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DISTRIBUTION AND ABUNDANCE OF CAPE HAKES (*Merluccius capensis and Merluccius paradoxus*) IN RELATION TO ENVIRONMENTAL VARIATION IN THE SOUTHERN BENGUELA SYSTEM

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Supervisor: Prof. J.G. Field

To my parents, Justin and Oonagh Millar,
for the gift of education.

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DECLARATION

This dissertation reports the results of research that I carried out in the Marine Biology Research Institute, Zoology Department, at the University of Cape Town. It has not been submitted for any other degree or examination at any other university. Most of the data that are presented were obtained from Marine and Coastal Management, Department of Environmental Affairs. Southern Oscillation Index data was obtained from the NOAA web page and has been referenced as such. All opinions expressed, unless otherwise acknowledged, are my own.

Signed by candidate

Dinah Millar

31/03/2000
Date

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ABSTRACT

Standard Geographical Information System (GIS) techniques and Generalized Additive Models (GAM), nonparameteric regressions without the assumptions of normality or linearity of traditional regression methods, were used to test the hypothesis that trends in hake (*M. paradoxus* and *M. capensis*) distribution and abundance are related to ocean environmental conditions (including bottom temperature, bottom oxygen concentration, sea surface temperature and sea surface temperature minus bottom temperature, as a measure of stratification or mixing) and location (including longitude, latitude and bottom depth). Hake and physical data, from seventeen biomass surveys undertaken by Marine and Coastal Management between 1984 and 1997 in the southern Benguela ecosystem, were used to test these relationships. Distinct patterns of distribution are evident for three different life history stages (juveniles, subadults and adults) of both species with juveniles occurring in shallow depths, inshore, and migrating to greater depths, offshore, as they grow older. A seasonal migration is also apparent in both species with the fish moving inshore and, in some cases, in a southerly direction in summer. No relationship between the physical data and the hake data in the GIS is consistently evident in all survey years and each life history stage is associated with a fairly wide range of preferred environmental conditions. *M. capensis* were found at sea surface temperature ranges of between 11.28 and 22.83°C, bottom temperatures of between 6.89 and 11.13°C, SST-BT values of between 1.34 and 13.34°C and bottom oxygen concentrations of between 1.13 and 4.65mg.l^{-1}. *M. paradoxus* were found at sea surface temperature ranges of between 13.08 and 22.04°C, bottom temperatures of between 5.76 and 9.69°C, SST-BT values of between 4.09 and 14.84°C and bottom oxygen concentrations of between 2.47 and 4.79mg.l^{-1}. However, there is some evidence, which requires further analysis, that hake distribution may have a relationship with the 16°C sea surface temperature isotherm, and hence the front. As the front is associated with high productivity levels it is thought that these movements may be prey-induced (it was hypothesized, however, that a change in current strength could be influencing these movements). The GAM provided reasonable fits to the spatial distribution of the Cape hakes, with bottom depth being observed as the primary determining factor for arranging the spatial distribution of the hakes and determining spatial density gradients. In addition, adult *M. capensis* and juvenile *M. paradoxus* were affected by the combined effect of depth and oxygen, and depth and latitude, respectively. However, these apparent relationships may only be due to the relationship that oxygen and latitude have with depth and not because of a direct relationship with the fish. These GAMs were used to try to increase the precision of existing biomass estimates by including detected trends in the model. The biomass and biomass variability estimates produced by the GAM are lower and the confidence intervals are tighter than those previously predicted by traditional methods but follow a similar trend.

Chapter One

Introduction

1.1. General

Over the last century an increasing number of marine resources have become depleted under intense fishing pressure as a result of escalating demands for food. Catches of those marine resources that have not been severely depleted, have undergone fluctuations which, in addition to escalated food demands, can also be attributed to changes in fishing fleets, technological developments of gear and past fishing intensity. It has been recognized, however, that stock size and availability are affected not only by fishing but also by variations in recruitment, changes in processes in the ecosystem (e.g. predation and competition), and by various changes in the environment on different space and time scales (Laevastu 1993).

In the past there has been a great amount of resistance to suggestions that non-fishery processes were at least as important as fishery effects. Recently this resistance has been questioned, with Sharp (1987) stating that not enough attention has been given to causes beyond the effects of overfishing in conventional fishery theory. Stromme and Hamakuaya (1998) have also noted that, although the idea of environmental effects influencing stock abundance has been present for a long time, the framework within which stock assessment models have developed has assumed that marine ecosystems are stable and that fish stocks, in pristine conditions, would not fluctuate dramatically. Fisheries scientists have only recently become more convinced that natural environmental variability is extremely important in controlling fish stock variation (Bakun 1998). Therefore, it is believed that the identification of consistent associations of fish species with particular ranges of environmental conditions is the first step towards incorporating the effects of environmental variability into improving fisheries management and stock assessment methods (Perry and Smith 1994). Environmental parameters that have been shown to affect fish stocks include sea temperature and oxygen concentration, wind and upwelling, and on a larger scale, the El Niño Southern Oscillation (ENSO) phenomenon.

1.2. Fisheries and the environment

As fish can perceive small changes in water temperature, it is thought that each species has a characteristic optimum temperature range and temperature tolerance limit (Scott 1982). In addition, juvenile and adult fish often have a different temperature tolerance and preference, which may result in a differing regional distribution (Laevastu and Hayes 1981). Temperature also affects various fish species by influencing spawning (Carscadden *et al.* 1997), growth rate (Bakken 1983, Lehodey and Grandperrin 1996), recruitment (Henderson and Corps 1997), abundance (Swartzman *et al.* 1992, 1994, Nilssen *et al.* 1993), distribution (Smith 1985, Perry and Smith 1994, Perry *et al.* 1994, Swartzman *et al.* 1995, Maravelias 1997, Stull and Tang 1996), aggregation (Macpherson *et al.* 1997) and catchability (Nathanial *et al.* 1990).

Another property of the aquatic environment that may influence fish is the level of dissolved oxygen, in particular hypoxic conditions. This occurs when oxygen levels are so low that they induce stress in aquatic living resources, most often, but not exclusively, when oxygen is less than approximately 2 $mg.l^{-1}$ or 1.4 ml O_2 l^{-1} (Tyson and Pearson 1991). In coastal habitats, lack of oxygen is also known to affect fish distribution (Kramer

1987, Mas Riera *et al.* 1990, Moller and Schloz 1991, D'Amour 1993, Shannon *et al.* 1993, Lee and Whitlatch 1995, Woodhead *et al.* 1998a), abundance (Roel and Bailey 1987, Woodhead *et al.* 1998a), spawning (Woodhead *et al.* 1998a), recruitment (Woodhead *et al.* 1998b, c), growth rate (Pauly 1981, 1984, 1997, 1998) and trophic interactions (Phil 1994).

Wind influences the vertical movement of fish shoals, usually sending them into deeper layers below the oscillatory wave movement during heavy winds because of its effect on turbulence and mixing in the surface layers of the ocean (Laevastu 1993). Wind and upwelling are closely associated because wind drives coastal upwelling. Hypoxic conditions often develop in upwelling regions so one or all of these conditions could directly or indirectly be considered as a driving force behind fish behavior. Recruitment (Martin and Kohler 1965), spawning (Carruthers 1938) and catch rate (Le Clus *et al.* 1998) are also believed to be related to wind anomalies.

Large-scale environmental perturbations such as the El Niño Southern Oscillation (ENSO) also affect fish distribution (Espino 1991) and recruitment (Wosnitza-Mendo and Espino 1996). The Pacific El Niño has a counterpart in the south-east Atlantic, the Benguela Niño that has a major impact on the biota of this region, although they are less frequent and less intense than the Pacific events (Shannon *et al.* 1996).

1.3. Pelagic and Demersal stocks and the environment

Although the relationship between environmental fluctuations and abundance of pelagic fish stocks has long been noted, it is only relatively recently that its importance has been recognized for demersal stock abundance. This is probably due to the fact that climatic fluctuations mainly affect the surface layers of the sea and therefore demersal fish may be less affected by climatic fluctuations than pelagic fish (Laevastu 1993). In addition, demersal species are generally longer lived with stocks consisting of more year classes then pelagic fish, so the impacts on the overall biomass would be far less dramatic (Stromme and Hamakuaya 1998). However, many demersal fish have pelagic larvae that are subjected to environmental conditions in the surface layers and more relationships are being observed between the trawled fish catch and environmental factors in several parts of the world (Bailey 1980, Hollowed and Bailey 1989).

Merluccius spp. are economically important components of the demersal fish communities inhabiting productive upwelling systems associated with eastern boundary currents in the Atlantic and Pacific Oceans (Bakun and Parrish 1981). In order to improve management of these stocks, it is essential to elucidate relationships between these demersal fish stocks and the oceanic environment.

1.4. Merluccius spp. and the environment

Brandhorst (1959) suggested that an oxygen-poor return flow between 200 and 400m adversely affected the migration and therefore the yield to the fishery of *Merluccius gayi gayi* off the Peruvian and Chilean coasts. Subsequently, only a few similar relationships between hake spp. and environmental conditions had been documented and, generally, only relationships between hake larvae or juveniles were tested. These relationships include: a correlation between *Merluccius productus* larvae off California and indices of Ekman transport (Bailey 1980), a positive effect on recruitment of *Merluccius gayi peruanus* off Peru caused by extensions of habitat during the El Niño of 1972/73 as a result of the oxygen minimum zone being depressed to greater depths (Wosnitza-Mendo and Espino 1985), and a significant correlation between *Merluccius bilinearis* off the Scotian shelf and sea temperature cycles (Dow 1977).

It has only been over the last decade that the number of studies, showing relationships of this nature, has increased. Year class strength of hake in the North Sea has been positively correlated with sea temperature (Thompson and Hilden 1988). Larvae of the Pacific hake, *M. productus*, have been shown to favour periods of weak offshore transport during January and February followed by periods of increased upwelling in March (Hollowed and Bailey 1989). Recruitment of the Pacific hake is also strongly correlated with environmental conditions. Juveniles are less abundant in upwelled water (Sakuma and Ralston 1997) and significantly more adult hake migrate when summers are warmer causing an increase in biomass in certain areas (Ware and McFarlane 1995). It has also been noted that *M. bilinearis*, the Silver hake found on the Scotian Shelf, maintains a similar temperature range between summer and winter by changing their seasonal depth distributions (Murawski and Finn 1988, Perry and Smith 1994).

More recently a number of observations have been made of *Merluccius capensis*, the shallow water hake in the Northern Benguela system, including a relationship between sea surface temperature and fish abundance. Gordoa and Hightower (1991) hypothesized that environmental factors could affect fish distribution in the water column and hence, their susceptibility to bottom trawling. Mas-Riera *et al.* (1990) stated that dissolved oxygen is an important factor affecting the distribution of *M. capensis* and it was later thought that juvenile *M. capensis* were apparently displaced from their typical inshore habitat in 1994 by hypoxic conditions that developed off Namibia (Hamukuaya *et al.* 1998). Temperature and oxygen were found to be the parameters most significantly influencing distribution of eggs and larvae (Oliver *et al.* 1998).

Little is known about environmental effects on hake distribution or recruitment in the Southern Benguela ecosystem. Botha (1980) considered the relationship between Cape hake and the hydrological environment. He found no clear dependence of hake catches on bottom temperature, salinity or oxygen. However, in a preliminary investigation by Roel and Bailey (1987), catches of *Merluccius paradoxus* were negatively correlated with bottom temperature and juvenile *M. capensis* abundance was negatively correlated with surface temperature. Moreover, juvenile *M. capensis* were more abundant in oxygen-deficient waters than adults. The authors stressed that these results may be circumstantial rather than causative. In a separate study, Shannon *et al.* (1988) found that changes in hake abundance are related to interannual variability of oceanic sea-surface temperature. Therefore, there is a large amount of uncertainty as to whether environmental factors affect the Cape hakes *M. paradoxus* and *M. capensis* in the Southern Benguela system.

1.5. Hakes in the Benguela Ecosystem

The Benguela Current upwelling system, off the west coasts of South Africa and Namibia, is a region of intense biological productivity. The region supports a great variety of commercially important fisheries, with an annual yield of over two million tonnes (Crawford *et al.* 1987). The three major resource groups caught in these waters are: hakes (*Merluccius* spp.) caught mainly by bottom trawl; horse mackerel (*Trachurus* spp.) fished mainly with mid-water trawl; and epipelagic shoaling fishes, notably pilchard (*Sardinops* *sagax*), anchovy (*Engraulis japonicus*), and young horse mackerel, the targets of purse-seine fleets (Woodhead *et al.* 1998b). The hake fishery is the most valuable demersal resource within the Benguela region with hakes generally being the principal target species for demersal trawlers (Hampton and Matthews 1997). The species involved in the fishery are *Merluccius polli* caught north of the Cunene River, *M. capensis* (shallow water Cape hake) and *M. paradoxus* (deep water Cape hake), which are caught south of 20°S (Roel and Bailey 1987). Off Namibia *M. capensis* is the most common hake species, whereas *M. paradoxus* predominates off the West Coast of South Africa. What is probably a second stock of *M. capensis* is found in the extreme southern Benguela, chiefly over the Agulhas Bank. The distribution of the three species can be seen in Figure 1.1.

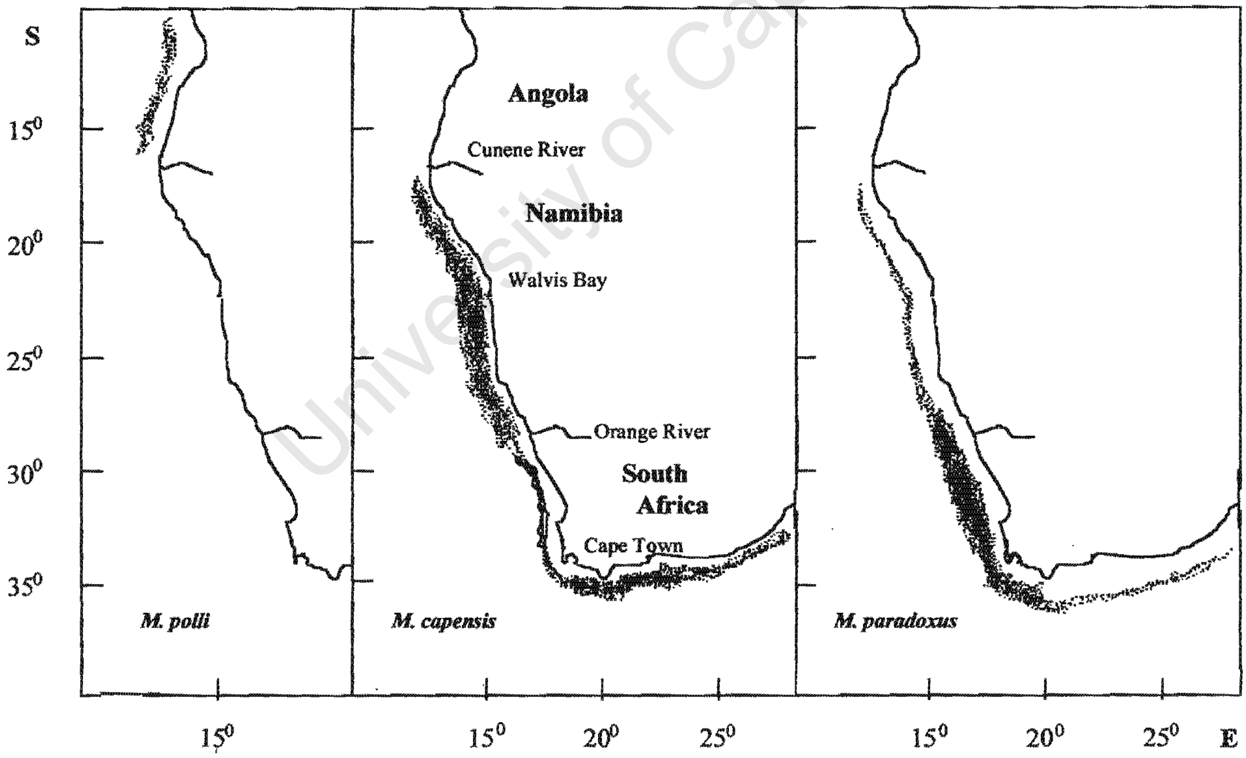


Figure 1.1: Distribution of three hake species in the Benguela ecosystem (redrawn after Payne 1989).

An overview of the history of the Cape hake fishery off southern Africa is provided by Botha (1980) and by Payne (1989). In addition the biology and population dynamics of the Cape hakes has been reviewed by Botha (1971, 1980, 1985, 1986), Payne (1986, 1989), Payne and Punt (1995), Payne *et al.* 1987a b, 1989), Punt and Leslie (1991), Punt *et al.* (1992) and Huse *et al.* (1998). There are currently two main methods used to assess the hake resource: an age-structured stock production model and Virtual Population Analysis (VPA) (Punt 1988, 1991, 1994). The production model is detailed in Butterworth and Andrew (1984) and the VPA approach is documented by Butterworth *et al.* (1990).

In recent decades hakes within the Benguela upwelling system have undergone large changes in distribution (Payne *et al.* 1989) and biomass (Figure 1.2), which cannot be attributed only to fishing. Although the exact mechanisms that cause these changes are uncertain, fluctuations in year-class strength of Cape hakes in the southern Benguela, under relatively stable conditions of exploitation (Leslie 1986), suggest an environmental modulation of the populations. Relatively little is known about the behavior of Cape hakes in the Benguela ecosystem and their responses to environmental variability and change. It has been hypothesized that both the deep water and shallow water hakes move seasonally inshore and offshore (Botha 1980), as well as latitudinally (north and south) along the west coast of South Africa (Japp, pers comm.). Cape hakes are also known to undergo diel migration through the water column, rising during the night to disperse and feed in midwater and returning to the bottom after dawn (Pillar and Barange 1997).

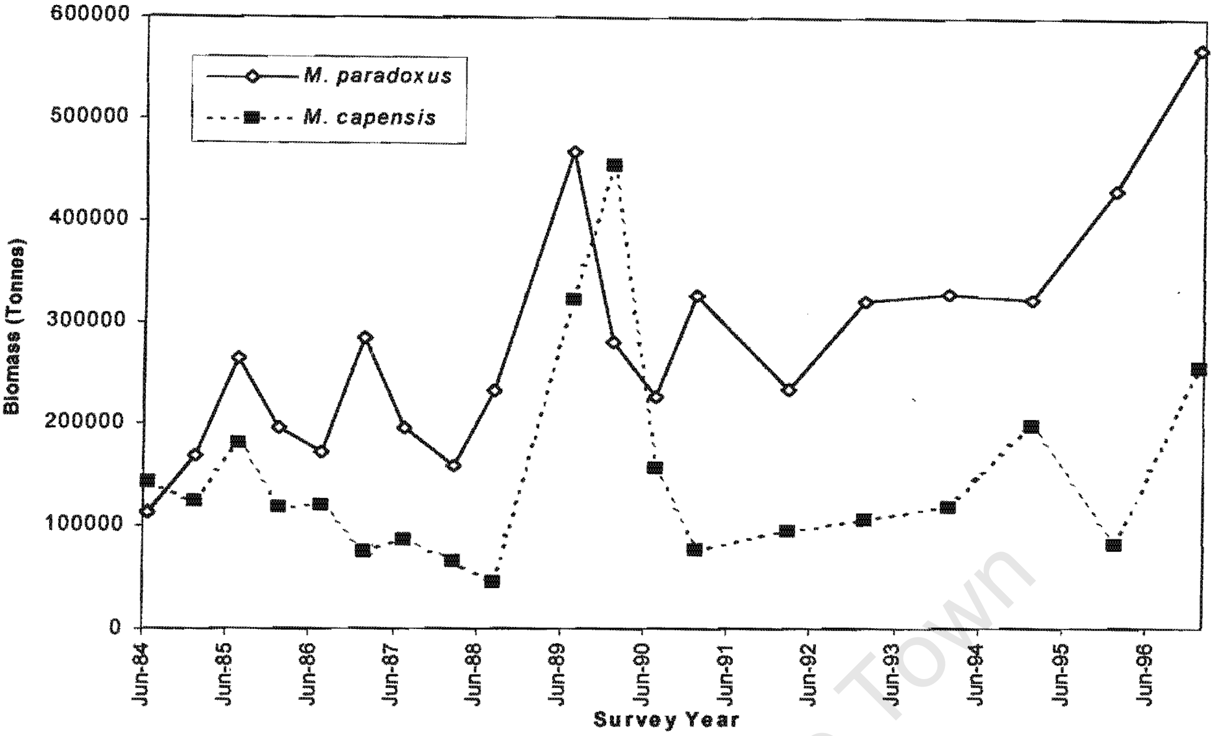


Figure 1.2: Changes in hake biomass between 1984 and 1997 in the southern Benguela ecosystem (MCM unpublished data).

The lateral and longshore migration of Cape hakes is believed to be influenced by upwelling (Japp, pers comm.). As coastal upwelling is associated with a reduction in temperature and oxygen levels, these may influence the distribution and abundance of demersal fish. In addition, because upwelling is closely linked to wind, availability of hake to the trawl fleet is also believed to switch on and off with changes in wind stress (Maree, pers. comm.). Changes in water quality could cause movements to be either horizontal with the onshore movement of cool upwelled water, or vertical to escape cold or warm bottom temperature.

As adult hakes are good swimmers, undergo vertical migrations, can tolerate a range of temperatures and are relatively opportunistic feeders, it is believed that hakes would be robust to all but major environmental perturbation (Hampton and Matthews 1997).

1.6. Spatial Analysis

Annual surveys conducted in the Benguela system by Marine and Coastal Management, Cape Town, provide a good opportunity to examine the spatial distributions of Cape hakes and how they might be related to environmental factors. The reason is that samples collected on fisheries survey are all geo-referenced (located explicitly in space by latitude and longitude) and are multivariate (both abundance data and physical data are collected at each sampling location). Spatial analytical methods to detect and correct for observed trends could lead to improved fisheries abundance estimates (Swartzman *et al.* 1992). A spatial approach that has become popular in many other disciplines is the use of Geographic Information Systems (GIS) although it has not yet been used extensively in fisheries science. This approach allows for the interpretation of georeferenced and multivariate data with greater speed and accuracy than conventional approaches (Isaak and Hubert 1997). In addition, an increasing trend in spatial analysis is in the form of spatial statistics (Sullivan 1991, Swartzman *et al.* 1992, Swartzman *et al.* 1994), in particular Generalized Models (Hastie and Tibshirani 1986). These model a response variable such as fish density, as a function of two or more covariates (e.g. physical variables).

1.7. Aims of this study

The primary objective of this study is to explore variations in the distribution and abundance of three life history stages (juveniles, subadults and adults) of the Cape hakes, *M. paradoxus* and *M. capensis*, off the west coast of South Africa in both summer and winter and to relate these variations to environmental conditions within the Benguela ecosystem during these seasons.

1.8. Thesis Outline

This thesis is divided into five chapters. Chapter 2 describes the study area and material and methods used in the study. Moreover, it describes the sampling strategy and choice of sampling sites. The main tools being used to explore the objectives of this study are standard Geographic Information System (GIS) methods and Generalised Additive Modelling (GAM). These make up the main subject of Chapters 3 and 4 respectively. Chapter 3 qualitatively assesses spatial and temporal patterns of hake abundance for three life history stages and of environmental conditions in the southern Benguela. It also explores whether there are consistent associations of fish species with particular ranges of environmental conditions. In Chapter 4 fish density is quantitatively modelled as a function of selected environmental parameters and trends observed will be incorporated into generating biomass estimates. This is done through the use of GAM. Lastly, these results are described in Chapter 5 in relation to their implications for management and stock assessment methods.

Chapter Two

2.1. Study Area

The Benguela region (Figure 2.1) lies off the west coast of South Africa and Namibia extending south from Angola to Cape Agulhas. The Benguela current is the major large-scale current which occurs in this region and makes up one of four major eastern-boundary current systems in the world (Hampton and Matthews 1997).

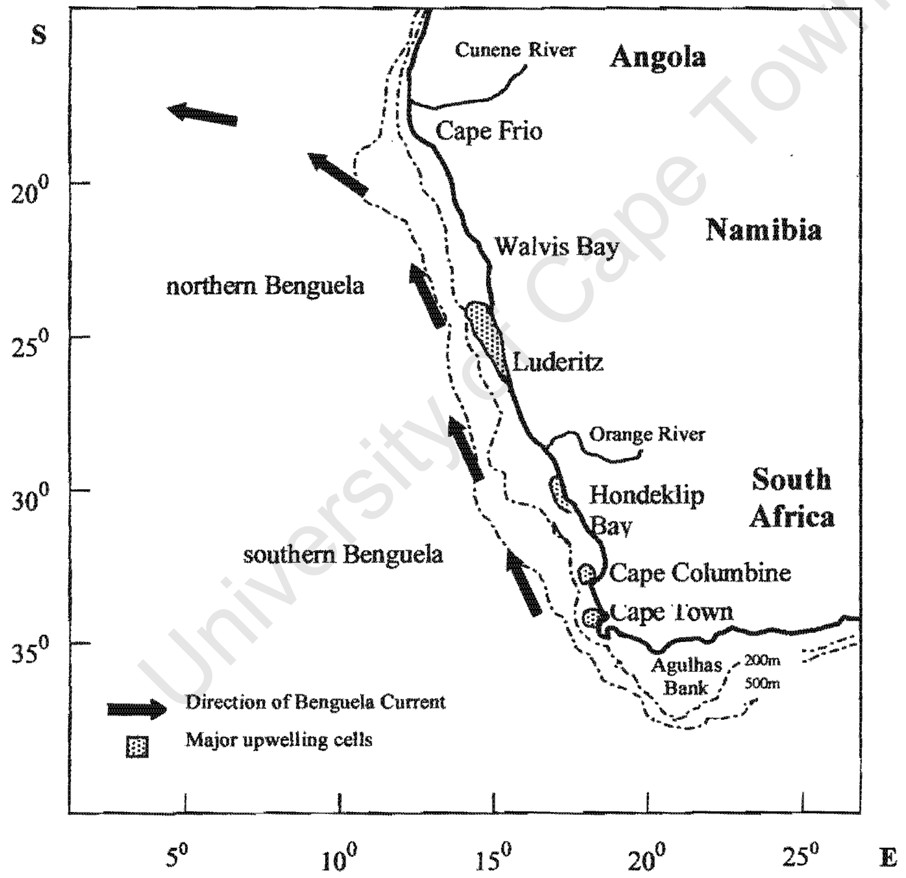


Figure 2.1: Map of the Benguela upwelling region with the arrows representing the flow direction of the Benguela current and the dotted areas representing the major upwelling cells (modified from Hampton and Mathews 1997).

The current flows equatorwards from the western tip of Africa to the Angolan front where it diverges offshore in a westerly direction. This water movement occurs within and on the outer margin of the Benguela upwelling system (Boyd and Nelson 1998). This upwelling system is unlike other eastern boundary upwelling systems as it has warm frontal systems along both its northern and southern borders due to the termination of the African continent at a relatively low latitude (Shannon *et al.* 1988). The Benguela system is divided into the northern and southern Benguela by cool and turbulent surface waters of the Lüderitz upwelling cell (Shannon and Pillar 1986).

This study was undertaken within the southern Benguela region. This includes the area on the west coast of South Africa from Cape Agulhas to the Orange River, covering a distance of 780km and excludes the central and eastern Agulhas Bank regions. The 500m isobath was taken as the seaward boundary indicative of the most productive part of the southern Benguela. This area has a surface area of approximately 105 000km^2 (Ware 1992). The southern Benguela has a deep shelf being narrowest in the south near Cape Town and broadest in the area around the Orange River (Shannon 1995). Coastal upwelling in this region is driven by south-easterly winds, which occur most prominently during summer (Jury 1985). The intensity of upwelling varies with locality, with the main upwelling cells occurring at Hondeklip Bay, Cape Columbine and off the Cape Peninsula. It is a region of intense biological productivity with the upwelled waters having high concentrations of nutrients and supporting high plankton production and high abundances of fish. The southern Benguela ecosystem is also characterized by oxygen-depleted waters that possibly originate in Angola and move south along the shelf or are locally generated (Field, pers comm.).

2.2. Sampling Methods

Biomass survey data used in this analysis were collected on the west coast of South Africa from the Orange River to Cape Agulhas out to 500m water depth (Figure 2.2).

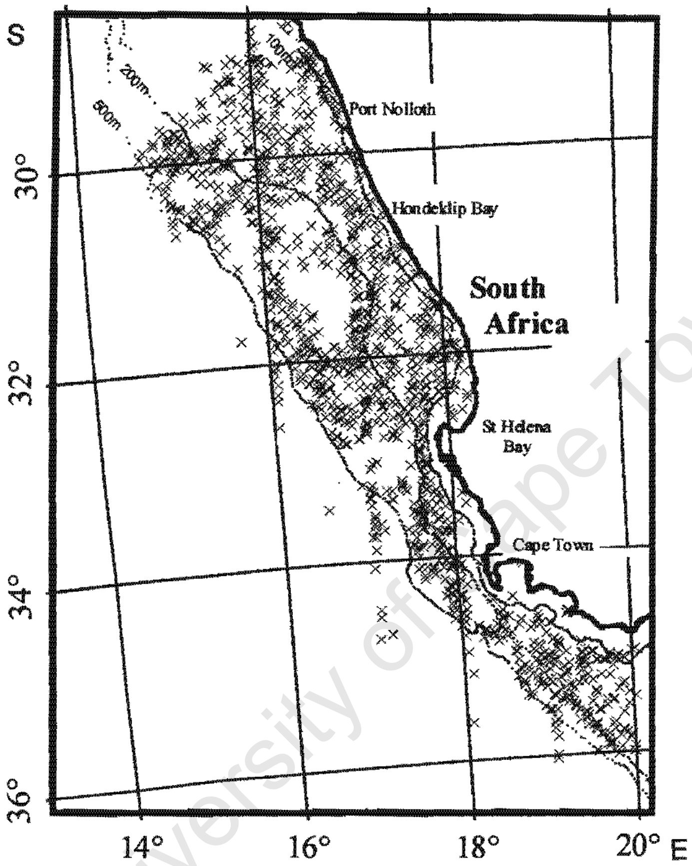


Figure 2.2: Trawl locations (represented by crosses) from 1984 to 1997 in the southern Benguela (MCM unpublished data).

This was collected during bi-annual (summer and winter) biomass assessment surveys between 1984 and 1990 and annually (summer) between 1991 and 1997 by the South African research vessel F.R.S. Africana (a 2452 GRT stern trawler). A weakness of these surveys is that they do not cover the whole distribution range of *M. paradoxus* and *M.*

capensis and this makes it difficult to interpret migration and interannual changes in biomass estimates. Data from the first survey (summer 1983) was not used as this was regarded as a learning survey. In addition, biomass estimates from 1983 and 1984 may not be compatible with the rest of the time series, as the selectivity of the bobbin-gear used for the first two years is different from that of the footrope-trawl gear used thereafter. During the summer survey of 1989, the vessel broke down after only 25 stations were completed and the survey was aborted (Leslie, MCM, pers comm). Thus, this data was not used.

The areal expansion method was applied to the hake biomass survey. The method involves a semi-random stratified selection of trawling positions at intervals along the coast, the number of stations per depth and latitude stratum being directly proportional to its total area. The same geographical range is covered each year from the coast out to the 500m isobath, and from the international border between South Africa and Nambia to Cape Agulhas (20°E). The survey area was subdivided into 100m depth strata, namely 0-100m, 100-200m, 200-300m, 300-400m and 400-500m. Each stratum was further subdivided into blocks of 5x5 nautical miles. Trawling stations were assigned to blocks in each of the strata on a semi-random basis, the number of stations per depth and latitude stratum being directly proportional to its total area. A 180-ft German trawl net with 1500kg polyvalent doors was used. The time the net actually spends on the bottom for each trawl is limited to 30 minutes. Occasionally some trawls were one hour in duration so all data were standardized to one hour. As a consequence of changes in trawl duration, the proposed correction might still result in a biased estimate for reasons such as the effect of fish exhaustion when swimming for longer periods of time in the trawl mouth.

The trawls took place during full daylight hours, with trawls commencing in full daylight and being raised before sunset to avoid possible vertical migration by hake off the bottom during the night. The catch from each trawl was sorted and identified to species, weighed and length frequencies in centimeter size classes were collected for all commercial species. Physical data, including temperature, salinity, dissolved oxygen and depth were collected at each trawl station (immediately following all trawls) using a conductivity, temperature and depth (CTD) rosette sampler, which was lowered to within 5m of the sea bed. Dissolved oxygen was determined by Winkler titration. Estimates of biomass and the associated standard errors were calculated (Leslie, pers. comm.) by the swept-area survey method. Two basic assumptions of the swept area method are that all fish in the path of the net are caught, and that the fish are distributed homogeneously over the survey area.

The density of hake (d_{si}) was calculated for each station by

$$d_{si} = \frac{c_{si}}{a_{si}}$$

where c_{si} is the catch of hake (kg) and a_{si} the area swept by the trawl net (n mile^{-2}) at the *i*-th station in stratum *s*. The swept area was calculated as the product of the length (estimated by towing speed multiplied by trawl duration) and breadth (given by the mouth opening of the net and assumed to be 26m) of the trawl track. The average density per stratum ($d_{s.}$) was then calculated as

$$\overline{d_{s.}} = \frac{\sum_{i=1}^{n_s} d_{si}}{n_s}$$

and extrapolated over the total area of the stratum (A_s) to yield the biomass index per stratum (B_s), and summed over strata to yield the estimated total biomass index (B).

$$B = \sum_{s=1} B_s = \sum_{s=1} A_s \overline{d_{s.}}$$

The standard error (*SE*) of the biomass index per stratum was taken as the product of the stratum area and the standard deviation of the mean density for that stratum. The *SE* for the survey biomass estimate was calculated as

$$SE(B) = \sqrt{\sum_{s=1}^{n_s} \left(A_s \sqrt{\frac{\sum_{i=1} \left(\overline{d_{s.}} - d_{si} \right)^2}{n_s - 1}} \right)^2}$$

To relate hake catches to environmental variables, standard Geographic Information System methods and Generalized Additive Models (GAM) were used. A more detailed account of the methodology involved in these techniques can be found in Chapters 3 and 4 respectively. Hake abundance was split into three life history stages so as to explore the various effects that each variable had on each life history stage. These stages included juveniles, those fish of lengths smaller than 24cm; subadults, those fish between 25cm and 45cm; and adults, those fish greater than 46cm (sexual maturity for males and females of both species occurs at a length class of between 30 and 50cm (Payne and Punt 1995)). Environmental variables included in this analysis are bottom depth, bottom oxygen concentration, bottom temperature, sea surface temperature, sea surface temperature minus bottom temperature, longitude and latitude. Sea surface temperature minus bottom temperature (SST-BT) is used to characterize areas dominated by stratified water (i.e. large SST-BT), transition zones (intermediate SST-BT) and deep mixing (SST-BT close to zero) (Maravelias 1997). However, because good mixing never occurs all the way to the bottom on the outer shelf, these waters would always show high SST-BT values. Therefore, the variable of SST-BT would only be a good indication of mixing/stratification on the inner shelf. In addition, waters in summer may appear more stratified (high SST-BT) due to an increase in heating of the surface layers between upwelling bouts and these factors should be taken into consideration when referring to this variable in later chapters of this thesis.

Chapter Three

The relationship of hake abundance and distribution to environmental parameters using a Geographical Information System

3.1. Introduction

All natural resources, including those found in marine ecosystems, are firmly established in some sort of ecological and economical system. An understanding of the dynamics of these resources, in this case fish stocks, is vital in order to make informed management decisions. A Geographical Information System (GIS) can be used to manipulate spatial data that relates to any one of these aspects of resource dynamics and therefore can be used for scientific investigations and resource management.

An information system is a chain of operations starting from planning the observation and collection of data and ending in using the derived information in some decision-making process. If this definition is used, a GIS can be considered as an information system that is specifically designed to work with data referenced by spatial or geographical co-ordinates (Booth 1998). This powerful tool is capable of organising, analyzing, and displaying spatial data with outputs being in the form of maps and other graphical, textual and tabular products (Isaak and Hubert 1997). The essential usefulness of GIS, however, lies in its ability to manipulate data in a large number of ways and to perform various analytical functions, thus providing output which makes for more efficient decision making (Meaden and Do Chi 1996). In addition, it is able to bring data from large spatial data sets together in an integrated way, faster and more accurately than conventional approaches (Long *et al.*

1994, Isaak and Hubert 1997). GIS provides a natural framework for the acquisition and analysis of georeferenced biological, oceanographic and environmental data.

GIS is useful in fisheries because it allows for the integration of coastline, bathymetry, trawl sets and oceanographic measurements (Kieser *et al.* 1995), but it has not been used extensively in fisheries science. Although limited, examples of GIS use in fisheries do exist with most of these involving freshwater fisheries (Isaak and Hubert 1997, Giles and Nielsen 1992). Examples are increasing since the use of GIS in marine fisheries was first suggested in 1992 (Simpson 1992, Meaden 1993). Kieser *et al.* (1995) have shown how a GIS can produce maps of sampling locations, acoustic fish density measurements, catch samples, fish habitat and oceanographic measurements. Castillo *et al.* (1996) used GIS techniques to analyze the distribution of three pelagic resources and their relation to physical oceanographic conditions, while Booth (1998) developed a GIS to analyze panga distribution and abundance patterns on the Agulhas Bank off South Africa. Due to the successful documented use of GIS in the above mentioned studies, I will use this tool to analyze the response of Cape hakes in the Benguela ecosystem to environmental variables.

In this chapter I examine the intra-seasonal and geographical distributions of three life history stages of *M. capensis* and *M. paradoxus* over the survey period using a GIS. Similarly, I examine the intra-seasonal change in physical conditions within the Benguela and test whether a particular range of temperatures is associated with high hake abundance. In addition, I test the effect of wind and the Southern Oscillation index, as a measure of the El Niño-Southern Oscillation, on hake abundance.

3.2. Data Analysis

Collection and calculation methods of hake biomass survey data and physical data used in this analysis can be found in Chapter 2. All information was processed using GIS techniques. A Geographical Information System was developed using ArcView 3.0 (ESRI). Each trawl was treated as a point on the latitude-longitude plane with each biomass survey being converted into a point coverage using decimal degree coordinates. The latitude and longitude of the starting of the trawl was used for the points to represent the trawl path vector. The area of the trawl and other attributes such as CTD and biological data were appended as an attribute file. Coastline and bathymetry coverages were digitized from available nautical maps.

