a small scale warming event (water temperature ~21°C, compared to seasonal mean of ~19°C (Figure 3.4)) in June 2010, diving observations confirmed the decrease in abundance of *A. coronus* in the region as suggested by lowered CPUE.

3.4.3. Determining a proxy for spatial distribution of *A. coronus*

When identifying a proxy for the spatial distribution of a species it is essential that accurate and consistent data is available for the selected variable. Furthermore it is important that variability in the selected parameter describes the expected changes in spatial distribution of the study species.

Pörtner and Knust (2007) indicated that physiological processes in fish were aerobically limited when individuals were exposed to warming water temperatures, as a result of decreased oxygen levels (as oxygen solubility decreases with increasing temperature). This was described as the first process causing fish to move into cooler waters, and highlights the appropriateness of temperature as well as dissolved oxygen data in estimating spatial distribution of fishes. Dissolved oxygen was not however, considered the best suited environmental parameter to describe the variability in spatial distribution of *A. coronus* in southern Angola. This was due to the lack of accurate *in situ* dissolved oxygen data in the study region. The ROMS BIOBUS outputs did not resolve the variability of dissolved oxygen in the nearshore zone at depth. The WOA dataset did however provide a better understanding of subsurface seasonal variability in dissolved oxygen. *In situ* monitoring stations will need to be established throughout the study region in order to determine the accurate seasonal variability of dissolved oxygen.

Surface salinity data (ROMS BIOBUS)(Figure 3.3b) showed similar regional variability to MODIS Terra SST estimates (Figure 3.3a) in the northern Benguela study region (Figure 3.1(A)),and could prove to be a potential proxy for the spatial distribution of west coast dusky kob in the future. This is due to the launch (August 2011) of the first satellite borne surface salinity sensors on board Aquarius (Aquarius 2011). Aquarius uses microwave radiometers to detect changes in the thermal emissions of the ocean as a result of altered conductivity (Aquarius 2011). Fisheries managers could therefore use the two satellite datasets (MODIS SST and Aquarius sea surface salinity (SSS)) concomitantly in the future to determine the potential spatial distribution of *A. coronus*. *In situ* salinity monitoring programmes will need to be established rapidly in order to allow validation of newly available SSS data in the study region.

During this study temperature was the one variable which was well represented in both the WOA and ROMS BIOBUS datasets. This combined with the excellent coverage of surface

variability through MODIS data as well as the existence of an *in situ* temperature dataset meant that temperature was considered the best suited environmental variable to determine spatial distribution of west coast dusky kob in southern Angola. This was further confirmed as the variability in surface temperature data (Figure 3.3a) described potential spatial distribution shifts which were similar to those associated with the seasonal migration described by Potts *et al.* (2010).

3.4.4. Summary of the Seasonal spatial distribution of *A. coronus*

Based on the results of this study, west coast dusky kob individuals would be expected to occupy the following regions during the respective seasons (Figures 3.3, 3.7, 3.8, 3.9 ,3.10):-

- Summer (DJF): Individuals would potentially be situated in the vicinity of the Cape Frio upwelling cell (17.5-18.5°S) where the inshore temperatures up to a depth of ~30-100m were above 16°C , the dissolved oxygen and salinity values , where available were above 190mmol.m^{-3} and ~35.4 40-60m below the surface respectively (Figure 3.10a,b). Temperatures within the optimum thermal ranges of the study species were also present in ROMS BIOUBUS outputs at the Cape Frio study site (Figure 3.9a,b), where seasonal variability was considered relatively accurate (compared to that of the Flamingo Lodge study site (Figure 3.7). Suitable conditions did exist off the coast of the Flamingo Lodge study site during summer and autumn (Figure 3.8a,b). Although the conditions at depth (40-100m) in the Flamingo Lodge study region appear to be suited to the presence of *A. coronus*, being an inshore species is expected to follow the retreating cooler waters and is potentially located in shore in the vicinity of the Cape Frio upwelling cell (17.5-18.5°S).
- Autumn (MAM): West coast dusky kob are expected to remain in the Cape Frio upwelling cell vicinity during this period as the conditions remain similar to those of the summer months in both the Cape Frio upwelling cell and the Flamingo Lodge study regions.
- Winter (JJA): The conditions in the Flamingo Lodge study region are within the optimum environmental ranges described for the study species. Temperatures are between 16-22°C in the upper 50m of the water column (Figure 3.8c), the water column is well aerated (>220mmol.m^{-3}) and salinity is not lower than 35.4.

Individuals of the study species are expected to move into the Flamingo Lodge region during this time, as the water column at the Cape Frio upwelling cell was observed to have cooled to below 16°C as far as ~100km offshore (Figure 3.10c). ROMS BIOBUS outputs suggest temperatures within the optimum thermal range of the study species only exist >160km offshore (Figure 3.9c).

- Spring (SON): The study species is expected to remain in the vicinity of the Flamingo Lodge study region during spring as the conditions at both study sites remain relatively similar to the winter conditions.

The proposed movements (above) are consistent with the regional variability the surface conditions (Figure 3.3,3.6).

3.4.5. Relative accuracy of the datasets

The accuracy of the datasets used in this study determines the accuracy of the predicted spatial distribution range of the study species.

The satellite derived SST values are considered to be the most accurate of the four datasets used here. This is because these values have been corrected according to a validation study (Chapter 2). The same cannot be said of the ROMS BIOBUS model outputs. The model outputs are used to give a general understanding of the variability of salinity, dissolved oxygen and temperature during the different seasons and should be viewed with caution due to the paucity of validation data. The establishment of *in situ* monitoring projects in the study region are therefore critical. The ROMS BIOBUS data appeared to represent the seasonality of the Cape Frio region better than that of the Flamingo Lodge region (Figures 3.7, 3.9, Appendix 1).

The World Ocean Atlas (2009) dataset provides an accurate representation of sub surface profiles as it comprises observational data collected during scientific research cruises. Temperature values were especially well represented and were successfully used to determine potential subsurface regions suitable for west coast dusky kob. Unfortunately salinity and dissolved oxygen data were not recorded as frequently as temperature measurements and did not provide good spatial coverage. Although poor data was removed for the analysis, a problem with using this dataset in the study region, as mentioned earlier, was the low number

of sampling stations available. This resulted in the possibility of a small number (~3) of research stations having an unrealistic influence on the seasonal averaging of the data. This problem was exacerbated by the large temporal gaps between data points which were in some locations as much as 42 years. This dataset was therefore also used for providing a general view of the variability in subsurface oceanographic conditions in the region and highlights the need for *in situ* monitoring programmes to be established in the coastal zone of the northern Benguela as a matter of urgency. A way forward is presented in the final chapter.

Long-term, accurate CPUE datasets from different locations along the coastline, collected concomitantly with environmental variability parameters would help to improve the accuracy of the optimum environmental ranges described in this study and could provide further insights into changing distributional patterns.

3.4.6. Extreme events:

It should be noted that all intrusions of warm Angola current water may not manifest themselves in the same manner as described by the monthly averaged climatologies and fisheries managers should use a combination of variables in order to establish a more accurate estimate of the spatial distribution of *A. coronus* during anomalous events (such as Benguela Niños). This is especially true for dissolved oxygen as Monteiro *et al.* (2008) describe the potential threat of LOW events that occur on the coastal shelf during warming periods. The spatial extent of which would not necessarily be visible through SST monitoring.

3.4.7. Considering additional environmental variables

The distribution of species is not solely related to temperature (Wootton 1990 Jensen *et al.* 1993, Pörtner and Knust 2007, Nye *et al.* 2009), but to the dynamic processes which exist between temperature and other environmental variables. Although temperature does provide a good indication of the seasonal movement of the study species and is easily measured with existing datasets, it is important to consider as many potentially influential variables as possible when attempting to accurately determine species distribution in relation to environmental variability. The environmental variables selected for this study are traditionally (Wootton 1990, Jensen *et al.* 1993, Helfman *et al.*2009) the most influential of fish physiological processes and were also selected because of their relative ease of measuring (low cost, low personnel requirements). However a vast number of other

environmental variables are available to be measured and could also indicate the spatial distribution of *A. coronus*.

3.4.7.1. Hydrogen sulphide

One such variable which is especially relevant to the northern Benguela region is Hydrogen sulphide, this gas escapes from the ocean sediments after excessive anaerobic oxidisation of sulphur by bacteria occurs. The gas forms a layer above the sediment and can subsequently erupt into the water column, and result in large scale fish kills and displacements (Jensen *et al.* 1993, Bruchert *et al.*2009). These events originate in the northern Benguela and may spread southwards on the continental shelf (Monteiro *et al.* 2008). The finding of *A. coronus* individuals south of their expected distribution limit in the Berg and Olifants River estuaries in South Africa may be the result of such events (Lamberth *et al.*2008).

3.4.7.2. Chlorophyll

The monitoring of chlorophyll is another variable that could be a potential spatial distribution indicator. Although the diet of the west coast dusky kob was dominated by pelagic fishes (specifically Sardinella aurita), it was found to be a generalist predator feeding on a range of prey types, including cephalopods (e.g. octopus, Octopus vulgaris and squid, Loligo vulgaris reynaudiii) and crustaceans (estuarine prawn Nematopalaemon spp. and swimming crab Callinetes spp.) in the inshore zone (Potts *et al.* 2010). Therefore, although a higher quantity of pelagic fishes are generally associated with increased productivity, alternative food sources, not determined by the spatial extent of chlorophyll, could be found utilised during times of reduced productivity.

Once the salinity, dissolved oxygen and temperature tolerance limits have been more narrowly defined it will be important to determine the optimum ranges or tolerance levels of secondary environmental variables such as Hydrogen sulphide gas and chlorophyll concentrations. As the ability to monitor a greater number of environmental variables in relation to the optimum environmental ranges of this species improves, the understanding and predictability of its spatial distribution will also improve. This is especially important in an ocean where inter annual variability is increasing (Parmesan and Yohe 2003, Shannon 2008, Monteiro *et al.* 2008). Monitoring programmes need to be initiated as a matter of urgency in order to gain a better understanding of the environmental variability of the study region and changes in the relative abundance of its inshore fishes.

Chapter 4

Assessing the rate of warming, and predicting its impacts on the distribution of *Argyrosomus coronus* in the northern Benguela

4.1. Introduction to Key Question 3:

Global air and sea surface temperatures have risen by 0.56-0.92°C in the past 100 years (1906-2005), and these trends are expected to accelerate in the current century (Harley *et al.* 2006, IPCC 2007). By the end of the century temperatures may have increased by a further 1.4 -5.8°C, and are currently increasing globally at an average rate of 0.13°C.decade^{-1} (1656-2005) (IPCC 2007, Burrows *et al.* 2011). Warming is not occurring uniformly across the globe and some regions are experiencing temperature changes at faster rates than others (Burrows *et al.* 2011). The northern Benguela experienced a rise in surface temperature between 0.8-1°C between 1982 and 2007, and large scale ecosystem changes appear to have taken place as a result (Hutchings *et al.* 2002, van der Lingen *et al.* 2006a, Shannon *et al.* 2008, Hutchings *et al.* 2009). These changes and warming trends are documented particularly in the offshore region of the northern Benguela while the ecosystem effects and rate of warming in the nearshore and inshore zones are relatively understudied.

Organisms are expected to respond to regional changes in temperature by changing their spatial distribution in order to maintain their thermal niches (Loarie *et al.* 2009, Burrows *et al.* 2011). Shifts in spatial distribution (especially a shift in temperate species towards the poles) as a result of climate change are well documented (Parmesan and Yohe 2003, Pörtner and Knust 2007, Nye *et al.* 2009, Link *et al.* 2010, Potts and Gotz 2011) and are expected to increase in occurrence if current global warming trends continue (IPCC 2007, Hare *et al.* 2010, Link *et al.* 2011). In order to effectively manage important inshore linefish species, such as the west coast dusky kob (Potts *et al.* 2010), it is essential to know the extent and possible direction of potential spatial shifts as well as the rate at which these may take place. A challenge in the northern Benguela, especially in the inshore zone, is separating the long term climate change trends from the strong decadal cycle in temperature trends as a result of the limited length of temperature datasets.