Map projections were used to allow areas on the surface of the earth (a spheroid) to be represented on a map (a flat surface). In this way the precise position of features on the earth's surface can be obtained from the map. The Transverse Mercator projection was used, as it is commonly used for large-scale mapping. The central meridian is centred on the region to be highlighted. This centering on a specific region minimizes distortion of all properties in that region. As meridians run north and south, this projection is best suited for landmasses, such as Africa, that stretch north to south (ESRI 1997).

The map projection can only be set if the map units it contains are decimal degrees (i.e. degrees of longitude-latitude expressed as a decimal rather than in degrees, minutes and seconds). This is because data in decimal degrees are in a spherical coordinate system and so are, by definition, unprojected. Therefore, longitude and latitude data were converted from degrees, minutes and seconds to decimal degrees using the equation

$$\text{Decimal degrees} = \text{degrees} + \text{minutes}/60 + \text{seconds}/3600$$

To make calculations easier, the earth is often treated as a sphere although its diameter is slightly larger at the equator than the poles. The assumption that the earth is a sphere can be used for small-scale maps. At this scale, the difference between a sphere and a spheroid cannot be detected on a map, however, to maintain accuracy for larger-scale maps, the earth must be treated as a spheroid. The predefined spheroid, Clarke 1880, was used (ESRI 1997). Maps for each survey year of fish numbers per nautical mile^{-2} were drawn to track the migration of hake.

Physical data were interpolated. Interpolation is undertaken to estimate values for locations where there are no measurements. Data were interpolated using the Inverse Distance Weighted (IDW) interpolator (ESRI 1997). This assumes that each input point has a local influence that diminishes with distance. It weights the points closer to the processing cell greater than those farther away. A specified number of points, or optionally all points within a specified radius, can be used to determine the output value for each location (Star and Estes 1990). To mark the boundary between the cool, productive coastal water and the warmer oceanic regime, the 16°C sea surface temperature isotherm, which is almost always present off the west coast of South Africa (Agenbag 1996) is shown as a dotted line on all sea surface temperature maps.

Using overlaying procedures characteristic of GIS, relationships among variables can be investigated. Both point and polynomial interpolated physical data (to allow for better visual interpretation) were overlaid with the density of fish.n mile^{-2} for each life-history stage.

Raster data are used to represent discrete and continuous variables. Continuous variables are represented in a GIS as surfaces, where the value for each cell is the value for a point at the centre of the cell, and the value of other locations within the same cell can be interpolated from the cell center and the centers of neighboring cells. Grid themes representing continuous surfaces were created and analyzed using the Spatial Analyst (ESRI 1997) in order to determine the relationship between environmental factors and hake data. Trends were identified using Boolean logic to select alternative combinations of values within the different coverages to identify zones of physical preference.

Relationships of hake biomass to windrun were analyzed and wind data were obtained from the Cape Point lighthouse (MCM, unpublished data). Windrun is the total distance that the wind has travelled during a particular period of time in a particular direction and is measured in kilometres.

In addition, hake biomass was related to the Southern Oscillation Index (SOI). This index is calculated as the normalized difference in surface pressure between Tahiti, French Polynesia and Darwin, Australia and is a measure of the strength of the trade winds which have a component of flow from regions of high to low pressure. These data were obtained from the NOAA web page.

3.3. Results

3.3.1. General patterns of hake biomass in relation to average environmental parameters

Hakes were heavily exploited during the 1960s and 1970s with subsequent decreases in catch rates and biomasses thereafter (Crawford *et al.* 1987). The trends in biomass for the 1980s and 1990s (1984-1997) are plotted together with a standard error in Figure 3.1 (dotted lines representing *M. capensis* and solid lines representing *M. paradoxus*). *M. capensis* followed a declining trend in the mid to late 1980s. This was abruptly interrupted by an increase in abundance of hake in the shallower areas (<200m) in 1989/1990 (Figure 3.2). After this, *M. capensis* biomass dropped to its original levels and has over recent years shown a slight increase.

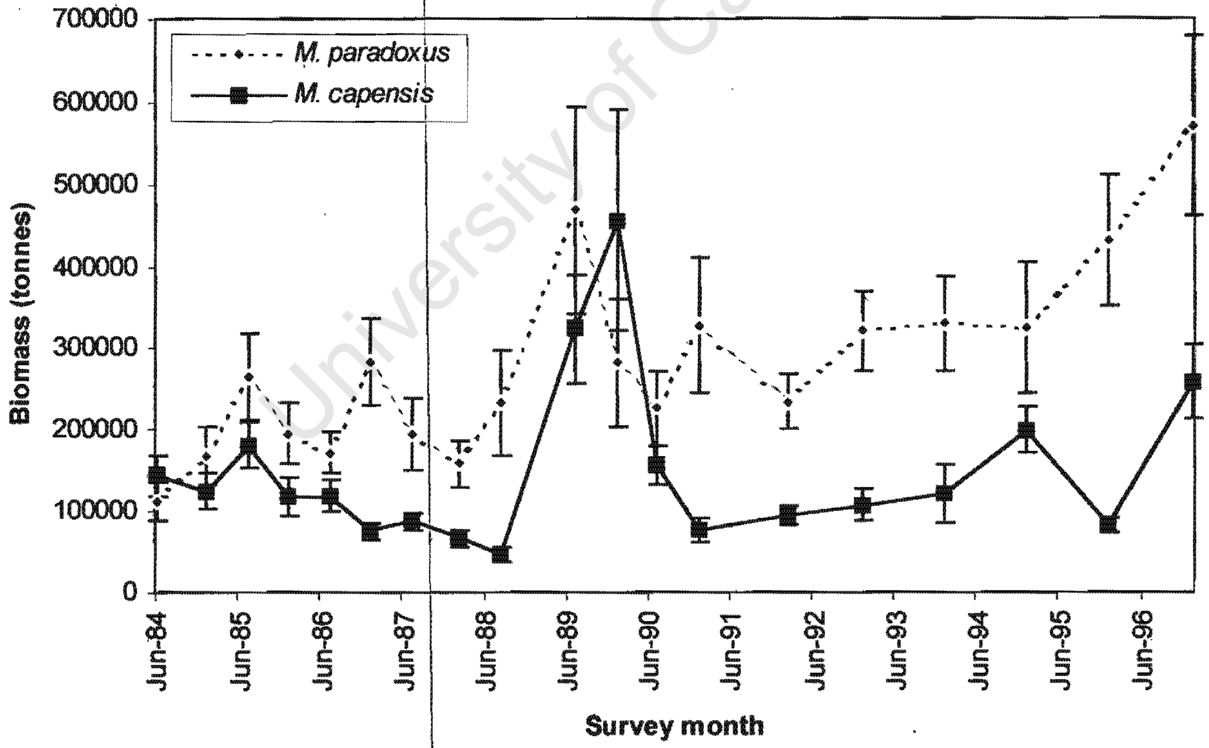


Figure 3.1: Total biomass and standard error for both *M. capensis* (straight line) and *M. paradoxus* (dotted lines) between 1984 and 1997 (MCM unpublished data) off the west coast of South Africa.

Figure 3.2: Pie charts representing the percentage of total biomass of *M. capensis* at each depth range surveyed off the west coast of South Africa between 1984 and 1997 (MCM unpublished data).

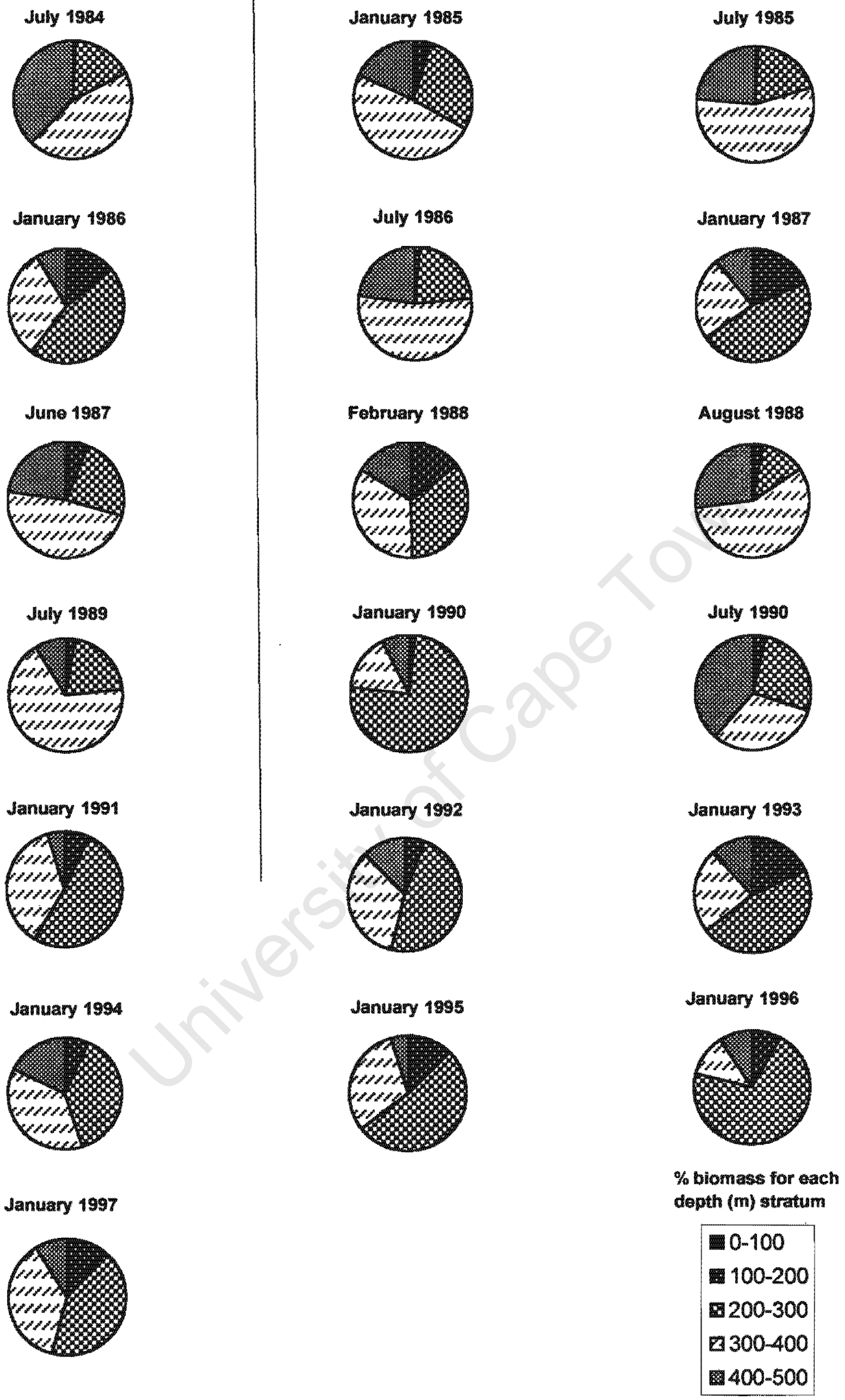


Figure 3.3: Pie charts representing the percentage of total biomass of *M. paradoxus* at each depth range surveyed off the west coast of South Africa between 1984 and 1997 (MCM unpublished data.

M. paradoxus have undergone a steady increase in biomass over the last two decades (Figure 3.1) but have also showed a sudden increase of fish in the 200-400m zone in June 1989 and January 1990 (Figure 3.3). The percentage contribution of *M. capensis* to the total catch (Figure 3.4) follows a similar trend to the biomass data (Figure 3.1) which shows that the variability occurring is caused mainly by the hake and not by other fish in the trawl. This implies that the variability is not a result of changes in fishing method or wind hampering the trawl, but is due to actual changes in the catchability, abundance or distribution of the species. In contrast, the percentage contribution of *M. paradoxus* does not show the same increase in 1989/1990, which implies that there was a general increase in all trawl species at that time.

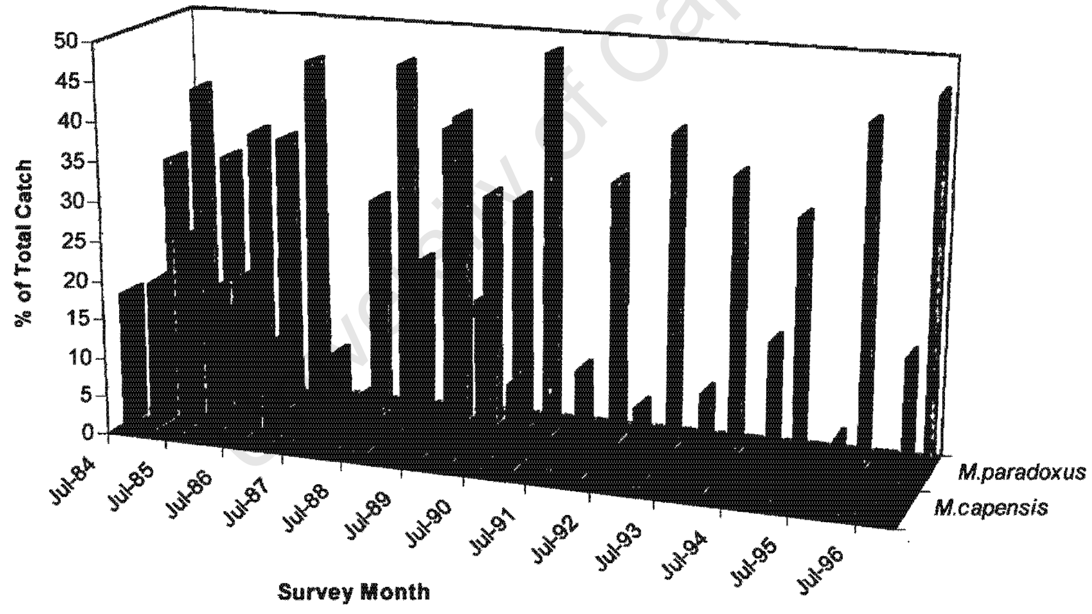


Figure 3.4: The percentage hake biomass of the total catch for both *M. capensis* and *M. paradoxus* off the west coast of South Africa between 1984 and 1997(MCM unpublished data).

Over this period, both hake species represent *ca.* 80% of the total catch, and so this decrease in the contribution of *M. paradoxus* is probably rather due to the observed increase in *M. capensis* and not to an increase of all trawl species.

A summary of all trawl survey physical data collected is presented in Table 3.1. Overall, the average depth surveyed (≈200m) was similar during summer and winter, except for February 1992 where the average depth was *ca.* 50m deeper. Average sea surface temperature is cooler in winter (15.26°C) than in summer (17.71°C). Average bottom temperatures are only 0.1°C cooler in summer (8.62°C) than in winter (8.71°C) with very similar values occurring throughout the survey years. SST-BT values are higher in summer (9.13°C) than in winter (6.22°C), which shows that waters are more stratified in summer. Bottom oxygen concentrations are also very similar between winter (3.38mg.l^{-1}) and summer (3.4 mg.l^{-1}) months.

Changes in biomass of both hake species over all survey years are compared to anomalies occurring over all years for sea surface temperature, bottom temperature, SST-BT and bottom oxygen concentrations in Figure 3.5. As seen in Figure 3.1, major increases in hake biomass are observed in January 1990 for *M. capensis* and July 1989 and January 1996, 1997 for *M. paradoxus*. However, there were no corresponding anomalies in the physical data that could be corresponded to these changes. Large differences occurred in all physical data in January 1992 but no anomalies were seen in the hake data. Overall, no clear relationships were observed between changes in hake biomass and environmental anomalies (Table 3.2).

Table 3.1: Mean (± standard error) of environmental variables collected during each survey month between 1984 and 1997 (MCM unpublished data) off the west coast of South Africa.

Year and Month	N	Depth (m)	Sea Surface Temperature (°C)	Bottom Temperature (°C)	SST-BT (°C)	Bottom Oxygen (mg.l^{-1})
July 1984	59	196.47 ± 80.46	15.27 ± 1.57	8.36 ± 1.52	5.91 ± 2.26	3.65 ± 1.21
January 1985	46	197.89 ± 70.49	*	*	*	*
July 1985	55	197.61 ± 70.83	*	*	*	*
January 1986	68	204.85 ± 77.05	18.65 ± 2.28	8.81 ± 0.64	9.85 ± 2.52	3.27 ± 0.90
July 1986	62	208.69 ± 87.01	15.75 ± 1.11	8.80 ± 1.26	6.95 ± 1.88	3.11 ± 1.21
January 1987	71	194.25 ± 69.01	17.86 ± 2.79	8.95 ± 1.05	8.90 ± 3.05	3.70 ± 1.11
June 1987	58	217.22 ± 75.05	16.06 ± 1.40	8.70 ± 1.20	6.92 ± 1.99	3.55 ± 0.97
February 1988	75	189.35 ± 66.21	17.74 ± 2.99	8.62 ± 0.70	9.12 ± 3.22	3.26 ± 0.85
August 1988	65	204.42 ± 87.61	14.78 ± 1.35	8.87 ± 1.11	5.92 ± 1.99	3.22 ± 0.93
January 1989	#	#	#	#	#	#
July 1989	60	200.08 ± 76.40	15.28 ± 1.13	8.97 ± 1.05	6.25 ± 1.83	3.32 ± 0.92
January 1990	72	193.06 ± 78.57	16.85 ± 2.35	8.45 ± 0.82	8.40 ± 2.60	3.35 ± 1.02
July 1990	48	195.08 ± 95.53	14.41 ± 1.44	8.53 ± 1.72	5.34 ± 2.40	3.43 ± 1.01
January 1991	73	186.07 ± 59.33	16.79 ± 2.66	8.67 ± 0.72	8.93 ± 2.21	3.44 ± 0.96
February 1992	71	250.25 ± 94.70	19.83 ± 2.07	8.06 ± 1.01	11.27 ± 2.37	3.70 ± 0.80
January 1993	65	202.20 ± 84.22	18.39 ± 3.20	8.71 ± 0.9	9.68 ± 3.36	3.41± 1.00
January 1994	77	201.35 ± 81.33	16.49 ± 2.54	8.65 ± 0.89	7.85 ± 2.61	3.46 ± 1.15
January 1995	87	199.67 ± 87.95	17.17 ± 2.60	8.62 ± 0.98	8.56 ± 2.99	3.30 ± 0.97
January 1996	73	197.49 ± 81.58	17.45 ± 2.53	8.72 ± 0.64	8.74 ± 2.79	3.07 ± 0.95
January 1997	62	195.32 ± 76.23	17.64 ± 2.94	8.54 ± 0.84	9.10 ± 3.15	3.47 ± 0.92

*No environmental data available
Survey aborted

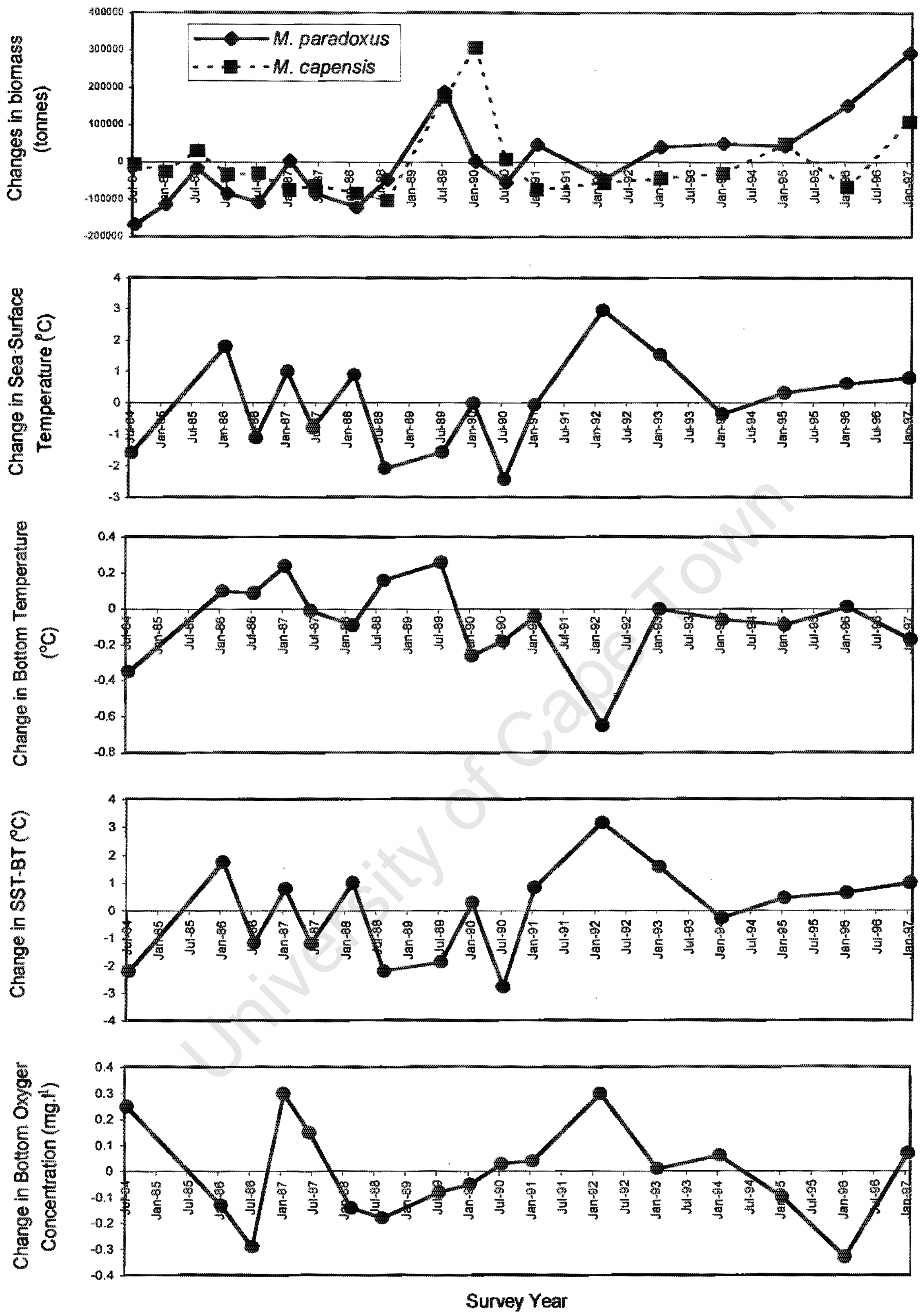


Figure 3.5: Anomalies of hake biomass and all environmental variables off the west coast of South Africa between 1984 and 1997 (MCM unpublished data).

Table 3.2: Correlation coefficients showing the relationship between hake biomass and the environmental variables.

Environmental variable	*M. capensis*	p	*M. paradoxus*	p
Sea Surface Temperature	-0.14	p>0.05	0.13	p>0.05
Bottom Temperature	-0.02	p>0.05	0.21	p>0.05
SST-BT	-0.07	p>0.05	0.26	p>0.05
Bottom Oxygen Concentration	-0.02	p>0.05	0.17	p>0.05

3.3.2. Hake distribution in relation to environmental parameters using a GIS

Distinct patterns of distribution are evident within the various life history stages of *M. capensis* (Figure 3.6) and *M. paradoxus* (Figure 3.7) when all trawl surveys are pooled. The greatest density of juvenile *M. capensis* is found in a very narrow depth range between 0m and 100m. Subadults are distributed between 0m and 250m and adults are distributed over the widest range between 200m and 500m. Similar life history segregation with depth is found for *M. paradoxus*, although they are generally found in deeper depth ranges than *M. capensis*. The greatest density of juvenile *M. paradoxus* is found between 150m and 300m. Subadults are distributed over a wider area, between 200m and 500m. Adults extend from 300m offshore.

A variety of differences in distribution between summer and winter are also observed for each life history stage. Not much difference occurs between summer and winter in the distribution of *M. capensis* juveniles (Figure 3.8a). However, between St Helena Bay and Hondeklip Bay, a greater density of juveniles is found extending further offshore in winter than in summer.

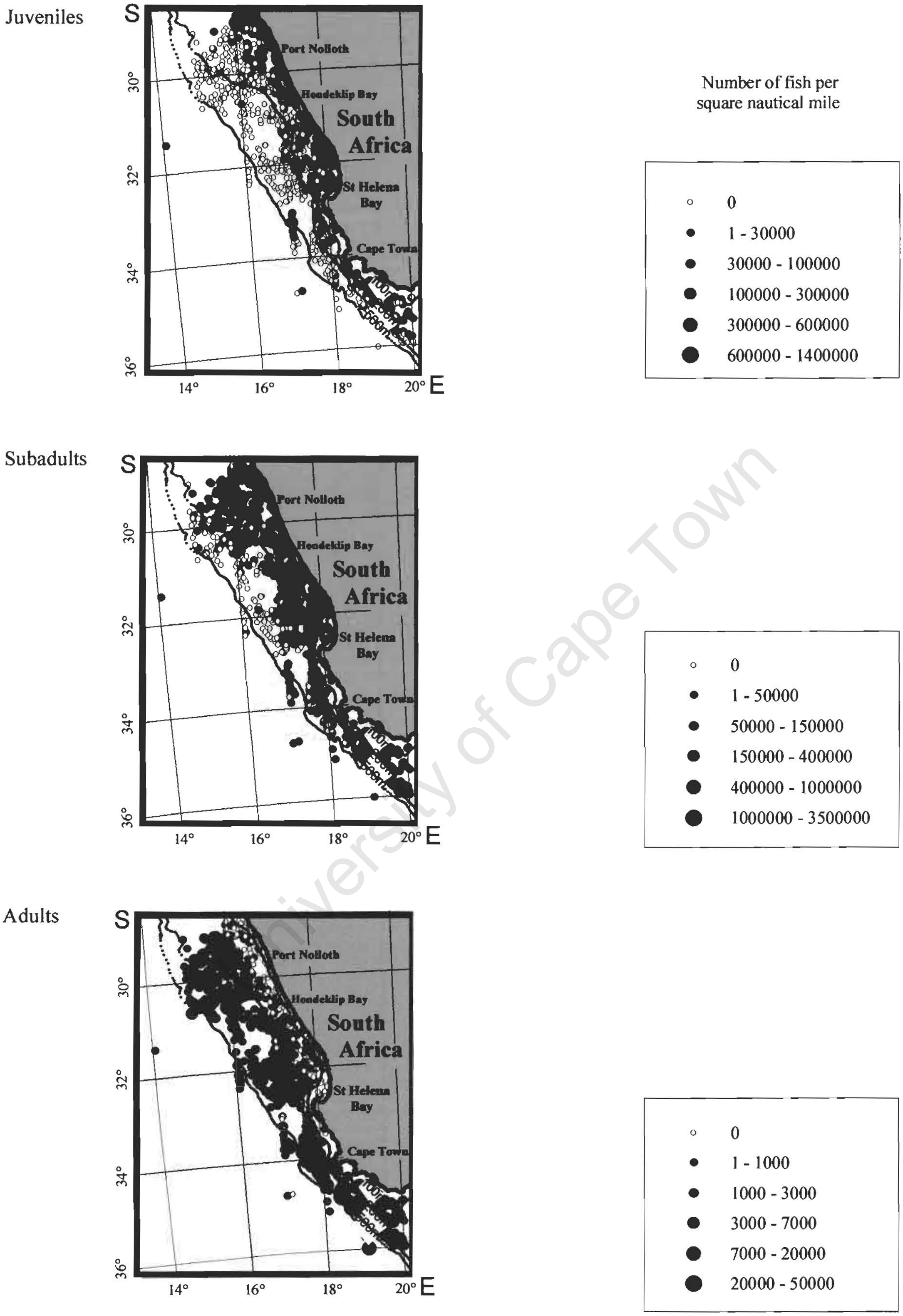


Figure 3.6: Distribution of three life history stages of *M. capensis* combining all data from 1984 to 1997 on the west coast of South Africa (MCM unpublished data)

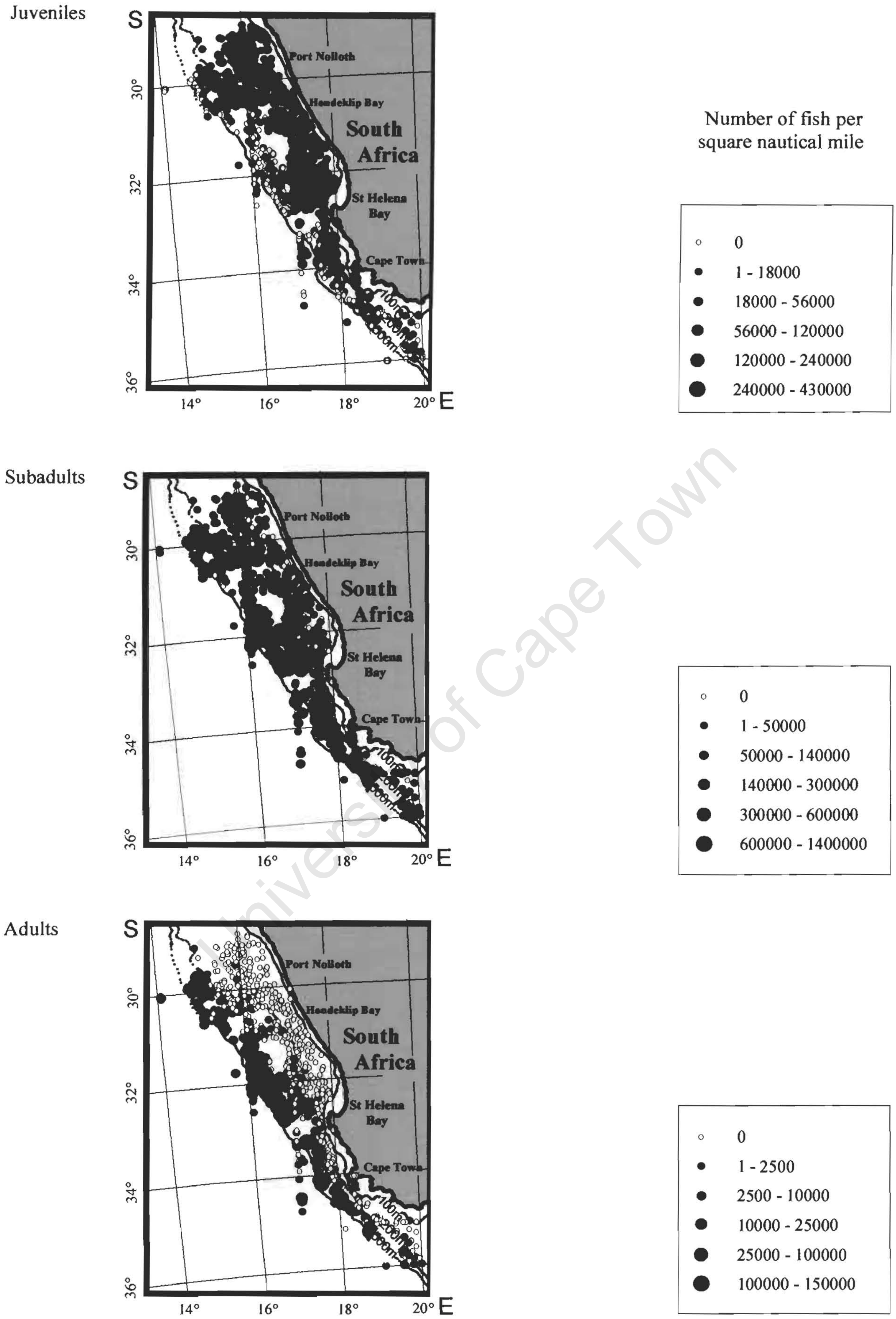
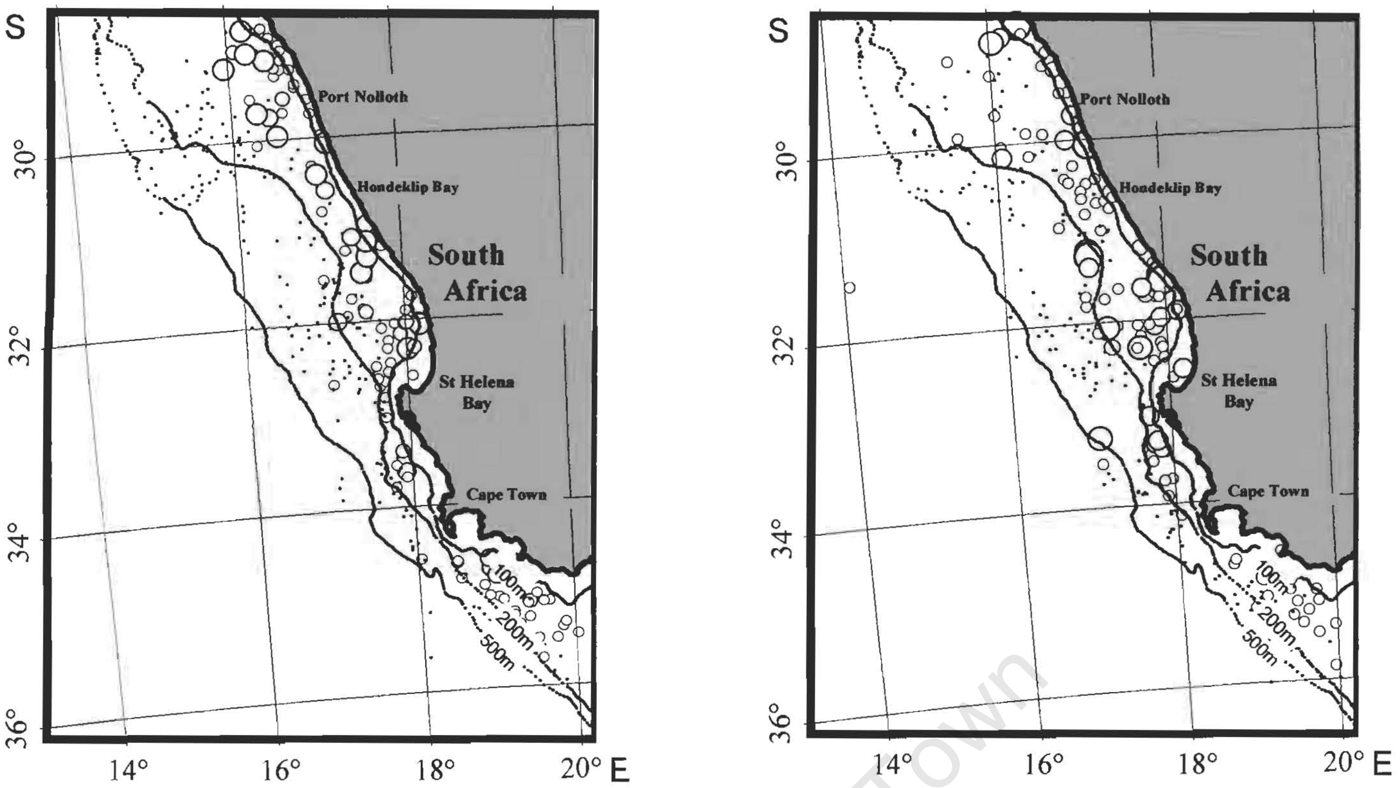


Figure 3.7: Distribution of three life history stages of *M. paradoxus* combining all data from 1984 to 1997 on the west coast of South Africa (MCM unpublished data).