4.1.1. Recent changes and the observed ecosystem response:

4.1.1.1. Trends in the Benguela Current Large Marine Ecosystem (BCLME)

The availability of satellite derived datasets (>20years) of sea surface temperature (SST) allow trends in the variability of water temperatures to be calculated. Using such datasets, a warming trend (0.6-1°C increase since 1982) (Monteiro *et al.* 2008, Shannon *et al.* 2008) has

been identified in the northern Benguela, while a cooling trend (-0.5°C.decade^{-1} from January to August (1982-2009)) (Rouault *et al.* 2010) appears to exist in the coastal regions of the southern Benguela (Shannon *et al.* 2008, Hutchings *et al.* 2009, Rouault *et al.* 2010).

The present warming trends described in the northern Benguela are believed to be a result of intensifications and longer residence times of the seasonal intrusions of Angola current water into the region (Monteiro *et al.* 2008) (see Figure 1.1). In contrast, changes in the central and southern Benguela are likely to be driven by different mechanisms. Variability in the south is driven by the advection of Agulhas current water entering the Benguela system, and the central sector is governed by the prevailing wind strength and direction (Jury and Courtney 1995).

4.1.1.2. Regime shifts

The changes in temperatures and oceanographic conditions associated with global change and increasing anthropogenic pressure (including fishing and mining) on the BCLME can result in ecosystem changes. These ecosystem changes, termed regime shifts, result in a shift in the dominant species of the region. Regime shifts in the northern and southern Benguela have been identified and are expected to become more established if current trends continue (Lynam *et al.* 2006, Heileman and O'Toole 2000) (see Chapter 1). These changes have had significant socio-economic impacts on the region especially since the new dominant species were less valuable and because of the geographic mismatch between processing facilities and the maximum biomass yields (van der Lingen *et al.* 2006a, Heileman and O'Toole 2009, Hutchings *et al.* 2009). The inshore region may be experiencing similar changes, west coast rock lobster, in the central and southern Benguela have shifted their distribution, south and eastwards in the same direction as the offshore small pelagics (Hutchings *et al.* 2009) (see Chapter 1). The variability of the inshore region of the northern Benguela, however, remains relatively poorly understood and these changes need to be investigated further.

While distributional changes of marine resources described above could be driven solely by environmental variability, it is likely that other anthropogenic factors, such as overexploitation and pollution are believed to have amplified the effects of environmental change (Sherman 2003, Heileman and O'Toole 2009). Mining activities, in particular diamond, on the Namibian and South African coasts are believed to have played a role in the depletion of marine living resources, most notably west coast rock lobster, (*Jasus lalandii*) as

a result of habitat disturbance (Heileman and O'Toole 2009). Oil transportation, exploration and extraction are also a problem in the region as spills and pollution negatively affect marine resources. Recent climatic trends have already triggered significant changes in the spatial distributions of global biota. Since future climatic induced changes are expected to be of a much greater magnitude (IPCC 2007, Harley *et al.* 2006); it is critical to predict changes in the BCLME to sustainably manage the exploitation of its marine resources.

4.1.2. Predicting changes to the system:

Knowledge of historical climate change is necessary to predict and model future changes (Worm *et al.* 2010). The earth is currently in an early inter-glacial period, historically characterised by increasing global temperatures. In the Benguela region specifically, more developed interglacial periods have been characterised by a weakened temperature gradient between the poles and the equator which resulted in a weak Benguela current veering west in the Cape Basin, south of its modern position (Krammer *et al.* 2006) (see Chapter 1). During this scenario, it is most likely that the central and northern Benguela would have been dominated by warm, tropical waters such as those associated with the Angola Current. The influence of anthropogenic greenhouse gas emissions however, may have altered the causal mechanisms of change that characterised the historical interglacial periods. Consequently the future changes in temperature could manifest themselves slightly differently (possible amplifying the historical trends), and ecosystem responses may be similar but not identical to the historical responses (Bakun 1990).

Outcomes of global climate models (GCMs) predict trends in the warming of the global ocean to continue, and even increase in intensity in the future (IPCC 2007). The impact of further change is likely to manifest through changes in inter-annual variability as well as through mean climatic shifts (IPCC 2007). Recent (2006) observational data which has been compared to model outputs from the 2001 IPCC summary suggests that the global climate system may be responding faster than expected to increases in greenhouse gas emissions (Rahmstorf *et al.* 2007). This means that the rates of change predicted by the models may be conservative estimates and the Benguela system could in fact undergo changes at a faster rate. An analysis of the rate of change in the Benguela would enable resource managers to plan for such changes.

If warming trends are to continue in the Benguela system a variety of oceanographic and ecosystem changes are likely to take place, however the decadal variability currently experienced in the region may have greater influence over shorter time periods, and the effects of this long term warming will only become apparent in the future. Increased coastal upwelling in the central Benguela is expected as a result of an increase in alongshore windstress caused by the strengthening of the South Atlantic Anticyclone (SAA, high pressure cell) (Bakun 1990).

A warming trend in the northern Benguela of ~0.8°C (1982-1989) (Monteiro *et al.* 2008), and ~0.3°C.decade^{-1} (1982-2005) (Rouault 2007, Hutchings *et al.* 2009) suggests a longer residence time of seasonal intrusion of the southerly flowing Angola Current. Shannon *et al.* (2008) highlighted the expected increase in frequency and intensity of anomalous warming events, such as Benguela Niños in the northern Benguela, should the warming trends continue. These changes have major implications for marine organisms in the region as changes in the seasonal cycle and rapid increases in average temperature will necessitate alterations to life history strategies in order to ensure continued optimal reproductive and growth functioning (Pörtner and Knust 2007, Burrows *et al.* 2011). With a global increase in temperature, species' spatial distributions are shifting towards the cooler poles (DEAT 2004, Harley *et al.* 2006, Pörtner and Knust 2007, Link *et al.* 2010, Potts and Gotz 2011).

Current global climate model scenarios may suggest an increase of red tides on the west coast of South Africa (Pitcher and Calder 2000, DEAT 2004). These will continue to increase if the current rate of urban population expansion continues and an increasing amount of nutrients (untreated sewage, industrial effluent) are discharged into the sea. The decomposition of such events can result in anoxic conditions which effect fish respiration and spatial distribution (Pitcher and Calder 2000, Heileman and O'Toole 2009, Helfman *et al.* 2000). However, if upwelling winds continue to increase as the high pressure cell (atmospheric) shifts southwards, these effects may not become apparent as turbulence and disturbance of coastal water would increase, reducing the occurrence of harmful algal blooms.

The prediction of impacts caused by a changing environment is critical for the mitigation and adaptation required to reduce the vulnerability of inshore species. Examples of management interventions to reduce vulnerability include changing the positioning of marine protected areas or the timing of closed fishing seasons (Link *et al.* 2010). If management strategies are

able to adapt to ecosystem changes, the sustainable exploitation of resources may still be possible (Link *et al.* 2010).

4.1.3. Specific aims

This chapter aims to answer Key Question 3 by quantifying the temperature related changes in the northern Benguela. These results will then be used to predict potential shifts in the spatial distribution of *Argyrosomus coronus*.

4.2. Methods

4.2.1. Temperature datasets

Satellite derived values for sea surface temperatures (SST) were used to investigate regional warming trends. This is because of the large spatial coverage obtained by satellite swaths and the consistency of their data collection (see chapter 2 for details). Temperature estimates from two different datasets were investigated, namely the Pathfinder SST reanalysis dataset as well as moderate resolution imaging spectroradiometer (MODIS) data from the National Aeronautics and Space Administration's (NASA) Terra satellite.

Pathfinder reanalysis SST data was selected because of its good temporal and relatively cloud-free coverage of 25 years (1985-2009). Monthly advanced very high resolution radiometer (AVHRR) data are reprocessed, as part of the Ocean Pathfinder SST project, a joint venture undertaken by NASA and the National Oceanic and Atmospheric Administration (NOAA) (Kilpatrick *et al.* 2001). Monthly 4x4km resolution data from Pathfinder version 5, with a quality flag of greater or equal to 4 was downloaded (http://www.nodc.noaa.gov) to form the dataset used in this study (Kilpatrick *et al.* 2001). This dataset has a great advantage over the MODIS Terra data in terms of temporal coverage, but lacks the ability to accurately describe temperature variability in the inshore zone or areas with steep temperature gradients (such as the Angola-Benguela Frontal Zone). This is because it is a global dataset and regions of steep temperature gradients are considered to be erroneous data.

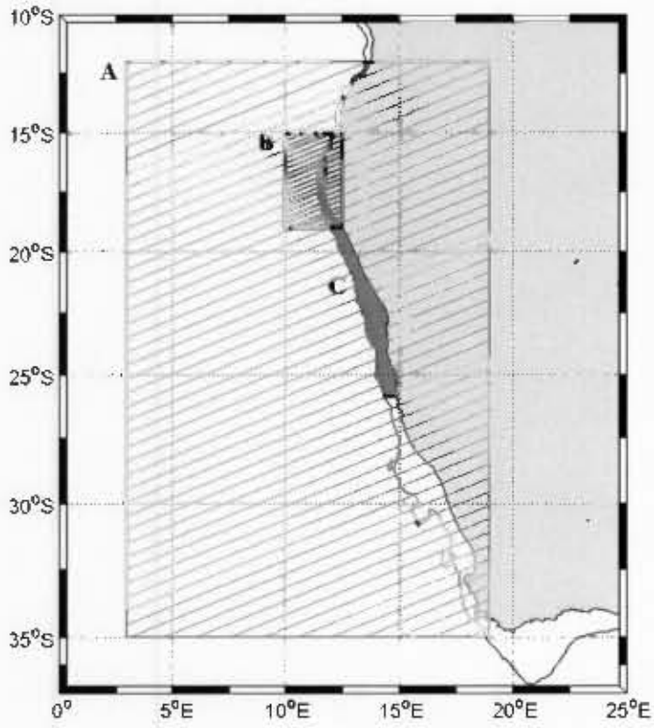
The MODIS Terra data (2000-present), extracted for the study region (see Chapter 2) was selected as opposed to MODIS Aqua data (2002-present) as the Terra dataset has a greater temporal range. All MODIS Terra data used in this study was corrected according to the

seasonal correction factors calculated in Chapter 2 (Table 2.5). Monthly averaged data from the MODIS Terra 2x2km as well as 4x4km resolution datasets were used in this study as this limited the effects of a seasonal bias caused by cloud cover in the extracted data. This also allowed a more robust comparison with the Pathfinder dataset as it too was comprised of monthly averaged data.

4.2.2. Study regions

Warming trends of a variety of study areas were compared in order to identify regions with an accelerated rate of change. The four areas selected for inclusion in this study were the southern African region (5-47°S and 3-55°E); the Benguela current large marine ecosystem (BCLME) region (12-35°S and 3-19°E); the Angola-Benguela Frontal Zone (ABFZ) (15-19°S, 10-13°E) and the inshore region of the northern Benguela between 12 and 26°S, inshore of the 200m isobath (Figure 4.1). MODIS Terra SST data (2x2Km resolution) was used to describe the ABFZ region, while 4x4km MODIS Terra SST data was used in the BCLME region as well as the inshore region of the northern Benguela. Temperature variability in the general southern Africa region was described using AVHRR Pathfinder 4x4km resolution data.

a)



b)

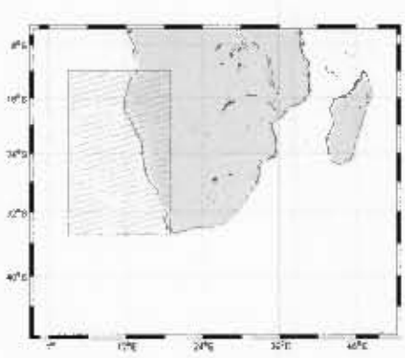


Figure 4.1 Study areas for sea surface temperature (SST) variability. a) (A)The Benguela Current Large Marine Ecosystem (BCLME) (12-35°S and 3-19°E) region, (B) the Angola-Benguela Frontal Zone (ABFZ) (15-19°S and 10-13°E) and (C) the inshore (<200m depth) region of the northern Benguela (12-26°S). b) The southern African region (5-47°S and -3-55°E), where the highlighted area represents the study area (A) of image a).

4.2.3. Analysis of warming trends in the northern Benguela

Linear regressions were fitted to the annually averaged temperature data in order to determine the extent of any warming trend present in the extracted data. Trends were assumed significant at the 95% level. Regionally averaged annual averages of SST were extracted from the different regions as necessary and were plotted in 2 dimensions in order to obtain a visual representation of the calculated trend. The linear trends exhibited by each pixel in each of the three domains were also represented in three dimensions. All computer analyses (and maps) were undertaken (created) using MATLAB R2009a.

To determine the relative rate of warming (°C.decade^{-1}) in the northern Benguela, the average global ocean warming trend (0.07°C.decade^{-1} (1960-present)) (Burrows *et al.* 2011) was subtracted from the regional data. To examine the relative rate of warming within the northern Benguela region, the global mean was subtracted from the average warming trend observed in each individual 4x4 km pixel.

Warming in the inshore region between 12 and 26°S was determined by examining the SST in the pixels between the coast and the 200m isobaths (Figure 4.2 (area C)). The rate of inshore warming in different areas on the northern Benguela coast were compared by subtracting the regionally averaged (inshore zone) warming signal of each pixel in the inshore region. To compare the warming rates in different sections of this inshore zone the significance of the per pixel linear trends were calculated using Spearman's rank correlation and the p values of the 90 and 95% significance levels were plotted.

4.2.4. Determining the potential spatial distribution of *A. coronus*

The results of Chapter 3 showed that the northernmost spatial distribution of adult *A. coronus* individuals can be approximately determined by the extent of the 22°C isotherm. Therefore, the northern extent of the spatial distribution of this species was mapped by tracking the annually averaged latitudinal extent of this isotherm, estimated from both MODIS Terra

4x4km resolution data (2000-2010) as well as the Pathfinder reanalysis data (1985-2009) in the ABFZ region (Figure 4.1 (B)) of the study area. The relative position of the Angola-Benguela Frontal Zone (ABFZ) was also assessed by plotting the annual position of the 20°C isotherm. This isotherm is thought to represent the approximate position of the front (Lass *et al.* 2000).

4.3. Results

4.3.1. Surface temperature trends exhibited by the different datasets

A warming trend was evident in the Northern Benguela (Figure 4.2a,b,c). Both the AVHRR (25 year study period) and the MODIS Terra (11 year study period) data (Figure 4.2,b) indicated that there has been extensive inshore and offshore warming of the northern Benguela. In addition, the region associated with the seasonal migration of the ABFZ (12-20°S) was warming faster over the last decade (2000-2010) than the rest of the northern Benguela (Figure 4.2a,b). The offshore zone of southern and central Benguela region was cooling, with the most marked cooling in the St Helena Bay area (~32-35°S) and the Luderitz upwelling cell (~26°S) (Figure 4.2b). In contrast, the inshore zone in the Luderitz upwelling region was warming at a rate of ~0.5°C.decade^{-1}. However, this trend was not evident in the longer term Pathfinder dataset (Figure 4.2a).

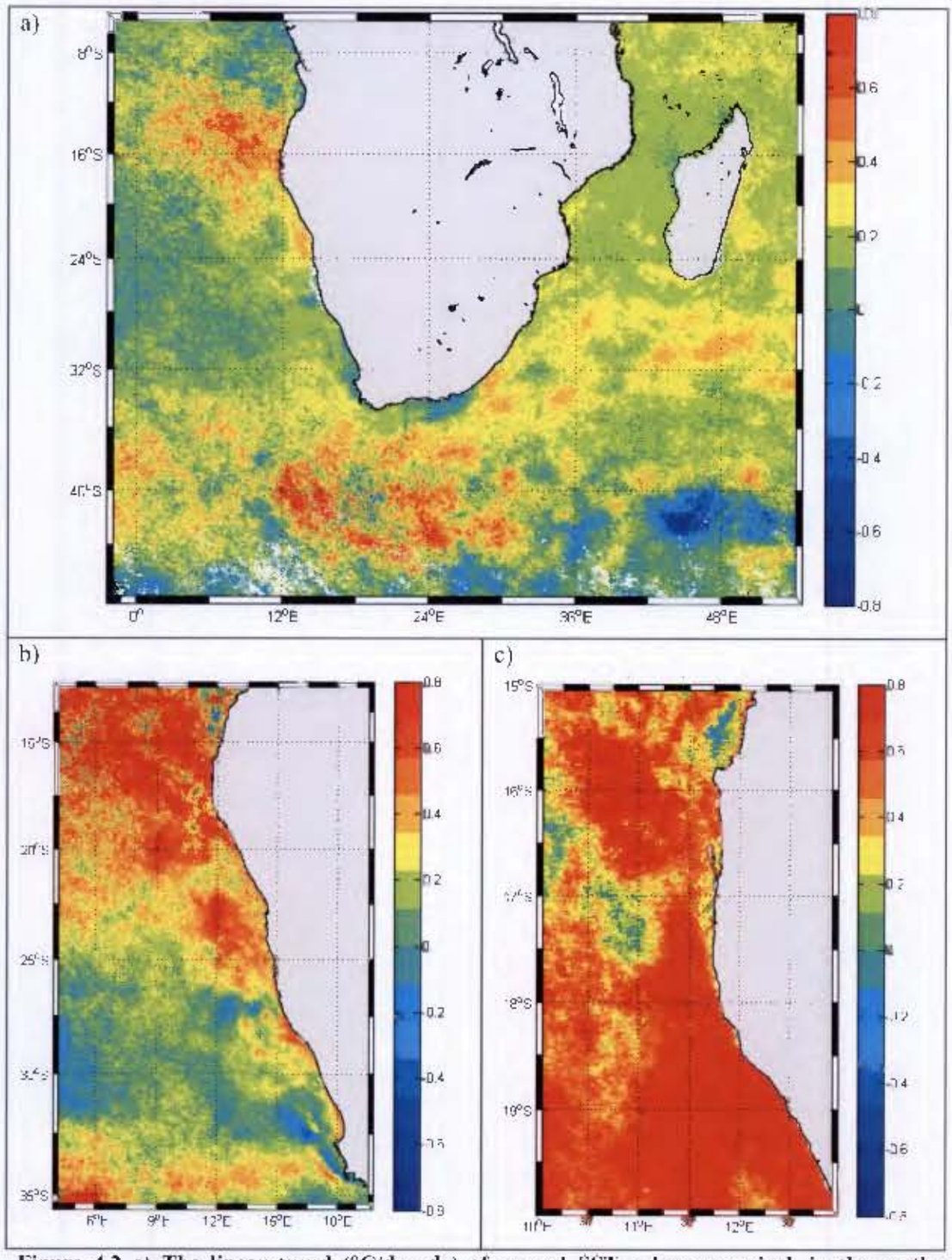


Figure 4.2 a) The linear trend (°C/decade) of annual SST values per pixel, in the southern African region (5-47°S and -3-55°E) measured from the Pathfinder reanalysis data (version 5, level 4) between 1981 and 2009. b) Linear trend of monthly averaged Modis Terra 4x4km SST data (2000 – 2009) for the Benguela Current Large Marine Ecosystem (BCLME) region (12-35°S and 3-19°E). c) Linear trend of annual SST values from Modis Terra 2x2km resolution (2000 – 2009) daily averaged data for the ABFZ region (15-20°S and 10-13°E).

The linear trend evident the Angola-Benguela frontal zone (ABFZ) region (15-20°S and 10-13°E), differed between the two datasets. A significant (Spearman's rank correlation ($p<$ 0.01, R=0.66) warming trend (0.35°C.decade^{-1}) was found using the Pathfinder data (Figure 4.3a), while a warming trend of 0.55°C.decade^{-1} (not significant, Spearman's rank correlation (p=0.11, R=0.52)) was estimated using the MODIS Terra data (Figure 4.3b).

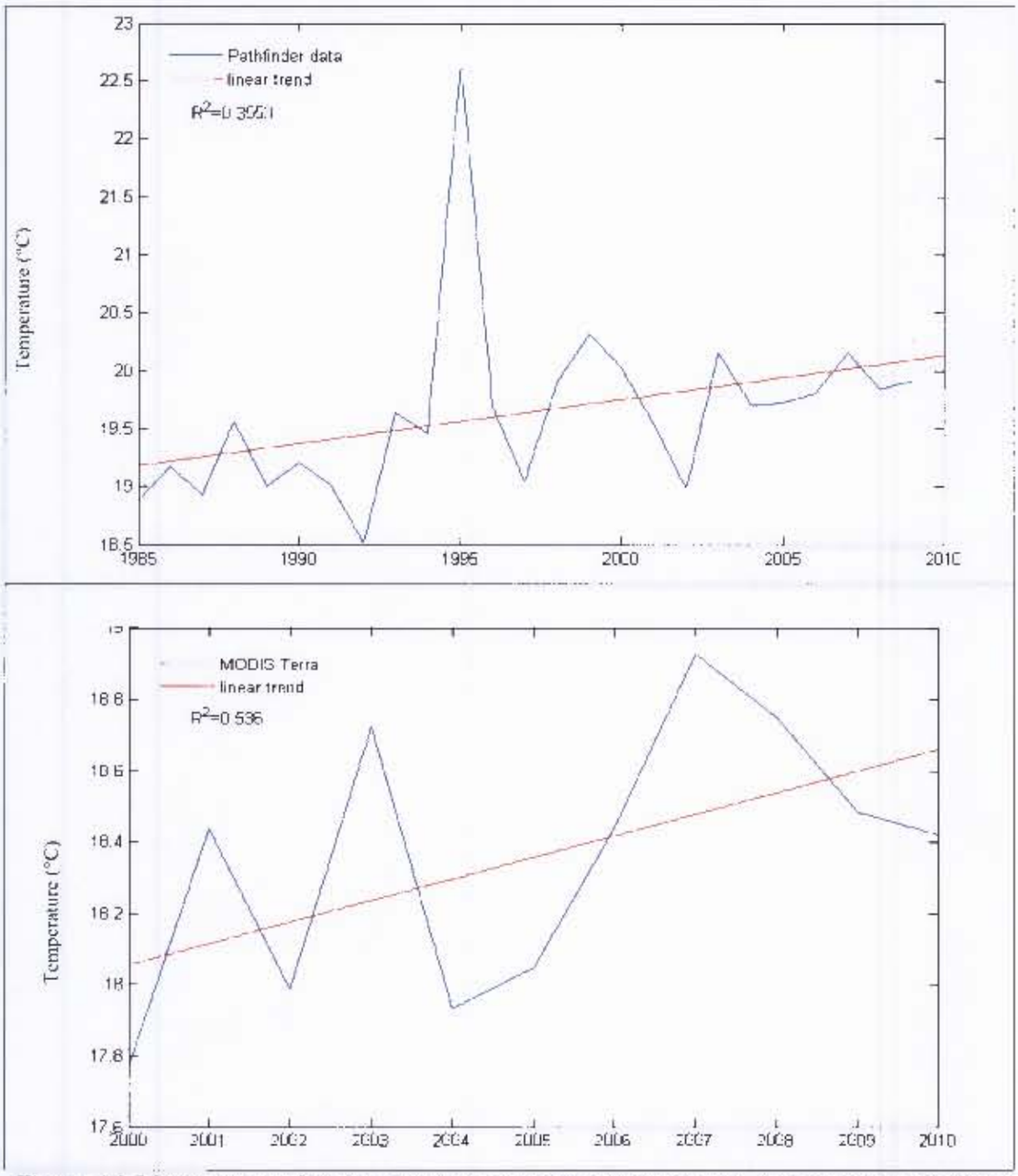


Figure 4.3 Linear sea surface temperature warming trends for the Angola Benguela Frontal Zone (coordinates) estimated at a 4 x 4 km resolution using a) Pathfinder reanalysis data and b) MODIS Terra data.

The SST warming in the ABFZ over the last 25 years was ~0.6°C.decade^{-1} greater than the global average (0.07°C.decade^{-1}) (Burrows *et al.* 2011) (Figure 4.4a). While the trend calculated over the last decade (2000-2010) was 0.6-0.8°C.decade^{-1} relative to the global average (Figure 4.4c).