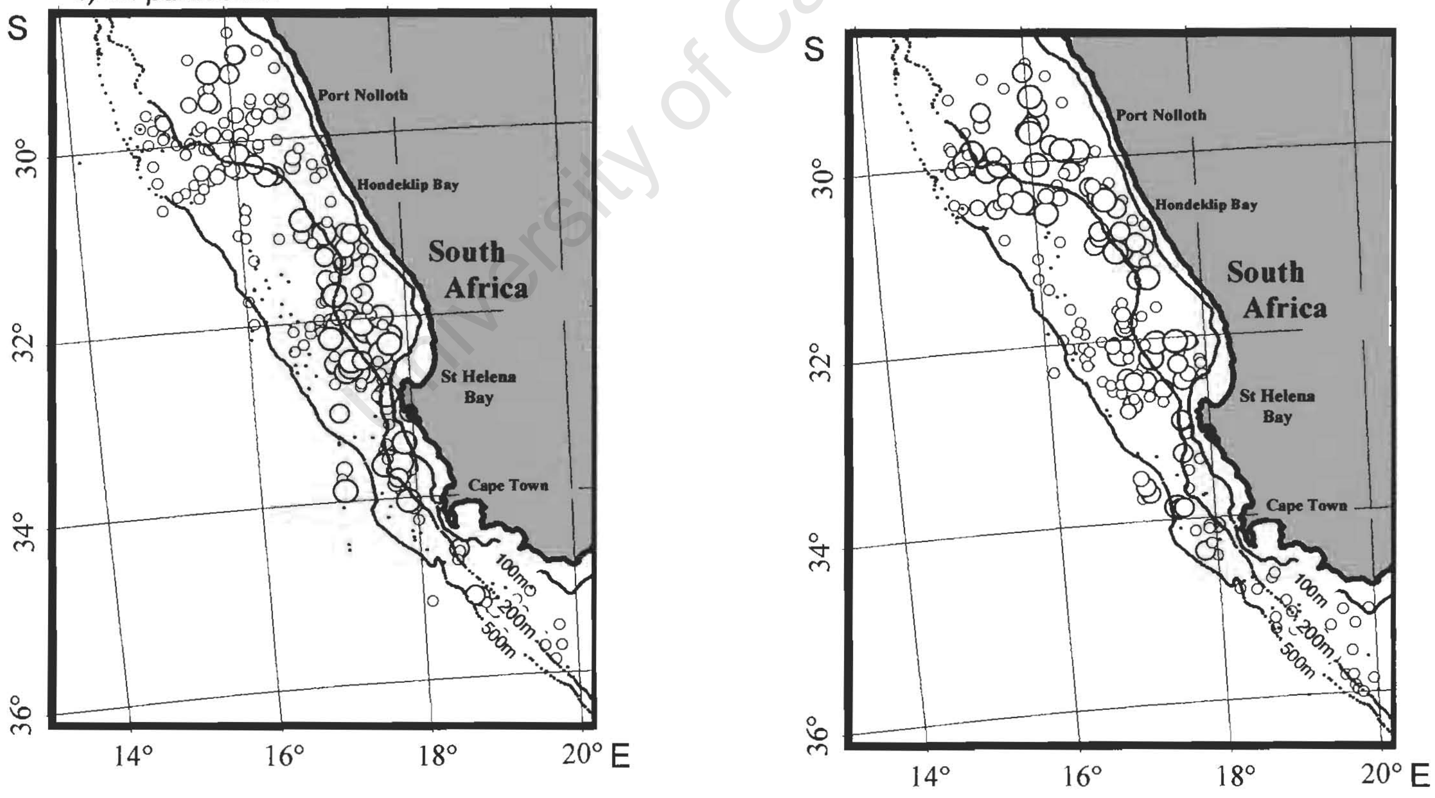
a) *M. capensis*



Summer

Winter

b) *M. paradoxus*



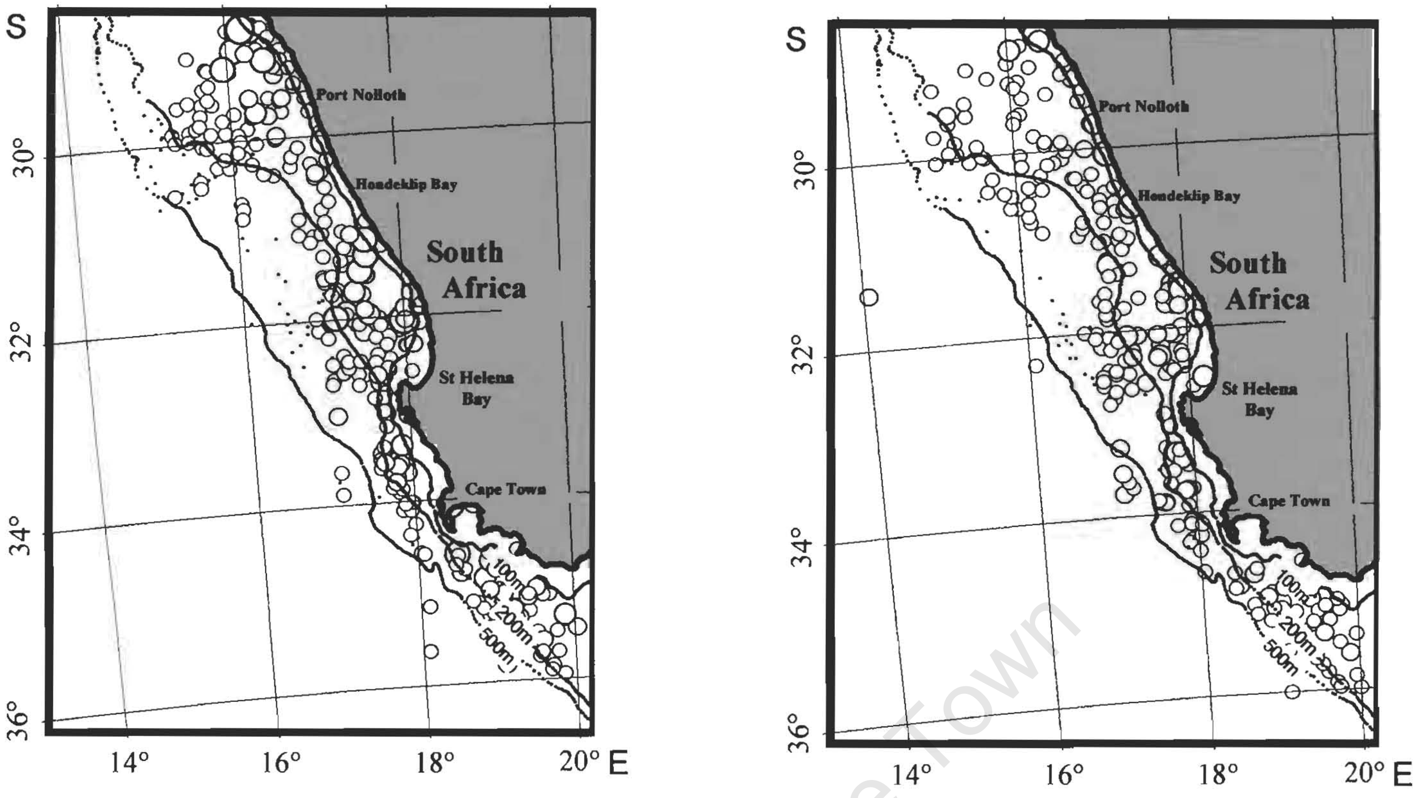
Summer

Winter

Figure 3.8: Distribution of hake juveniles in summer and winter off the west coast of South Africa (MCM unpublished data). (Fish No's per square nautical mile: · 0, ○ 1 - 10000, ○ 10000 - 20000, ○ 20000 - 50000, ○ 50000 - 500000, ○ 500000 - 1337400)

[redacted]

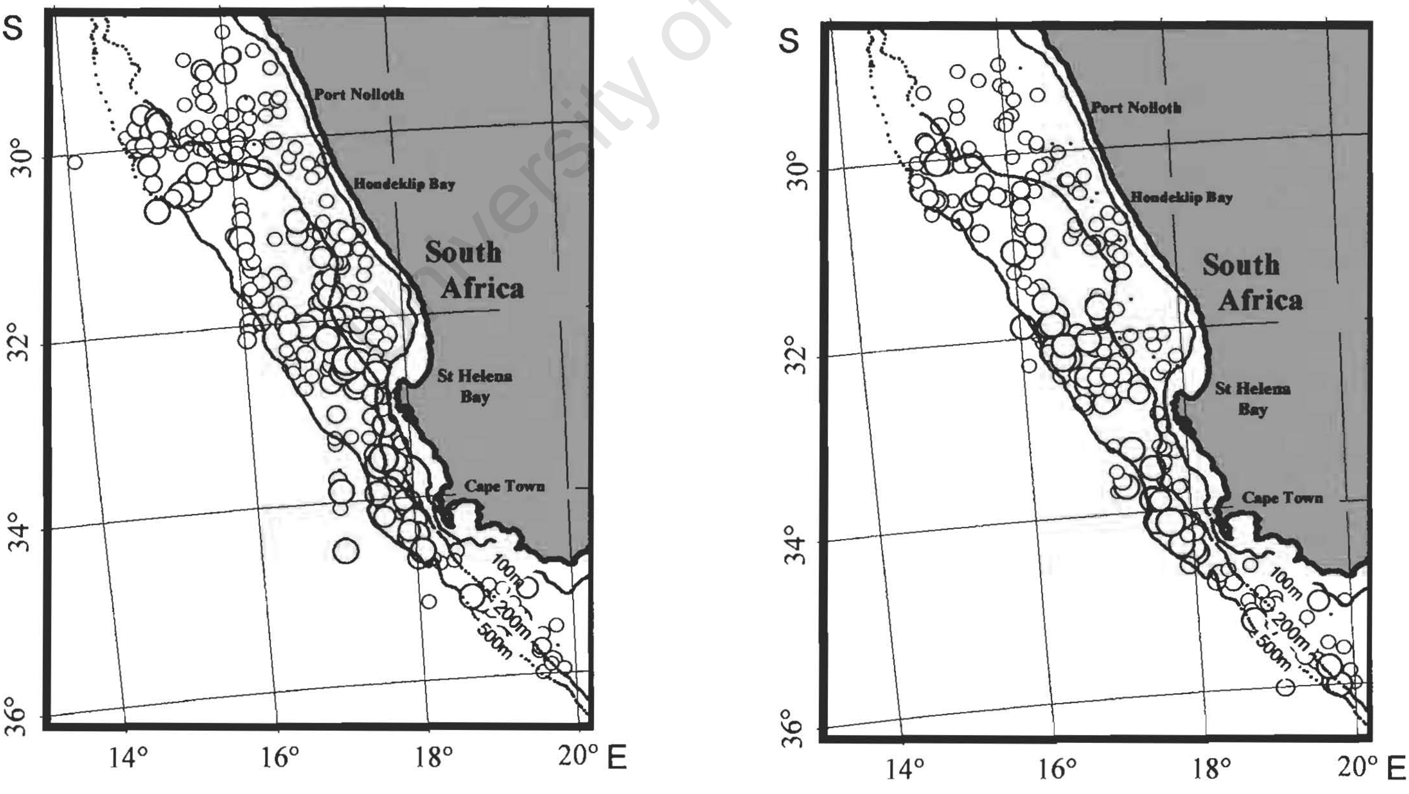
a) M. capensis



Summer

Winter

b) M. paradoxus

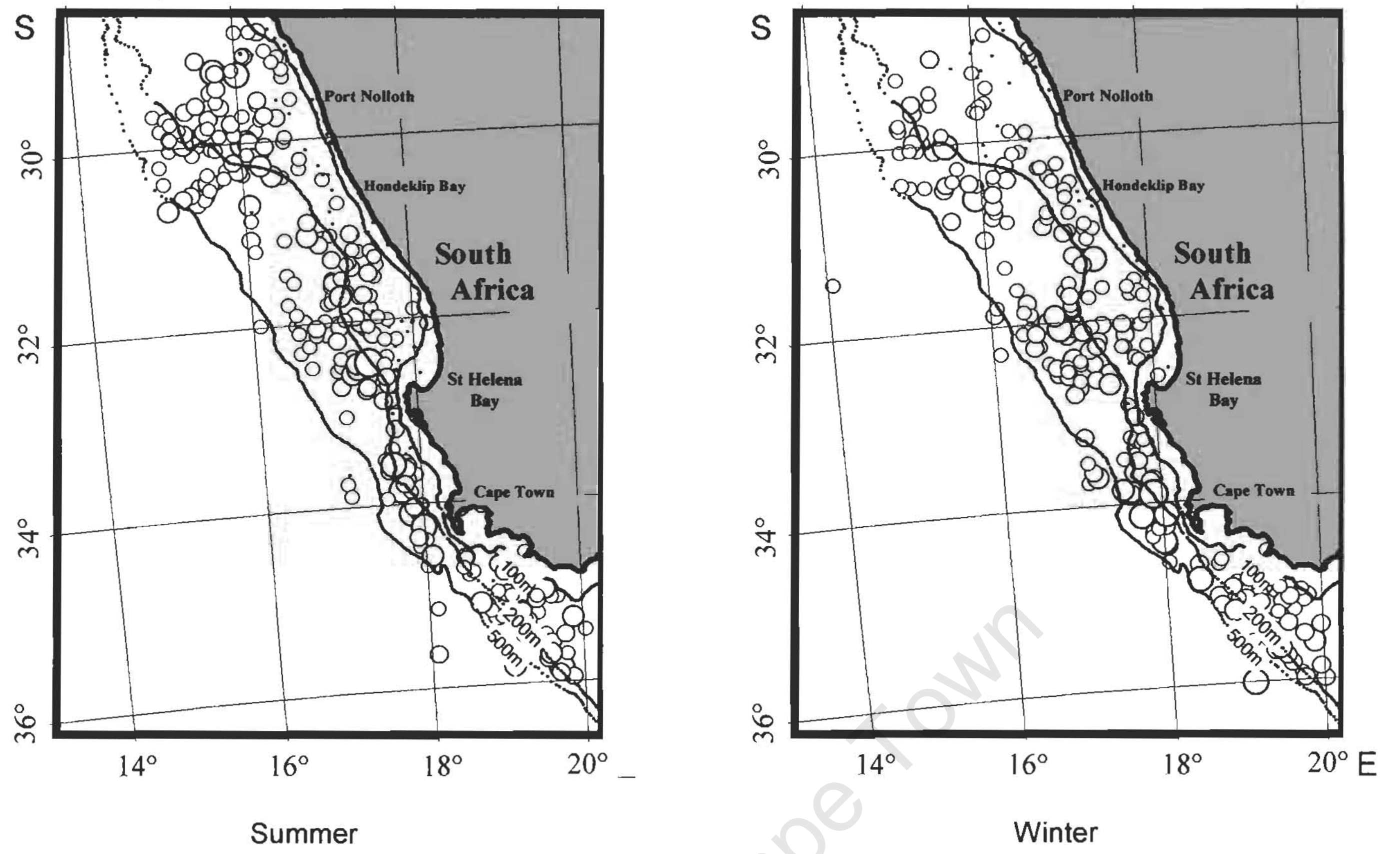


Summer

Winter

Figure 3.9: Distribution of hake subadults in summer and winter off the west coast of South Africa (MCM unpublished data). (Fish No's per square nautical mile: · 0, ○ 1 - 10000, ○ 10000 - 50000, ○ 50000 - 100000, ○ 100000 - 500000, ○ 500000 - 3443000)

a) *M. capensis*



b) *M. paradoxus*

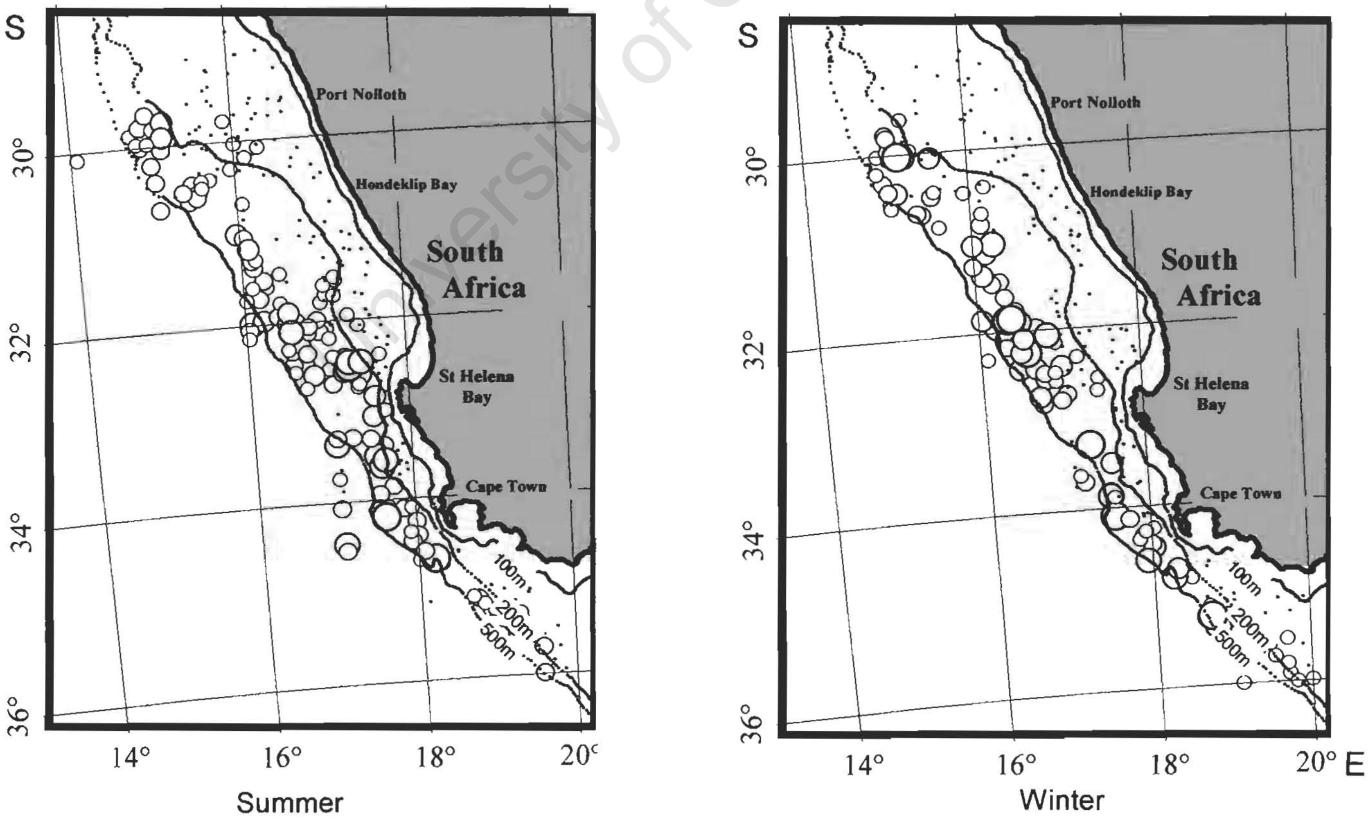


Figure 3.10: Distribution of hake adults in summer and winter off the west coast of South Africa (MCM unpublished data). (Fish No's per square nautical mile: · 0, ○ 1 - 1000, ○ 1000 - 4000, ○ 4000 - 8000, ○ 8000 - 20000, ○ 20000 - 145000)

The greatest density of *M. paradoxus* juveniles (Figure 3.8b) moves south, from a further offshore position in winter between the Orange River and Hondeklip Bay, to a further inshore position in summer between Hondeklip Bay and St Helena Bay. There is not much difference between the distribution of *M. capensis* subadults (Figure 3.9a) in summer and winter, although there is a slight narrowing in the distribution towards the coast in summer with more fish being observed further offshore than the 200m isobath in winter. A greater density of *M. paradoxus* subadults (Figure 3.9b) extends further inshore in summer than in winter with the greatest density at 32°S in winter moving further south in summer. A greater density of adult *M. capensis* (Figure 3.10a) extends further inshore around Port Nolloth in summer than in winter with the greatest density at 32°S in winter also moving further south in summer. A greater density of adult *M. paradoxus* (Figure 3.10b) extends slightly further inshore in summer with the greatest density at 32°S in winter also moving further south in summer.

Therefore the general trend for both species is that the distribution range seems to extend further inshore in summer. Moreover, adult *M. capensis* and all life history stages of *M. paradoxus* seem to move further south in summer.

The on - and offshore movement can be seen more clearly in Figures 3.2 and 3.3. The greatest *M. capensis* biomass (Figure 3.2) is between 100m and 200m in summer and between 200m and 300m in winter. The majority of *M. paradoxus* biomass (Figure 3.3) is found between 200m and 300m in summer and between 300m and 400m in winter. ANOVA was used to test whether there was a significant difference in fish biomass between summer and winter in a depth category of less than 200m and greater than 200m for *M. capensis* and between summer and winter in a depth category of less than 300m and greater than 300m for *M. paradoxus*. A significant difference occurs between all categories for both *M. capensis* (F=10.97, $p<0.001$) and *M. paradoxus* (F=16.05, $p<0.001$). A Student-Newman-Keuls test revealed that all pairs were significantly different ($p<0.05$), showing that a difference in fish density occurs above and below 200m for *M. capensis* and above and below 300m for *M. paradoxus* between summer and winter. Other than the above mentioned factors, little difference in distribution is observed for each hake species over all the survey months (Appendix A). All data in the Appendix was standardized so as to compare survey years. These maps show major changes between years but lose a large amount of the finer detail (i.e. showing migration). Large increases in density occur in *M. capensis* juveniles in St Helena Bay in February 1988 and January 1996. Large increases in density are also observed in July 1989 and January 1990 and 1995, with a higher density being observed further offshore than usual along the coast between Port Nolloth and St Helena Bay. The subadults of this species show a slight increase in abundance between Hondeklip Bay and St Helena Bay in January 1990 and 1995. *M. paradoxus* juveniles increased in density in February 1988, July 1989 (further north), January 1990 and January 1991 and a large increase in January 1996 (Appendix A).

The polynomial interpolated point estimates of bottom temperature, bottom oxygen concentration, sea surface temperature and sea surface temperature minus bottom temperature (Figures 3.11 and 3.12) provide a general description of the physical conditions in the southern Benguela. Whilst only two surveys during summer (January 1995) and winter (June 1987) have been illustrated, a description of all the surveys is presented as follows.

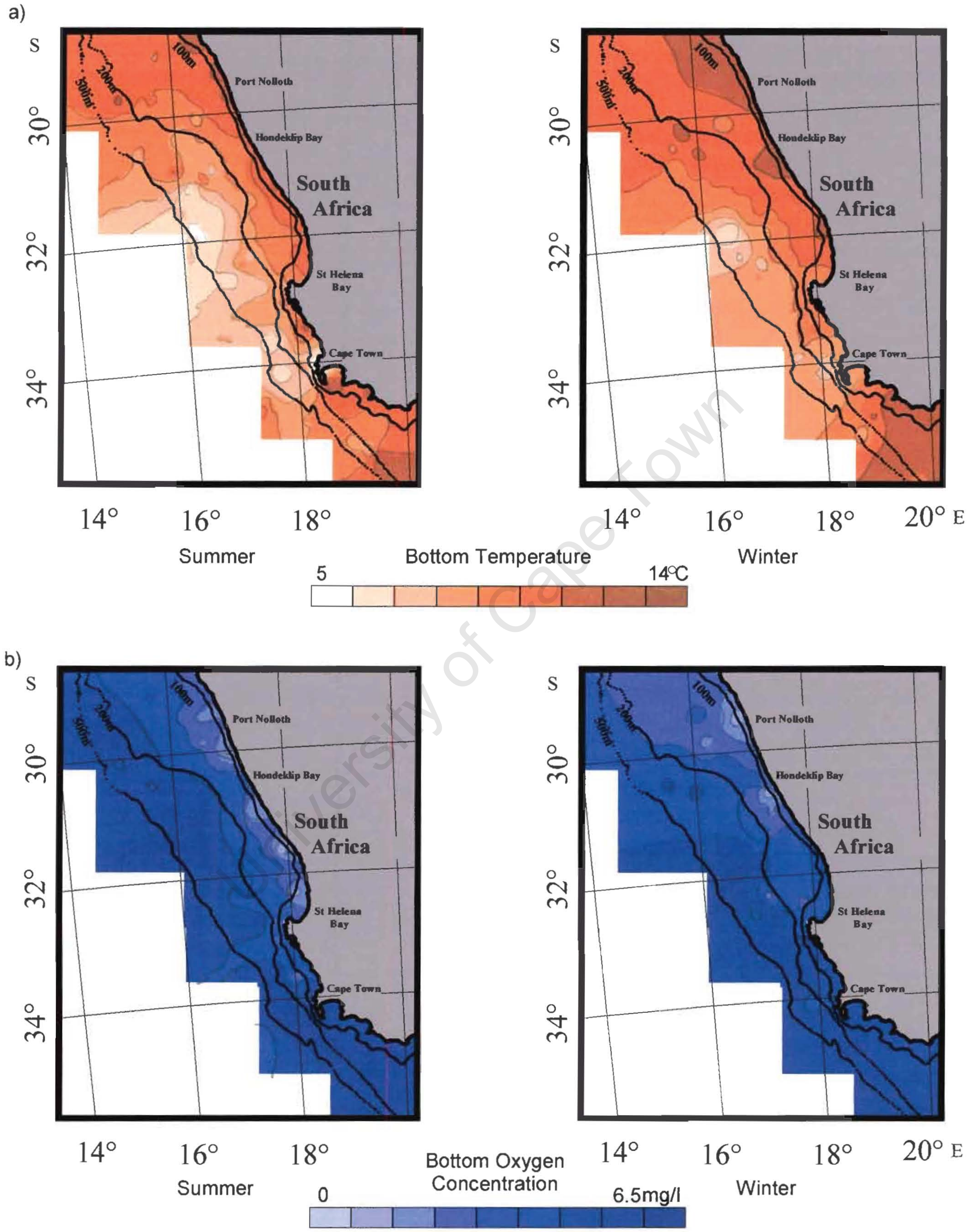


Figure 3.11: Bottom temperature (a) and bottom oxygen concentration (b) for summer (January 1995) and winter (June 1987) off the west coast of South Africa (MCM unpublished data).

Bottom temperatures (Figure 3.11a) in the southern Benguela region are generally warmer inshore and become cooler further offshore. Warmer bottom temperatures intrude along the coast in winter between Cape Agulhas and Cape Town as well as between the Orange River and Port Nolloth. Cooler bottom waters offshore, that extend between St Helena Bay and Hondeklip Bay, are found to extend further south to Cape Town in summer. This movement of water of cooler bottom temperatures may be the reason why all life history stages of *M. paradoxus* and adult *M. capensis* show a southerly seasonal movement.

Bottom Oxygen concentrations (Figure 3.11b) are lower inshore, with pockets of very low oxygen concentrations occurring along the coast. These oxygen concentrations increase from 200m to 500m depth offshore. There is little variation in bottom oxygen concentration between summer and winter. Bottom oxygen concentration is highest in the inshore region between Cape Town and St Helena Bay.

Sea surface temperatures (Figure 3.12a) are cooler at the coast than further offshore. These cooler waters extend further offshore in winter, with particularly cool sea surface temperatures in July 1990 between St Helena Bay and the Orange River (Appendix A). In summer, very warm sea surface temperatures occur between Cape Agulhas and Cape Town, as well as offshore from 200m between Hondeklip Bay and Port Nolloth. In January 1990 and 1991 the temperatures off Hondeklip Bay and Port Nolloth were cooler than usual. Very warm temperatures were found over most of the area in January 1992. The 16°C isotherm (Figure 3.12a) is found further offshore from the Orange River to St Helena Bay in winter where it starts to form closer inshore and eventually disappears south of St

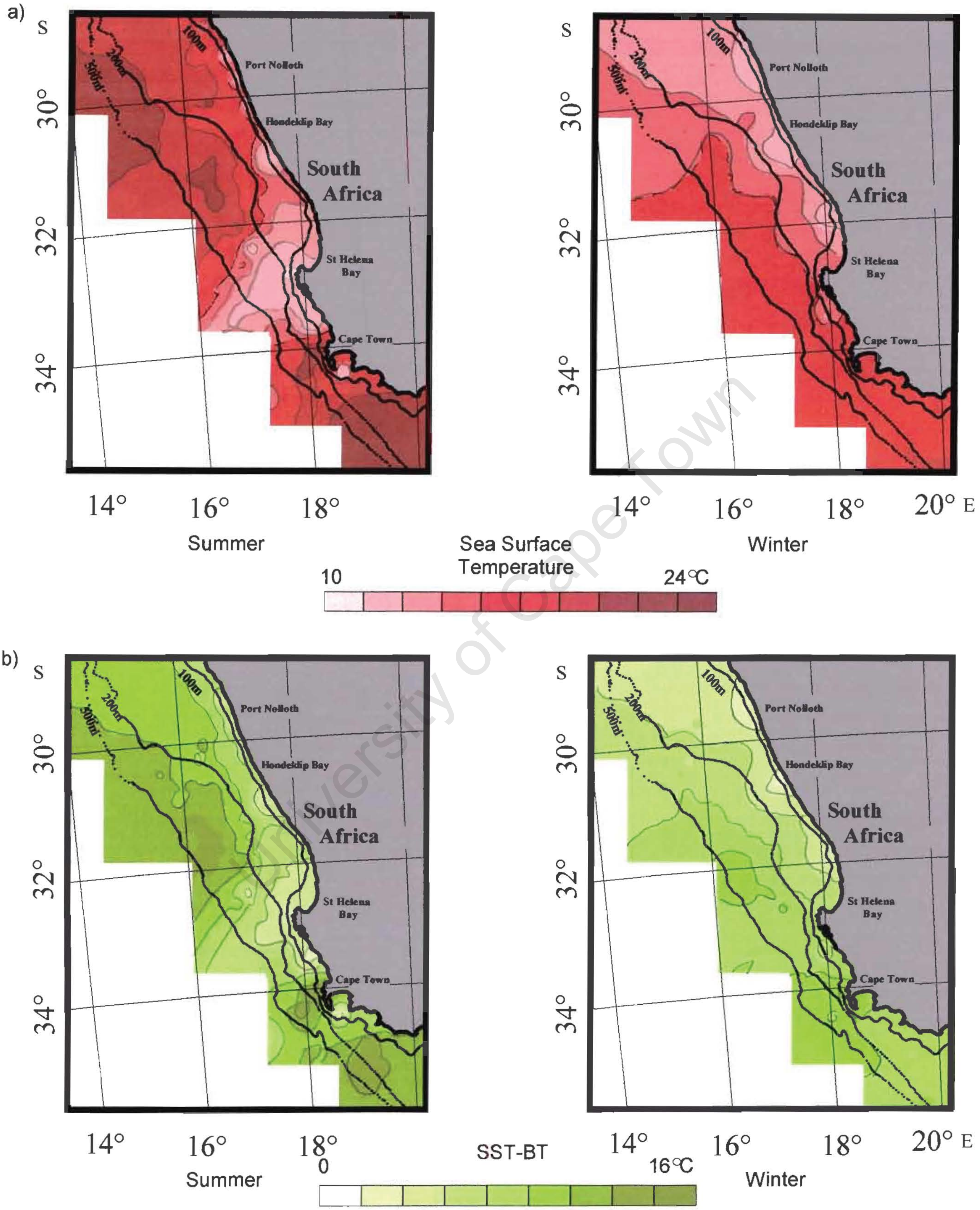


Figure 3.12: Sea surface temperature (a) and sea surface temperature minus bottom temperature (SST-BT) (b) for summer (January 1995) and winter (June 1987) off the west coast of South Africa (MCM unpublished data). The 16 C SST isotherm is represented as a dotted line.

Helena Bay. In summer the 16°C isotherm is very close inshore between the Orange River and Hondeklip Bay and is then found further offshore, south of this, between St Helena Bay and Cape Town (Figure 3.12a). In January 1990, 1994 and 1995 and July 1989 the isotherm moves further offshore between Cape Town and St Helena Bay than usual and, in February 1988 and January 1996, it is closer inshore than normal (Appendix A). Therefore, it seems that the increase in density of *M. capensis* juveniles in St Helena Bay in certain years may be due to the closer than usual inshore movement of the 16°C isotherm, whereas the general increase in density occurring for juveniles of both species and subadult *M. capensis* in July 1989 and January 1990 may be due to lower values of SST-BT extending further offshore, implying that greater mixing of the water column occurred further offshore than usual.

SST-BT (Figure 3.12b) values are lower at the coast, suggesting more mixing of waters at the coast than offshore where values are higher. Generally, in winter, the values are lower than in summer. In summer, the values are higher offshore so greater stratification of waters occurs from 250m offshore. However, in July 1989 and January 1990 and 1991, values were lower offshore between St Helena Bay and Port Nolloth than normal for both seasons and suggest an increase in mixing of the water column (Appendix A). No consistent relationships between hake density and physical variables are apparent in all survey years. This can be seen more clearly in Tables 3.3-3.8, which show the values of each environmental factor corresponding with the highest value of hake density for all survey years. It appears that each species and life history stage does not have consistent associated environmental variables and that each has a fairly wide range of preferred environmental factors. These ranges are summarized in Table 3.9.

Table 3.3: Preferred zones of environmental conditions (with SE in parenthesis) of *M. capensis* juveniles off the west coast of South Africa obtained by overlaying procedures in ArcView3.

Year and Month	Sea Surface Temperature (°C)	Bottom Temperature (°C)	SST-BT (°C)	Bottom Oxygen (mg.l^{-1})
July 1984	11.30	9.82	1.48	1.81
	(0.15)	(0.01)	(0.16)	(0.03)
January 1985	*	*	*	*
January 1986	21.15	8.97	12.18	3.33
	(0.03)	(0.04)	(0.03)	(0.04)
July 1986	13.59	11.13	2.46	2.78
	(0.11)	(0.19)	(0.30)	(0.12)
January 1987	20.83	10.02	10.81	4.48
	(0.11)	(0.16)	(0.05)	(0.01)
June 1987	13.53	9.43	4.11	2.93
	(0.12)	(0.04)	(0.15)	(0.09)
February 1988	15.70	8.92	6.79	2.25
	(0.01)	(0.01)	(0.01)	(0.01)
August 1988	12.59	9.77	2.82	1.28
	(0.09)	(0.05)	(0.14)	(0.08)
January 1989	*	*	*	*
July 1989	12.76	9.89	2.87	2.97
	(0.12)	(0.08)	(0.20)	(0.02)
January 1990	15.08	8.99	6.08	2.52
	(0.80)	(0.88)	(1.68)	(0.86)
July 1990	12.49	10.99	1.50	4.12
	(0.30)	(0.38)	(0.68)	(0.09)
January 1991	20.39	8.05	12.34	4.34
	(0.02)	(0.03)	(0.03)	(0.02)
February 1992	*	*	*	*
January 1993	13.36	9.22	4.14	1.41
	(0.06)	(0.02)	(0.08)	(0.04)
January 1994	14.34	9.92	4.42	1.84
	(0.25)	(0.05)	(0.30)	(0.06)
January 1995	16.77	9.34	7.44	1.46
	(0.04)	(0.01)	(0.04)	(0.07)
January 1996	15.31	9.59	5.72	1.68
	(0.13)	(0.10)	(0.05)	(0.07)
January 1997	11.78	9.55	2.23	1.48
	(0.23)	(0.06)	(0.28)	(0.12)

* No environmental data available
\# Survey aborted

Table 3.4: Preferred zones of environmental conditions (with SE in parenthesis) of *M. capensis* subadults off the west coast of South Africa obtained by overlaying procedures in ArcView3.

Year and Month	Sea Surface Temperature (°C)	Bottom Temperature (°C)	SST-BT (°C)	Bottom Oxygen (mg.l^{-1})
July 1984	11.28	9.94	1.34	1.28
	(0.47)	(0.29)	(0.76)	(1.19)
January 1985	*	*	*	*
January 1986	20.59	8.45	12.14	3.59
	(0.05)	(0.02)	(0.07)	(0.04)
July 1986	13.62	11.07	2.55	2.73
	(0.14)	(0.26)	(0.39)	(0.22)
January 1987	15.84	8.28	7.57	4.05
	(0.04)	(0.01)	(0.05)	(0.01)
June 1987	12.71	9.81	2.90	3.66
	(0.26)	(0.10)	(0.35)	(0.13)
February 1988	17.41	9.74	7.68	2.08
	(0.23)	(0.15)	(0.08)	(0.07)
August 1988	12.59	9.77	2.82	1.28
	(0.09)	(0.05)	(0.14)	(0.08)
January 1989	*	*	*	*
July 1989	12.76	9.89	2.87	2.97
	(0.12)	(0.08)	(0.20)	(0.02)
January 1990	14.64	9.51	5.13	2.02
	(0.05)	(0.01)	(0.06)	(0.04)
July 1990	11.48	9.53	1.95	1.82
	(0.17)	(0.06)	(0.24)	(0.12)
January 1991	19.98	9.24	10.74	3.96
	(0.01)	(0.04)	(0.05)	(0.05)
February 1992	*	*	*	*
January 1993	21.86	9.69	12.17	4.16
	(0.02)	(0.13)	(0.11)	(0.01)
January 1994	13.01	9.46	3.56	4.65
	(0.42)	(0.10)	(0.43)	(0.03)
January 1995	15.90	9.47	6.43	1.13
	(0.18)	(0.05)	(0.13)	(0.13)
January 1996	17.38	8.90	8.49	1.69
	(0.16)	(0.02)	(0.14)	(0.28)
January 1997	19.62	9.08	10.54	4.41
	(0.01)	(0.01)	(0.01)	(0.01)

* No environmental data available
# Survey aborted

Table 3.5: Preferred zones of environmental conditions (with SE in parenthesis) of *M. capensis* adults off the west coast of South Africa obtained by overlaying procedures in ArcView3.

Year and Month	Sea Surface Temperature (°C)	Bottom Temperature (°C)	SST-BT (°C)	Bottom Oxygen (mg.l^{-1})
July 1984	16.06	9.75	6.32	4.11
	(0.14)	(0.06)	(0.14)	(0.14)
January 1985	*	*	*	*
January 1986	22.83	9.49	13.34	4.17
	(0.09)	(0.01)	(0.07)	(0.01)
July 1986	16.34	8.08	8.25	4.50
	(0.01)	(0.07)	(0.06)	(0.02)
January 1987	17.48	9.56	7.92	3.34
	(0.03)	(0.02)	(0.01)	(0.02)
June 1987	15.85	9.43	6.43	2.46
	(0.15)	(0.02)	(0.13)	(0.05)
February 1988	15.04	8.76	6.28	4.21
	(0.03)	(0.04)	(0.06)	(0.01)
August 1988	15.76	7.29	8.46	3.82
	(0.02)	(0.04)	(0.06)	(0.01)
January 1989	*	*	*	*
July 1989	16.20	6.89	9.31	4.51
	(0.04)	(0.16)	(0.14)	(0.06)
January 1990	13.57	7.89	5.68	3.97
	(0.02)	(0.01)	(0.02)	(0.01)
July 1990	14.29	8.43	5.86	4.23
	(0.31)	(0.13)	(0.38)	(0.01)
January 1991	18.16	8.21	9.95	4.21
	(0.78)	(1.50)	(2.28)	(0.33)
February 1992	*	*	*	*
January 1993	18.91	7.89	11.02	3.84
	(0.01)	(0.01)	(0.01)	(0.01)
January 1994	15.39	7.68	7.71	4.13
	(0.04)	(0.04)	(0.08)	(0.12)
January 1995	20.96	8.35	12.61	4.19
	(0.19)	(0.12)	(0.31)	(0.01)
January 1996	20.24	9.04	11.20	3.47
	(0.03)	(0.04)	(0.02)	(0.04)
January 1997	21.59	9.48	12.11	3.98
	(0.01)	(0.01)	(0.01)	(0.01)

* No environmental data available
\# Survey aborted

Table 3.6: Preferred zones of environmental conditions (with SE in parenthesis) of *M. paradoxus* juveniles off the west coast of South Africa obtained by overlaying procedures in ArcView3.

Year and Month	Sea Surface Temperature (°C)	Bottom Temperature (°C)	SST-BT (°C)	Bottom Oxygen (mg.l^{-1})
July 1984	15.66	8.16	7.49	3.76
	(0.01)	(0.03)	(0.02)	(0.01)
January 1985	*	*	*	*
January 1986	16.98	8.35	8.63	2.91
	(0.19)	(0.04)	(0.23)	(0.03)
July 1986	16.44	8.82	7.62	4.52
	(0.01)	(0.02)	(0.01)	(0.01)
January 1987	15.52	8.34	7.18	3.29
	(0.20)	(0.06)	(0.25)	(0.08)
June 1987	15.32	9.69	5.64	2.96
	(0.82)	(0.38)	(1.19)	(0.68)
February 1988	14.48	8.47	6.01	2.85
	(0.36)	(0.02)	(0.38)	(0.03)
August 1988	15.30	8.51	6.80	3.07
	(0.09)	(0.03)	(0.12)	(0.05)
January 1989	#	#	#	#
July 1989	15.88	8.85	7.04	3.70
	(0.36)	(0.39)	(0.17)	(0.89)
January 1990	16.76	8.12	8.64	3.33
	(0.13)	(0.11)	(0.23)	(0.21)
July 1990	13.08	8.99	4.09	3.31
	(0.07)	(0.04)	(0.07)	(0.15)
January 1991	17.81	8.47	9.35	4.33
	(0.09)	(0.02)	(0.11)	(0.04)
February 1992	17.42	7.98	9.44	3.42
	(0.44)	(0.45)	(0.77)	(0.92)
January 1993	16.53	8.37	8.16	2.47
	(0.12)	(0.08)	(0.20)	(0.19)
January 1994	17.79	8.54	9.25	3.42
	(0.10)	(0.03)	(0.13)	(0.02)
January 1995	16.83	9.14	7.70	2.72
	(5.10)	(0.87)	(4.29)	(0.33)
January 1996	19.64	8.92	10.72	3.04
	(4.64)	(0.13)	(4.77)	(1.14)
January 1997	15.54	8.72	6.82	3.31
	(1.26)	(0.33)	(1.59)	(0.77)

* No environmental data available
\# Survey aborted

Table 3.7: Preferred zones of environmental conditions (with SE in parenthesis) of *M. paradoxus* subadults off the west coast of South Africa obtained by overlaying procedures in ArcView3.