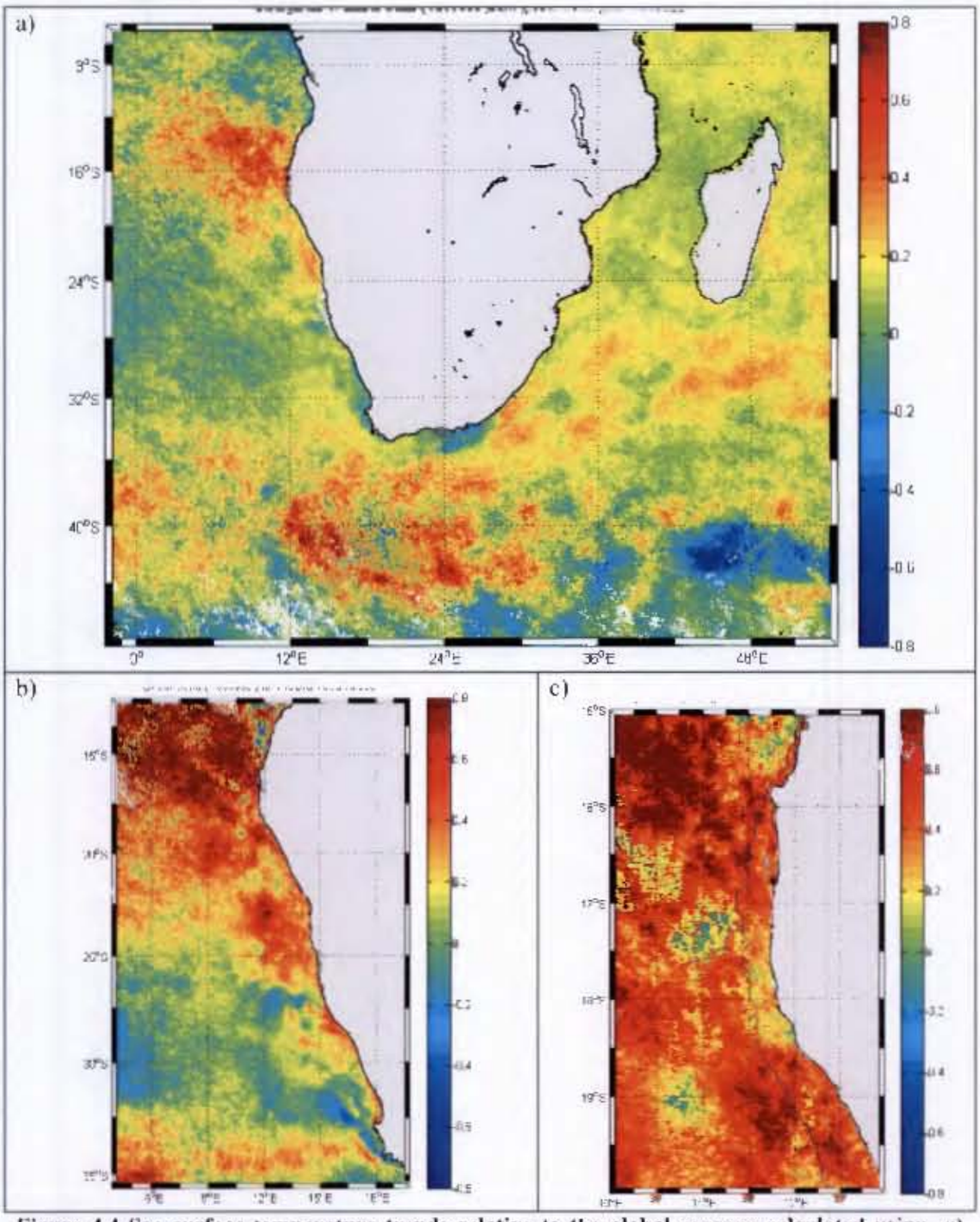


Figure 4.4 Sea surface temperature trends relative to the global average calculated using a) Pathfinder 5 reanalysis data for southern Africa, b) Pathfinder 5 reanalysis data for the BCLME region and c) the MODIS Terra SST data for the ABFZ region.

4.3.2. Investigation into coastal warming

The coastal zone (<200m) of the northern Benguela appears to be warming at a faster rate than the rest of the region in two areas, 15.5-17°S and 18.5-20°S (Figure 4.5). Although these trends were only calculated over an 11 year period (2000-2010) many of the pixels within these two regions indicate significance of the warming trend at the 90 and 95% levels (Figure 4.7). An exception to the warming which has occurred in the majority of the coastal zone of the ABFZ region is the area associated with the Cape Frio upwelling cell ~17.5-18.5°S (Figure 4.5a,b).

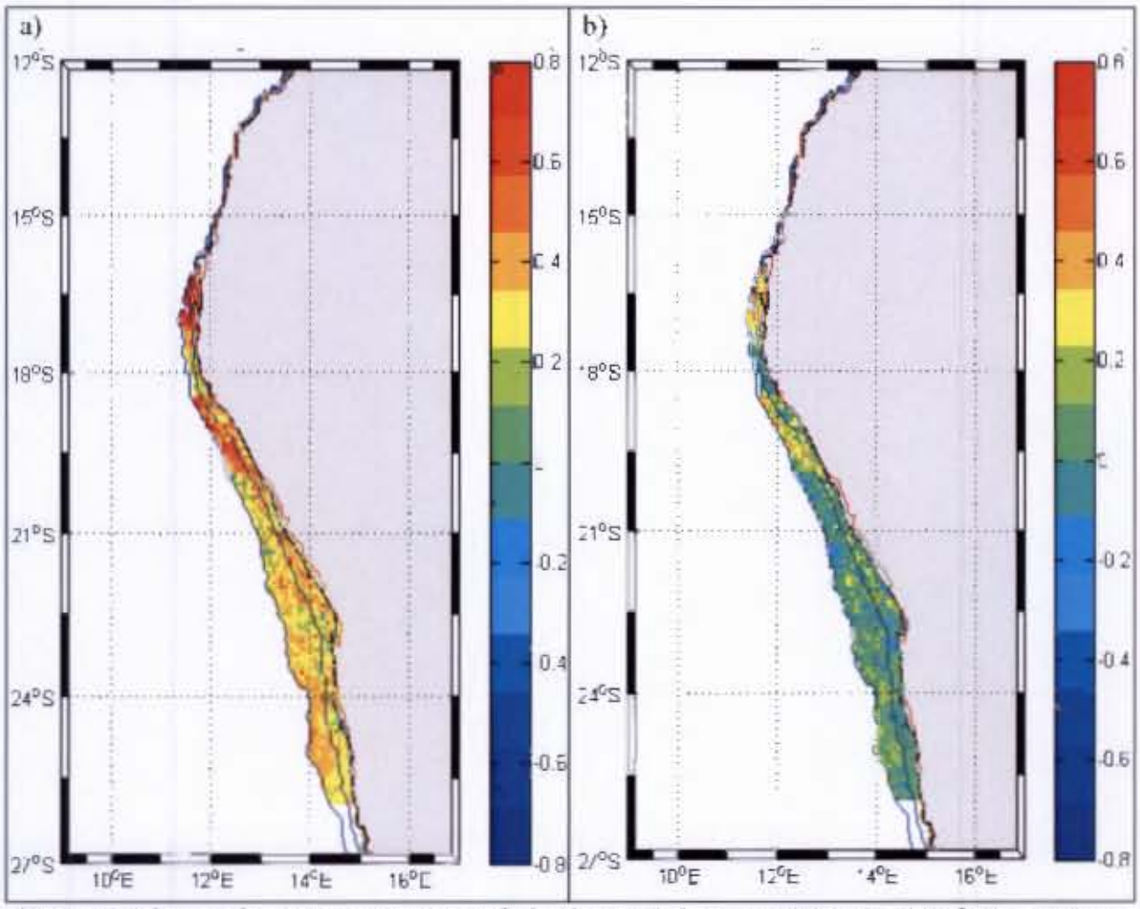


Figure 4.5 Sea surface temperature trends in the coastal zone (<200m depth) of the northern Benguela (21-26°S) relative to a) the global mean and b) the regional average of the northern Benguela coastal zone, from MODIS Terra 4x4km resolution data (2000-2010).

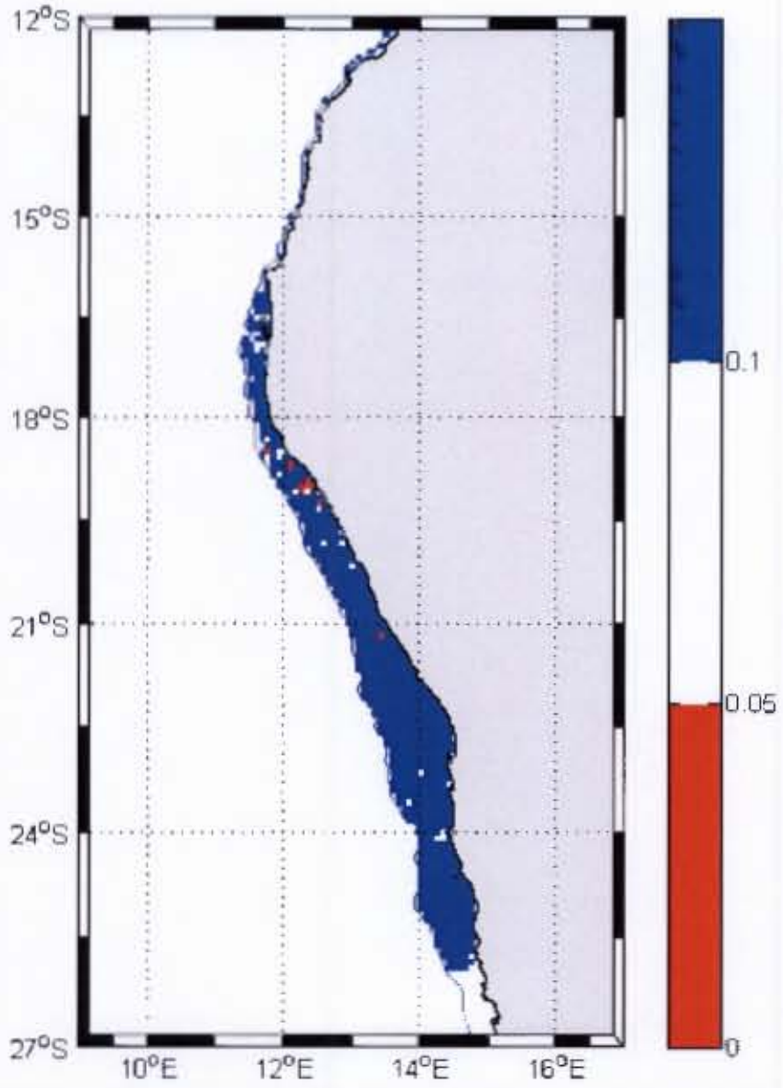


Figure 4.6 The relative significance levels (indicated by alpha values 0.1 and 0.05) of the linear warming trends experienced in the inshore region (<200m) of the northern Benguela (21-26°S) over the last decade (2000-2010) calculated using MODIS Terra SST data. Red pixels indicate significance at the 95% level, white pixels the 90% level and the linear trends of the blue region showed no significant trend.

4.3.3. Effects of regional change on the spatial distribution of *Argyrosomus coronus*

Based on the position of the 22°C isotherm (Figure 4.7) it appears that a southerly shift in the distribution of the west coast dusky kob was likely between 2002 and 2003 as well as between 2004 and 2007. A ~0.9° latitude shift (~100km) in the position of this isotherm between from ~15-15.9°S was noted during these periods. Besides these two warm events, a

general southward shift of ~0.5° latitude (~15-15.5°S) was observed for the 22°C isotherm during the study period (2000-2010). Similar displacements of the ABFZ (represented by the 20°C isotherm) (Lass *et al.* 2000) were observed, over the periods 2002-2003 and 2004-2007, however the 20°C isotherm appears only to have undergone a ~0.5° (16°S to 16.5°S) latitude shift over these periods. A general southerly shift of <0.5° latitude is evident for this isotherm (Figure 4.7).