Year and Month	Bottom Temperature (°C)	SST-BT (°C)	Sea Surface Temperature (°C)	Bottom Oxygen (mg.l^{-1})
July 1984	8.30	7.85	16.14	3.99
	(0.31)	(0.31)	(0.03)	(0.11)
January 1985	*	*	*	*
January 1986	8.59	11.29	19.88	2.95
	(0.85)	(1.14)	(0.92)	(0.79)
July 1986	8.82	7.62	16.44	4.52
	(0.02)	(0.01)	(0.01)	(0.01)
January 1987	8.45	10.13	18.58	3.54
	(0.07)	(0.16)	(0.21)	(0.05)
June 1987	7.97	8.94	16.91	3.88
	(0.52)	(0.18)	(0.38)	(0.39)
February 1988	8.71	10.41	19.12	3.58
	(0.01)	(0.01)	(0.01)	(0.01)
August 1988	7.29	8.46	15.76	3.82
	(0.04)	(0.06)	(0.02)	(0.02)
January 1989	*	*	*	*
July 1989	6.91	9.30	16.21	4.50
	(0.21)	(0.17)	(0.05)	(0.01)
January 1990	7.78	8.31	16.09	3.75
	(0.06)	(0.09)	(0.06)	(0.04)
July 1990	8.77	6.07	14.83	3.92
	(0.02)	(0.08)	(0.08)	(0.22)
January 1991	7.55	10.17	17.72	3.94
	(0.07)	(0.05)	(0.02)	(0.01)
February 1992	7.82	14.02	21.83	4.13
	(0.02)	(0.29)	(0.31)	(0.07)
January 1993	7.68	10.17	17.85	3.81
	(0.02)	(0.11)	(0.09)	(0.01)
January 1994	7.40	13.21	20.61	4.79
	(0.26)	(0.74)	(0.48)	(0.04)
January 1995	8.33	12.66	20.99	4.20
	(0.07)	(0.16)	(0.10)	(0.01)
January 1996	8.73	11.45	20.17	3.40
	(0.41)	(4.27)	(4.67)	(0.47)
January 1997	6.43	14.61	21.04	4.32
	(0.11)	(0.20)	(0.10)	(0.02)

* No environmental data available
\# Survey aborted

Table 3.8: Preferred zones of environmental conditions (with SE in parenthesis) of *M. paradoxus* adults off the west coast of South Africa obtained by overlaying procedures in ArcView3.

Year and Month	Bottom Temperature (°C)	SST-BT (°C)	Sea Surface Temperature (°C)	Bottom Oxygen ($mg.l^{-1}$)
July 1984	7.07	8.96	16.03	4.49
	(0.18)	(0.31)	(0.14)	(0.11)
January 1985	*	*	*	*
January 1986	8.37	11.02	19.40	3.39
	(0.06)	(0.24)	(0.18)	(0.05)
July 1986	6.65	9.37	16.02	4.28
	(0.01)	(0.01)	(0.01)	(0.01)
January 1987	8.45	10.13	18.58	3.54
	(0.07)	(0.16)	(0.21)	(0.05)
June 1987	7.75	9.12	16.87	4.04
	(0.67)	(0.47)	(0.24)	(0.53)
February 1988	8.23	12.79	21.02	4.02
	(0.10)	(0.49)	(0.50)	(0.06)
August 1988	8.68	6.41	15.09	3.91
	(0.08)	(0.13)	(0.06)	(0.06)
January 1989	*	*	*	*
July 1989	9.48	6.68	16.16	3.79
	(0.04)	(0.08)	(0.04)	(0.01)
January 1990	7.84	6.99	14.83	3.86
	(0.11)	(2.66)	(2.56)	(0.24)
July 1990	6.12	9.18	15.30	4.31
	(0.21)	(0.26)	(0.05)	(0.02)
January 1991	7.72	12.64	20.35	4.41
	(0.01)	(0.01)	(0.01)	(0.01)
February 1992	5.76	14.84	20.6	4.75
	(0.01)	(0.01)	(0.01)	(0.01)
January 1993	7.98	14.06	22.04	4.35
	(0.22)	(0.40)	(0.18)	(0.06)
January 1994	6.89	11.43	18.32	4.22
	(0.26)	(0.35)	(0.10)	(0.05)
January 1995	8.77	9.36	18.14	4.08
	(0.22)	(0.99)	(0.79)	(0.06)
January 1996	6.87	10.17	17.04	4.64
	(0.09)	(0.11)	(0.20)	(0.07)
January 1997	7.38	10.56	17.94	4.62
	(0.04)	(0.19)	(0.18)	(0.13)

* No environmental data available
\# Survey aborted

Table 3.9: Preferred environmental ranges at which greatest hake abundance was observed off the west coast of South Africa obtained by GIS overlaying techniques described in the text.

Species and Life history stage	Sea Surface Temperature (°C)	Bottom Temperature (°C)	SST-BT (°C)	Bottom Oxygen concentration (mg.l^{-1})
M. capensis				
Adults	13.57-22.83	6.89-9.75	5.68-13.34	2.46-4.51
Subadults	11.28-21.86	8.28-11.07	1.34-12.14	1.13-4.65
Juveniles	11.30-21.15	8.05-11.13	1.48-12.34	1.28-4.48
M. paradoxus				
Adults	14.83-22.04	5.76-9.48	6.41-14.84	3.39-4.75
Subadults	14.83-21.83	6.43-8.82	6.07-14.61	2.95-4.79
juveniles	13.08-19.64	7.98-9.69	4.09-10.72	2.47-4.52

ANOVA was used to test whether there is a significant difference between the preferred environmental conditions of the three life history stages for both hake species. Significant differences occur between the three life history stages of *M. capensis* and bottom temperature (F=9.72, $p<0.05$), SST-BT (F=4.65, $p<0.05$) and bottom oxygen concentration (F=8.89, $p<0.05$). No significant relationship occurred between the three life history stages for sea surface temperature (F=2.42, $p>0.05$). Significant differences occur between the three life history stages of *M. paradoxus* and sea surface temperature (F=4.56, $p<0.05$), bottom temperature (F=7.4, $p<0.05$), SST-BT (F=7.94, $p<0.05$) and bottom oxygen concentration (F=15.31, $p<0.05$). A Student-Newman-Keuls test revealed that for all environmental variables *M. paradoxus* subadults and adults preferred the same ranges while both differed from those ranges preferred by juveniles (Table 3.10). In contrast, *M. capensis* juveniles and subadults preferred the same ranges for all environmental variables while both differed from those ranges preferred by adults (Table 3.10).

Table 3.10: Results of the Student-Newman-Keuls test (qstat) to show where the significant difference in preferred environmental range occurs between the three life history stages of both hake species (Combinations: 1=juveniles, 2=subadults and 3=adults).

Environmental variables	*M. capensis*			*M. paradoxus*		
Combinations	1&2	1&3	2&3	1&2	1&3	2&3
Sea surface temperature	2.99	0.77	2.22	4.02	3.24	0.78
	ns	ns	ns	s	s	ns
Bottom temperature	0.58	5.67	5.09	3.55	5.35	1.8
	ns	s	s	s	s	ns
SST-BT	0.85	4.09	3.24	4.93	4.83	0.11
	ns	s	s	s	s	ns
Bottom oxygen concentration	1.21	5.66	4.45	5.6	7.53	1.93
	ns	s	s	s	s	ns

ns=not significant, s=significant

3.3.3. Hake abundance in relation to windrun

Monthly N/S and E/W wind-runs are given in Figure 3.13. Winds in the summer months were all upwelling-favourable (equatorward), whereas in winter they were mostly poleward winds, with the exception of July 1989, which was southerly. Easterly winds dominate in summer while westerly winds are more prevalent in winter. Both the south-easterly and north-westerly winds generally increase in magnitude over the survey years. There is a reduction in the NW wind between January 1988 and January 1991. As the magnitude of the SE and NW increases, so does the biomass of *M. paradoxus*. A relationship is observed between *M. paradoxus* biomass and the N/S windrun ($r=0.42$, $p<0.05$) and the E/W windrun ($r=0.43$, $p<0.05$) but not for *M. capensis*. These relationships should be quantified in further analysis. Fishery industry members argue that persistent winds adversely affect catch rates and anecdotal evidence from trawler captains is that hake are seen on their echosounders to migrate off the bottom during the onset of strong south easterly winds at Cape Point. Once the wind drops again, size and quantity of fish caught improve. These effects are not apparent in the data because Marine and Coastal Management research ships do not stay in one area long enough to detect such behaviour during routine surveys.

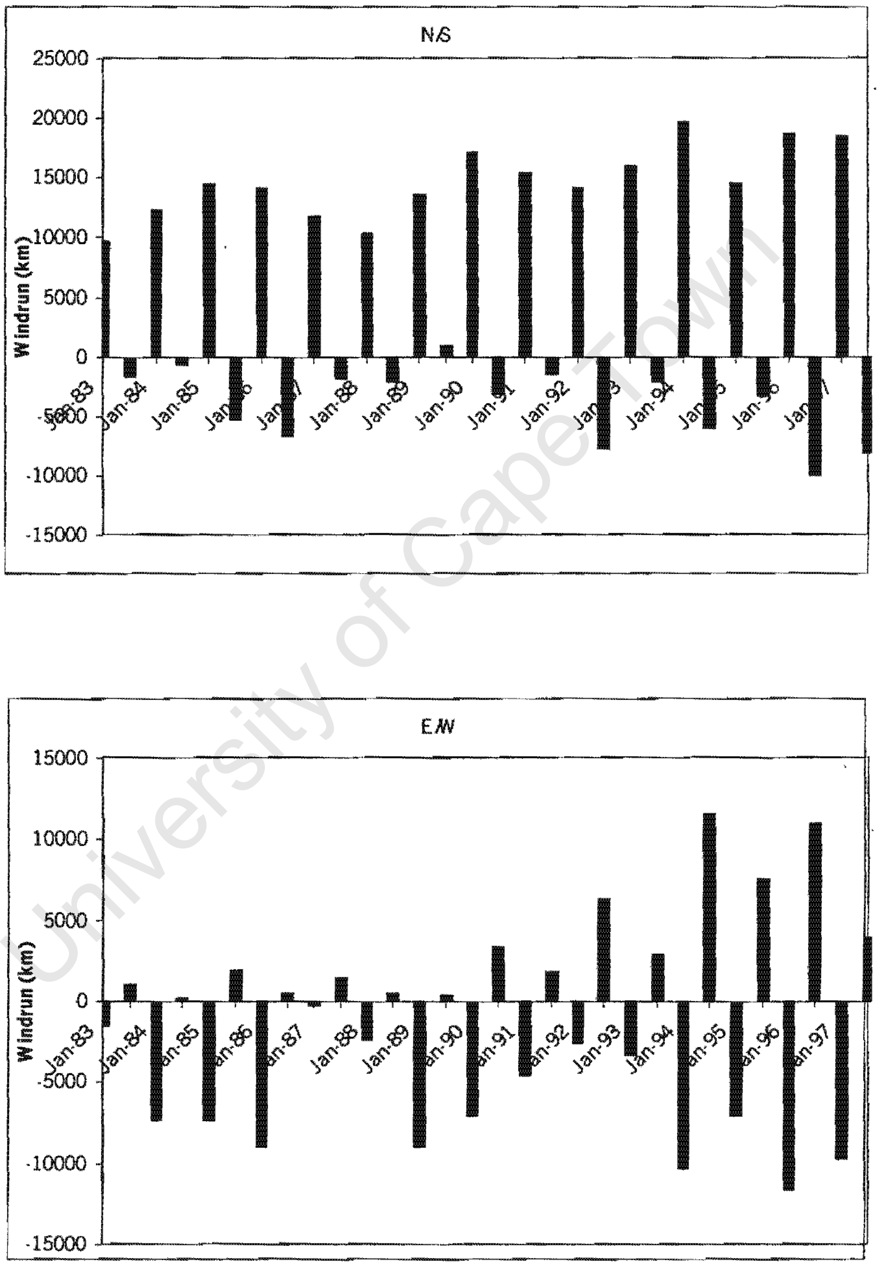


Figure 3.13: North/South and East/West windrun for each survey month between 1984 and 1997 obtained from Cape Point lighthouse (MCM unpublished data).

3.3.4. Hake abundance in relation to the Southern Oscillation Index

The Southern Oscillation Index (SOI) is presented in Figure 3.14 along with hake biomass over all the survey months. High SOI (large pressure difference) is associated with stronger than normal trade winds and La Niña conditions and low SOI (smaller pressure difference) is associated with weaker than normal trade winds and El Niño conditions. Thus, El Niños occurred during 1986-1987, 1991-1992, 1993 and 1994 and that a La Niña occurred during 1985-1986, 1988-1989 and the 1995-1996 (weak La Niña). No linear relationship was observed between the SOI and *M. capensis* (r=0.13, p>0.05) and *M. paradoxus* (r=0.32, p>0.05) biomass.

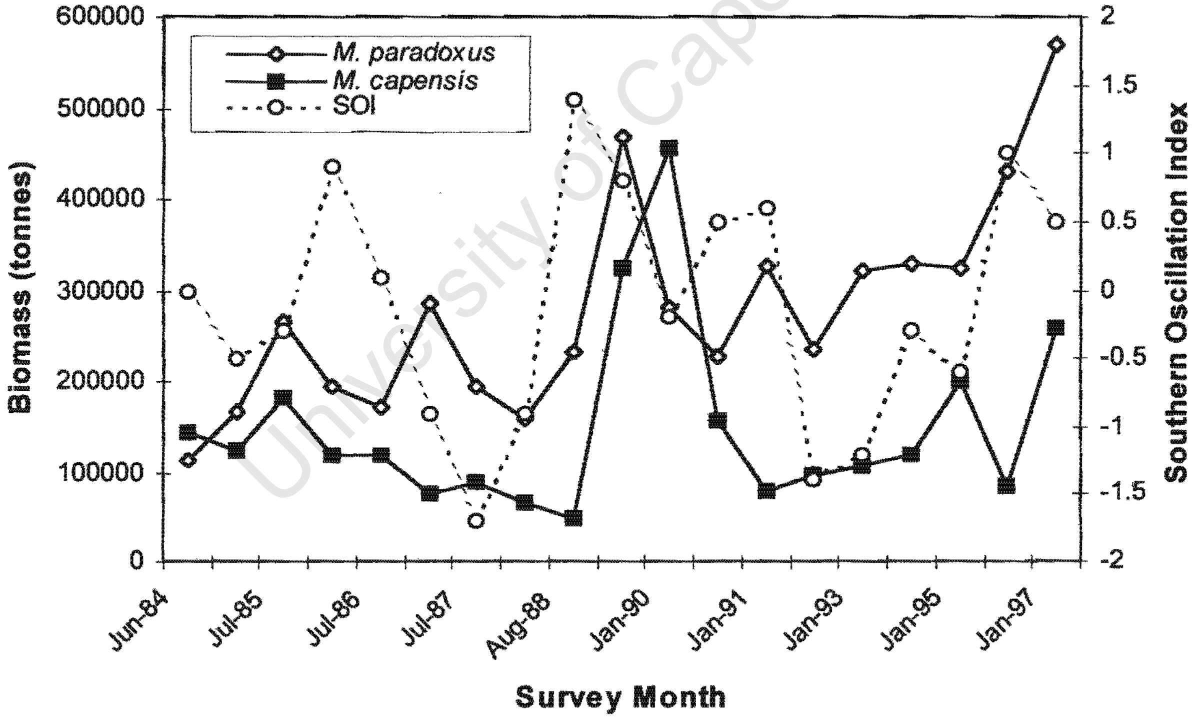


Figure 3.14: Total biomass of *M. capensis* and *M. paradoxus* off the west coast of South Africa in relation to the Southern Oscillation Index for each survey month between 1984 and 1997(MCM unpublished data and NOAA data, respectively).

However, *M. paradoxus* biomass seems to follow a similar pattern to the SOI index with increases in biomass occurring approximately one year after each of the documented La Niña. *M. capensis* shows a large increase in biomass a year and a half after the SOI index is at its highest in the time series studied.

3.4. Discussion

3.4.1. General patterns of hake biomass in relation to average environmental parameters

The apparent downward trend in biomass of *M. capensis* has been ascribed at least partially, to poor recruitment since the early 1980s, which was thought to be possibly as a result of environmental perturbations (Payne *et al.* 1989). However, it may have also been as a result of longlining, which started in 1985 with *M. capensis* being the most common catch (in particular, large mature fish) when species other than kingklip are targeted (Japp 1989). In contrast, increase in biomass of *M. paradoxus* is almost entirely based on recruitment (Payne *et al.* 1989). *M. capensis* biomass seems to be slowly recovering, with the large increase in biomass in both species between 1989 and 1990 still unaccounted for, but with possible explanations below.

Changes in average physical data for each survey do not seem to have an effect on the hake biomass. Anomalies occurring in physical data in January 1992 are because the depths sampled on this survey were on average 50m deeper than normal. Therefore, one would expect that sea surface temperature would be higher, bottom temperature would be lower, bottom oxygen concentration would be higher and SST-BT would be higher than normal due to the correlation of these physical factors with depth (see Chapter 4). However, these anomalies did not appear to influence the hake in any way.

Results of bottom trawl surveys show that the distribution of the shallow water Cape hake *M. capensis* is continuous from Cape Town to Mossel Bay (Punt *et al.* 1995). It has been hypothesized that favourable environmental conditions favoured a shift of the resource from the south coast to the west coast (Japp pers. comm.). The stock seemed reduced in size on the south coast in early 1989 and only in mid 1990 did the stock there appear to increase only after situation appeared to normalize on the west coast (Japp pers. comm.). Sustained cooling of shelf waters occurred in the southern Benguela from autumn 1989 (Hampton and Matthews 1997) and this may have caused favourable conditions which may, in turn, have encouraged the migration of hake from the south coast. In addition, over this period, a change in SST-BT occurred with more mixing of the water column. So, either this or the fact that hake appear to prefer cooler periods may have encouraged *M. capensis* to move from the south coast to the west coast. This may also explain why the biomass of *M. capensis* showed a large increase in comparison to the rest of the trawl biomass early in 1990.

3.4.2. Hake distribution in relation to environmental parameters using a GIS

Hake undergo a marked change in depth distribution as they grow older, with smaller hake occurring in shallower water than larger hake (see possible explanation in Chapter 4). Both species of hake also tend to move further inshore during summer and occupy a narrower distribution range. In addition, all life history stages of *M. paradoxus* and adult *M. capensis* extend further south in summer. Stauffer (1985) found that *M. productus* make seasonal offshore migrations as well as migrating to higher latitudes and inshore in summer and towards the equator and offshore in winter. These inshore and offshore movements are also seen in the Cape hakes with *M. paradoxus* migrating in a southerly direction in summer; Pitcher and Alheit (1995) believed that this occurred because the hake were following the pelagic production cycle.

If the migratory pattern of hake is associated with environmental factors, differences in their distribution over the survey years may reflect fluctuations in oceanic conditions. A possible pattern was observed between cooler bottom temperatures and distribution of all life history stages of *M. paradoxus* and adult *M. capensis*. However, there is no consistency between highest hake density and a particular range of physical factors. A relationship may exist between the inshore movement of hake in summer and the positioning of the sea surface 16°C isotherm. In summer, a combination of offshore warming together with strong inshore upwelling, the penetration of Agulhas Bank water and a steep shelf break close to the coast, cause the formation of a strong thermal front and an associated equatorward, shelf edge jet current (Bang and Andrews 1974, Hulley and Lutjeharms 1989). This thermal front, which is found at the boundary between cool, productive coastal water and the warmer oceanic regime, usually occurs with the 16°C sea surface temperature isotherm which is almost invariably present off the coast. The 16°C isotherm and, thus, the front moves offshore in winter (indicative of cool conditions) and inshore in summer which has been documented by Agenbag (1992) and it appears that the hakes mirror this movement. This is evident when considering the inshore and southerly movement of all life history stages of *M. paradoxus* and adult *M. capensis* in summer and the positioning of the 16°C sea surface temperature isotherm. It moves very close inshore in summer between the Orange River and Hondeklip Bay and extends slightly further offshore in the southern regions around St Helena Bay and Cape Town where it seems that the hakes migrate towards.

The frontal interface, occurring between waters of different densities (e.g. between cooler upwelled waters and warmer oceanic surface waters), is one of the most significant areas of food concentration in upwelling regions like the Benguela. This occurs because a zone of convergence, which sustains the distinct character of the front, is formed by buoyancy driven flows directed from each water type towards the interface (Bakun 1998). These frontal zones have been found to influence fish distribution and may be as a consequence of water types or currents (Laevastu 1993); this is discussed in Section 3.4.3.

In addition, small weak organisms, which would normally be unable to resist being passively swept along in the horizontal ocean flow, accumulate in the energetic, slowly sinking waters of the convergent frontal zone. This then causes a high concentration of food particles in this area, where small organisms such as fish larvae benefit dramatically (Bakun 1998). As a result, it is well known that plankton and nekton aggregate at oceanic fronts (Uda 1952). Hence, the existence of a frontal system close to the shelf break in the southern Benguela region is associated with increased biomass and zooplankton productivity. Magnuson *et al.* (1981) tested the hypothesis that frontal aggregations at the Gulf Stream front resulted from the response of organisms to the front itself rather than to a geographically fixed feature of the region. They found that more species and individuals of fish were observed when the front was present. In addition it seems that about 60% of the fish species moved back and forth with the front.

Shelton (1986) has stated that the most noticeable feature of the Benguela system is the contraction of the area occupied by cool waters in summer and the expansion of the zone in winter. In the southern Benguela region, the seasonal difference in the distribution of

Lampanyctodes hectoris (lantern fish) follows an inshore movement in summer and it appears to be geared to the effect of frontal dynamics on the availability of food in summer (after periods of prolonged upwelling). Hulley and Lutjeharms (1989) postulated that this inshore movement by the mesopelagic fish during summer was related to the availability of suitable quantities of food at the front. Owen (1981) has suggested that periodic relaxation or breaching of the front may be biologically important, since they allow for the release of nutrients and plankton into offshore waters, resulting in the formation of a wider productive zone than in summer. During winter, the offshore distribution of mesopelagic fish expands, but this does not appear to be correlated with the position of the front and wider productive zone. However, this offshore migration is considered to be a spawning migration (Hulley and Lutjeharms 1989).

As *M. paradoxus* on the west coast progress from juvenile to adult their prey choices change. They progress from being typically zooplanktivorous, preferentially preying on large crustaceans (i.e. euphausiids and amphipods), to mesopelagic fish (light and lantern fish in the case of *M. paradoxus*) (Hulley and Lutjeharms 1989) and pelagic fish (anchovy in the case of *M. capensis*) (Pillar and Barange 1993), to preying on progressively larger fish prey and an increase in cannibalism. As both *M. paradoxus* and *M. capensis* have shown signs of inshore migration in summer and offshore migration in winter, it is thought that they may also be following the front and hence may be moving to an area of high concentration of their main prey items. It has been previously noted by Payne *et al.* (1987) that centres of hake abundance, particularly juveniles, relate closely to known concentrations of amphipods and euphausiids and lanternfish with their distribution mirroring that of their prey. Therefore it is thought that the summer inshore movement of hake could be in response to the movement of their principal prey. As the front moves inshore in summer there would be a higher concentration of euphausiids at the front and further inshore and this could explain why hake moves inshore in summer and has a high amount of euphausiids in the diet during this season. As subadult *M. paradoxus* consume a large amount of lantern fish which are known to move with the front, it is thought that they are also following the movements of their prey. There is a high rate of cannibalism in large deep-water hake during summer, which may reflect a greater overlap of large and small hake in the inshore region. The juvenile *M. paradoxus* seem to be most affected by the movement of the front inshore in summer. This may be due to the fact that their main prey (i.e. euphausiids) are more directly influenced by the frontal movement whereas older fish prey on mesopelagics, pelagics, other demersal fish or hakes which are less directly influenced by the front.

M. capensis consume a similar diet to *M. paradoxus,* however, the smaller *M. capensis* ingest more pelagic fish with the larger *M. capensis* ingesting progressively large demersal prey, particularly other hake. In winter their diet seems to be more mixed while during summer other hake become more prevalent in their diet, which also suggests greater overlap during this season (Pillar and Barange 1997). Similar migrations towards feeding grounds have been noted for the Argentine hake (*Merluccius hubbsi*), which take advantage of productive ocean features (Podesta 1989). However, the fact that it seems that hakes follow their prey inshore with the front may be circumstantial and it could be that prey and predator are responding to the same oceanographic processes such as increased inshore flow at depth during periods of upwelling. As this relationship between the 16°C isotherm and hake movement is not always clear, it is suggested that more detailed analysis be undertaken to conform this. No clear relationships could be observed between hake distribution and abundance and bottom oxygen concentration and it is felt that the GIS analysis may not be sufficiently sensitive to detect relationships. This is further analyzed in Chapter 4.

3.4.3. Hake abundance in relation to windrun

The offshore southerly or southeasterly winds off the west coast in summer cause an uplift of water at the coast and hence upwelling. In contrast, the onshore northerly or north westerly winds in winter cause sinking at the coast or downwelling. Upwelling causes the nutrients necessary for phytoplankton growth to be brought to the surface and, as phytoplankton is the primary food source of most pelagic species, it would make this a very productive area. Therefore wind driven effects lead to high biological productivity (Brink 1998). The general trend in increased biomass as the south easter increases could thus be a result of increased upwelling and therefore increased food supply, causing the hake to be more concentrated closer to the coast and once again suggesting that the movement of hake is prey-related.

Wind stress acting on the surface of the sea is the major mechanism whereby mechanical energy and momentum from the wind is transferred to the ocean (Bakun 1998). Therefore it is important to realize that causes influencing hake abundance and distribution may be part of a process which is driven by the action of the wind on the sea. Such surface winds have been known to influence fish behaviour through their effects on the ocean, mainly by wave action and associated turbulence and oscillatory movement within the water column, or by the generation of currents or changes in the mixed layer depth (Le Clus 1988).?

Not there

Few wind-demersal fish relationships have also been reported. Mohr (1964) reported that in the Lofoten area, saithe dispersed from fishing grounds, probably by dispersing into a water mass above the bottom when the wind shifted to a northerly direction. This dispersal sometimes occurred before the wind shifted. Mohr (1964) believed that this dispersal was caused by internal waves, excited by travelling surface pressure systems, rather than by local winds and this may also be the explanation of why fishers fishing off the west coast of South Africa see hakes moving off the bottom when the SE blows. Ralton Maree (BEP, pers. comm.) has suggested that a mechanism exists whereby wind-induced physical forcing may be transferred in the form of bottom currents to as deep as 500m within a relatively short period. This may directly or indirectly (e.g. because of resuspension of fine bottom sediment) cause the hake to move.

In the Benguela current, north of the Cape peninsula region, a strong northward flowing jet current is found several hundred kilometers offshore which is often found associated with the oceanic front. This jet, which is thought to persist throughout the summer after its initiation in spring (Brundrit 1981) appears to extend upwards from the shelf edge (250m) towards the surface, where some modification occurs under direct wind action (Nelson and Polito 1987). It has become known as the Good Hope jet and derives its energy from the upwelling system in summer and disappears in winter (Bang and Andrews 1974). The strengthening of the jet in summer is caused by injection of water with high steric heights from the Agulhas current on the offshore side of the jet and by upwelled water with low steric heights on the inshore side of the jet (Strub *et al.* 1998). It is thought that current dynamics such as the increased inshore flow at depth during periods of upwelling may indirectly be a migration mechanism for hake. Boyd et al. (1992) have shown that both summer and winter current patterns may play a role in facilitating hake recruitment. Currents may also affect adults by possibly aiding in orientation while they migrating from feeding grounds to spawning grounds.

3.4.4. Hake abundance in relation to the Southern Oscillation Index

The most dramatic expression of interannual variability of the Pacific system is the El Niño-Southern Oscillation phenomenon. The term ENSO is used to describe the full range of variability observed in the Southern Oscillation index, including both El Niño and La Niña events. El Niño is characterized by a large scale weakening of the trade winds and warming of the surface layers in the eastern and central equatorial Pacific Ocean. Stronger than normal trade winds and cool sea surface temperatures characterize La Niña (Philander 1990). The effects of El Niño are felt most directly in Peru and Ecuador but, because the Pacific is so large, its effect on the earth's climate system is global. Additional effects may be transferred via teleconnections within the earth's coupled atmosphere-ocean system to marine ecosystems throughout the world (Bakun 1998).

It is believed that ENSO phenomena can be used as a holistic index of environmental conditions in the southern Benguela. In particular, ENSO events, La Niña or El Niño, affect the climate and oceanography in a specific way (Korrûbel 1995). Episodic equatorial warm events, which are El Niño-like in character, occur in the Atlantic. Warm events that coincide with the time period of this study occurred in 1984 and 1995 and Shannon *et al.* (1986) have suggested that the term Benguela Niño be used to describe these events. Benguela Niños are generally intrusions of warm saline, less productive tropical surface waters on the Namibian shelf, which do not appear to have much of an effect in the

Southern Benguela. Rather than being triggered by variation in local wind-stress, the Benguela Niño is believed to be associated with large-scale remote changes in the wind patterns (i.e. relaxation of the stronger than normal trade winds) (Gammelsrod *et al.* 1998). Empirical studies on large scale teleconnections have revealed some physical inter-relationships, some of them acting nearly simultaneously and some with a time lag (Laevastu 1993). It appears that an El Niño in the Pacific may initiate a tropical warm event in the Atlantic the following year (Bakun 1996). However, these El Niño-type episodes seem to be less frequent in the Atlantic than in the Pacific. Therefore, an ENSO event occurring in the Pacific could only have an effect on the Southeast Atlantic a year (or some lag period) later.

A reduction of the easterly wind in the Southeast Atlantic coincides with a warm phase ENSO in the Pacific. So, it may be possible that an increase in the easterly winds could be coincidental with a cold phase ENSO. A single cold phase event occurred in 1988-1989 in the Pacific. Agenbag (1996) noted increased easterly winds in the southern Benguela at that time, although maximum deviation occurred during the summer of 1989-1990. Therefore the effects of La Niña may affect the South east Atlantic (in particular the Southern Benguela), with a time lag similar to that of The Benguela Niño. Hampton and Matthews (1997) have noted that sustained cooling of shelf waters occurred in the southern Benguela from autumn 1989. In the past it has been noted that hake favour cooler periods (Crawford *et al.* 1990) and this may explain the favourable catch rates over this time. However, as my results do not appear to show any direct relationships with temperature (see Chapter 4), it may be that some other factor associated with cooler waters (e.g. possible La Niña conditions) affects hake.

It has been reported that there is about a 6-month lag between a temperature switch in the tropical Pacific, and its effect globally (Kerr 1988). After the 1988/89 La Niña an increase in hake abundance occurred approximately a year later in the southern Benguela. It is believed that this increase was a consequence of greater abundance of young hake (Hutchings and Hampton 1998); in section 3.3.2 it is shown that during this year there was an increase in juveniles (which would mainly include 0 and 1 year olds). Therefore it would seem that this La Niña event did not have an immediate effect on the juveniles as an increase in their biomass is only noted *ca.* 6 months after the affects of the La Niña would have been felt in the Benguela. However it is possible that the ENSO event may have a direct positive influence on eggs and larvae of hakes and then this affect would only be evident in the large number of juveniles caught 6 months to a year later.

Hampton and Matthews (1997) also noted that there was a two month period of below average reversal in flow at a current meter site at 33°S, which was completely uncharacteristic of the record, occurred during winter 1989. This may have some connection with an apparent "La Niña" event occurring in the southern Benguela but, even so, as this event was totally uncharacteristic of the record, it may have caused the irregularities seen in the hake abundance between 1989 and 1990.

Thus there remains a large number of unanswered questions concerning the causes of changes in hake distribution and abundance. In Chapter 4, GAM will be used to look at the relationship between hake biomass and environmental variables in more detail.

Chapter Four

Environmental effects on hake distribution and abundance: a quantitative analysis using Generalized Additive Modeling

4.1. Introduction

One major shortcoming of using environmental data in fisheries is that attempts have been made to analyse the effects of only one environmental feature on fish behavior and distribution at a time. Because interactions of fish and the environment are extremely complex, not just one but a number of features and processes affect fish populations simultaneously.

Generalized Additive Modeling (GAM) has only recently been applied to analyse spatial trends in fisheries science (Booth 1998). These GAMs allow for a response variable (fish abundance) to be modelled as a function of two (such as latitude and longitude), or more covariates (environmental variables) simultaneously. Many relationships have been found using this modeling technique. These include relationships between environmental factors and panga (*Pterogymnus laniarius*) abundance on the Agulhas Bank (Booth 1998), egg density of western mackerel and horse mackerel on the European continental shelf region of the Northeast Atlantic Ocean (Borchers *et al.* 1997), abundance and distribution of North Sea Herring (Maravelias 1997), abundance of a number of different groundfish species in the Bering Sea (Swartzman *et al.* 1992, 1994, 1995) and recruitment of Californian northern anchovy (Cury *et al.* 1995).

Quantifying these spatial relationships strengthens our understanding of factors that influence the distribution and abundance of fish species. In doing so, a degree of explanation of the distribution is given, which may serve to reduce the variance in biomass estimates because it provides additional information concerning the distribution of abundance through covariates that are easily measurable (Swartzman *et al.* 1992).

GAMs have proven useful in examining and testing relationships found during exploratory data analysis. They have also been used in smoothing abundance outliers and including spatial trends in abundance, both of which appear to improve abundance estimates (Swartzman *et al.* 1992). GAMs also have advantages over traditional methods because they are model-based rather than design-based. Thus they do not require a random survey design but, instead, require sufficient coverage of exploratory variables to allow for reliable estimation (Borchers *et al.* 1997). In addition, GAMs are very flexible as they do not assume linearity.

The objective of this chapter is to establish quantitative relationships between the spatial distribution of hake density (*M. paradoxus and M. capensis*) and environmental factors over a wide geographical area, using biomass survey data and CTD data collected on the west coast of South Africa. GAM will then be used to estimate hake biomass and in so doing, try to improve on existing biomass estimates.

4.2. Data Analysis

Hake data used for this study, from trawl surveys undertaken by Marine and Coastal Management, Cape Town, were collected on the west coast of South Africa from 1984 to 1997. All trawl details are covered in Chapter 2. Densities of life history stages were log-transformed and these values were used for all further analysis.

Suggested relationships in Chapter 3 were further examined and tested using Generalized Additive Modeling (GAM). GAM was used to model the spatial distribution and abundance of *Merluccius capensis* and *Merluccius paradoxus* on the west coast of South Africa in response to various covariates. Details regarding the use of GAM in this study follow below.

4.2.1. Generalized Additive Modeling (GAM) – an overview for spatial data.

GAM is a nonparametric generalization of multiple linear regression. Both methods relate the dependent variable or a response to covariates or predictors (Hastie and Tibshirani 1990). However, the GAMs extend the usual collection of likelihood-based regression models by replacing the usual linear function of a covariate with an unspecified smooth function (estimated by a scatterplot smoother). The additive model consists of a sum of such smooth functions of each covariate in the model (Hastie and Tibshirani 1990). The theory of GAM requires that the dependent variable be transformed by a link function (Hastie and Tibshirani 1990). Therefore, a known function of the expected value, called the link function, is modeled as the sum of smooth functions of the covariates.

The general form of a GAM is

$$g(E(Y/x)) = g(\mu) = \alpha + \sum_{i=1} f_i(x_i)$$

Where g is the link function, α is a constant intercept term and f_i corresponds to the nonparametric or smooth function describing the relationship between the transformed mean response (the link transform function) and the ith predictor (Venables and Ripley 1994). Because the forms of the f_i are generally unknown, they are estimated using some form of scatterplot smoother. In this application, the data were assumed to come from a non-homogeneous Poisson distribution. This distribution was chosen because it is often appropriate for count data (ie. estimates of fish abundance represented by fish numbers) and spatial data.

The parameter of the Poisson distribution is calculated as

$$\Lambda(x) = \int_{Ax} \lambda(u) du$$

where $\lambda(x)$ is the intensity of the underlying Poison process and A_x is the area of the observations. The expected value of the Poisson distribution is Λ (x) and the natural link function is its logarithm. Thus, the Poisson Generalized Additive Model (Swartzman *et al.* 1992) relates the expected counts to the covariates as

$$\log[E(Y|x_1,\ldots,x_p)] = \log[\Lambda(x)] = \sum_{i=1}^{p} f_i(x_i)$$

A general and efficient algorithm for fitting a GAM consists of a hierarchy of three modules – scatterplot smoothers, the backfitting algorithm and the local scoring algorithm.

4.2.1.1. Smoothing algorithm

Smoothing functions, as mentioned above, are estimated by scatterplot smooths and in GAM, they replace the least-square fits in regression. The idea behind a scatterplot smoother is that it exposes the functional dependence without imposing a rigid parametric assumption about the dependence. It therefore relies on the data to specify the form of the model. One of the main uses of scatterplot smoothers is to estimate the dependence of the mean of Y on the predictors, and to then serve as a building block for the estimation of additive models (Hastie and Tibshirani 1990). A number of different smoothing functions exist, but the one chosen to estimate the smooths in this thesis is the cubic *B*-spline smoother which is an indirect method of smoothing driven by penalized least squares (Hastie and Tibshirani 1990). This approach seeks a function f that minimizes the penalized residual sum of squares (PRSS)

$$\mathrm{PRSS} = \sum_{i=1}^{n}\left[\left(y_i - f(x_i)^2\right) - \lambda \int f''(t)dt\right]$$

over all functions with continuous first and integrable second derivatives. In so doing, it minimizes the compromise between the fit and the degree of smoothness of the form over all functions f (Venables and Ripley 1994). The degree of smoothing, performed by the smoother, is determined by the degrees of freedom associated with the smooth

(Maravelias 1997, Borchers *et al.* 1997). In this case df=4 (defining a more flexible function) was found to result in a better fit than using df=1 (a less flexible function).

The smoothing spline does not actually smooth the data, but rather prepares for the backfitting algorithm used by GAMs to fit multiple covariates (the terms) in the model.

4.2.1.2. Backfitting algorithm

The backfitting algorithm fits the smoothing functions one at a time by taking the residuals and smoothing them against X (Venables and Ripely 1994) using a scatterplot smoother (in this case, the cubic smoothing spline). Known as the Gauss-Seidel algorithm in numerical analysis, this cycle continues until a threshold level of the deviance is achieved (ie. none of the functions change from one iteration to the next) (Chambers and Hastie 1992). The measure of fit for the GAMs is the deviance, twice the natural logarithm of the likelihood ratio between the saturated model and the current model (Swartzman *et al.* 1992). For a Poisson process this can be calculated as follows:

$$\text{Deviance}(x,\mu) = 2\sum_{i=1}^{n} x_i \ln\left[\frac{x_i}{\mu_i}\right] - (x_i - \mu_i)$$

The updating iterations are continued until the deviance fails to change.

4.2.1.3. Local-scoring algorithm

The backfitting algorithm occurs within the local-scoring procedure. The local scoring algorithm, a generalization of the usual Fisher scoring procedure for computing maximum likelihood estimates (Hastie and Tibshirani 1986), uses backfitting to iteratively fit weighted additive models. Each iteration produces a new working response and weights, which are handed to the backfitting algorithm, which then produces a new additive predictor (Chambers and Hastie 1992).

The theory of GAMs is described in detail in Hastie and Tibshirani (1990) and, for an application in fisheries or in ecology, in Swartzman *et al.* (1992), and Cury *et al.* 1995. In this thesis, GAMs are used to model trends in abundance as functions of position as well as oceanographic or environmental variables. The covariates available for inclusion in the model are depth, bottom oxygen concentration, bottom temperature, sea surface temperature (SST), sea surface temperature minus bottom temperature (SST-BT), longitude and latitude. Data from all survey months from 1984 to 1997 were lumped to form one large sample size and to see what trends were observed over this period. Initially, fish abundance was modelled separately with each covariate and scatterplot smoothers were used to show the individual relationships that exist between the two. The 95% confidence interval of the smoothing function was also plotted. A rug plot was included on the x-axis, which shows the density of points for each covariate (fewer points results in larger standard errors). The absolute magnitude on the y-axis reflects the relative importance of each covariate. A value of zero on the vertical axes corresponds to no effect of the explanatory variable (Maravelias 1997). For comparison, a standard linear regression analysis was conducted to test the relationships between depth and the other four covariates (bottom oxygen concentration, bottom temperature, SST, SST-BT).

GAM was then preformed for all survey months combined, using all covariates in the model to show the conditional effect, that is, the effect of a variable, given that the other variables are included in the model. In order to obtain the best fitting model, all variables were initially included in the model (this was labelled Model 1). To provide a familiar measure of model fit, a pseudo-coefficient of determination (Swartzman *et al.* 1992) was calculated (a good fit is defined by a small deviance). This allows for a measure of the ratio of variation explained by the model to the total variation explained by both the model and any associated error. It is calculated as follows:

$$\text{Pseudo} - \text{coefficient of determination} = \frac{\text{Best model residual deviance}}{\text{Overall mean or null model deviance}}$$

Although this pseudo-coefficient is not identical to the classical R^2, this measure is bound between 0 and 1 and is used as a surrogate for R^2. The spatial coordinate system given by longitude and latitude is arbitrary. Since most spatial data are referenced in two dimensions, isotropy of any spatial process is important. In this case, isotropy refers to a spatial process that evolves similarly in all directions (Kaluzny *et al.* 1996). Therefore, the latitude-longitude axes were rotated to correct for directional invariance or isotropy. This has the effect of maximizing the pseudo- R^2.

A second model was also considered. Only bottom temperature, bottom oxygen concentration, SST and SSTBT were included in this model in order to examine the effect of removing the variables of position from the model. Pseudo-R^2 values were calculated for both models. Backward, stepwise elimination was used to select a set of significant covariates and a final best-fitting model was selected for each life history stage of both hake species. Different models were required for each hake species and each life history stage. This is not surprising when one considers the differences in the observed distribution of each species and each life history stage.

Once a best-fitting model was established for each life history stage, it was used to generate estimates of mean fish abundance at each sampling point for the two hake species. This was then used to generate biomass estimates that could be compared to currently used biomass estimates calculated by Marine and Coastal Management (MCM), Cape Town. To allow comparisons with the biomass estimates of MCM, the same stratified estimation technique to estimate overall biomass was used. A mean abundance estimate was generated for each survey point with the log-transformed estimates transformed back into direct abundance. These point abundance estimates were then multiplied by the average mass per fish in each life history stage to generate the density of hake (Kg.nmile^{-2}) for each station. From there, the total biomass index and standard error were calculated using the same methology as explained in Chapter 2. The standard error was calculated but not the coefficient of variation as it was felt that calculating both may result in conflicting interpretations.

4.3. Results

4.3.1. Patterns in hake abundance in relation to environmental variables

Figures 4.1 for *M. paradoxus* and Figures 4.2 for *M. capensis* are scatterplot smoothes showing the individual effect that each covariate has on the logarithm of hake density over the whole survey period observed in this study. These plots summarize the data for the entire time period and show which covariates have the greatest effect on hake density. Both the scatterplots for each survey and the scatterplot smoothes for all surveys combined suggested the following relationships for each factor examined:

1) Depth (Figure 4.1a and 4.2a)

The density of adults of both species increased with increasing depth, leveling off at a highest density from about 320m out to 500m for *M. paradoxus* and between about 200 and 300m (decreasing on either end of this range) for *M. capensis*. *M. paradoxus* subadults follow a similar pattern to the *M. capensis* adults. Juvenile *M. paradoxus* and *M. capensis* and subadult *M. capensis* all decrease with increasing depth, with the highest density of *M. paradoxus* juveniles and capensis subadults being found between 100 – 250m and *M. capensis* juveniles in highest density between 0-150m.

2) Longitude (Figure 4.1b and 4.2b)

No clear relationship was found between all life history stages of *M. paradoxus* and adults of *M. capensis* and longitude. Both *M. capensis* juveniles and subadults showed an increase in density further east.

3) Latitude (Figure 4.1c and Figure 4.2c)

All life history stages of *M. capensis* and the subadults of *M. paradoxus* show no real relationship with latitude. This can be explained by the low ranges on the y-axis.

However, *M. paradoxus* juveniles showed an increase in density further north whereas adults showed an increase in density further south (32°S to 34°S).

4) Degree of stratification (SST-BT) (Figure 4.1d and 4.2d)

Adults of both species occur in greatest density over a wide range of values with more being found in more stratified waters. Juveniles seem to occur where mixing of the water column is far greater. *M. paradoxus* occurs in waters which are slightly more stratified the *M. capensis*.

5) Bottom temperature (Figure 4.1e and 4.2e)

Adult *M. paradoxus* were found over a fairly wide range of bottom temperatures, with highest density at cooler bottom temperatures (between 5 and 7.5°C) and decreasing thereafter with warmer bottom temperatures. *M. capensis* adults and *M. paradoxus* subadults show no clear relationship with bottom temperature. This can be explained by the low range on the y-axis. *M. capensis* subadults and juveniles and *M. paradoxus* juveniles are all seen to increase in density with increasing bottom temperatures, with *M. paradoxus* having its highest density at temperatures of between 8-9°C and *M. capensis* juveniles and subadults having their highest density at bottom temperatures of between 9-10°C. All three have their highest density in a narrower range of bottom temperatures than the adults. *M. capensis*, however, has its highest density at bottom temperatures which are slightly warmer than *M. paradoxus*.

6) Sea surface temperature (Figure 4.1f and 4.2f)

Adults of both species were found in greatest density further offshore at warmer SSTs, with the juveniles being found in greatest density further inshore at cooler SSTs. No clear relationship occurred between subadults of both species and SST. This can be explained by the low range on the y-axis. *M. paradoxus* were found at slightly warmer SST than *M. capensis*.

7) Bottom oxygen concentration (Figure 4.1g and 4.2g)

Density of adults of both species increases with increasing bottom oxygen concentration with greatest density between 3.5 and 5.5mg.l^{-1}. In contrast, juveniles of both species are found in greatest density in lower bottom oxygen concentrations and decrease with increasing oxygen concentrations (highest abundance between 0 and 3mg.l^{-1}). No clear relationship is observed between subadult density of both species and bottom oxygen concentrations. Greatest density of *M. capensis* occurs at lower bottom oxygen concentrations than *M. paradoxus*.

By observing the y-axis of the scatterplot smoothes, it is evident that depth is the most important covariate for both hake species and all life history stages. To a lesser degree, relationships between the following are also seen to occur: *M. capensis* juveniles and longitude, bottom oxygen concentration and SST-BT; *M. capensis* subadults and longitude; *M. capensis* adults and bottom oxygen concentration, SST, SST-BT, latitude; *M. paradoxus* juveniles and bottom temperature, latitude, bottom oxygen; and *M. paradoxus* adults and bottom temperature, SST, SST-BT, latitude and bottom oxygen concentration.

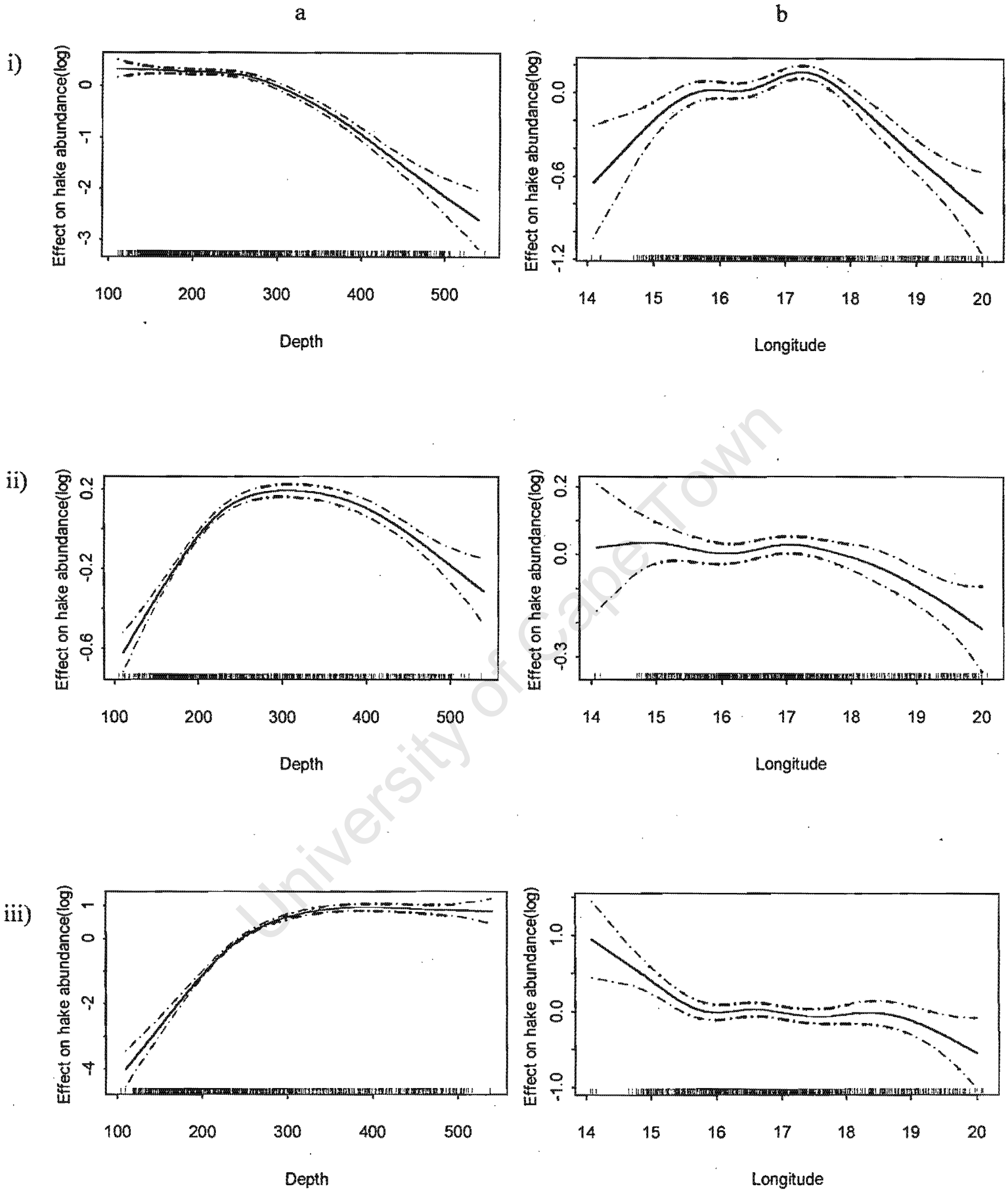


Figure 4.1: Scatterplot smoothes showing the individual effect that each environmental variable has on abundance of *M. paradoxus* i) juveniles, ii) subadults and iii) adults. The 95% confidence interval is represented by the dotted line and a rug plot is included on the x-axis.

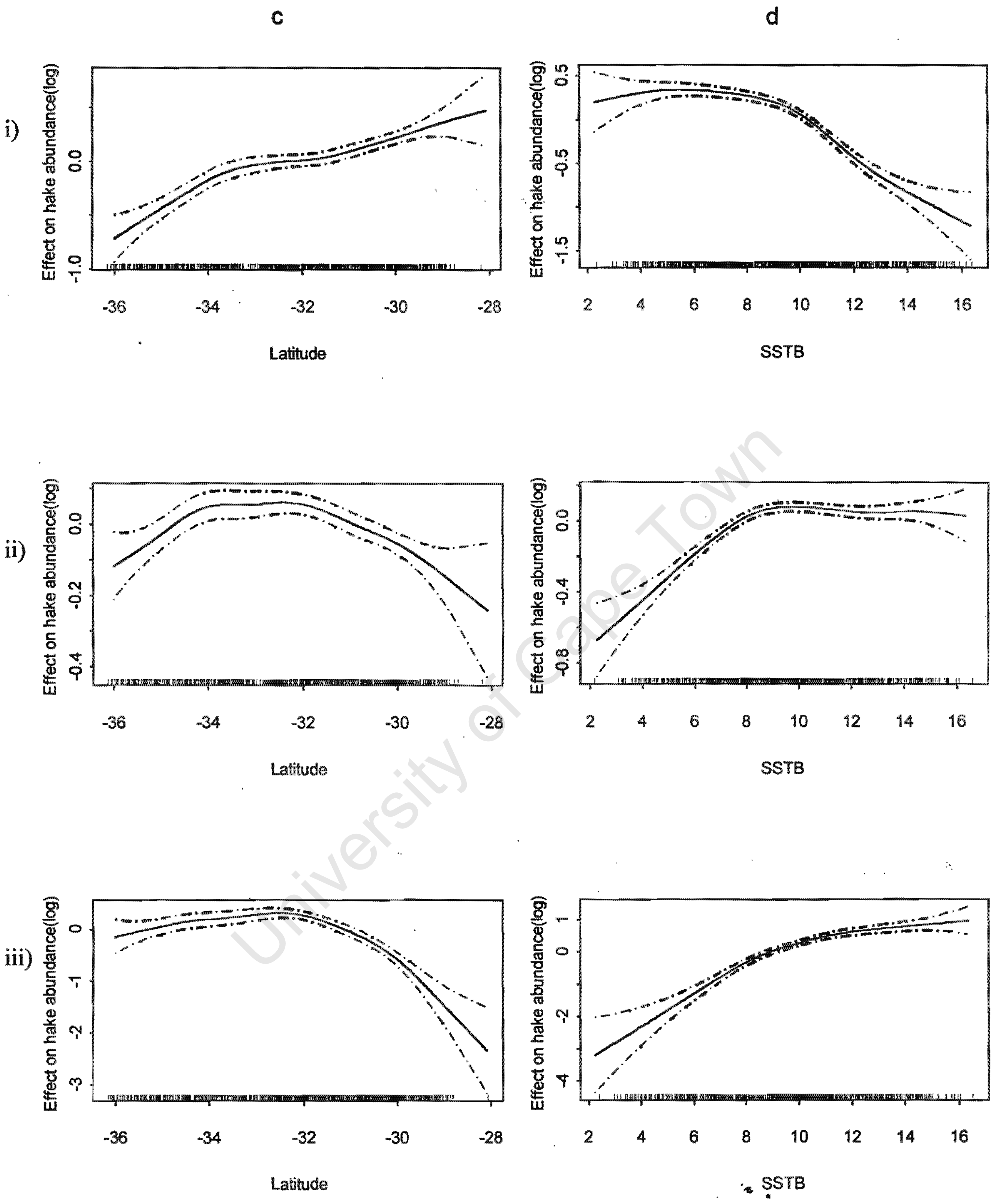


Figure 4.1 (cont.) : Scatterplot smoothes showing the individual effect that each environmental variable has on abundance of *M. paradoxus* i) juveniles, ii) subadults and iii) adults. The 95% confidence interval is represented by the dotted line and a rug plot is included on the x-axis.

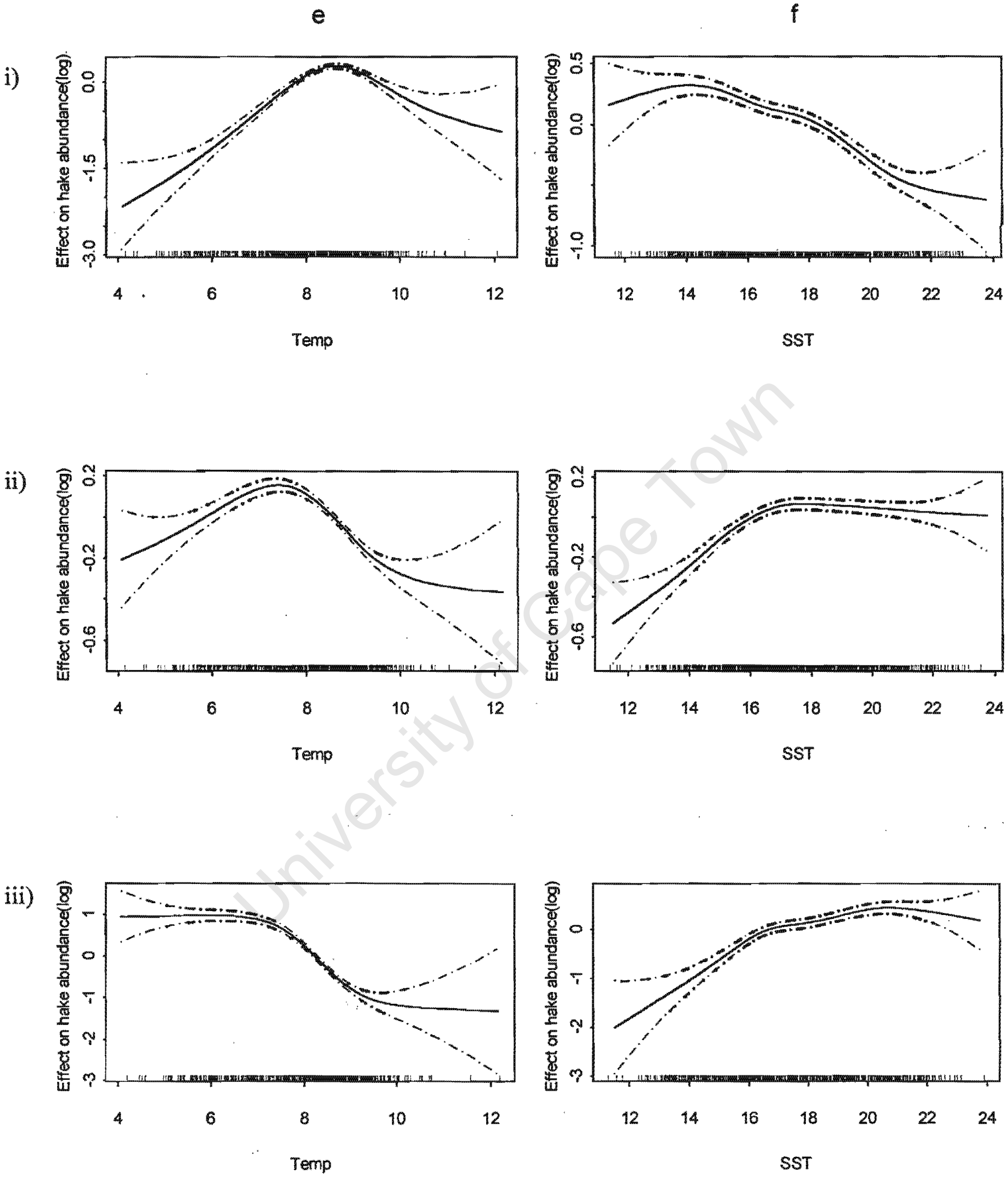


Figure 4.1 (cont.): Scatterplot smoothes showing the individual effect each environmentalvariable has on abundance of *M. paradoxus* i) juveniles, ii) subadults and iii) adults. The 95% confidence interval is represented by the dotted line and a rug plot is included on the x-axis.

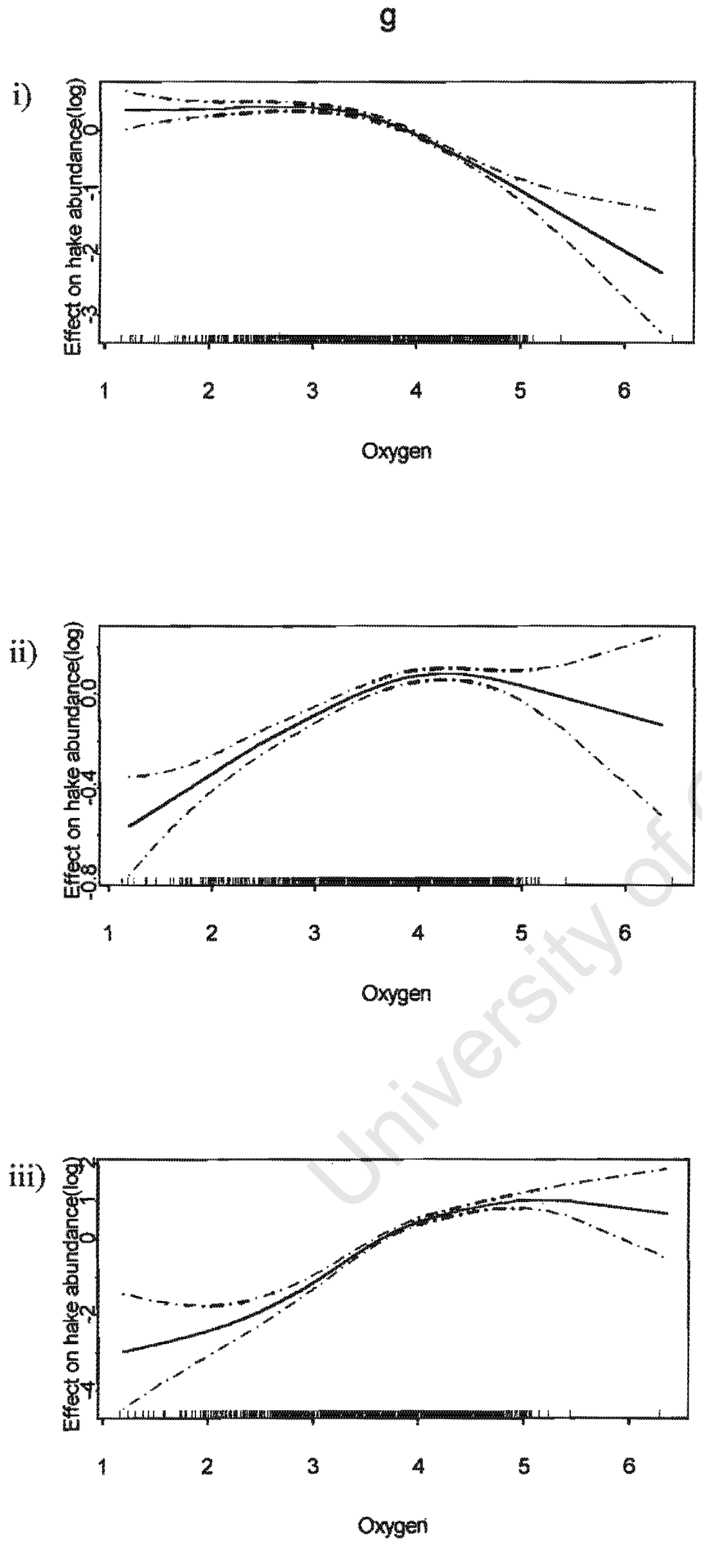


Figure 4.1 (cont..): Scatterplot smoothes showing the individual effect each environmental variable has on abundance of *M. paradoxus* i) juveniles, ii) subadults and iii) adults. The 95% confidence interval is represented by the dotted line and a rug plot is included on the x-axis.

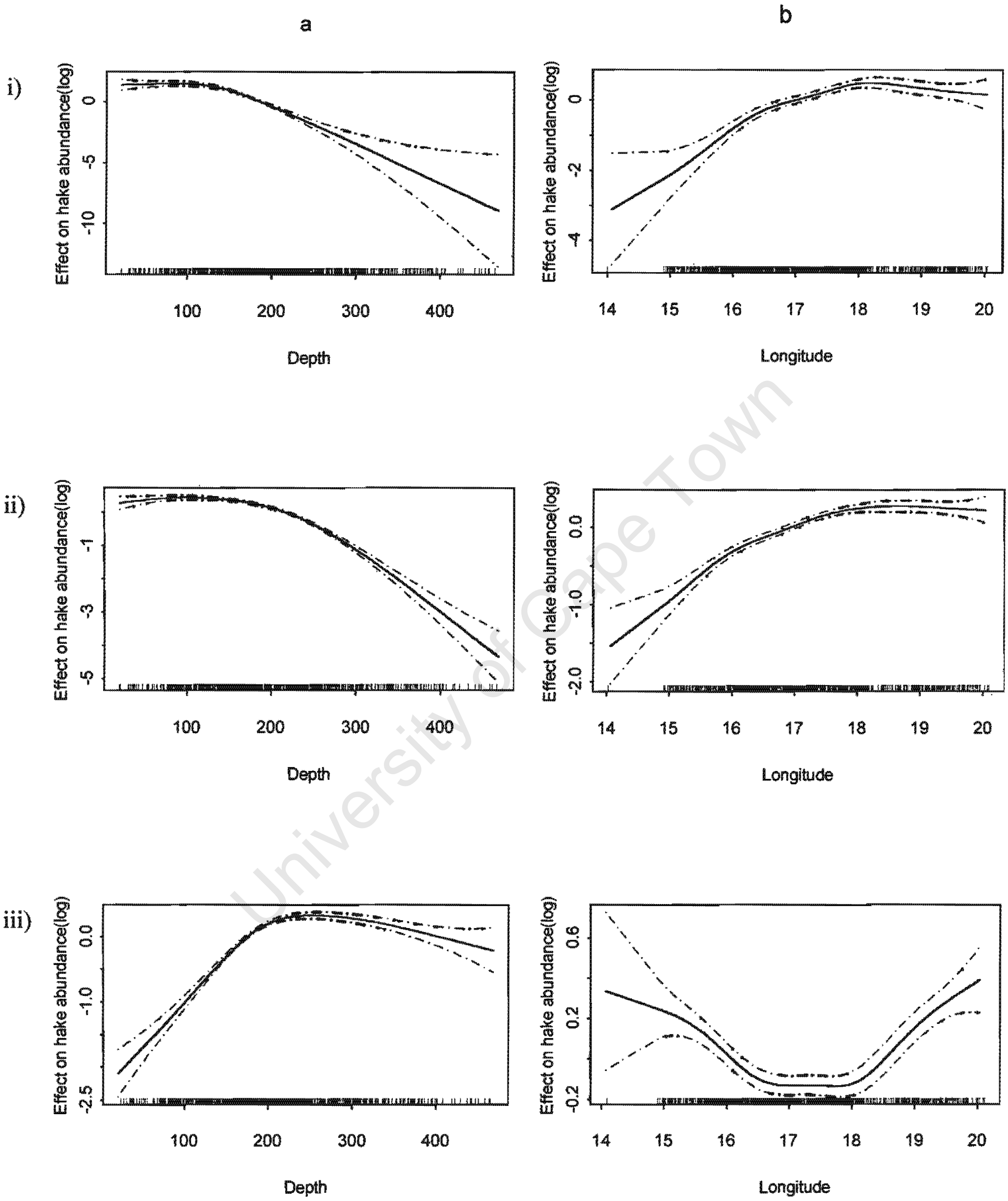


Figure 4.2: Scatterplot smoothes showing the individual effect each environmental variable has on abundance of *M. capensis* i) juveniles, ii) subadults and iii) adults. The 95% confidence interval is represented by the dotted line and a rug plot is included on the x-axis.

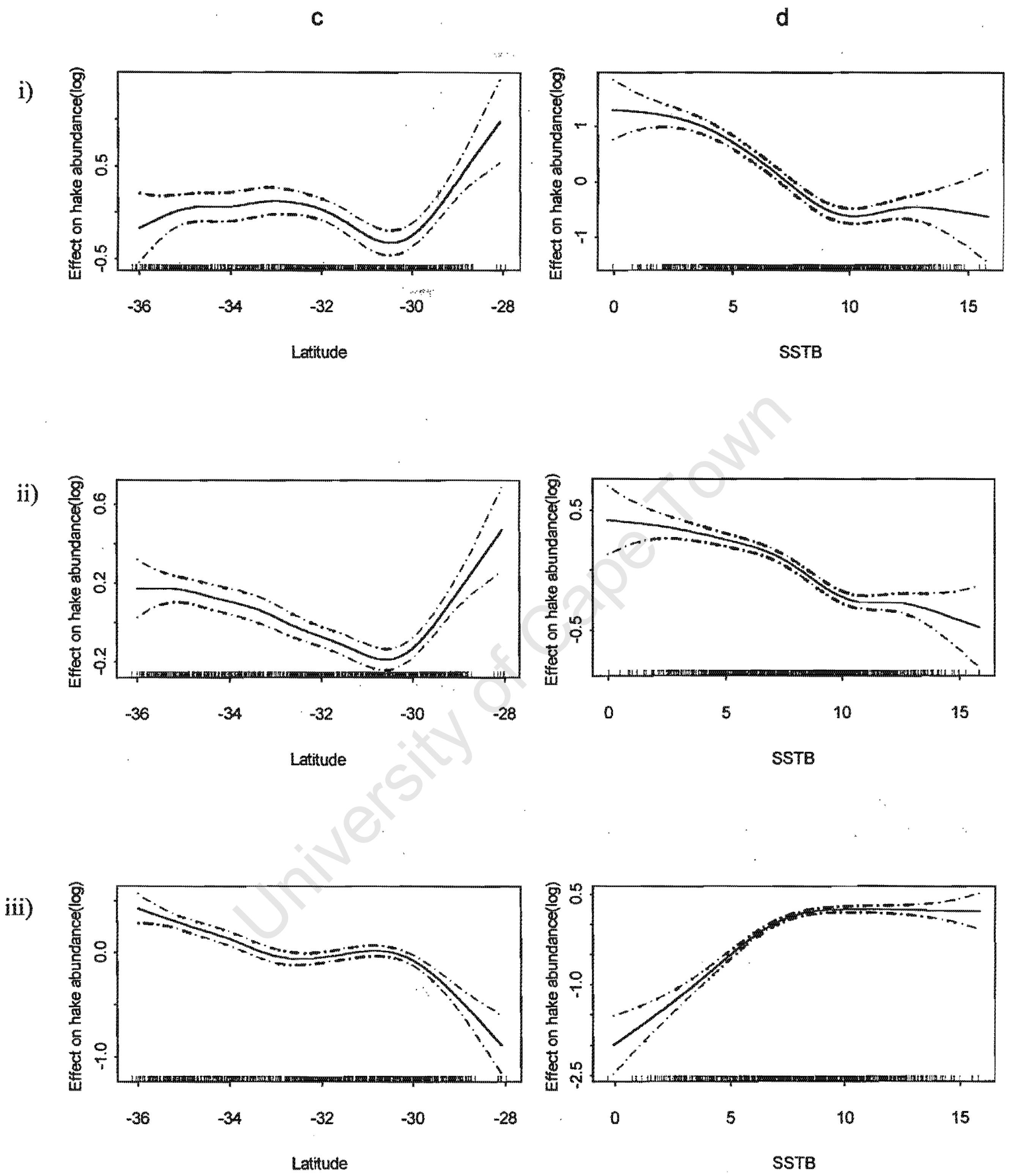


Figure 4.2 (cont.): Scatterplot smoothes showing the individual effect each environmental variable has on abundance of *M. capensis* i) juveniles, ii) subadults and iii) adults. The 95% confidence interval is represented by the dotted line and a rug plot is included on the x-axis.

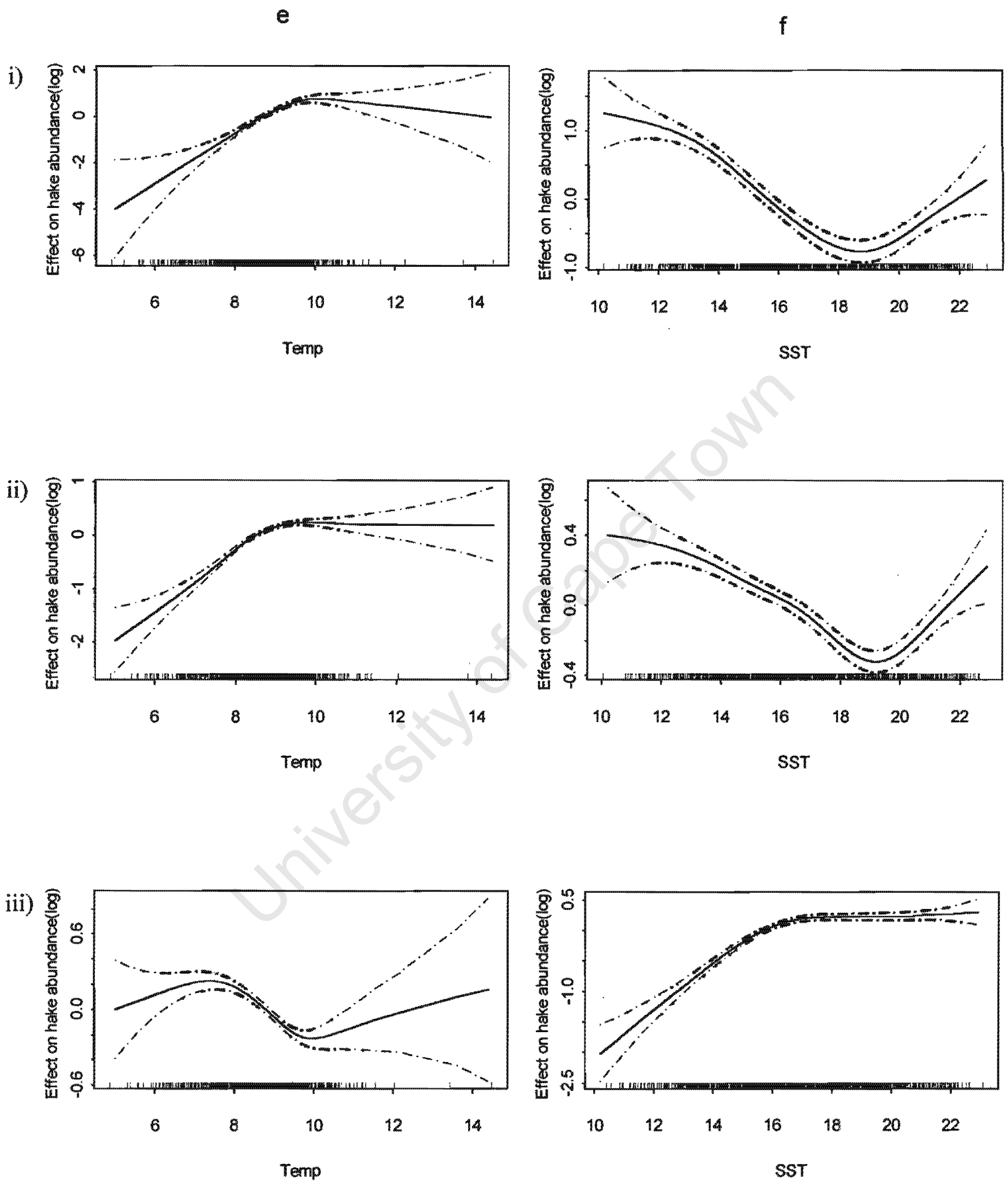


Figure 4.2 (cont.): Scatterplot smoothes showing the individual effect each environmental variable has on abundance of *M. capensis* i) juveniles, ii) subadults and iii) adults. The 95% confidence interval is represented by the dotted line and a rug plot is included on the x-axis.