When examining the long-term trend in the position of both the 20 and 22°C isotherms in the ABFZ region (Figure 4.8) an average southerly shift of ~0.9° latitude (~100km) was evident for both isotherms (20°C:15.6-16.5°S; 22°C:15-15.9°S). The relative influence of warming and cooling events could be seen in the northward and southward displacements of both isotherms. The pathfinder data clearly showed the severity of the 1995 Benguela Niño, as the 20°C and 22°C were displaced southwards of 20°S (Figure 4.8).

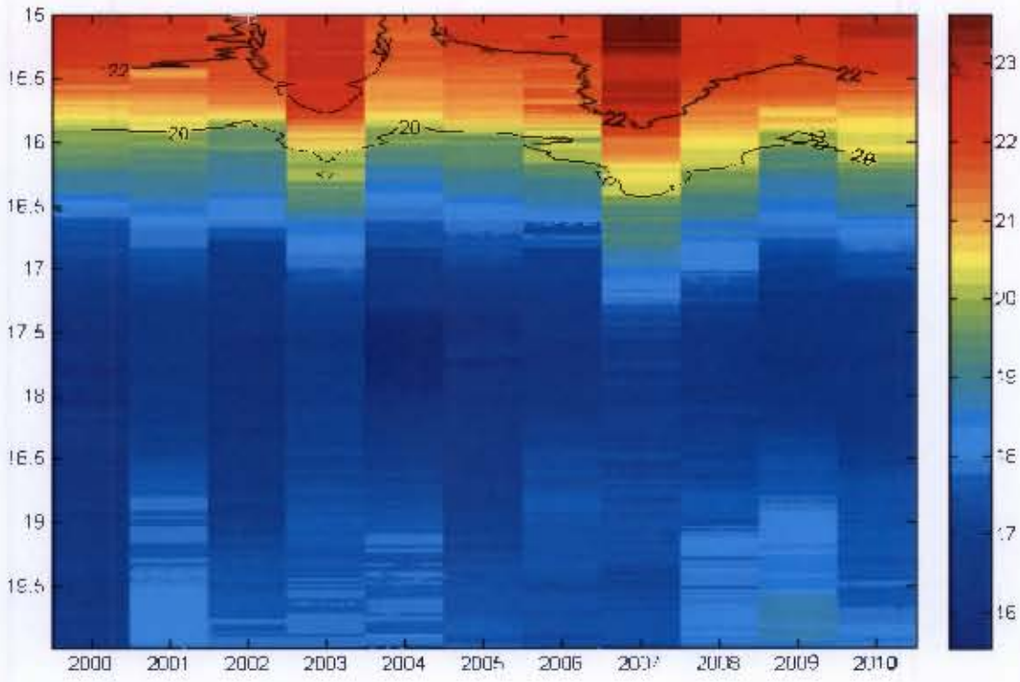


Figure 4.7 Location of the 20 and 22°C sea surface temperature (SST) isotherms (between 15 and 20°S), calculated from monthly averaged 2x2km Modis Terra data along a longitude of 11.58°E from 2000 until 2010.

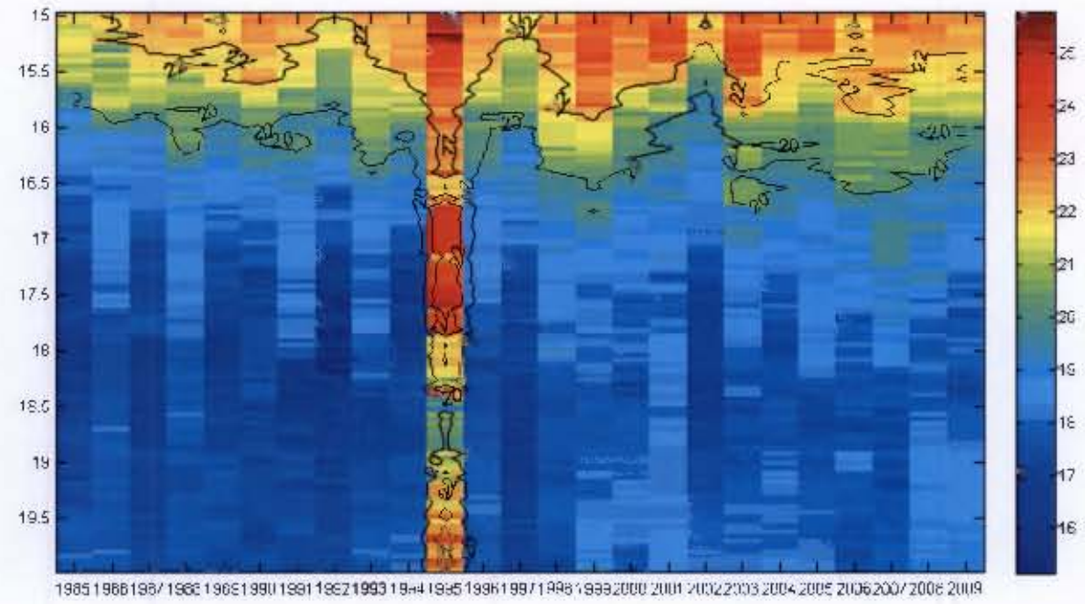


Figure 4.8 Location of the 20 and 22°C sea surface temperature (SST) isotherms for the region between 15 and 20°S, along a latitude of 11.58°S over the period between 1985 and 2009, calculated using Pathfinder (5) reanalysis data. The extreme warming event associated with the 1995 Benguela Niño is visible.

4.4. Discussion

4.4.1. Identification of warming hotspots in the northern Benguela

Global change does not manifest itself in uniformly across the globe and different regions and systems respond in a variety of ways to climate variability (IPCC 2007, Loarie *et al.* 2009, Burrows *et al.* 2011). The northern Benguela was found to be warming at an average rate of ~0.6-0.8°C.decade^{-1} above the global mean in the offshore and inshore regions (Figure 4.4b). Monteiro et al (2008), using optimally interpolated sea-surface temperature (OI-SST) (Reynolds *et al.* 2002) from 1982-1999 reported similar rates of warming in this region. In contrast to the northern Benguela, a weak cooling trend (~-0.2°C.decade^{-1} below the global mean) was observed offshore in the southern and central Benguela regions, and a slight warming trend (~0.3-0.6°C.decade^{-1}above the global mean) was observed in the inshore zone (Figure 4.4b). While the warming in the inshore region of the southern and central sectors is in contrast to Rouault *et al.*'s (2010) findings, this may be because the two studies had

different temporal ranges and used different datasets used to calculate the trends. Only 11 years of data were used to calculate a trend in this study, while Rouault's dataset spanned 25 years. Despite the shorter dataset, the selection of the most accurate satellite product for the inshore zone and the use of *in situ* validation (Chapter 2) suggests that this study provided a better estimate of inshore temperature variability (see Chapter 2), compared to the optimally interpolated sea-surface temperature (OI-SST) (Reynolds *et al.* 2002) used by Rouault *et al.* (2010). Results of this current study show that the surface waters of the southern Benguela inshore zone have warmed rapidly in the last decade.

Not all regions in the Benguela region were warming at the same rate (Figures 4.2, 4.4). For example, the ABFZ is warming at a much faster rate (>1.5°C.decade^{-1}) than the rest of the northern Benguela (0.6-0.8°C.decade^{-1}) (Figures 4.2b,c; 4.4b,c). The fastest warming trend in the inshore zone was observed between 15.5-17°S and 18.5-20°S (Figure 4.5). With rapid warming (>0.8°C.decade^{-1} above the global ocean average (0.07°C.decade^{-1}) over the last decade (2000-2010), these areas could be identified as local warming "hotspots". Hotspots of temperature warming are areas where the long term warming trend is greater than the global mean, one such hotspot has been identified off the Tasmanian coast where warming of 0.23°C.decade^{-1} has been identified since the 1940s (Last *et al.* 2010).). Although the data does not extend as far back, according to this definition, this region can be categorised as an ocean warming hotspot (Figure 4.2c). The development of local warming hotspots has significant impacts on the biology of the area as organisms become most stressed in these regions (Harley *et al.* 2006). Hotspots are therefore ecologically important as the changes happening in these areas could be used to predict likely changes in other areas where temperature warming is slower. While the MODIS dataset was short term (11 years), the similar trends (Figure 4.2) observed when using the 25 year long Pathfinder dataset suggest that the identified warming "hotspots" are not part of a decadal cycle, but are in fact long-term features.

The influences of natural inter and intra annual variability in the study regions are not considered when using linear trends to identify trends in temperature variability. Bakun (1990) warns against solely relying on this approach, which is why the natural variability of this system was assessed by examining the annual latitudinal position of the 20 and 22°C isotherms. The position of these isotherms appeared to migrate southwards during the period

between 2002 and 2003 as well as 2004 and 2007 (reaching a maximum of ~16.4°S (20°C) and ~15.8°S (22°C)), while experiencing ~0.5° latitude over the study period (2000-2010) (Figure 4.7). The non- linear variability of the average position of the 20 and 22°C isotherms provided evidence of the variable nature of the warming that occurs in the region. The southerly migration of these two isotherms was further evident in the longer term (1985-2009) Pathfinder dataset, where their average positions appear to have shifted southwards by ~0.9° latitude (Figure 4.8).

It is interesting to note that the two identified coastal warming hotspots in the northern Benguela (15.5-17°S and 18.5-20°S) were separated by a region which has experienced minimal change over the last decade and even slight cooling in comparison to the average rate of change in this inshore region (Figure 4.5a,b). The position of this 'gap' is in the vicinity of the Cape Frio upwelling cell (~18°S) and the results of this study suggest that the upwelling cell is not warming at the same rate as the rest of the region.

4.4.2. Limitations of the methods and datasets

As the Pathfinder reanalysis data is a global product the quality flags assigned to the data are very sensitive to strong temperature gradients. This means that in frontal regions or areas of upwelling this satellite product does not provide the most accurate SST retrievals (Kilpatrick *et al.* 2001). This should be considered when regarding the results of this study. The long time span of the dataset (25 years) however, provides a useful method of confirming the trends observed during the shorter (11 years), but more accurate MODIS Terra dataset.

The Pathfinder data used in this study had a quality flag level of 4. The selection of the quality level was a trade off between very accurate data but very few data points or a large dataset which contained erroneous data. Quality level 4 provides sufficiently accurate data for this study while still providing an abundance of data points. The differences between the results of this study, especially Figure 4.2a, and those of Rouault *et al.* (2010) could be the result of the use of different levels of quality flags. The quality flag level of Pathfinder data used in future studies is therefore an important point to consider, as conflicting results may be found depending on the flag level selected. It is recommended that future studies use data from more than one quality flag level in order to compare the different results.

A limitation associated with the MODIS Terra dataset was the short time period covered by the data, as NASA's Terra satellite was only launched in 2000 (MODIS 2011). Therefore any

of the identified trends in temperature variability in the BCLME may be a result of decadal variability of the system, and not long term. However, the longer time period associated with the pathfinder dataset, means that where an identified trend is present in both datasets, it would be more likely to continue in the future.

4.4.3. Potential causes of the warming trend in the northern Benguela

Patterns of ecosystem change which have taken place in the BCLME historically, suggest that the system undergoes phases of relative warming and cooling periods which are expected to alternate on a decadal basis (Hardman-Mountford *et al.* 2003, Heileman and O'Toole 2009, Hutchings *et al.* 2009). The evidence presented in this study describes partial decadal cycles in the MODIS Terra data, as well as in the longer time series of the Pathfinder dataset, but no obvious decadal variability was identified. Longer term datasets are required in order to accurately identify the decadal variability of SST in this region. The warming ocean temperatures observed worldwide (Burrows *et al.* 2011) supports this theory. To verify the warming trend, further monitoring in the region is required. Decadal variability may still be evident in future changes in the rates of regional warming and cooling, but the underlying rise in average annual temperatures, in the identified hotspot regions particularly, appears to be unquestionable.