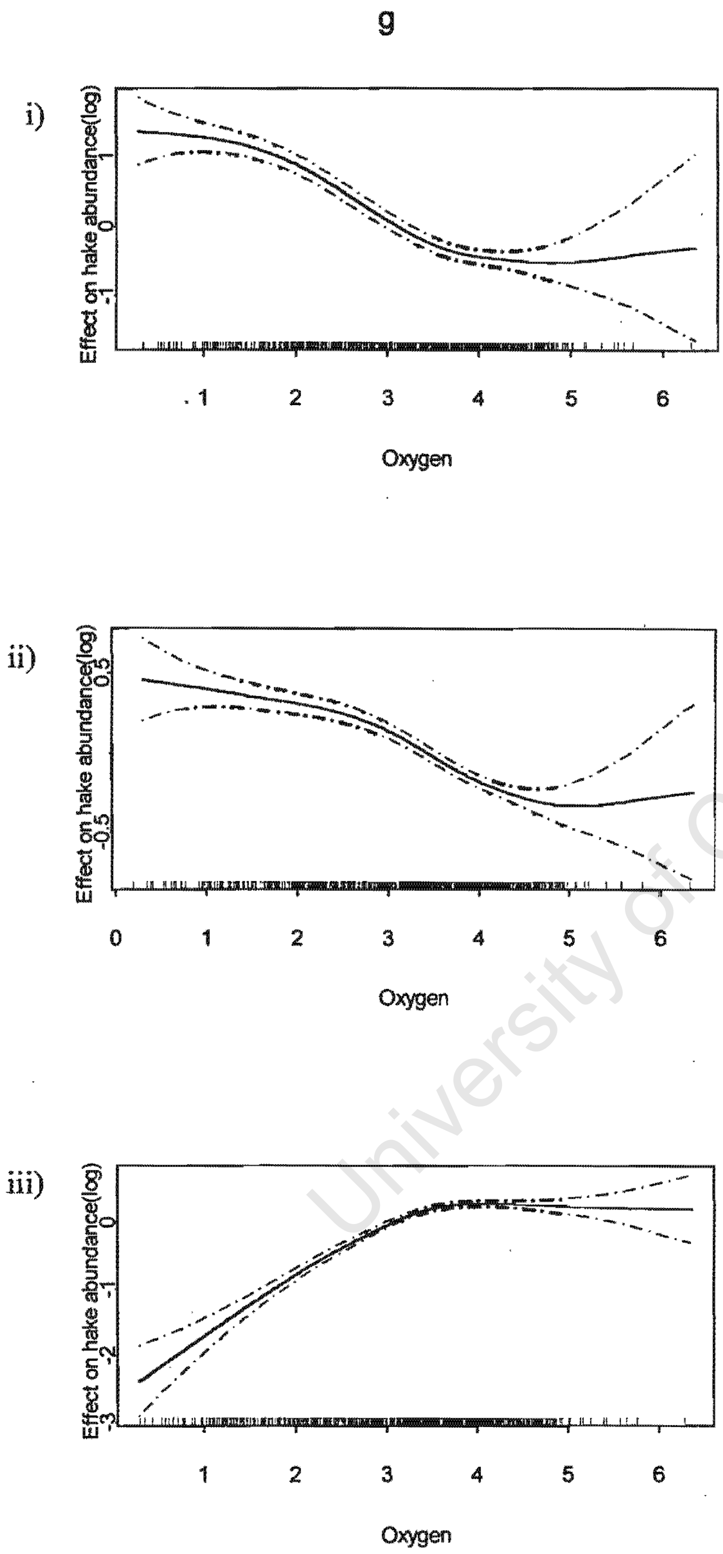


Figure 4.2 (cont.): Scatterplot smoothes showing the individual effect each environmental variable has on abundance of *M. capensis* i) juveniles, ii) subadults and iii) adults. The 95% confidence interval is represented by the dotted line and a rug plot is included on the x-axis.

However, if one regresses depth against bottom oxygen concentration (Figure 4.3a), bottom temperature (Figure 4.3b), SST-BT (Figure 4.3c) and SST (Figure 4.3d), it is clear that a strong relationship exists between depth and the other covariates. Bottom oxygen concentration increases as depth increases ($r=0.65$, $n=1264$, $p<0.05$), bottom temperature decreases as depth increases ($r=0.78$, $n=1264$, $p<0.05$) and sea surface temperature minus bottom temperature ($r=0.63$, $n=1264$, $p<0.05$) values increase as depth increases. The relationship between SST and depth is not as strong as the others but is still considered significant ($r=0.16$, $n=1264$, $p<0.05$), with SST increasing as depth increases. Therefore, it is possible that these other variables only appear to have an effect on hake density because of their relationship with depth. Because depth is consistently the most significant effect, it would seem that is the most important of the factors determining the spatial density of hake.

4.3.2. GAM to show the relationship between hake abundance and environmental variables

Two GAMs were constructed for each hake species and life history stages for all survey months (Tables 4.1–4.3). Model 1 represents the average fish density related to longitude, latitude, bottom depth, bottom oxygen concentration, bottom temperature, sea surface temperature and sea surface temperature minus bottom temperature. Model 2 removes latitude, longitude and bottom depth as covariates. For the first GAM, the latitude-longitude axes are rotated to maximize pseudo–R^2. Tables 4.1-4.3 display the pseudo- R^2 for each of the GAM runs, and also gives the rotation angle giving the highest pseudo-R^2 for model 2.

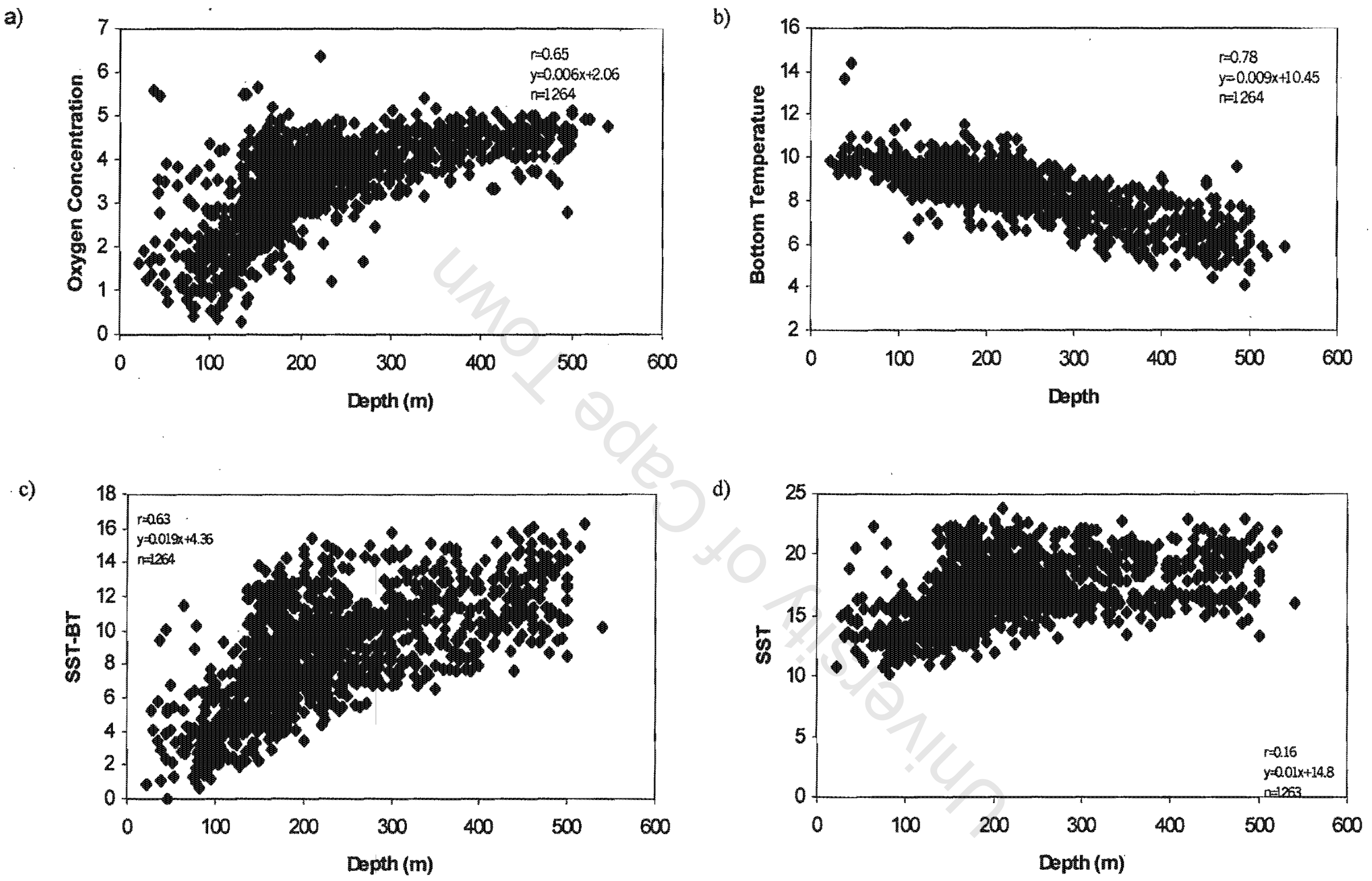


Figure 4.3: The regression relationship between depth and a) bottom oxygen concentration, b) bottom temperature, c) sea surface temperature Minus bottom temperature and d) sea surface temperature.

Table 4.1: R^2 values from the GAM for juveniles of each species and survey month (Model 1 ~ longitude + latitude + depth + bottom temperature + bottom oxygen + SST + [SST-BT] and Model 2 ~ bottom temperature + bottom oxygen + SST + [SST-BT]).

Survey Month	*M. paradoxus*			*M. capensis*		
	Model 1	angle	Model 2	Model 1	angle	Model 2
June 1984	0.806	23	0.721	0.853	1	0.542
January 1985	*	*	*	*	*	*
July 1985	*	*	*	*	*	*
January 1986	0.679	1	0.552	0.915	21	0.663
July 1986	0.577	1	0.344	0.909	1	0.450
January 1987	0.860	1	0.821	0.956	16	0.550
July 1987	0.634	21	0.485	0.970	1	0.803
February 1988	0.821	1	0.449	0.943	1	0.652
August 1988	0.661	26	0.403	0.816	23	0.527
January 1989	*	*	*	*	*	*
July 1989	0.667	1	0.369	0.847	1	0.695
January 1990	0.759	19	0.660	0.894	23	0.562
July 1990	0.998	1	0.994	0.805	14	0.376
January 1991	0.637	1	0.396	0.960	12	0.696
February 1992	0.703	22	0.638	*	*	*
January 1993	0.807	1	0.505	0.970	2	0.637
January 1994	0.722	19	0.501	0.642	1	0.471
January 1995	0.590	23	0.457	0.915	11	0.705
January 1996	0.766	4	0.667	0.772	2	0.555
January 1997	0.829	7	0.725	0.623	1	0.456

*no data available

Table 4.2: R^2 values from the GAM for subadults of each species and survey month (Model 1 ~ longitude + latitude + depth + bottom temperature + bottom oxygen + SST + [SST-BT] and Model 2 ~ bottom temperature + bottom oxygen + SST + [SST-BT]).

Survey month	*M. paradoxus*			*M. capensis*		
	Model 1	angle	Model 2	Model 1	angle	Model 2
June 1984	0.810	1	0.639	0.917	24	0.411
January 1985	*	*	*	*	*	*
July 1985	*	*	*	*	*	*
January 1986	0.728	10	0.644	0.814	1	0.496
July 1986	0.794	1	0.533	0.744	13	0.533
January 1987	0.640	8	0.466	0.839	12	0.561
July 1987	0.676	16	0.486	0.760	8	0.211
February 1988	0.592	1	0.376	0.701	18	0.315
August 1988	0.607	1	0.426	0.701	1	0.484
January 1989	*	*	*	*	*	*
July 1989	0.789	13	0.660	0.735	1	0.555
January 1990	0.559	1	0.354	0.745	22	0.500
July 1990	0.999	1	0.884	0.787	1	0.409
January 1991	0.583	17	0.327	0.847	27	0.390
February 1992	0.661	20	0.472	*	*	*
January 1993	0.640	14	0.362	0.815	16	0.342
January 1994	0.651	1	0.455	0.713	1	0.563
January 1995	0.450	2	0.246	0.833	6	0.635
January 1996	0.688	1	0.320	0.746	28	0.440
January 1997	0.615	6	0.468	0.803	1	0.420

*No data available

Table 4.3: R^2 values from the GAM for adults of each species and survey month (Model 1 ~ longitude + latitude + depth + bottom temperature + bottom oxygen + SST + [SST-BT] and Model 2 ~ bottom temperature + bottom oxygen + SST + [SST-BT]).

Survey month	*M. paradoxus*			*M. capensis*		
	Model 1	angle	Model 2	Model 1	Angle	Model 2
June 1984	0.936	1	0.639	0.853	15	0.803
January 1985	*	*	*	*	*	*
July 1985	*	*	*	*	*	*
January 1986	0.847	27	0.769	0.694	1	0.592
July 1986	0.901	28	0.704	0.699	5	0.611
January 1987	0.759	27	0.641	0.805	7	0.767
July 1987	0.876	17	0.664	0.774	1	0.714
February 1988	0.781	1	0.532	0.681	16	0.554
August 1988	0.939	35	0.773	0.581	21	0.435
January 1989	*	*	*	*	*	*
July 1989	0.943	5	0.874	0.665	26	0.559
January 1990	0.813	6	0.484	0.622	1	0.485
July 1990	0.999	35	0.999	0.598	5	0.495
January 1991	0.815	2	0.687	0.726	12	0.458
February 1992	0.840	8	0.549	*	*	*
January 1993	0.651	1	0.542	0.780	1	0.599
January 1994	0.832	1	0.674	0.580	1	0.512
January 1995	0.720	13	0.529	0.442	1	0.340
January 1996	0.739	1	0.473	0.636	4	0.490
January 1997	0.809	10	0.689	0.673	1	0.540

*No data available

The difference in pseudo – R^2 between models 1 and 2 gives an indication of how well bottom oxygen concentration, bottom temperature, sea surface temperature and sea surface temperature minus bottom temperature alone explains the distribution. Having a small decrease in Pseudo-R^2 suggests that little additional information is provided by including latitude, longitude and depth. Having a large decrease in pseudo-R^2 suggests that longitude, latitude and bottom depth have a strong effect on the distribution (Swartzman et al. 1992). A large decrease from model 1 to model 2 was noted in the majority of survey months for the three life history stages, showing that longitude, latitude and depth appear to improve the significance to the GAM models. This shows their importance in predicting hake density.

Selecting which of the predictor variables to include in a GAM to select the best-fitting model is fairly complicated. The covariates available for inclusion in the model are latitude, longitude, depth, bottom oxygen concentration, bottom temperature and sea surface temperature minus bottom temperature (SST-BT). Backward stepwise elimination was used to estimate the best-fitting model for each life history stage and the covariates chosen for each model are described in figures 4.4-4.7. Density of *M. paradoxus* adults and subadults and *M. capensis* juveniles and subadults is best described by depth. *M. paradoxus* adults have a strong positive relationship with depth (shown by the large range in y-axis values), having highest density between 300 and 500m. *M. paradoxus* subadults do not have such a strong relationship with depth (shown by the smaller y-axis values) with highest density found between 250 and 350m, after which they begin to decrease again.

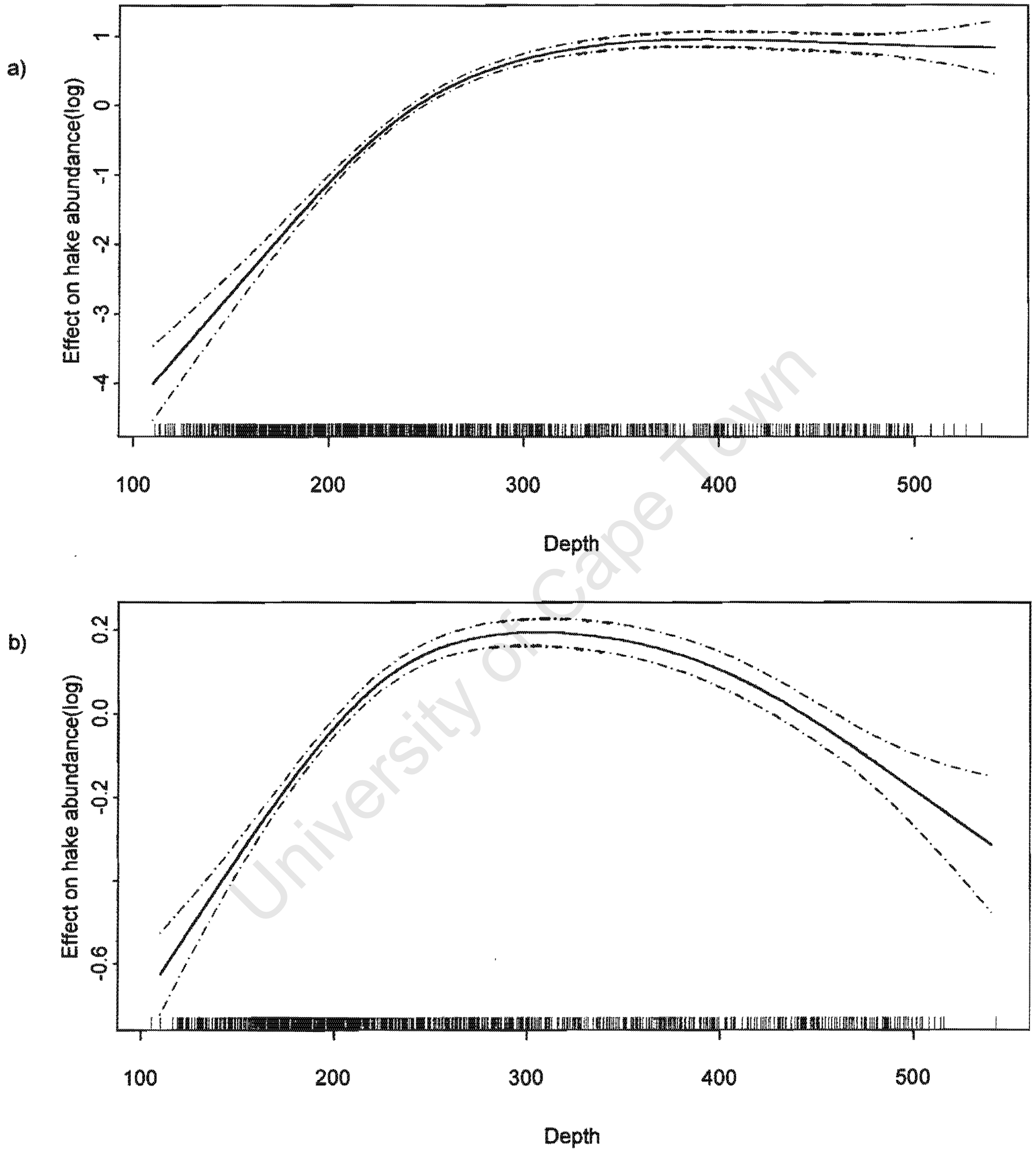
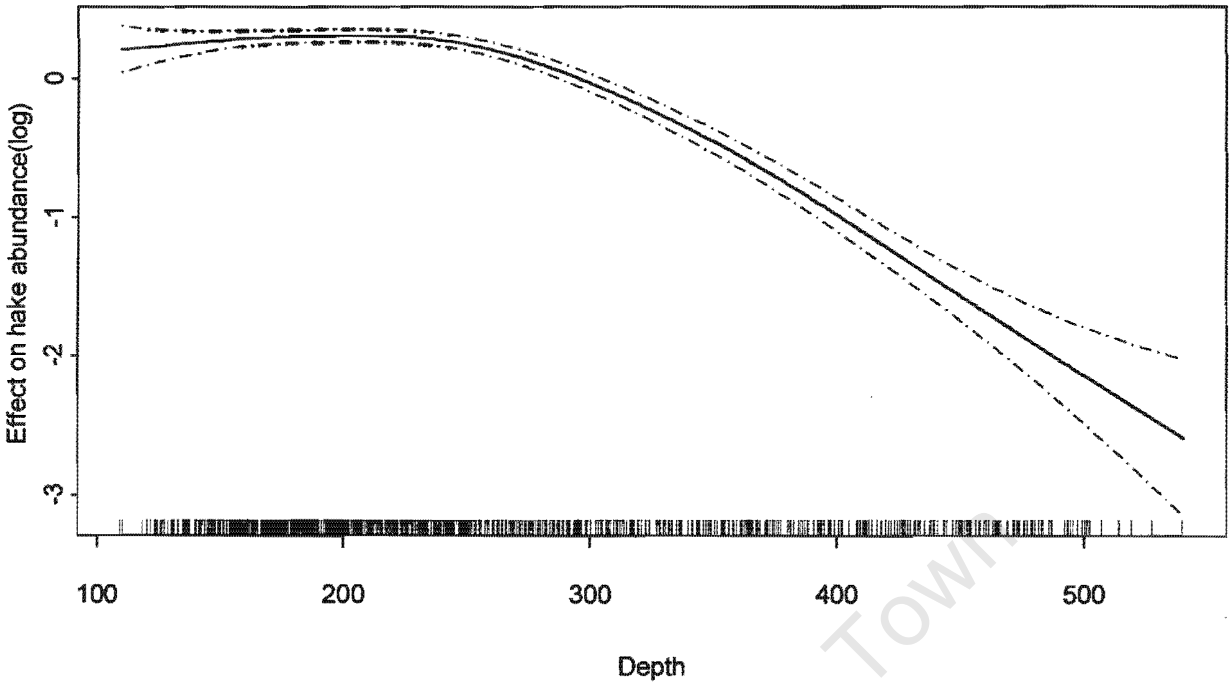


Figure 4.4: Plots of the best fitting GAM smoothes for the abundance of *M. paradoxus* a) adults and b) subadults as a function of depth. The 95% confidence interval is represented by the dotted line and a rug plot is included on the x-axis.



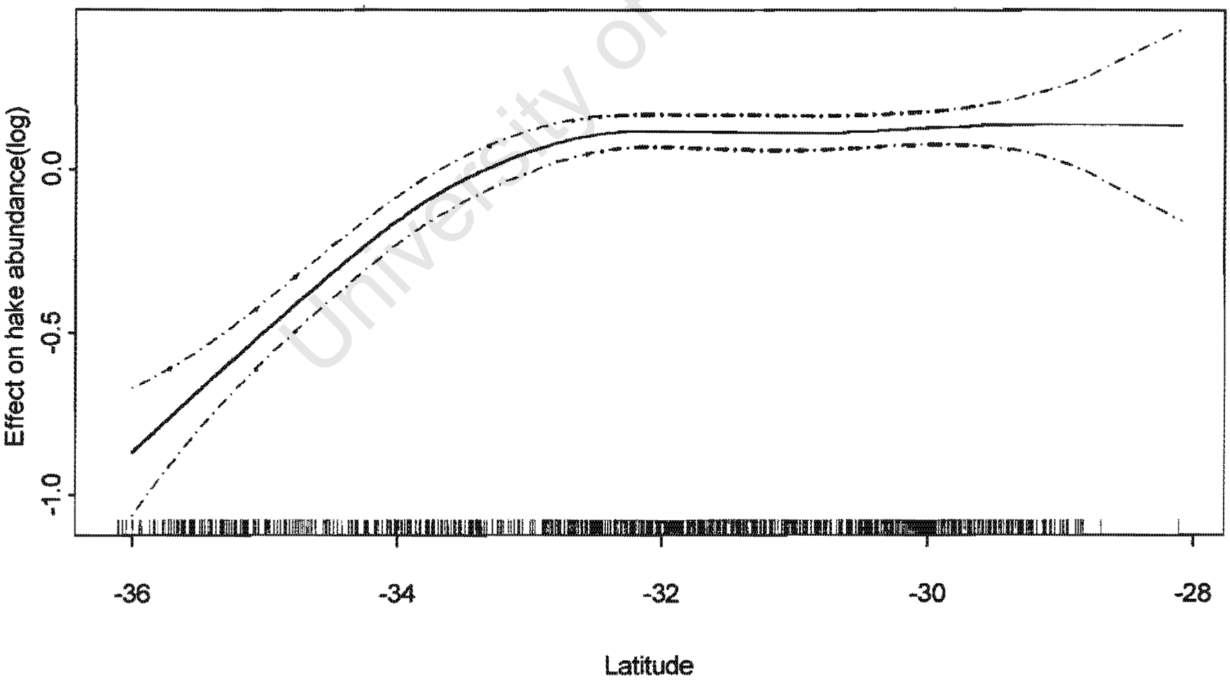
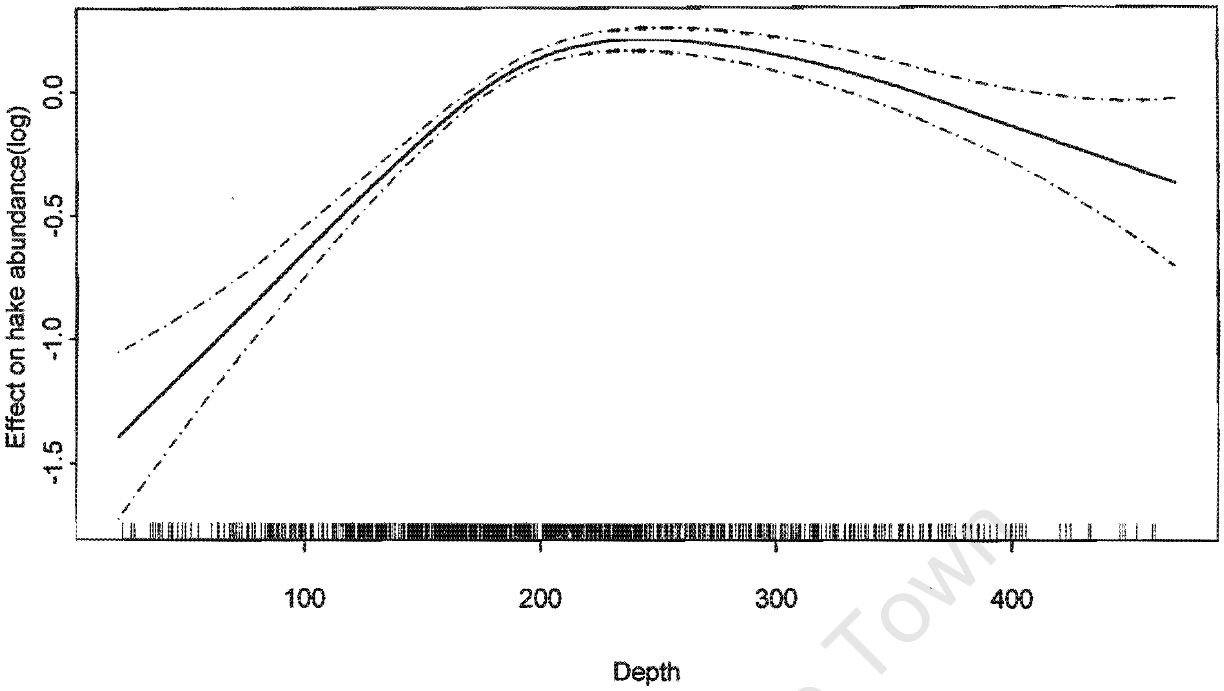


Figure 4.5: Plots of the best fitting GAM smoothes for the abundance of *M. paradoxus* juveniles as a function of depth and latitude. The 95% confidence interval is represented by the dotted line and a rug plot is included on the x-axis.



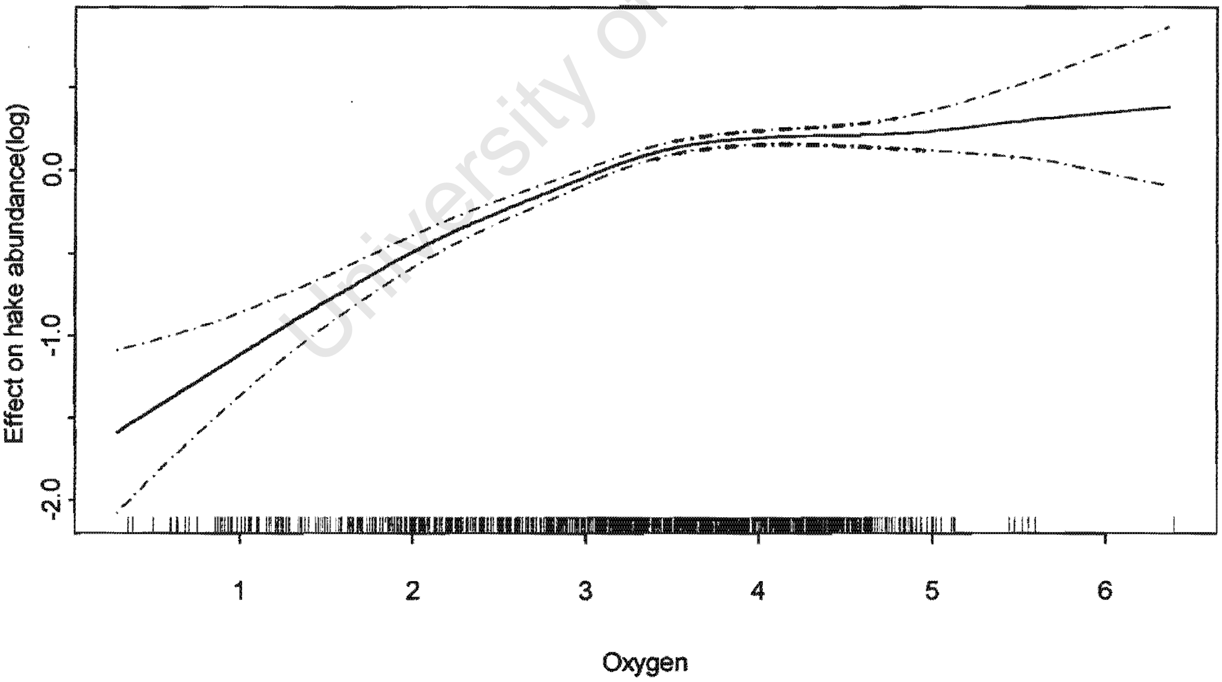


Figure 4.6: Plots of the best fitting GAM smoothes for the abundance of *M. capensis* adults as a function of depth and oxygen. The 95% confidence interval is represented by the dotted line and a rug plot is included on the x-axis.

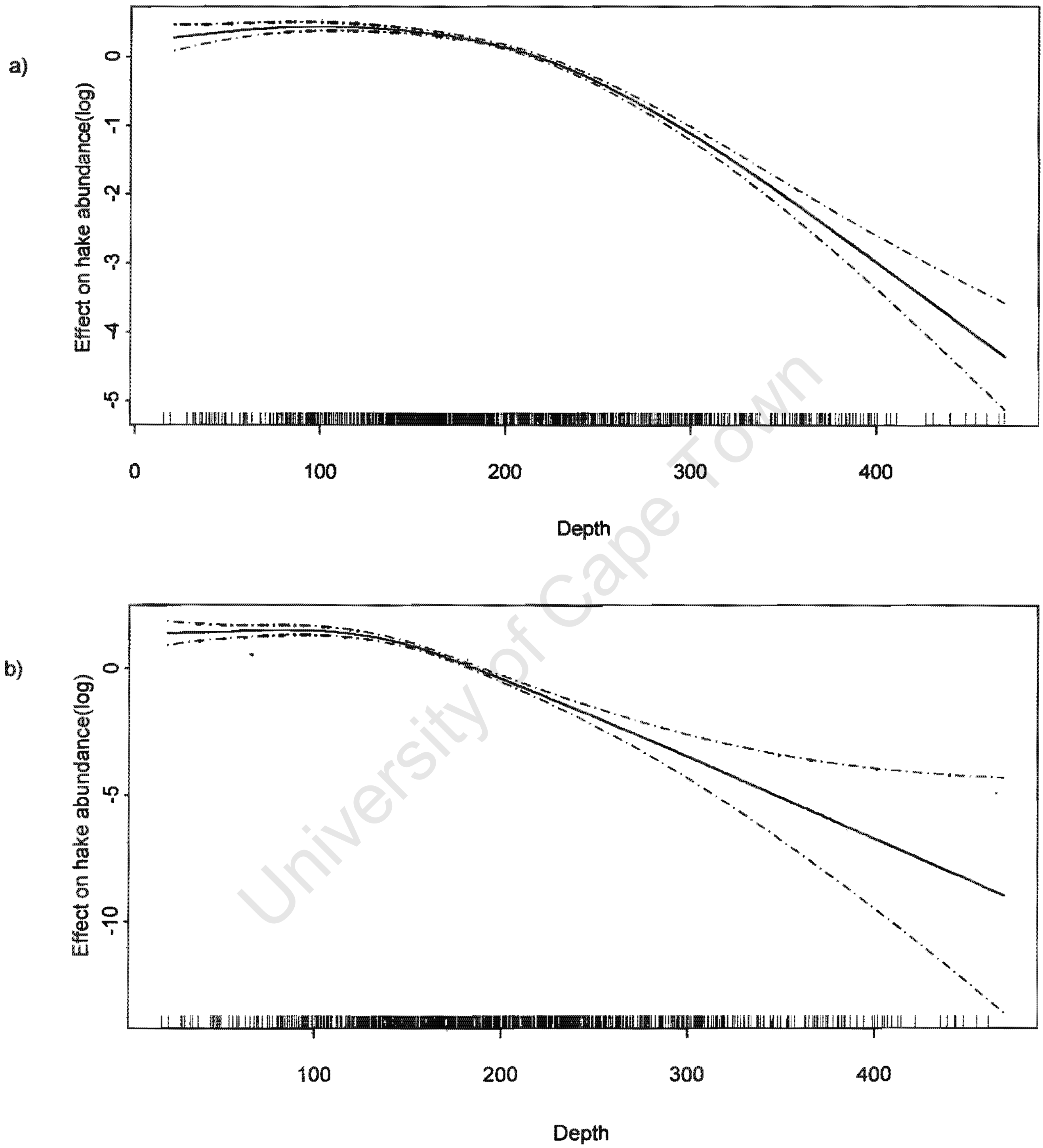


Figure 4.7: Plot of the best fitting GAM smoothes showing the abundance of *M. capensis* a) subadults and b) juveniles as a function of depth. The 95% confidence interval is represented by the dotted line and a rug plot is included on the x-axis.

M. capensis juveniles and subadults both decrease with depth, with subadults having greatest density between 50-150m and the juveniles between 50 and 100m. *M. paradoxus* juveniles are found in greatest density between 30°S and 33°S at a depth between 150 and 250m. *M. capensis* adults are found at greatest density at depths between 200 and 280m at oxygen concentrations of between 3.5 and 4.5mg.l^{-1}. It needs to be emphasized that the effect of each variable shown in the above figures is the conditional effect, that is, the effect that this variable has, given that the other variables are included in the model. Because depth is consistently the more significant effect, it is suggested that depth is the primary determining factor for arranging the spatial distribution of the hakes and determining spatial density.

4.3.3. GAM used to predict hake biomass

Table 4.4 summarize the GAM predicted (based on the best fitting GAMs) and currently used estimates of biomass calculated using the swept area method (SAM). Biomass estimates are presented together with their coefficients of variation. The GAM predicted biomass estimates were remarkably similar to those obtained by the SAM, except the GAM estimates were lower. Looking at both biomass estimation methods for *M. paradoxus*, biomass showed increases in June 1985 and June 1989 and then a general increase between January 1992 and January 1997. Both methods used for *M. capensis* showed a slight decrease in biomass between June 1984 and June 1988 with a significant increase in June 1989. After this, biomass dropped and from January 1990 to January 1997 showed a steady increase.

Table 4.4: Comparison of variation in biomass estimates by species and year between GAM and the swept area method.

Year	*M. paradoxus*				*M. capensis*			
	SAM		GAM		SAM		GAM	
	Biomass	SE	Biomass	SE	Biomass	SE	Biomass	SE
June 1984	112912	23925	84606	25881	143405	25544	104655	18883
January 1985	*	*	*	*	*	*	*	*
July 1985	*	*	*	*	*	*	*	*
January 1986	196151	36366	80631	18939	117829	23639	65809	13487
July 1986	172522	24129	147048	67196	119609	18492	66837	27891
January 1987	284859	53108	143742	21626	75705	10242	43702	13355
July 1987	195530	4425	140151	27590	87407	11201	64887	14006
February 1988	158796	27390	97444	34197	66737	10767	31802	5106
August 1988	233103	64016	115852	26012	47129	9570	21801	5416
July 1989	468928	124878	296978	142089	323879	67303	193781	110707
January 1990	282225	78956	160899	87786	455861	135253	149309	56658
July 1990	226910	46016	122953	41760	157826	23565	97317	25687
January 1991	327105	82209	92249	13151	77369	14997	25514	6859
February 1992	234699	33963	124339	28454	*	*	*	*
January 1993	321767	48800	143214	18536	106963	19049	55777	10583
January 1994	329927	58332	188724	34539	120206	35885	58082	15503
January 1995	324626	80370	149343	35598	199173	26816	118495	56838
January 1996	430971	80614	213258	34520	83347	9287	54809	33947
January 1997	570091	108230	304877	72792	257332	46062	152942	56621

*No data available

4.4. Discussion

4.4.1. Patterns in hake abundance in relation to environmental variables

From the data presented, it is evident that both species of hake have a distinct spatial distribution. Although *M. capensis* shows no clear relationship with latitude, the adult population of *M. paradoxus* was found in highest density between 32°S and 34°S. It has long been debated as to whether hake undergo horizontal migration. To some extent they have to, because large numbers of males and females must move to the same geographical location for spawning to be successful (Payne 1989). Latitudes where *M. paradoxus* were found in highest density correspond with the main spawning area for this species, which is found between 32°S and 36°S (Payne and Punt 1995). As hake spawn mainly between August and March on the west coast, with spring and early summer being the preferred seasons (Payne 1989), and the majority of the surveys undertaken in this study occurred in this time period, it would make sense that the highest density of adult *M. paradoxus* would be found in this area. According to Botha (1986) there are two peaks in spawning activity, the first late in the year by both species and the other in February/March, sustained mainly by the deep-water hake. This may explain why no clear pattern was observed for *M. capensis* adults, as most surveys occurred either in Jan/Feb or June/July, outside their peak spawning times. As nursery areas are predominantly downstream of the spawning areas (Payne and Punt 1995), it is understood why juvenile *M. paradoxus* are found in lower latitudes.

The large concentration of *M. capensis* juveniles and subadults found in higher longitudes close to the shore, particularly around areas such as St Helena Bay and around the Orange River mouth, probably arise from the passive transport of eggs and larvae by currents to these areas. It is also believed that the juvenile fish actually seek out these areas of favourable conditions, which are relatively protected from competitors located further offshore (Roel and Bailey 1987).

It is clear that both species have a clear depth preference. *M. capensis* lives inshore and is distributed mainly up to the margin of the continental shelf (Botha 1980), apparently preferring the area where the shelf is widest and the slope is steepest. In contrast, *M. paradoxus* prefers to be further offshore over the continental margin, where the shelf is narrower and less sloped (Payne *et al.* 1987). In addition there is a size graduation by depth whereby the average fish size increases with depth. The observation of smaller fish close to shore implies an inshore migration of early life stages. As fish become older, their depth range is probably influenced by physiological constraints. *M. paradoxus* moves further inshore in summer and is found in deeper waters in winter. This inshore-offshore migration is well documented in other hake species (Pitcher and Alheit 1995) and, in the case of Namibian hake, shoreward migration is considered to be a spawning migration, whereas the offshore migration is thought to be related to feeding (Gordoa *et al.* 1995).

Temperature is a major factor in fish metabolism and behavioural responses. Fish tend to congregate in thermal ranges that offer them the opportunity for maximum activity and this is manifested in their abundance and distribution (Maravelias 1997). The data show that *M. paradoxus* adults are found in lower bottom temperatures than their juveniles. *M.*

capensis juveniles are also found in warmer waters than their adults. It would appear, therefore, that these differences in the distribution of juveniles and adults may be caused by having different temperature tolerances and preferences. It is well documented that large fish show greater preferences for colder waters than smaller fish of the same species. It has been suggested that older fish live in colder waters as a result of a physiological need where they benefit from lower metabolic costs and therefore greater longevity (Wise 1980). In contrast, younger fish live in warmer waters where food supply and growth rates are often greater (Macpherson and Duartė 1991).

Bottom waters with low levels of dissolved oxygen characterize upwelling areas, such as the southern Benguela system. Very low levels of bottom oxygen concentration have been known to not only affect the distribution and abundance (Mas Riera *et al.* 1990) of certain species but also their activity (Roel and Macpherson 1988). In Namibia, hypoxic water has been seen to displace juvenile *M. capensis* offshore from their typical inshore habitat (Hamukuaya *et al.* 1998). The scatterplot smooths show that adults of both species are found in higher bottom oxygen concentrations than their juveniles. This is probably because growth of fish is oxygen limited (Pauly 1984). The major cause for this oxygen limitation is that fish gills do not grow as fast as the body they have to supply with oxygen (Pauly 1984, 1998). As a result, larger fish are not able to take up oxygen as efficiently as smaller fish. Thus older hake require areas of higher bottom oxygen concentration than juveniles that are able to survive in waters of lower oxygen concentration. As oxygen in excess of routine requirements is required for growth, the latter will cease when a certain size is reached at which relative gill area is just sufficient to cover routine metabolism. Hence, any factor which reduces routine metabolism, such as lower temperatures, will have the effect of increasing that certain size (Pauly 1997). This may also explain why adult hake prefer lower temperatures as this reduces their metabolism and hence lowers requirements for oxygen. Juvenile *M. capensis* are able to withstand lower bottom oxygen concentrations than juvenile *M. paradoxus* which seem to avoid these areas and stay further offshore. Roel and Bailey (1987) speculated that *M. capensis* must possess some physiological means of tolerating oxygen deficiency which is not possessed by juvenile *M. paradoxus*. Hake juveniles seem to remain in coastal areas of low oxygen concentration instead of occupying a wider, more comfortable, range of depth distribution and this may be as a result of the juveniles trying to avoid predation and cannibalism by larger fish. It must be noted, however, that the hakes might not actually be responding to the changes in oxygen concentration. This is because the availability of oxygen is not linearly related with its concentration because it changes with partial pressure which changes with depth.

Adults of both species were found in greatest density at higher sea surface temperatures than juveniles. In the past, relationships have been observed between sea surface temperature and hake (Macpherson *et al.* 1991, Roel and Bailey 1987). A similar observation was made by Roel and Bailey (1987) in their study on *M. capensis* off northern South Africa and southern Namibia. The effect of sea surface temperatures on adults may be causative but, as juveniles are known to undertake stronger daily vertical migrations than adults and are considered semipelagic, sea surface temperature is more likely to have a direct effect on juveniles.

Macpherson *et al.* (1991), in their study of *M. capensis* in Namibia, found that hake distribution was not affected by sea surface temperature, but that biomass definitely was. They believed that warm conditions could induce hake to concentrate closer to the seabed, making them more susceptible to bottom trawl. They therefore challenged the hypothesis that hake density is related to biomass, implying that abnormally warm summers could suggest higher catches, regardless of the state of the stock. In addition, during warm periods, the upwelling-oceanic front occurs nearer the coast and Shannon *et al.* (1988) believed that this could lead to increased densities of hake and their prey in these areas.

Adults of both species tend to occur in waters with high surface minus bottom temperature values, representative of more stratified waters at a given depth. Spawning rarely occurs in areas of strong turbulent mixing of the water column (Parish *et al.* 1981) and this may be the reason as to why adults seem to prefer deeper waters.

4.4.2. GAM to show the relationship between hake abundance and environmental variables

Whilst there appears to be a fair amount of correlation between bottom temperature, bottom oxygen concentration, sea surface temperature, SST-BT and depth, depth was a consistently significant effect in all the GAM fits. In addition, the consistent large decrease in pseudo-R^2 between model 1 and model 2, suggests how important longitude, latitude and depth are in determining hake density. Furthermore, all the best fitting models for both species, and each life history stage, included depth as the main determinant of hake density. It is therefore suggested that depth is a primary factor in determining spatial hake density gradients in the southern Benguela system. Similarly, depth was the main covariate to determine panga density on the Agulhas Bank (Booth 1998), flatfish density in the Bering Sea (Swartzman *et al.* 1992) and pollock schools in the Bering Sea (Swartzman *et al.* 1994, 1995).

A large number of demersal fish species show a general tendency to increase in size towards deeper waters (Macpherson and Duarte 1991). This positioning of fish within their depth range appears to reflect a general behaviour pattern. Consideration of several hypotheses to account for the general pattern suggests that it reflects a migratory movement towards deeper waters during ontogeny, where fish benefit from the extended lives and lower metabolism at lower temperatures. However, as so many studies, including this one, show depth as being the primary predictor above all other environmental factors examined, I agree with Macpherson and Duarte (1991) who suggested that the size-depth relationship observed represents an evolutionary response of the fish, independent of the depth changes in habitat conditions in the particular location inhabited by the fish. Therefore, as Macpherson and Duarte (1991) suggested, this pattern is more likely to be evolutionary in nature and due to inherited behaviour.

4.4.3. GAM used to predict hake biomass

The spatial trends that have been highlighted can be incorporated into the generation of biomass estimates. The trends in GAM biomass estimates show an increase of both *M. paradoxus* and *M. capensis* over the last 13 years, being more evident in *M. paradoxus*.

A similarity was observed in abundance estimates between the two biomass estimators compared in this study. This is probably due to the fact that depth was the primary determining factor in the GAMs and that the depth stratification method is the method used to calculate current biomass estimates by Marine and Coastal Management, Cape Town (Booth 1998). Therefore, these results support the use of depth as the characteristic to be used when defining the strata for the stratified sampling technique.

Although the GAMs provide realistic fits to the data, it would be wrong to say that depth was the only main factor involved in determining spatial hake density gradients and arranging spatial distribution. It is more than likely other factors such as currents, thermocline depth, prey movements etc., that were not examined here, may also be important. Further investigation is needed of additional environmental factors which may influence hake distribution.

Chapter 5

Conclusions

Because it is very important to understand the dominant factors that control variability in fish populations, interpreting behavioural responses of fish to environmental circumstances is essential (Crawford *et al.* 1990). However, the variability that has been observed in fish stocks has proven difficult to understand in the past and has led some to believe that it will be a long time before these problems are solved. Bakun (1996) has listed a number of reasons for this, including; 1) conditions within the ocean are not agreeable to any sort of experimental control, 2) the varying degrees of motion occurring in the ocean make it impossible to maintain the integrity of the volume of water in which an experiment is taking place unless it is contained in some way (but this just restricts the scales of processes and alters essential mechanisms) and 3) the conventional fisheries science paradigm relies heavily on temporal-spatial averaging (e.g. one data point per stock per year etc), whereas major changes could be occurring between these sampling periods. In addition, it is difficult to separate the effects of man from those of the environment (Crawford *et al.* 1990).

It is essential that fisheries biologists understand these fluctuations and the interactive impact of environmental factors for management purposes, and more and more studies such as this one, on differing fish stocks, are being undertaken in an attempt to get closer to finding a solution to this problem. Therefore, this study provides a start to quantifying the environmental effects that may influence the abundance and distribution of the Cape hakes, *M. capensis* and *M. paradoxus* in the southern Benguela system.

Of all the environmental variables tested in this study, depth was found to be the primary factor in determining hake spatial density gradients and arranging spatial distribution by both the GIS and the GAM. Individual relationships for hake density against each environmental variable were observed in scatterplot smoothes but, in all cases, depth was seen to be the most important factor affecting the hakes. It is difficult to understand why fish should associate closely with particular depths alone. As all the environmental variables examined are depth-related, it is hard to say whether the fish occur in greatest density at certain depths because of one or more of these environmental variables or for some other reason not tested here. The fact that depth is the primary factor affecting hake and that there could be a logical explanation due to environmental variables that smaller hake occur in shallower waters (i.e. can tolerate low oxygen levels) and larger hakes in deeper waters (where they benefit from lower metabolic costs and greater longevity), it would seem that their distribution could be an evolutionary response due to inherited behaviour (Macpherson and Duarte 1991). However, because there are so many environmental parameters that weren't tested in this study, one cannot rule out the fact that depth serves as a proxy for other variables (Perry *et al.* 1994) not measured in this study.

One environmental variable that did seem to have more of an effect on *M. capensis* adult density was bottom oxygen concentration. *M. capensis* occur closer inshore where oxygen levels are lower and so would be subject to more adverse conditions on occasion. As juveniles handle lower oxygen concentrations better than adults do (Pauly 1984), their distribution and abundance would not be effected by changes in oxygen concentration as much as adults. The reason why *M. capensis* occur closer inshore than *M. paradoxus* is unknown, but it has been suggested that *M. capensis* juveniles must possess some physiological means of tolerating oxygen deficiency which is not possessed by juvenile *M. paradoxus* which seem to avoid these areas (Roel and Bailey 1987). The structures of the gills of each species differ (Botha 1980, Van Eck 1969) and these differences could influence their ability to take up dissolved oxygen.

When looking at sea surface temperature it appears that the distribution of hake, in particular that of *M. paradoxus*, is possibly related to the movement of the 16°C isotherm. As this isotherm is associated with the oceanic front and, therefore, increased productivity associated with the front, the need to find an adequate food supply for maintenance, growth and reproduction may have contributed to shaping the migratory pattern of hake (Podesta 1989). Because it is unlikely that fish distribution is determined by physical factors alone, it is important to also consider biotic factors such as prey abundance which have also been shown to be important determinants of distribution. However, further analysis is required to confirm this.

The hakes appear to also be in some way connected to the ENSO index but with a 1 year time-lag. In particular, they appear to have more of a relationship with the cold phase El Niño or La Niña. Similar conditions to an El Niño occur in the Benguela a year after the Pacific El Niño, thus, it is suggested that the Benguela may also experience similar conditions to a Pacific La Niña the year after that occurs. Unfortunately, many countries have shown little if any interest in cold events (Kiladis 1998), including South Africa where no literature can be found on their effects. With respect to the southern Benguela, trends in the southern oscillation index are likely to reflect changes in the flux of Agulhas Current water into the SE Atlantic (Shannon *et al.* 1988). Effects are thought to be brought about by teleconnections which are the influence of sea surface temperature variation in the tropical Pacific on regional and local climate regimes around the world. However, the reliability of ENSO teleconnection signals becomes less as one moves away from the tropical Pacific. In addition, weak and moderate La Niña events might not be strong enough to generate climate anomalies in distant locations such as the Benguela ecosystem. In general, robust signals have appeared as far away from the tropical Pacific as Africa. (Kiladis 1998). Therefore, it is likely that only the effects of strong La Niña events would be apparent in the Benguela and so weak Pacific La Niñas would not be apparent.

Wind has also been documented in having an effect on hake abundance. Therefore it must have some sort of effect on the ocean which in turn then affects the hake. Ralton Maree (BEP, pers. comm.) has suggested that wind-induced currents could influence hake abundance. It has also been shown that, in years when the southeasterly wind has been at its strongest, biomass, in particular that of *M. paradoxus*, has increased during those years. However, those working in the fishing industry have documented that on a shorter time-scale, when the southeasterly wind blows, catchability seems to drop. Therefore it seems from this statement, that there may be an inverse relationship between biomass and catchability. It has been suggested by Gordoa and Hightower (1991) that catchability of some demersal fish may be inversely related to abundance.

The best fitting GAM models were used to generate biomass estimates and these have been plotted in Figure 5.1.

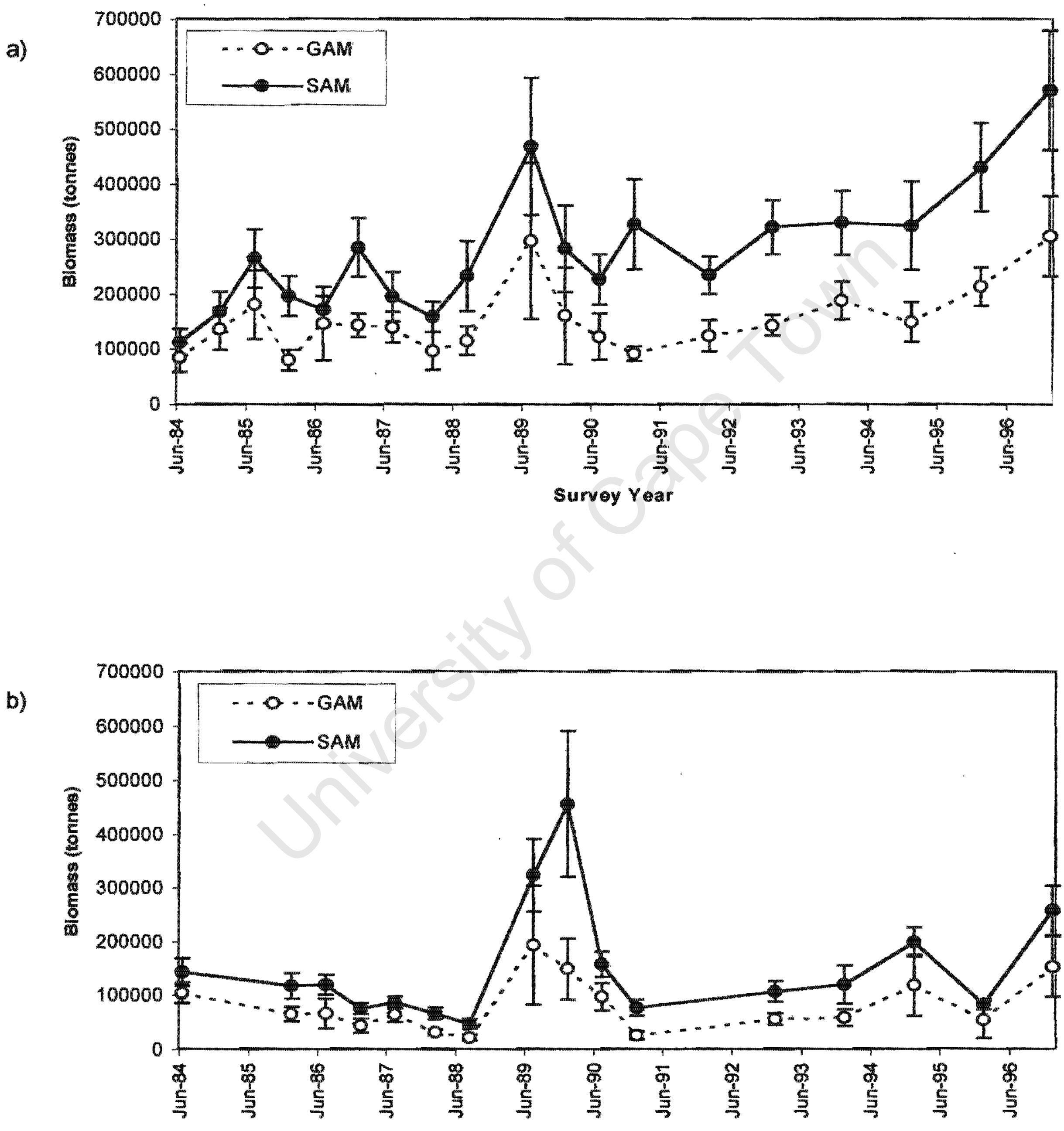


Figure 5.1. Results of the GAM estimates (dotted lines) for a) *M. paradoxus* and b) *M. capensis* for each survey year compared with the swept are method (SAM) (solid line) ± SE.

The GAM derived biomass estimates were shown to be more constant with a reduction in variability when compared to the swept area method estimates. This is felt to be as a result of the smooth of the GAM which tends to downplay the effect of extremely large counts at individual trawl stations which would normally strongly influence the biomass estimate (Booth 1997). Booth (1997) debated whether or not there is an improvement in the estimation of abundance over the swept area method and it is agreed with him that the averaging effect of the GAM may mask any significant changes in biomass within the years analyzed. Therefore, in agreement with Booth's (1997) conclusion, it is felt that the swept area method estimates should be used in the short term until simulation can provide results as to whether or not the GAM abundance estimates are preferable.

Hake on the west coast of South Africa are assessed using a Shaeffer type surplus production model based on catch per unit effort and tuned with survey estimates. A potential limitation of the surplus production model used to manage the hake fishery is the assumption that catchability is constant. As it appears that this might not be true for the Cape hakes, management problems would be greatest when the stock declined to low levels because 1) biomass and catch quotas obtained from traditional surplus production models would tend to be overestimated and 2) further management errors would be likely when setting either effort or catch quotas because of the rapidly changing relationship between effort and fishing mortality (Gordoa and Hightower 1991). It is agreed with Butterworth (1988) that conservative management is needed until the factors affecting catchability are fully understood.

The criticism by Sharp (1987) that fisheries management procedures and forecasting techniques that fail to directly account for causal short- and long-term environmental processes will remain speculative and sustain wishful thinking is widely supported. Therefore the identification of strong associations of fish with particular habitat conditions is essential. Not only environmental processes but also other factors such as food availability, bottom type and seasonal migration, all interrelated with physical factors, may also play a role (Scott 1982). It is, therefore, important to continue investigating additional variables that may influence Cape hakes.

This study has provided additional insights into the effect of the environment on the Cape hakes, but has also raised questions that suggest avenues for further research. First, what other factors related to depth may cause different life history stages to choose preferential depth ranges? Second, is the inshore summer movement that follows the front, related to food availability or some other factor related to the front such as the jet current? Third, the effect of wind-induced currents needs to be investigated more closely, in particular the possibility that hakes may make use of them as a measure of orientation for their movements to spawning or feeding grounds. Fourth, more attention needs to be paid to the effects that southern oscillation index and teleconnections have on the Benguela, particularly the possibility that the La Niña could have an effect in the southern Benguela. If these effects can be established then they could be related to hake abundance and distribution. In addition, connections between ENSO events and local winds should be investigated. Last, from a physiological perspective, the differences between the gills of both species need to be examined in terms of their ability to take up dissolved oxygen more efficiently. Once these questions have been answered, we will be closer to understanding the variability in biomass and distribution that is observed in both of the Cape hakes.

References

AGENBAG, J.J. 1996 - Pacific ENSO events reflected in meteorological and oceanographic perturbations in the southern Benguela system. *S. Afr. J. Sci.* 92: 243-246.

BAILEY, G. 1998 – Variability of hypoxia in response to physical and biogeochemical processes in the Benguela upwelling system. Abstracts of the International Symposium on Environmental Variability in the South-east Atlantic, Swakopmund, Namibia. 30 March – 1 April.

BAILEY, K.M. 1980 - Recent changes in the distribution of hake larvae: Causes and consequences. *Calif. Coop. Oceanic Fish. Investig. Repts.* 21.

BAKKEN, E. 1983 – Recent history of Atlanto-Scandian herring stocks. *FAO Fish. Rept.* 291(2): 521-536.

BAKUN, A. 1996 - Patterns in the Ocean: Ocean Processes and Marine Population Dynamics. University of California Sea Grant Program, San Diego, California, USA, in co-operation with Centro de Investigaciones Biologicas de Noroeste, La Paz, Mexico: 323pp.

BAKUN, A. 1998 – Global climatic teleconnections and fisheries ecology: a perspective (with comments on the Benguela System). Abstracts of the International Symposium on Environmental Variability in the South-East Atlantic, Swakopmund, Namibia. 30 March – 1 April.

BAKUN, A. and R.H. PARRISH. 1981 – Environmental inputs to fishery population models for eastern boundary current regions. In *Report and Supporting Documentation of the Workshop on the Effects of Environmental Variation on The Survival of Larval Pelagic Fishes, Lima*, 1980. Sharp, G.D. (Conv. Ed). Paris; UNESCO: 67-104 (I.O.C. Workshop Rep. 28).

BANG, N.D. and W.R.H. ANDREWS. 1974 - Direct current measurements of an oceanic frontal jet in the upwelling regime west of Cape Town. *J. Mar. Res.*32: 405-417.

BOOTH, A.J. 1997 - Biology, stock assessment and management of the panga *Pterogymnus laniarius* on the Agulhas Bank, South Africa. Ph.D thesis, Rhodes University: 173pp.

BOOTH, A.J. 1998 - Spatial analysis of fish distribution and abundance: A GIS approach. In *Fisheries Stock assessment models*. Funk, F., Quinn, I., Heifetz, J., Ianelli, J.N., Powers, J.E., Schweigert, J.F., Sullivan, P.J. And C.I. Zhang (Eds.). Alaska Sea Grant College Program Report No. AK-SG-98-01, University of Alaska, Fairbanks.

BORCHERS, D.L., BUCKLAND, S.T., PRIEDE, I.G. and S. AHMADI. 1997 - Improving the precision of the daily egg production method using generalized additive models. *Can. J. Fish. Aquat. Sci.* 54: 2727-2742.

BOTHA, L. 1971 - Growth and otolith morphology of the Cape hakes *Merluccius capensis* Cast. and *M. paradoxus* Franca. *Investl Rep. Div. Sea Fish. S. Afr.* 97: 32pp.

BOTHA, L. 1980 – The biology of the Cape hakes *Merluccius capensis* Cast. *And M. paradoxus* Franca in the Cape of Good Hope area. Ph.D thesis, University of Stellenbosch: 182pp.

BOTHA, L. 1985 - Occurrence and distribution of Cape hakes *Merluccius capensis* Cast. and *M. paradoxus* Franca in the Cape of Good Hope area. *S. Afr. J. mar. Sci.* 3: 179-190.

BOTHA, L. 1986 - Reproduction, sex ratio and rate of natural mortality of Cape hakes *Merluccius capensis* Cast. and *M. paradoxus* Franca in the Cape of Good Hope Area. *S. Afr. J. mar. Sci.* 4: 23-35.

BOYD, A.J., TAUNTON-CLARK, J. and G.P.J. OBERHOLSTER. 1992 - Spatial features of the near-surface and midwater circulation patterns off western and southern South Africa and their role in the life histories of various commercially fished species. *S. Afr. J. mar. Sci.* 12: 189-206.

BOYD, A.J. AND G. NELSON. 1998 - Variability of the Benguela current off the Cape Peninsula, South Africa. *S. Afr. J. mar. Sci.* 19: 27-40.

BRANDHORST, W. 1959 – Relationship between the hake fishery and a southerly subsurface return flow below the Peru Current off the Chilean Coast. *Nature*. 183: 1832–1833.

BRINK, K.H. 1998 - Wind-driven currents over the continental shelf. In *The global Coastal ocean: Processes and methods*. Brink, K.H. and A.R. Robinson (Eds.). John Wiley and Sons Inc. USA.

BRUNDRIT, G.B. 1981 - Upwelling fronts in the southern Benguela region. *Trans. Roy. Soc. S. Afr.* 44(3): 309-313.

✓BUTTERWORTH, D.S. 1988 - Some recommendations regarding the assessment methodologies used by ICSEAF. *Collect. Sci. Pap. Int. Comm. SE Atl. Fish.* 15(1): 107-155.

✓BUTTERWORTH, D.S. and P.A. ANDREW. 1984 - Dynamic catch-effort models for the hake stocks in ICSEAF division 1.3-2.2. *Colln scient. Pap. Int. Comm SE Atl. Fish.* 11(1): 29-58.

✓BUTTERWORTH, D.S., HUGHES, G. and F. STRUMPFER. 1990 - VPA with ad hoc tuning: implementation for disaggregated fleet data, variance estimation, and application to the Namibian stock of Cape horse mackerel *Trachurus trachurus capensis*. *S. Afr. J. mar. Sci.* 9: 327-357.

CARRUTHERS, J.N. 1938 – Fluctuations in the herring of the East Anglian autumn fishery, the yield of the Ostend spent herring fishery, and the haddock of the North Sea – in the light of relevant wind conditions. *Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer.* 107(3): 10–15.

CARSCADDEN, J., NAKASHIMA, B.S. and K.T. FRANK. 1997 – Effects of fish length and temperature on the timing of peak spawning in capelin (*Mallotus villosus*). *Can. J. Fish. Aquat. Sci.* 54(4): 781–787.

CASTILLO, J., BARBIERI, M.A. and A. GONZALEZ. 1996 - Pelagic fish resources distribution related to some sea surface characteristics. *ICES J. Mar. Sci.* 53: 139-146.

CHAMBERS, J.M. and T.J. HASTIE. 1992 - Statistical Models in S. Wadsworth and Brooks/Cole Advanced Books and Software. Pacific Grove, California. 608pp.

CRAWFORD, R.J.M., SHANNON, L.V. and D.E. POLLOCK. 1987 - The Benguela Ecosystem. Part IV. The major fish and invertebrate resources. *Oceanogr. Mar. Biol. Ann. Rev.* 25: 252-505.

✓CRAWFORD, R.J.M., SIEGFRIED, W.R., SHANNON, L.V., VILLACASTIN-HERRERO, C.A. and L.G. UNDERHILL. 1990 – Environmental influences on marine biota off Southern Africa. *S. Afr. J. Sci.* 86: 330–339.

CURY, P. and C. ROY. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.* 46(4): 670-680.

CURY, P., ROY, C., MENDELSSOHN, R., BAKUN, A., HUSBY, D.M. and R. H. PARRISH. 1995. Moderate is better: exploring nonlinear climatic effect on Californian anchovy. *Can. J. Fish. Aquat. Sci. 121*: 417-424.

D'AMOURS, D. 1993 – The distribution of cod (*Gadus morhua*) in relation to temperature and oxygen level in the Gulf of St. Lawrence. *Fish. Oceanogr.* 2(1): 24–29.

DOW, R.L. 1977 – Effects of climatic cycles on the relative abundance and availability of commercial marine and estuarine species. *J. Cons. CIEM.* 37(3): 274–280.

ESPINO, M. 1991 – El Niño phenomena: Its impact on the demersal fishes of Peru. *Lima.* 3(6): 19–24.

ESRI. 1997. Getting to Know ArcView GIS. ESRI Press. 675pp.

GAMMELSROD, T., BARTHOLOMAE, C.H., BOYER, D.C., FILIPE, V.L.L. and M. J. O'TOOLE. 1998 - Intrusion of warm surface water along the Angolan-Namibian Coast in February-March 1995: The 1995 Benguela Niño. *S. Afr. J. mar. Sci.* 19: 41-56.

GILES, R.H. and L.A. NIELSEN. 1992 - The uses of Geographic information systems in Fisheries. American Fisheries Society Symposium, Rhode Island, Nov 12-15: 81-94.

GORDOA, A. and J.E. HIGHTOWER. 1991 - Changes in catchability in a bottom-trawl fishery for Cape hake (*Merluccius capensis*). *Can. J. Fish. Aquat. Sci. 48*: 1887-1895.

GORDOA, A., MACPHERSON, E. and M.P. OLIVAR. 1995 - Biology and fisheries of Namibian hakes (*M. paradoxus and M. capensis*). In *Hakes - Fisheries, Ecology and Markets.* Alheit, J. and T. Pitcher (Eds.). Chapman and Hall, London. 478pp.

HAMPTON, I. And S. MATTHEWS. (eds). 1997 – BENEFIT SCIENCE PLAN. Deutsche Gesellschaft fur Technische Zusammenarbeit GmbH (GTZ) GmbH. Germany: 90pp.

HAMUKUAYA, H., O'TOOLE, M.J. and P.M.J. WOODHEAD. 1998 – Observations of Severe hypoxia and offshore displacement of Cape hake over the Namibian shelf in 1994. *S. Afr. J. Mar. Sci.* 19: 57–59.

HASTIE, T.J. and R.J. TIBSHIRANI. 1986 - Generalized Additive Models. *Stat. Sci.* 1: 297-318.

HASTIE, T.J. and R.J. TIBSHIRANI. 1990 – Generalized Additive Models. Chapman And Hall. London. 335pp.

HENDERSON, P.A. and M. CORPS. 1997 – The role of temperature and cannibalism in interannual recruitment variation of bass in British waters. *J. Fish. Biol.* 50(2): 280–295.

HOLLOWED, A.B. and K.M. BAILEY. 1989 – New perspectives on the relationship between recruitment of Pacific hake (*M. productus*) and the ocean environment. *Can. Spec. Publ. Fish. Aquat. Scie.* 108: 207–220.

HULLEY, P.A. and J.R.E. LUTJEHARMS. 1989 - Lanternfishes of the southern Benguela region. Part 3. The Pseudoceanic-oceanic interface. *Anals S. Afr. museum*. 98 (10): 409-435.

HUSE, I., HAMUKUAYA, H., BOYER, D.C., MALAN, P.E. and T. STROMME. 1998 - The diurnal vertical dynamics of Cape hakes and their potential prey. *S. Afr. J. mar. Sci*. 19: 365-376.

HUTCHINGS, L. and I. HAMPTON. 1998 - Variability in fish resources in the southern Benguela region. Abstracts of the International Symposium on Environmental Variability in the South-east Atlantic, Swakopmund, Namibia. 30 March – 1 April.

ISAAK, D.J and W.A. HUBERT. 1997 – Integrating new technologies into fisheries science: the application of Geographic Information Systems. *Fish. Yr*. 22(1): 6–9.

JAPP, D. W. 1989 - An assessment of the South African longline fishery, with emphasis on stock integrity of kingklip *Genypterus capensis* (Pisces: Ophidiidae). M.Sc. Thesis, Rhodes University, Grahamstown: 138pp.

JURY, M.R. 1985 - Case studies of alongshore variation in wind-driven upwelling in the Southern Benguela region. In *South African Ocean Colour and Upwelling Experiment*. Shannon, L.V. (Eds.). Sea Fisheries Research Institute: 29-46.

KALUZNY, S., VEGA, S., CARDOSO, T. and A. SHELLEY. 1996 - S-Plus Spatial Stats. MathSoft, Inc. Seattle, Washington. 226pp.

KERR, R.A. 1988 - La Nina's big chill replaces El Nino. *Science*. 241: 1037-1038.

KIESER, R., LANGFORD, G. and K. COOKE. 1995 - The use of geographic information systems in the acquisition and analysis of fisheries acoustic data. ICES Int. Symp. on Fisheries and Plankton Acoustics, Aberdeen. 12-16 June.

KILADIS, 1998 - A La Nina Summit, Boulder Colorado: 15-17 July.

KORRUBEL, J.L. 1995 - Predicting recruitment in South Africa anchovy. M. Sc. Thesis. University of Cape Town. 190pp.

KRAMER, D.L. 1987 - Dissolved oxygen and fish behaviour. *Environmental Biol. Fishes*. 18: 81-92.

LAEVASTU, T. 1993 – Marine climate, weather and fisheries. Fishing News Books. Oxford. 204pp.

LAEVASTU, T. and M.L. HAYES. 1981. Fisheries Oceanography and Ecology. Fishing News Books. Oxford. 199pp.

LE CLUS, F., AGENBAG, J.J., HENNIG, H.F-K.O., ROBERTS, M.J., GRUNDLINGH, M.L., SIMS, P.F. and M.J. STRUTHERS. 1998 – Seasonal and interannual variability in wind field and commercial catch rates of *Austroglossus pectoralis* (Soleidae). *S. Afr. J. Mar. Sci.* 19: 377–390.

LEE, D.S and R.B. WHITLATCH. 1995 – Influence of hypoxia on the foraging ecology and movement of juvenile winter flounder. New York Sea Grant Inst. Stony Brook. New York. 90pp.

LEHODEY, P. and R. GRANDPERRIN. 1996 – Influence of temperature and ENSO events on the growth of the deep demersal fish alfonsino, *Beryx splendens*, off New Caledonia in the western tropical South Pacific Ocean. *Deep-Sea Res.* 43(1): 49–57.

√LESLIE, R.W.1986 – Stock assessments for Cape hakes in ICSEAF divisions 1.6 and 2.1 + 2.2. *Colln scient. Pap. Int. Comm SE. Atl. Fish.* 13(2): 27-36.

LONG, B., SKEWES, T.D. and I. POINER. 1994 - Geographic Information Systems helps manage Torres Strait fisheries. *Aust. Fish.* 53 (2): 14-15.

MACPHERSON, E., MASO, M., BARANGE, M. and A. GORDOA. 1991 – Relationship between measurements of hake biomass and sea surface temperature off Southern Namibia. *S. A. J. mar. Sci.* 10: 213-217.

MACPHERSON, E. and C.M. DUARTE. 1991 – Bathymetric trends in demersal fish size: is there a general relationship? *Mar. Ecol. Prog. Ser.* 71:103–112.

MAGNUSON, J.J., BRANDT, S.B. and D.J. STEWART. 1980 - Habitat preference and fishery oceanography. In *Fish Behaviour and its use in the capture and culture of Fishes.* Bardach, J.E., Magnuson, J.J., May, R.C. and J.M. Reinhart (Eds.). International center for living aquatic resources management, Manila.

MARAVELIAS, C.D.1997 – Trends in abundance and geographic distribution of North Sea herring in relation to environmental factors. *Mar. Ecol. Prog. Ser.* 159: 151-164.

MARTIN, W.R. and A.C. KOHLER.1965 – Variation in recruitment of cod (*Gadus morhua* L.) in southern ICNAF waters, as related to environmental changes. *ICNAF Spec. Publ.* 6: 833– 846.

MAS-RIERA, J., LOMBARTE, A., GORDOA, A. and E. MACPHERSON. 1990 – Influence of Benguela upwelling on the structure of demersal fish populations off Namibia. *Mar. Biol.* 104: 175–182.

MEADEN, G.J. 1993 - Instigation of the world's first marine fisheries GIS. *Counc. Meet. Of the Int. Counc. For the Exploration of the Sea, Dublin.* 13pp.

MEADEN, G.J. and T. DO CHI. 1996 – Geographical Information Systems: Application to marine fisheries. FAO Fisheries Technical Paper. Rome.

MENDELSSOHN, R. and P. CURY. 1987 - Fluctuations of a fortnightly abundance index of the Ivoirian coastal pelagic species and associated environmental conditions. *Can. J. Fish. Aquat. Sci.* 44: 408-421.

MOHR, H. 1964 - Changes in the behaviour of fish due to environment and motivation and their influence on fishing. ICNAF Environmental Symposium, Rome, Contrib. G-3.

MOLLER, H. and U. SCHOLTZ. 1991 - Avoidance of oxygen-poor zones by fish in the Elbe River. *J. Appl. Ichthyol.* 7: 176-182.

MURAWSKI, S. A. and J. T. FINN. 1988 – Biological bases for mixed-species fisheries: Species co-distribution in relation to environmental and biotic variables. *Can. J. Fish. Aquat. Sci.* 45: 1720–1734.

NATHANIEL, D. E., RAMANA, T. V. and M. P. M. REDDY. 1990 – Influence of some Bottom water oceanographic features on demersal fish catches in the Arabian Sea Off Manjeswar. *J. Mar. Biol. Ass. India.* 32 (1-2): 162–169.

NILSSEN, E.M., PEDERSEN, T., HOPKINS, C.C.E., THYHOLDT, K. and J.G. POPE. 1993 – Recruitment variability and growth of Northeast Arctic cod: Influence of physical environment, demography, and predator-prey energetics. *ICES Symposium*. 30.

NOAA WEB PAGE. Available: http://www.pmel.noaa.gov/toga_tao/el-nino/home.html

OLIVER, M.P., RUBIES, P. and J. SALAT. 1998 - Early life history and spawning of *M. capensis* in the northern Benguela current. *S. A. J. Mar. Sci.* 16: 245-254.

O'TOOLE, M.J. 1995 – The Benguela current and comparable eastern boundary upwelling ecosystems. Deutsche Gesellschaft fur Technische Zusammenarbeit (GTZ) GmbH. Germany. 154pp.

OWEN, R.W. 1981 - Fronts and eddies in the sea: mechanisms, interactions and biological effects. In *Analysis of Marine Ecosystems*. Longhurst, A.R. (Ed.). Academic Press, London. 197-233.

PARRISH, R.H., BAKUN, A., HUSBY, D.M and C.S. NELSON. 1981 - Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. *Ocean Scale and Regional Comparison*: 734-759.

PAULY, D. 1981 – The relationships between gill surface area and growth performance In fish: a generalization of von Bertalanffy's theory of growth. *Meeresforsch.* 28: 251–282.

PAULY, D. 1984 – A mechanism for the juvenile-to-adult transition in fishes. *J. Cons. Int. Explor. Mer.* 41: 280-284.

PAULY, D. 1997 – Geometrical constraints on body size. *Tree.* 12 (11): 442.

PAULY, D. 1998 – Tropical fishes: patterns and propensities. *J. Fish Biol.* 53 (A): 1-17.

✓PAYNE, A.I.L. 1986 - Biology, stock integrity and trends in the commercial fishery for demersal fish on the south-east coast of South Africa. Ph.D thesis. University of Port Elizabeth. 368pp.

✓PAYNE, A.I.L. 1989 – Cape hakes. In: *Oceans of Life off Southern Africa.* Payne, A.I.L. And R.J.M. Crawford (Eds.), Vlaeberg, Cape Town: 136-147.

✓PAYNE, A.I.L. and A.E. PUNT. 1995 - Biology and fisheries of South African Cape hakes (M.capensis and M.paradoxus). In *Hake - Fisheries, Ecology and Markets.* Alheit, J. and T. Pitcher (Eds.). Chapman and Hall, London. 478pp.

✓PAYNE, A.I.L., LESLIE, R.W. and C.J. AUGUSTYN. 1987 - Biomass index of Cape Hake and other demersal fish species in division 1.6 in 1986. *Colln scient. Pap. Int. Comm SE. Atl. Fish.* 14 (11): 169-191.