Decadal variability is thought to be the result of the influence of a number of different atmospheric forcing modes acting on the northern Benguela region. Hutchings *et al.* (2009) summarise four of the most important of these factors described by Colberg and Reason (2006) and Reason *et al.* (2006):

- Firstly the strength of trade winds in the equatorial Atlantic affects Benguela Niño events on a decadal scale;
- secondly migrations of the South Atlantic Anticyclone (high pressure) affect upwelling-favourable wind stress, the position of which appears to be linked to ENSO events;
- thirdly interdecadal variability displayed by a midlatidude mode acts on the northern Benguela and
- lastly the Southern Annular Mode in the southern Atlantic affects the paths of westerlies influencing the northern Benguela.

The northern Benguela is currently in a warming phase (since 1995) where cool events are less frequent and southerly displacements of the Angola-Benguela Front are more common (Rouault *et al.*2007, Hutchings *et al.* 2009). This has been attributed to the general decadal variability of the region influenced by the factors described above which have manifested in the weakening of southerly windstress at Luderitz during 1990-2006 (Hutchings *et al.* 2009). This warming trend in SST vales in the northern Benguela appears to be the direct result of increased frequency and residence time of the seasonal southward migrations of the ABFZ. During periods of weakened upwelling in the northern Benguela as a result of weakened southerly wind stress, Angola current water is possibly able to intrude further southwards and remain in the region for longer than usual. Evidence of this provided in the increased southerly extension of the 20 and 22°C isotherms into the northern periphery of the region (Figures 4.7, 4.8).

Global ocean-atmosphere system teleconnections across the Atlantic via Kelvin (ocean) and Rossby (atmospheric) waves associated with the modes mentioned previously have not been explored in this study. Increasing evidence and understanding of coupled ocean-atmosphere dynamics indicate that the influence of global atmospheric change on oceanographic systems (such as the BCLME) may increase in the future (IPCC 2007). Previous studies (Florenchie *et al.* 2003, 2004, Reason *et al.* 2006, Colberg and Reason 2007, Rouault *et al.* 2007) outline the existing implications of the complex coupled ocean–atmosphere effects which can lead to Benguela Niño events. In an environment that is warming however, the effects of extreme events could be amplified as warm water intrusions may reach further south along the west African coast than was the case during previous events. Research on the dynamic interactions that cause these extreme events is ongoing, and continued monitoring of both the offshore and inshore regions will help to gain a better understanding of the modes of variability at play in the region.

4.4.4. What are the effects of the regional warming?

The increasing southerly extent of the average annual position of the 22°C isotherm is apparent (Figure 4.7). Based on the results of Chapter 3, it is likely that this will result in a shift in the spatial distribution of *A. coronus*. The likelihood of finding *A. coronus* in the vicinity of Flamingo Lodge will be drastically reduced once the annual average temperature increases above 22°C. In this case, a southerly displacement in the spatial distribution of this species is expected.

The disappearance of keystone species such as large predators can have major ecosystem effects. This could be exacerbated if similar range shifts were undertaken by other species in the region. Large ecosystem changes have been observed in the offshore region of the northern Benguela (van der Lingen *et al.*2006a, Hutchings *et al.* 2009). With widespread inshore warming in the northern Benguela, shifts in the distribution of other species are likely. Warming trends have been shown to impact marine animals who respond by moving towards the poles. Organisms are thus likely to avoid unfavourable temperatures by shifting their distributions poleward (Parmesan 2006, Burrows *et al.* 2011). This trend may soon become apparent in the northern Benguela.

While warming is poised to alter the northerly distribution of *A. coronus*, changing conditions were also observed in the southern part of their distribution. The Luderitz upwelling cell, already the world's most vigorous wind driven cell, is expected to intensify under the influence of strengthened southerly wind stress (Bakun 1990). A cooling trend was observed in the offshore zone (>200m depth) using both the 11 and 25 year datasets (Figure 4.2a,b), while a cooling trend was observed with the 25 year (Pathfinder) dataset in the inshore region (Figure 4.2a). However, the MODIS terra data showed warming trend during the last decade (2000-2010) (Figure 4.2b).This may be a result of a short term warming cycle (such as the previously explained decadal variability) masking a long term cooling trend in the region. However, if the Luderitz upwelling cell does intensify, the study species would effectively become restricted to a narrow coastal region as the warming waters in the north continue to intrude southward and the southern distribution barrier at Luderitz strengthens. Such range contractions are becoming common in warming environments (Parmesan 2006). A southerly distributional shift (in the case of a weakening in intensity of the Luderitz upwelling cell) as well as a range contraction would have management implications for the west coast dusky kob, particularly as the species may become targeted by the already well established northern Namibian recreational fishery.

Besides the warming trend observed in the BCLME region, the Pathfinder results showed that infrequent extreme events (Such as the 1995 Benguela Niño, Figure 4.8) may open a gateway through the central Benguela which can be utilised by *A. coronus*. These gateways may explain why vagrants of the study species have been identified as far south as the Berg and Olifants estuaries in South Africa (Lamberth *et al.* 2008). Based on the results of this study, it

is likely that these extreme southerly movements could only occur during large scale warming events, such as Benguela Niños. Lamberth *et al* (2008) attributed the presence of adult *A. coronus* in the Berg River to a Benguela Niños event and added that the passage of these fish through the central Benguela is most likely when the extreme events are accompanied by toxic conditions associated with hydrogen sulphide eruptions.

The warming identified in the northern Benguela, has important implications for regional resource management. Existing management strategies would need to be adapted to changes in species spatial distributions if they are to protect marine resources (Nye *et al.* 2009, Link *et al.* 2010). A southerly distributional shift and range contraction (described above) would increase the vulnerability of the west coast dusky kob as it would be confined to a localised region in northern Namibia. This region is characterised by heavy recreational fishing pressure and this species may be rapidly overexploited without timely management intervention. This is especially true as the current management plans in place for the morphologically similar silver kob (*A.inodorus*) in northern Namibia are defined by this species' fast growth rate and small size at maturity and would not be suited to the slower growing and later maturing west coast dusky kob. Changes in the spatial distributions of marine resources need to be included in future management plans in order to promote sustainable fisheries (Link *et al.* 2010). Management interventions such as co management strategies, seasonally closed areas or the revision of the location of marine protected areas may help to conserve this species.

Chapter 5

Conclusions and recommendations for future work

5.1. Project findings:

This study aimed to determine the extent of environmental change in the inshore zone of the ABFZ and to predict the impact of this change on the distribution of *A. coronus*.

5.1.1. Key Question 1:-What is the most suitable satellite product to study surface temperature variability in the inshore zone of the northern Benguela, and what is the error associated with this product in coastal waters?

The Moderate Resolution Imaging Spectroradiometer (MODIS) sensors on board NASA's Terra and Aqua satellite were the most suitable tools for measuring SST variability in the inshore region of the northern Benguela. The applicability of the MODIS Terra dataset to biological spatial distribution studies was found to be greater than that of the MODIS Aqua data due to Terra's longer temporal range (2000-present). Seasonal correction factors for both of these products in each season, were determined through comparison with an *in situ* dataset (Table 2.5), thus accounting for the general overestimation of both the Aqua and Terra MODIS sensors of *in situ* temperature values. An average overestimation of 0.76 ± 1.06°C for the MODIS Terra data and 0.85 ± 0.85°C for the MODIS Aqua data was identified for the inshore region of the Angola-Benguela Frontal Zone (ABFZ). The correction factors calculated in Chapter 2 may be improved in future studies through the use of datasets which extend over longer time periods, allowing a greater number of match up days, as well as by calculating monthly correction factors rather than seasonal ones.

5.1.2. Key Question 2:- Is there a relationship between the catch rate of *A. coronus* and environmental parameters?

Surface temperature variability was relatively easy to measure in the region due to the spatial extent of MODIS Aqua and Terra data, and was thus considered a good indicator of the spatial extent of *A. coronus* in the northern Benguela (see Chapter 3). It was found that CPUE increased in waters cooler than 22°C and warmer than 16°C in the vicinity of Flamingo Lodge (15.57°S, 12.02°E). Based on the assumed "avoidance temperatures" west coast dusky kob are predicted to occur south of Flamingo Lodge, near the Cape Frio upwelling cell (~18°S, 11.8°E) during the summer and autumn months (DJF, MAM) and in the vicinity (15.57°S, 12.02°E) of Flamingo Lodge during winter (JJA) and spring (SON).

This relationship will need to be explored further using a longer term CPUE dataset, as the current dataset was limited to 4 years. Monitoring of other environmental variables will also

aid in understanding the relationships which exist between this species and its environment. *In situ* temperature, dissolved oxygen and salinity data are especially limited in the study region and monitoring programmes need to be initiated in order to monitor the physical changes in the coastal marine environment of the northern Benguela.

Recent model outputs of dissolved oxygen as well as the Regional Ocean Model System (ROMS) simulation outputs could also be used to determine the spatial distribution of marine species. However, these outputs need to be regionally validated and corrected according to the identified errors, before accurate estimations of regional oceanographic conditions can be made. The use of validated model outputs would allow a more accurate representation of the effects of salinity and dissolved oxygen variability on the spatial distribution of *A. coronus*. However, such validation studies cannot take place without accurate *in situ* datasets of the required variables, thus the establishment of inshore monitoring programmes is of utmost importance.

5.1.3. Key Question 3:- How rapidly are environmental conditions changing and what are the implications of these changes on the distributional patterns of *A. coronus* in the northern Benguela?

Using the corrected satellite SST retrieval data (Chapter 2), warming trends over the last 25 and 11 years were explored in the northern Benguela. A linear trend of ~0.6°C.decade^{-1} was found to have occurred between 1985 and 2009 in the Angola-Benguela frontal zone in particular (see Chapter 4) and this trend was found to have increased to >0.8°C for the last decade. The majority of the northern Benguela region has experienced warming at a much faster rate than the global mean (0.07°C.decade^{-1}) over the last decade. Furthermore, two inshore (<200m depth) hotspots of localised warming were identified at 15.5-17°S and 18.5-20°S where the linear trend of warming over the last decade (2000-2010) was found to be significant at the 90-95% level (Figure 4.6).

The warming trends observed over the last decade (2000-2010) are likely to be the caused by decadal variability in the region. However the existence of a significant linear warming trend over a 25 year period (Figure 4.3) indicated that the recent warming in the northern Benguela may be related to more than just decadal variability and may persist in future years. The localised warming in the ABFZ region is thought to be caused by an increase in the residence time of the seasonal intrusions by Angola Current water into the region. This is brought about

by a decadal scale trend in weakened upwelling in the central Benguela (Hutchings *et al.* 2009). These warming trends (and their persistence) pose a threat to the temperate biota of the region and may result in a shift of organisms to cooler waters at higher latitudes, which has been observed in other temperate regions of the world (Parmesan and Yohe 2003, Parmesan 2006, Burrows *et al.* 2011). This may very well be the case for the west coast dusky kob in the northern Benguela as the estimated upper optimum range of the species (the 22°C isotherm) has migrated further south during the last decade (see Chapter 4, Figures 4.7, 4.8). If current warming trends continue, this species is expected to shift its spatial distribution into northern Namibia with the continued southerly migration of the 22°C isotherm.

The southerly limit of a potential distributional shift of the study species would be the dispersion barrier at Luderitz, as annually averaged temperatures in this upwelling region are below the expected minimal thermal tolerance limit of *A. coronus*. Inshore warming experienced in the Luderitz region in the last decade, however, suggests that periods of weakened upwelling have existed. During these periods temperatures in the inshore zone of the Luderitz region may be greater than 16°C, potentially allowing west coast dusky kob individuals to pass through the identified dispersion barrier and into the southern Benguela. This could explain the findings of Lamberth *et al.* (2008) of extra-limital vagrants (Last *et al.* 2010) of the study species in South African estuaries. As the general warming phase of the inshore region of the central and southern Benguela may be related to decadal variability, and upwelling in the central Benguela could increase again in the near future, the southern limit of the potential displacement of *A. coronus* will have to be explored in terms of future scenarios of warming or cooling in the region. Upwelling cells are expected to strengthen in response to climate change (Bakun 1990) and if this is indeed the case in the long term, the study species may become trapped between its upper and lower optimum thermal range limits on the northern Namibian coast, and undergo an effective range contraction. The species would become increasingly vulnerable to capture as a result.

Dissolved oxygen and salinity changes over similar periods in the northern Benguela may too have significant effects of the biota of the region however, a lack of *in situ* data precluded detailed investigation. This further highlights the need to establish monitoring programmes of physical environmental variables in the inshore regions of the northern Benguela as soon as

possible. Surface salinity estimates are now available via satellite sensors on board the Aquarius satellite launched in 2011. This data should be utilised in the study region, in the future to investigate seasonal salinity changes once the regional accuracy of the salinity data has been assessed. The investigation of surface salinity in conjunction with SST variability will help to provide a more accurate estimation of the surface signal of the seasonal intrusion by Angola Current water into the northern Benguela, which in turn would enable estimates of spatial distribution changes in temperate organisms to be explored.

5.2. What are the ecosystem and socio-economic effects of changing distributional patterns of *A. coronus* in the northern Benguela?

Shifts in the distributional ranges of marine organisms have been observed in response to extreme warming events as well as general warming trends in temperate regions (Parmesan and Yohe 2003, Parmesan 2006, Pörtner and Knust 2007, Hutchings *et al.* 2009, Burrows *et al.* 2011). This has been especially apparent in pelagic species, or species with pelagic larval stages, and these species are expected to undergo further distributional variations in the future (Harley *et al.* 2006). The findings of this study suggest that a southerly distribution shift in *A. coronus* may occur if water temperatures continue to rise in the ABFZ region. Furthermore, continued warming of the nature identified in Chapter 3 may well result in an inshore regime shift similar to that which has occurred in offshore waters in recent years (van der Lingen *et al.* 2006a).

If warming trends in the region continue at present rates, current management strategies for *Argyrosomus coronus* would need to be adapted to encompass the expected changes in the species distribution. The vulnerability of a species generally increases if it undergoes a range contraction (Parmesan 2006). This is particularly relevant in the case of the west coast dusky kob as a southerly range shift and range contraction would concentrate this species in central and northern Namibia. This region has very well established recreational fisheries (Kirchner 1998). The Skeleton Coast National Park (17.5-21.1°S) in Namibia however, could provide some protection from fishing pressure unless the population shift extends further south of 22°S. On a positive note, the large size attained by the west coast dusky kob (max 77kg, common to 50kg) (Griffiths and Heemstra 1995), when compared with the Namibian kob species, the silver kob (*Argyrosomus inodorus*) (max 36.5kg, common to 15kg) (Griffiths and

Heemstra 1995) will provide the recreational fishery with a major boost. The Namibian recreational fishery is extremely important for the economy of coastal communities (Stage and Kirchner 2005) thus it is critical that a new resource such as this is well managed to maximise its long-term benefit. The required management plan is complicated by the extremely similar morphological characteristics of the two kob species and the vastly different life histories. For example, *A. coronus* matures at approximately 90 cm (Potts *et al.* 2010) compared with 40 cm (Griffiths and Heemstra 1995) for *A. inodorus*. Therefore, future management plans must recognise the potential of the *A. coronus* resource and will need to incorporate the seasonal trends in relative dominance of the two species. For example, the west coast dusky kob may be the dominant species during the summer and autumn months and fishery regulations should be designed towards this species during that time. This will ensure that this species is protected when it is dominant in the Namibian fishery.

Unfortunately, Namibia's gain is southern Angola's loss and a southerly shift in the distribution of *A. coronus* will negatively impact the artisanal fishery for this species in southern Angola (Potts *et al.* 2010). In addition, continued warming in the region could lead to similar spatial distribution shifts of other important fishery species in the future. Coastal communities and local economies would then suffer from a decrease in abundance of economically important fisheries resources. It is recommended that experimental fishing for tropical species be initiated in this area, to ensure that communities can quickly respond to the arrival of new fisheries resources from the north.

5.3. Project short comings

The use of various datasets to describe regional variability in oceanographic conditions overcame the paucity of data in the northern Namibian and southern Angolan nearshore regions. However, the findings of this study would have been more accurate if extensive *in situ* biological and physiochemical datasets had been available. The scarcity of *in situ* datasets of physical environmental variables especially water temperature, dissolved oxygen and salinity in the ABFZ region was particularly evident. The lack of environmental variability data at different depths in the water column was too noted as a major research gap in the northern Benguela region (see Chapter 3). Long-term biological monitoring information, including relative abundance estimates of fisheries species was also lacking, and the dataset used in this study was limited to a 4 year period from a single location. This

dataset is currently being temporally expanded, enabling future investigations into the response of *A. coronus* to environmental change. Ideally CPUE as well as environmental variability data should be continuously collected from a variety of locations and throughout the water column. This would enable the monitoring of shifts in species distribution and abundance as well as the determination of the magnitude of regional oceanographic changes. Estimates of spatial distribution would be further improved with the extension of existing conventional fish tagging studies in the region. Such studies, when involving numerous species, would improve our understanding of ecosystem response to environmental changes in the region.

The inability of infrared satellite sensors to gather SST information in cloudy conditions limited the validity of the estimation of satellite error in measuring inshore and nearshore waters of the northern Benguela. Clouds reduced the number of match up days available for satellite and *in situ* data comparison. Cloudiness can also cause a seasonal bias of annually averaged temperatures as accurate SST retrievals were less frequent during spring, possibly as a result of the increased frequency of fog. Microwave imaging technology, which is not affected by atmospheric conditions, is fast improving and microwave SST retrievals closer to the coast may become available in the near future. If this is the case, this data could be successfully used to provide year-round estimations of SST variability in the inshore region of the northern Benguela. The microwave data would first need to be investigated for regional satellite errors following the process outlined in Chapter 2. A further problem associated with the use of satellite data is the short temporal scale of datasets which restricts the confidence of trend calculations.

Programmes that monitor biological and physical characteristics of the water column are critical for our understanding of the inshore zone in this region. Although the majority of marine research has traditionally been located in the offshore zone of the northern Benguela, there is a growing need for inshore monitoring especially in the face of global change. This is primarily because of the great dependence of coastal communities on the inshore marine resources. Data from established inshore monitoring sites would help to improve the forecasting ability (through their input into forecasting models) of extreme events and provide information on distribution and abundance shifts of marine resources. In turn this

would allow the development of efficient management plans, enabling the sustainable exploitation of inshore marine resources.

5.4. Recommendations for future work

It is clear that a permanent and efficient coastal observation network needs to be established in the northern Benguela (Brundit *et al.* 2006). In order to identify the specific objectives of such a network it is important to assess what data is already available and which variables need to be focused on.

Remote sensing capabilities to monitor physical and to a lesser extent, biological variables have improved tremendously in recent years (Glenn *et al.* 2000). However, the inability of these sensors to monitor chemical and further biological variability and the fact that they can only measure the upper layers of the water column highlights the need for continued *in situ* monitoring (Glenn *et al.* 2000). This is especially true in data poor areas where validation studies of remotely sensed variables are limited.

Presently *in situ* monitoring in the form of one moored array of instruments exists and is currently collecting information on oceanographic and atmospheric data from the surface to the ocean floor in the tropical south east Atlantic (Figure 5.1). This forms part of the Prediction and Research Moored Array in the Tropical Atlantic (PIRATA) programme which involves the permanent installation of an Autonomous Temperature Line Acquisition System (ATLAS) buoys in the topical Atlantic. PIRATA provides important information on oceanographic conditions and wind forcing in the region. The information received from the new (2006) ATLAS buoy, Kizomba, can be used to infer conditions in the inshore zone, and its value in monitoring and gaining an understanding of the development of extreme events is unquestionable (PIRATA 2011, Rouault *et al.* 2009). However, it cannot directly describe the oceanographic state of the inshore zone and monitoring systems should be established further inshore for this purpose. In this regard, a recent proposal to design and implement an Argo float system for shelf seas has been submitted for governmental funding. Argo floats are lagrangian measuring devices which move through the water column sampling at predetermined intervals. Such instruments would provide invaluable information on the dynamics and physical oceanographic environment of the coastal zone.

Another monitoring programme in the early phases of design and implementation is one which involves the deployment of gliders in inshore regions of southern African waters. These instruments allow continuous monitoring along specified depth contours. South Africa has very recently been appointed a centre of excellence for marine glider instruments.

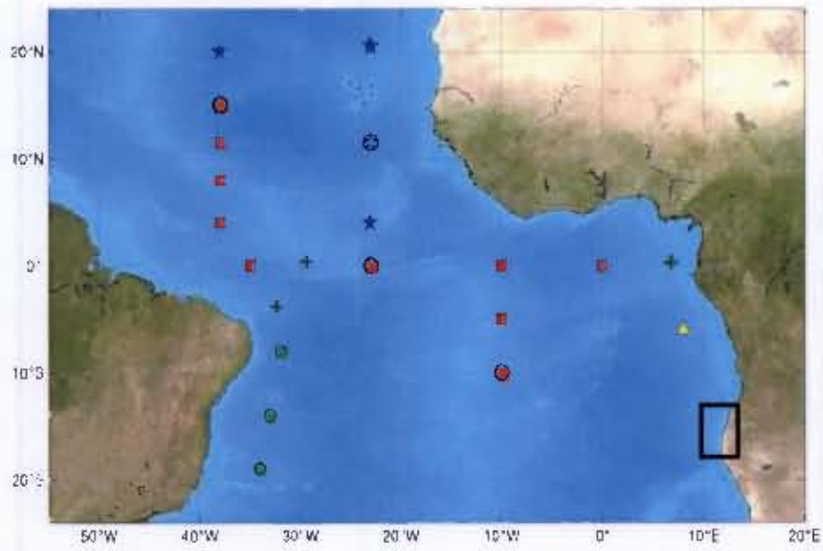


Figure 5.1 The position of the ALTAS buoys of the PIRATA programme. The yellow triangle indicates the Kizomba ATLAS buoy, the south east extension of the project. Black box indicates the current study region (adapted from PIRATA 2011).

Technology in the form of instruments, sensors and systems from which to monitor the inshore zone abound (Glenn *et al.* 2000). However, the lack of funding, institutional support and competent personnel restrict the establishment of effective monitoring programmes, especially in developing countries (such as Angola) where research funds are especially limited (Brundit *et al.* 2006). Internationally there are a number of programmes with specific mandates to monitor the coastal zone. In the Benguela specifically there are two bodies which are responsible for coastal monitoring, the Benguela Current Commission (BCC) formerly the Benguela Current Large Marine Ecosystem (BCLME) and the Global Ocean Observing System for Africa (GOOS-Africa).

5.4.1. Benguela Current Large Marine Ecosystem (BCLME), a past programme

The Benguela Large Marine Ecosystem project (BCLME) was aimed at monitoring and observing environmental and biological change in the cross boundary (political) Benguela system. The project, funded by Global Environmental Facility (GEF), and the Benguela Environment Fisheries Interaction and Training programme (BENEFIT) (a subsidiary

programme) supported by Germany and Norway, were extremely successful in identifying trends and monitoring oceanographic and biological variability within the BCLME (Hempel *et al.* 2008). The BCLME project ended in 2007 and research and management of the Benguela system is being continued by the Benguela Current Commission (BCC) (supported by the three national governments of Angola, Namibia and South Africa) (Iyambo 2008, Duda 2008). The focus of the BCLME and BENEFIT programmes was on commercially exploited stocks that were shared between the three participatory countries (Hampton 2008) and oceanographic variability related to abundance and distribution changes in these resources. The monitoring of the inshore region of the northern Benguela was therefore not a research priority. The significant warming which has been identified in the last decade especially, but in the last 25 years too, indicates the need to establish coastal monitoring in this region as a matter of urgency. The establishment of such a monitoring initiative is in line with the aims of the BCC as it would assist in gaining an understanding of the variability of coastal oceanographic conditions and the effects these have on economically important trans-boundary coastal resources.

5.4.2. Global Ocean Observing System (GOOS)

The Global Ocean Observing System (GOOS) funded and supported by the United Nations Environmental Programme (UNEP), the World Meteorological Organisation (WMO), the International Council for Science (ICSU) and the Intergovernmental Oceanographic Commission (IOC), is a permanent integrated global system of oceanographic observations and data products (GOOS 2011). GOOS forms the oceanographic component of the Global Earth Observing System of Systems (GEOSS), along with the Global Climate Observing System (GCOS) and the Global Terrestrial Observing System (GTOS) (Christian 2003). The specific aims of the GOOS programme are to describe and forecast the state of the ocean and its marine living resources as well as to improve the management of marine and coastal ecosystems and resources (GOOS 2011). A sub group of GOOS, the Coastal Global Ocean Observing System (CGOOS) exists with the aim of improving the ability to detect and predict the effects of climate and anthropogenic changes on coastal ecosystems (Malone and Cole 2000, IGOS report 2006). Improving coastal monitoring and management capacities therefore form a major part of the aims of the GOOS and CGOOS programmes, which is evident in their support of the African branch of the project.

GOOS-Africa, established in 1998, and its regional component, the Regional Ocean Observing and Forecasting Systems for Africa (ROOFS-Africa) bodies, supported by the CGOOS and the Integrated Global Observation Strategy (IGOS) programmes, are concerned with the monitoring and management of local coastal ecosystems (Ahanhanzo 2006). It seems, however, that the establishment of regional monitoring in the inshore zone of the northern Benguela has yet to take place. Even in the more studied inshore region of the southern Benguela authors have noted the scarcity of moored monitoring arrays which are dedicated to monitor environmental change, especially dissolved oxygen (van der Lingen *et al.* 2006b).

The ROOFS-Africa programme together with the BCC would be ideal frameworks in which to establish a permanent programme of coastal monitoring in the northern Benguela, which could focus on investigating change in identified hotspots of coastal warming. In fulfilment of the GOOS mandate to monitor ecosystem change (Christian 2003, Ahanhanzo 2006), it would be extremely beneficial to extend the mooring sites which exist in the southern Benguela into areas identified as warming hotspots, where environmental change is taking place at significant rates (Chapter 4).

As the ROOFS-Africa infrastructure needs to be locally funded, low cost instrumentation is essential for the success of such programmes (Ahanhanzo 2006). This is especially true in Angola, where one of the identified warming hotspots is positioned (15.5-17°S, inshore of 200m depth) as this country is the one member state of the BCLME that is most in need of development, both in terms of equipment and personnel (Brundit *et al.* 2006). Before the installation of any monitoring instrumentation, a monitoring programme should be properly laid out. This should include the allocation of funding as well as support, in the form of technical information and personnel for the duration of the programme. It is also important to ensure the capabilities of the selected instrumentation are fully understood and meet the needs of the study. The potential for bio fouling and vandalism should too be taken into account and measures to mitigate the effects of both should be implemented (Glenn *et al.*2000).

Based on the results of this study, the initial installation of temperature loggers at strategic positions along the coast, followed by the addition of dissolved oxygen and salinity sensors to the same mooring would be advised. The installation of temperature loggers at strategic

locations along the coast, corresponding with sites of ongoing CPUE monitoring would benefit studies such as this one immensely. Temperature loggers can be placed in the water column on a permanent basis and remotely relay data to a laboratory computer. The loggers can be set to specific satellite overpass times to encourage a direct comparison between locally observed sea surface temperatures and those derived from satellite sensors. This would improve the correction factors calculated here (see Chapter 2) and thus enable a more accurate understanding of surface temperature variability in the region. Temperature loggers also allow for the monitoring of temperature change with depth, and could shed light on the characteristics of warming events which are too thought to increase if the identified warming of the northern Benguela continues. Information collected using this equipment would significantly contribute to our understanding of the ecology of the northern Benguela. Without this, resource managers in the northern Benguela will not be able to plan for future scenarios of marine resource abundance and spatial distribution. This could lead to unsustainable exploitation of these resources and significant socioeconomic problems in the region.

Chapter 6
Appendix

6.1. Seasonal variability in oceanographic conditions described by ROMS BIOBUS outputs

ROMS BIOBUS seasonally averaged outputs from the Flamingo Lodge (Figure 6.1) and Cape Frio (Figure 6.2) study sites. Although the ranges of salinity and dissolved oxygen are not within the identified optimum ranges for *A. coronus*, a degree of seasonal variability is evident at both sites.

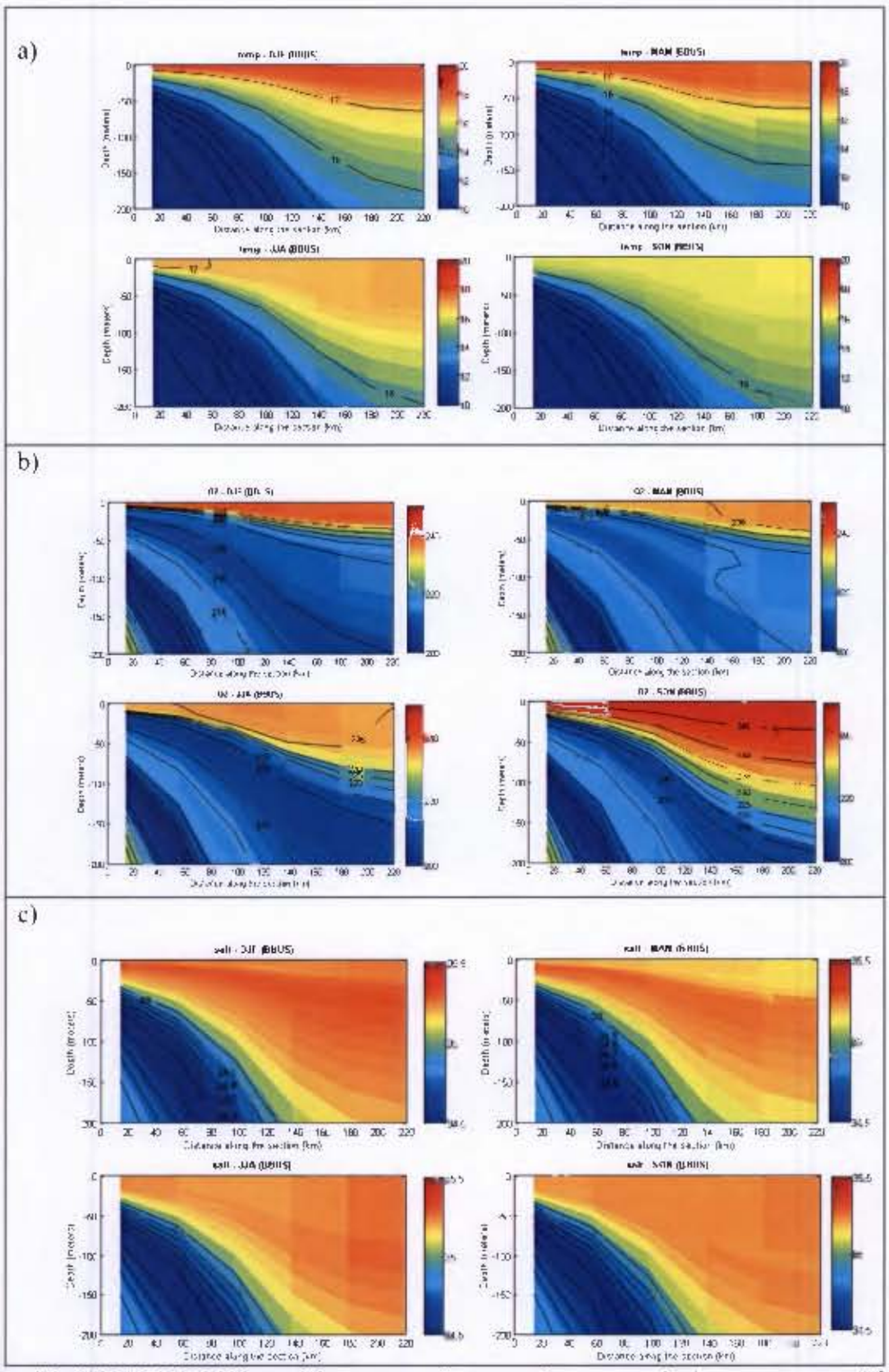


Figure 6.1 ROMS BIOBUS model outputs of seasonally averaged a) temperature (°C); b) dissolved oxygen (mmol.m-3) and c) salinity variability with depth and distance offshore directly offshore of Flamingo Lodge, southern Angola (10-12.5°E and 15-16°S).

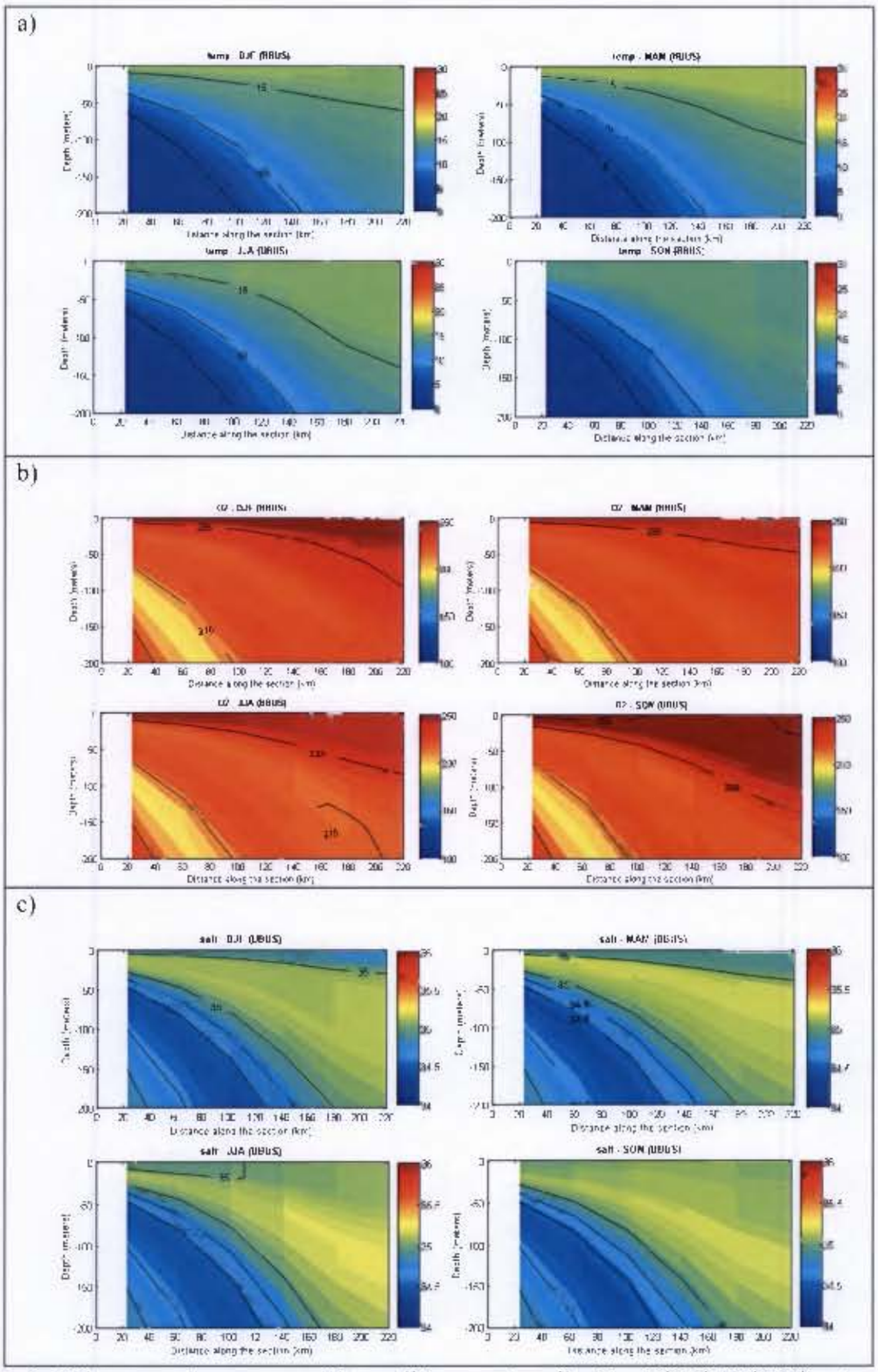


Figure 6.2 The seasonal oceanographic conditions as described by ROMS BIOBUS outputs in the vicinity of the Cape Frio upwelling cell (17.5-18.5°S and 10-12.5°E) in terms of by a) temperature (°C), b) dissolved oxygen (mmol.m^{-3}) and c) salinity.

Chapter 7

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