✓PAYNE, A.I.L., ROSE, B. and R.W. LESLIE. 1987 - Feeding of hake and a first attempt at determining their trophic role in the South African west coast marine environment. In *The Benguela and Comparable Ecosystems* (eds A.I.L. Payne, J.A. Gulland and K.H. Brink). *S. Afr. J. Mar. Sci.* 5: 471-501.

✓PAYNE, A.I.L., BADENHORST, A., AUGUSTYN, C.J. and R.W. LESLIE. 1989 – Biomass indices for Cape hake and other demersal species in South African waters in 1988 and earlier. *Colln scient. Pap. Int. Comm SE. Atl. Fish.* 16 (2): 25-62.

PERRY, R.I. and S.J. SMITH. 1994 – Identifying habitat associations of marine fishes using survey data: An application to the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* 51: 89-602.

PERRY, R.I., STOCKER, M. and J. FARGO. 1994 – Environmental effects on the distributions of groundfish in Hecate Strait, British Columbia. *Can. J. Fish. Aquat. Sci.* 1: 1401-1409.

PHIL, L. 1994 – Changes in the diet of demersal fish due to eutrophication-induced hypoxia in the Katteget, Sweden. *Can. J. Fish. Aquat. Sci.* 51 (2): 321-336.

PHILANDER, S.G.H. 1990 – El Nino, La Nina and the Southern Oscillation. Academic Press, San Diego, CA. 289pp.

✓PILLAR, S.C. and M. BARANGE. 1993 – Feeding selectivity of juvenile Cape hake *Merluccius capensis* in the Southern Benguela. *S. Afr. J. mar. Sci.* 13: 255-268.

✓PILLAR, S.C. and M. BARANGE. 1997 - Diel variability in bottom trawl catches and feeding activity of the Cape hakes off the west coast of South Africa. *ICES J. Mar. Sci.* 54: 485-499.

✓PITCHER, T. and J. ALHEIT. 1995 - Hake - Fisheries, Ecology and Markets. Chapman and Hall, London. 478pp.

PODESTA, G. P. 1989 - Migratory pattern of Argentine Hake *Merluccius hubbsi* and oceanic processes in the southwestern Atlantic Ocean. *Fish Bull.* 88: 167- 177.

✗ PUNT, A.E. 1988 - Model selection for the dynamics of southern African hake resources. *Rep. Benguela Ecol. Progm. S. Afr.* 15. 395pp.

✓PUNT, A.E. 1991 - Management procedures for Cape hake and baleen whale resources. Ph.D thesis, University of Cape Town. 875pp.

✓PUNT, A.E. 1994 - Assessment of the stocks of Cape hakes *Merluccius* spp. Off South Africa. *S. Afr. J. mar. Sci.* 14: 159-186.

✓PUNT, A.E. and R.W. LESLIE. 1991 - Estimates of some biological parameters for the Cape hakes off the South African west coast. *S. Afr. mar. Sci.* 10: 271-284.

✓PUNT, A.E., LESLIE, R.W. and S.E. DU PLESSIS. 1992 - Estimation of the annual consumption of food by Cape hake *M. capensis* and *M. paradoxus* off the South

African west coast. In Benguela Trophic Functioning (eds. A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn). *S. Afr. J. mar. Sci.* 12: 611-634.

✓ PUNT, A.E., BUTTERWORTH, D.S. and J. MARTIN. 1995 - The effects of errors in the placement of the boundary between the west and south coast hake *Merluccius* spp. stocks on the performance of the current hake management procedure. *S. Afr. J. mar. Sci.* 15: 83-98.

ROEL, B. and G.W. BAILEY. 1987 – Preliminary investigation of the relationship between hake abundance and hydrological parameters in the Benguela system. *Colln scient. Pap. Int. Comm SE. Atl. Fish.* 14(2): 193-201.

ROEL, B. and E. MACPHERSON. 1988 - Feeding of *M. capensis* and *M. paradoxus* off Namibia. *S. Afr. J. mar. Sci.* 6:227-243.

SAKUMA, K.M. and S. Ralston. 1997 - Vertical and horizontal distribution of juvenile Pacific whiting (*M. productus*) in relation to hydrography off California. *Cal. Coop. Ocean. Fish. Invest.*. 38: 137-146.

SCOTT, J. S. 1982 – Depth, temperature and salinity preferences of common fishes of the Scotian shelf. *J. Northw. Atl. Fish.* Sci. 3: 29-39.

X SHANNON, L.V. 1995 - The Benguela Current Ecosystem. In *The Benguela Current and Comparable eastern boundary upwelling ecosystems.* M.J. O'Toole (Ed). Deutsche Gesellschaft fur Technische Zusammenarbeit, Germany: 5-11.

X SHANNON, L.V. and G. NELSON. 1996 – The Benguela: large scale features and processes and system variability. In: *The South Atlantic: Present and Past Circulation.* Wefer, G., Berger, W.h., Siedler, G. and Webb, D.J. (Eds), Springer-Verlag, Berlin- Heidelberg: 163-210.

SHANNON, L.V. and S.C. PILLAR. 1986 - The Benguela ecosystem. Part III. Plankton *Oceanogr. Mar. Biol. Ann. Rev*, 24: 65-170.

SHANNON, L.V., BOYD, A.J., BRUNDRIT, G.B. and J. TAUNTON-CLARK. 1986 - On the existence of an El Niño-type phenomenon in the Benguela system. *J. mar. Res.* 44: 495-520.

SHANNON, L.V., CRAWFORD, R.J.M., BRUNDRIT, G.B. and L.G. UNDERHILL. 1988 – Responses of fish populations in the Benguela ecosystem to environmental change. *J. Cons. Int. Explor. Mer.* 45: 5-12.

SHANNON, L.V., CRAWFORD, R.J.M., POLLOCK, D.E., HUTCHINGS, L., BOYD, A.J., TAUNTON-CLARK, J., BADENHORST, A., MELVILLE-SMITH, R., AUGUSTYN, C.J., COCHRANE, K.L., HAMPTON, I., NELSON, G., JAPP, D.W. and R.J. TARR. 1992 – The 1980s – a decade of change in the Benguela ecosystem. In Benguela Trophic Functioning. Payne, A.I.L., Brink, K.H., Mann, K.H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* 12: 271-296.

SHANNON, L.V., NELSON, G., CRAWFORD, R.J.M. and A.J. BOYD. 1996 – Possible impacts of environmental change on pelagic fish recruitment: modeling anchovy transport by advective processes in the southern Benguela. *Global Change Biol.* 2: 407-420.

SHARP, G.D. 1987 – Climate and fisheries: Cause and effect or managing the long and short of it all. *S. Afr. J. mar. Sci.* 5: 811-838.

SHELTON, P.A. 1986 - Fish spawning strategies in the variable southern Benguela Current region. Ph.D. thesis: University of Cape Town.

SIMPSON, J.J. 1992 - Remote sensing and geographic information systems: Implications for global marine fisheries. *Report series. California Sea Grant College Program.* 27pp.

SMITH, R.J.F.1985 - The control of fish migration. In: *Zoophysiology*, Vol 17. Springer-Verlag, New York.

STAR, J. and J. ESTES. 1990 - Geographical information systems: an introduction. Prentice Hall, New Jersey.

✓STAUFFER, G.D. 1985 - Biology and life history of the coastal stock of Pacific Whiting, *M. productus*. *Mar. Fish. Rev.* 47(2): 2-7.

STROMME, T. and H. HAMAKUAYA. 1999 – Possible environmental impacts on abundance of shallow-water Cape hake (*Merluccius capensis*) in Namibian waters. Abstracts of the International Symposium on Environmental Variability in the South-east Atlantic, Swakopmund, Namibia. 30 March – 1 April.

STRUB, P.T., SHILLINGTON, F.A., JAMES, C. and S.J. WEEKS. 1998 - Satellite Comparison of the seasonal circulation in the Benguela and California Current Systems. *S. Afr. J. Mar. Sci.* 19: 99-112.

STULL, J.K. and C. TANG. 1996 – Demersal fish trawls off Palos Verdes, southern California, 1973-1993. *Calcofi Rep.* 37: 211-240.

✓SULLIVAN, P.J. 1991 – Stock abundance estimation using depth-dependent trends and spatially correlated variation. *Can. J. Fish. Aquat. Sci.* 48: 1691-1703.

✓SWARTZMAN, G., HUANG, C. and S. KALUZNY. 1992 – Spatial analysis of Bering Sea groundfish survey data using Generalized Additive Models. *Can. J. Fish. Aquat. Sci.* 49: 1366-1378.

SWARTZMAN, G., STUETZLE, W., KULMAN, K. and M. POWOJOWSKI. 1994 - Relating the distribution of pollock schools in the Bering Sea to environmental factors. *ICES J. mar. Sci.* 51: 481-492.

SWARTZMAN, G., SILVERMAN, E. and N. WILLIAMSON. 1995 – Relating trends in Walleye pollock (*Theragra chalcogramma*) abundance in the Bering Sea to Environmental factors. *Can. J. Fish. Aquat. Sci.* 52: 369-380.

THOMPSON, A.B. and M. Hilden. 1988 - The early life history of fish. Blaxter, J.H.S., Gamble, J.C., and H. Westernhagen (Eds.), ICES, Bergen.

UDA, M. 1952 - On the relation between the variation of the important fisheries conditions and the oceanographical conditions in the adjacent water of Japan. *J. Tok. Uni. Fish.* 38: 363-389.

VAN ECK, T.H. 1969 - The South African hake: *'Merluccius capensis'*- or "*Merluccius paradoxus*'? *S. Afr. Shipp. News Fishg Ind. Rev.* 24: 95-97.

VENABLES, W. N. and B.D. RIPELY. 1994 - Modern Applied Statistics with S-Plus. Springer-Verlag, New York. 462pp.

WARE, D.M. 1992 - Production characteristics of upwelling systems and the trophodynamic role of hake. *S. Afr. J. mar. Sci.* 12: 501-513.

WARE, D.M. and G.A. McFarlane. 1995 - Climate-induced changes in Pacific hake (*M. productus*) abundance and pelagic community interaction in the Vancouver Island upwelling system. *Can. Spec. publ. Fish. Aquat. Sci.* 121: 509-552.

WOODHEAD, P.M.J., HAMUKUAYA, H., O'TOOLE, M.J. and M. MCENROE. 1998 - Effects of oxygen-depletion in shelf waters on hake populations off central and northern Namibia. Abstracts of the International Symposium on Environmental

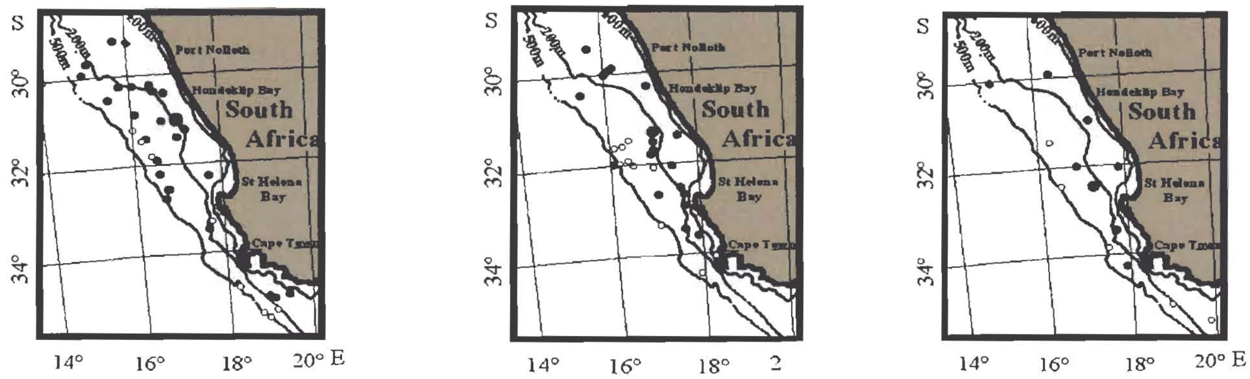
Variability in the South-east Atlantic, Swakopmund, Namibia. 30 March – 1 April.

WOODHEAD, P.M.J., HAMUKUAYA, H., O'TOOLE, M.J., STROMME, T. and S.S. KRISTMANNSSON. 1998 – Recruit mortalities in Cape hake, following exculsion from shelf habitat by persistent hypoxia in the northern Benguela Current. Abstracts of the International Symposium on Environmental Variability in the South-east Atlantic, Swakopmund, Namibia. 30 March – 1 April.

WOODHEAD, P.M.J., HAMUKUAYA, H., O'TOOLE, M.J., STROMME, T., SAETERSDAL, G. and M.R. REISS. 1998 – Catastrophic loss of two billion Cape hake recruits during widespread anoxia in the Benguela current. Abstracts of the International Symposium on Environmental Variability in the South-east Atlantic, Swakopmund, Namibia. 30 March – 1 April.

WOSNITZA-MENDO, C. and M. ESPINO. 1986 – The impact of "El Niño" on recruitment in the Peruvian hake (*Merluccius gayi peruanus*). *Meeresforsch.* 31: 47-51.

APPENDICES



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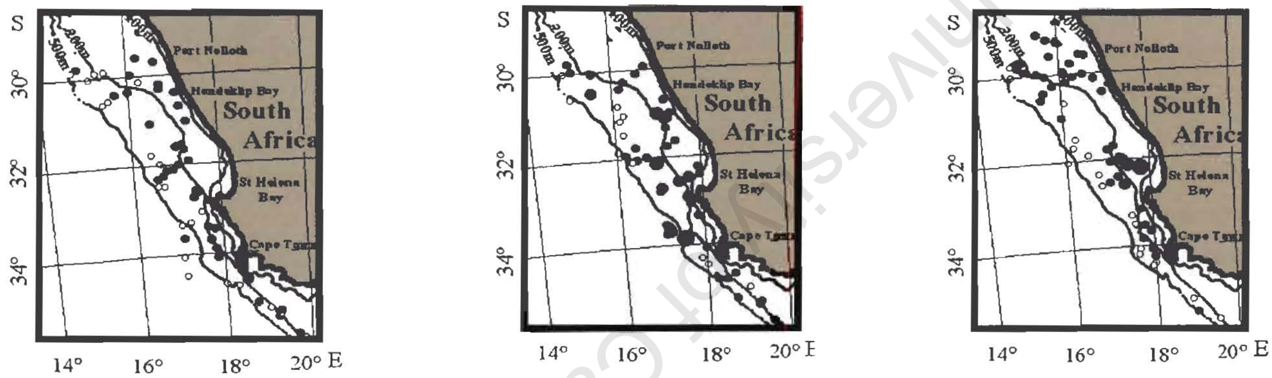

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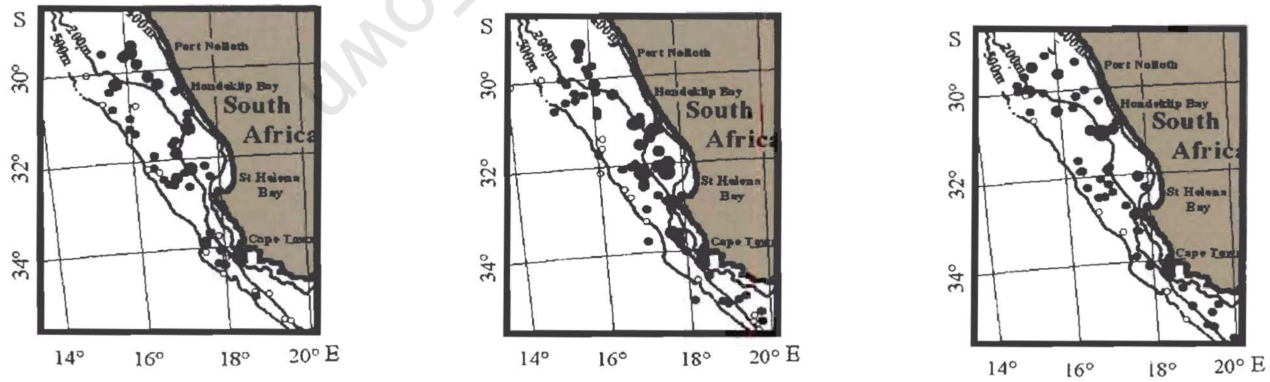

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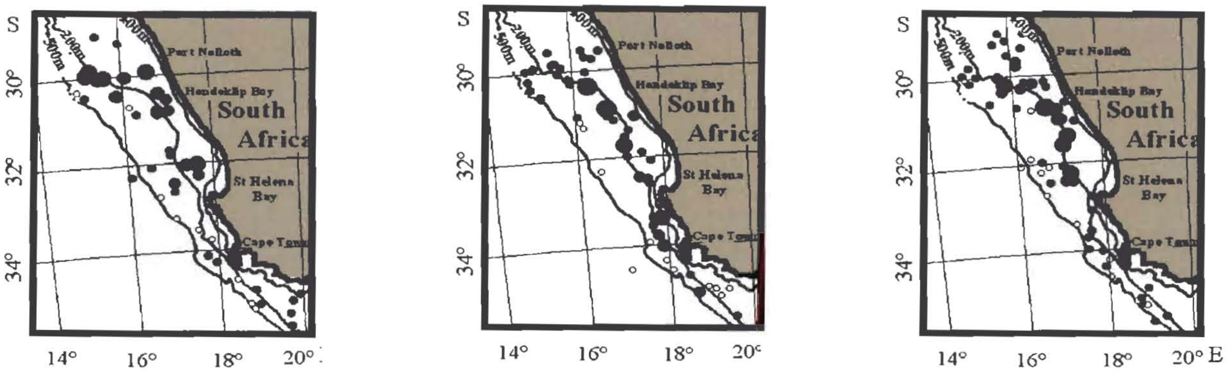
Figure A1: Distribution of *M. paradoxus* juveniles for all survey months on the west coast of South Africa (larger circles represent areas of higher fish density and smaller circles represent areas of lower fish density).



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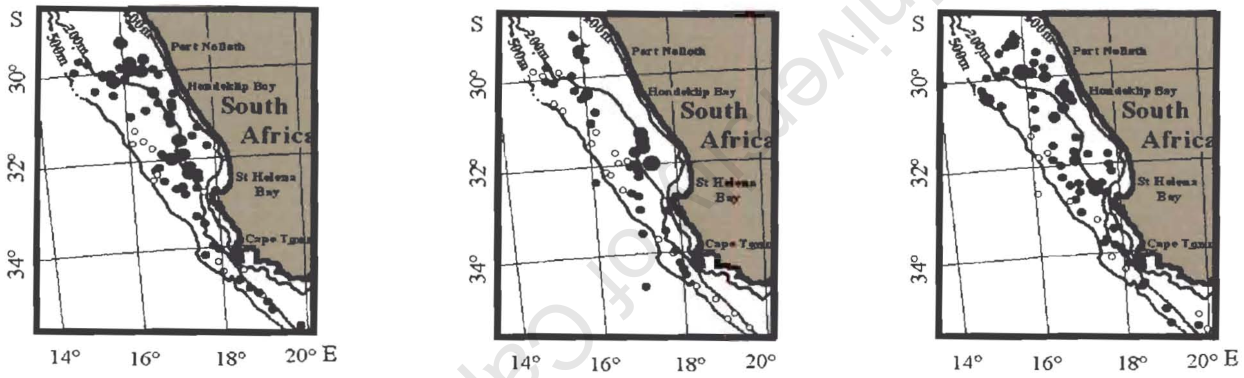

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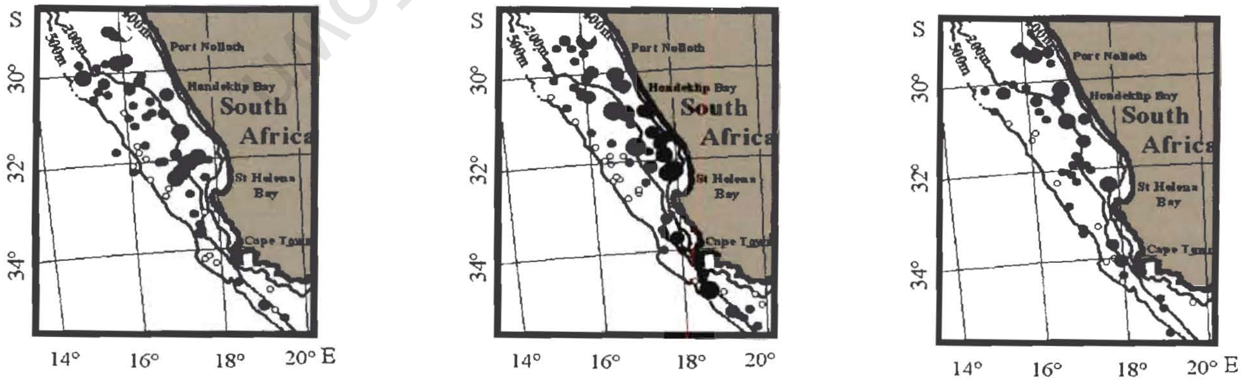

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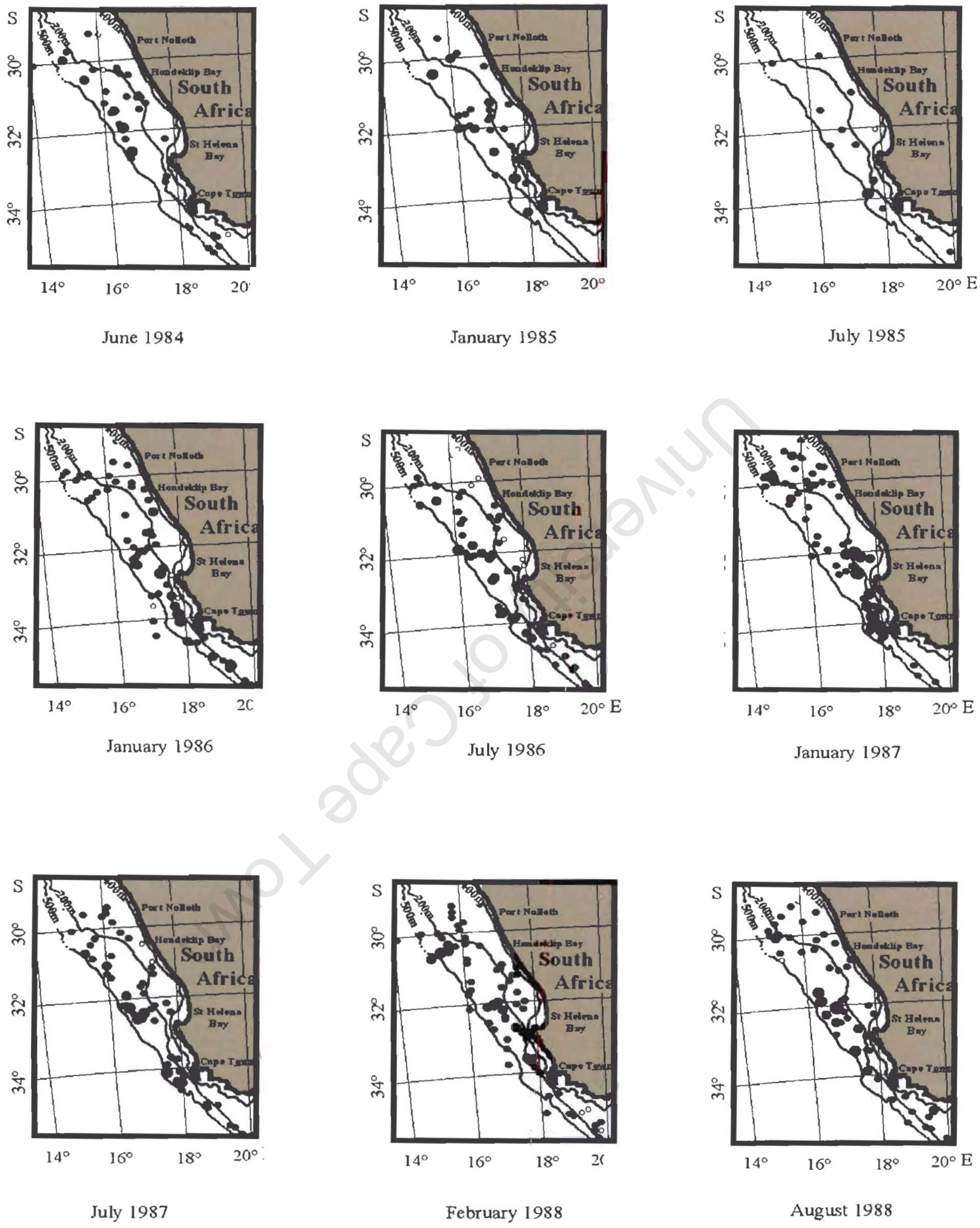

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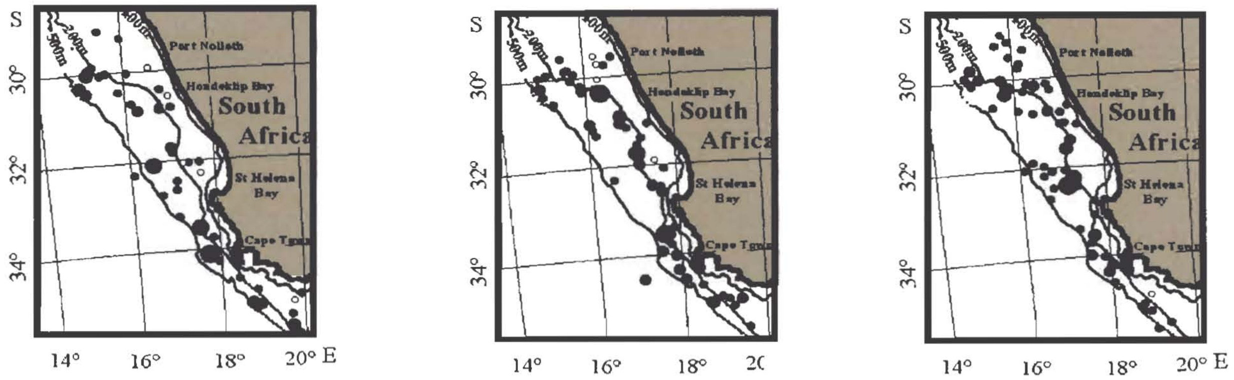

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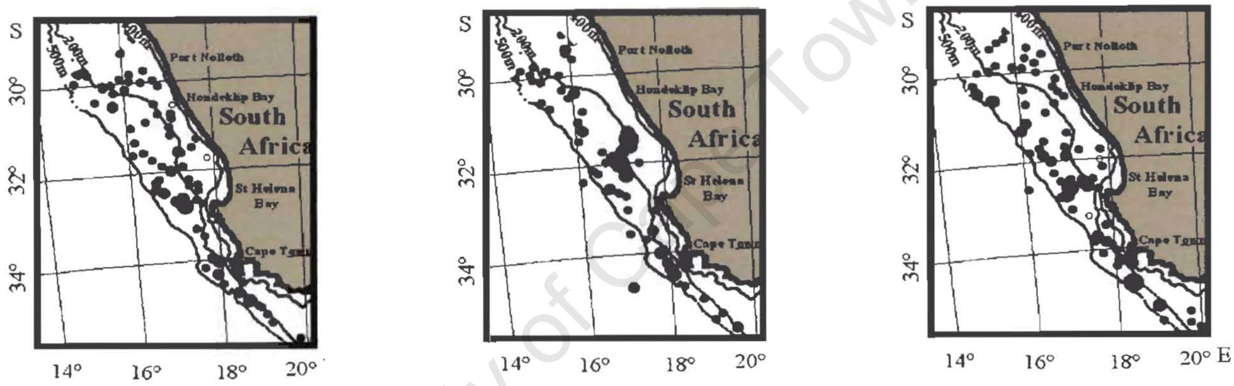

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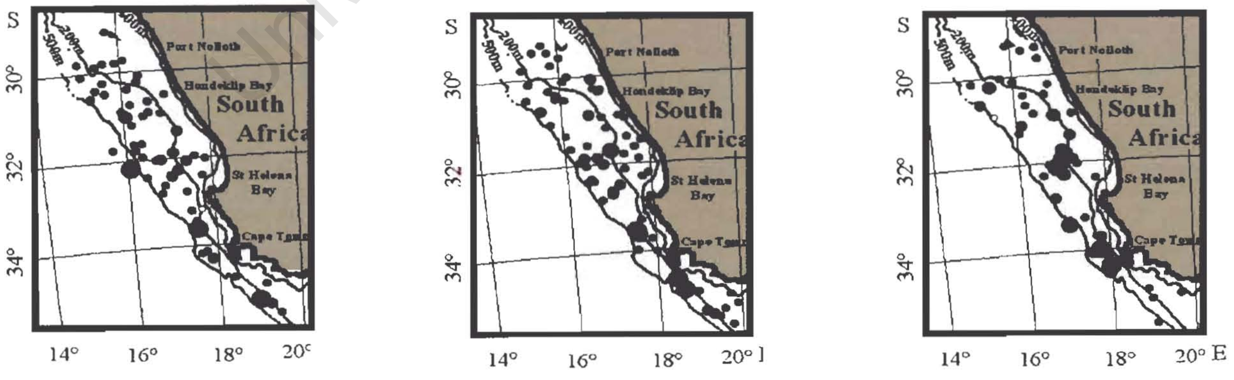

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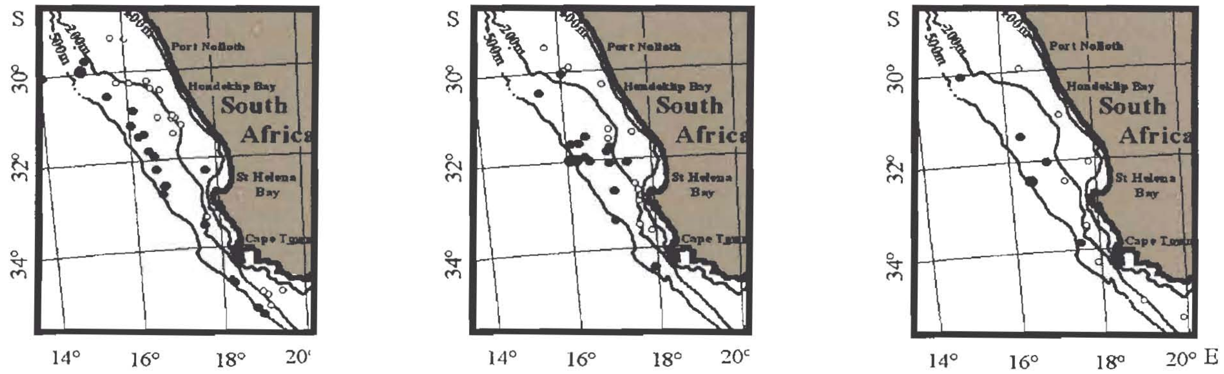
Figure A2 (cont.): Distribution of *M. paradoxus* subadults for all survey months on the west coast of South Africa.



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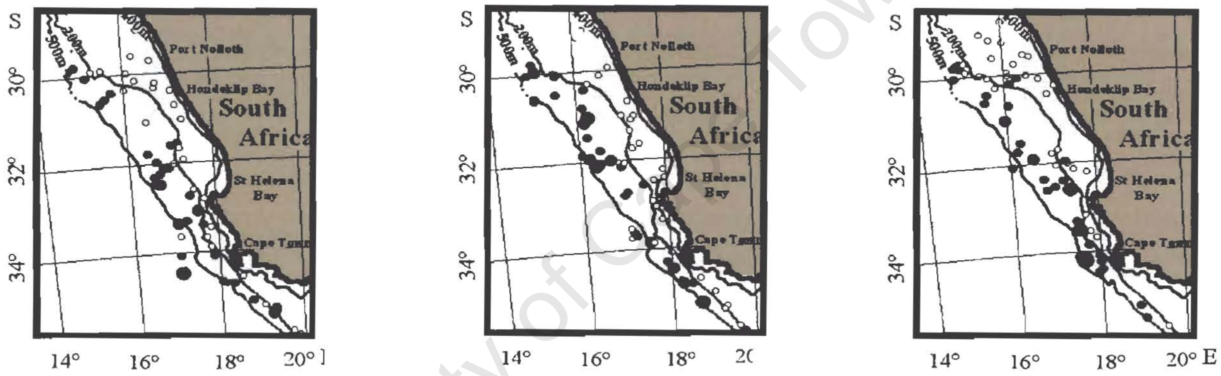

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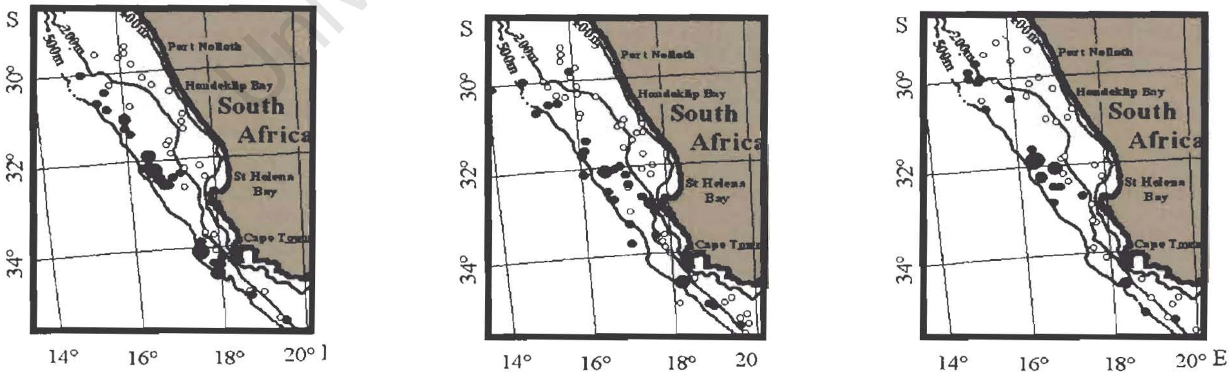

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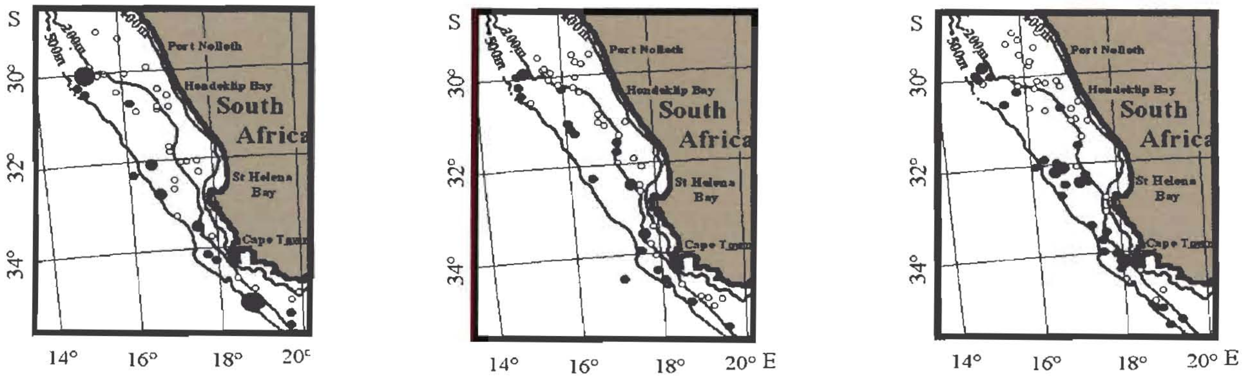
Figure A3: Distribution of *M. paradoxus* adults for all survey months on the west coast of South Africa (larger circles represent areas of higher fish density and smaller circles represent areas of lower fish density).



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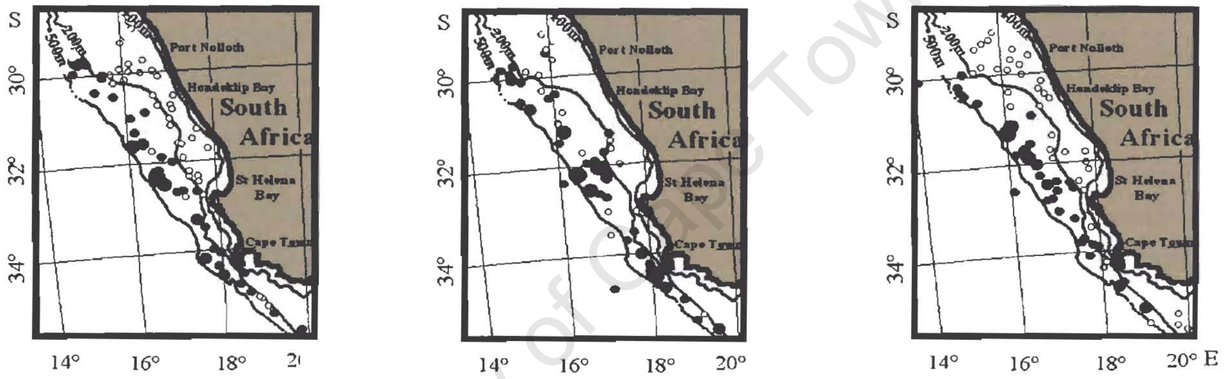

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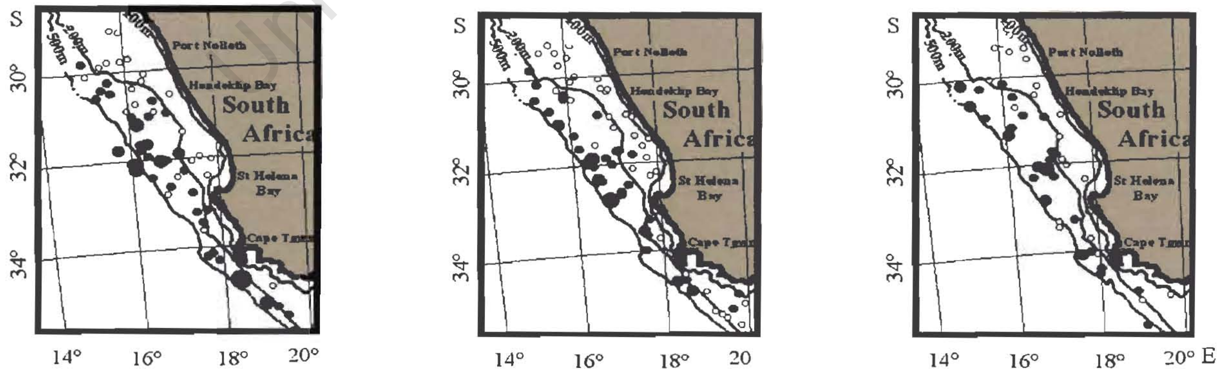

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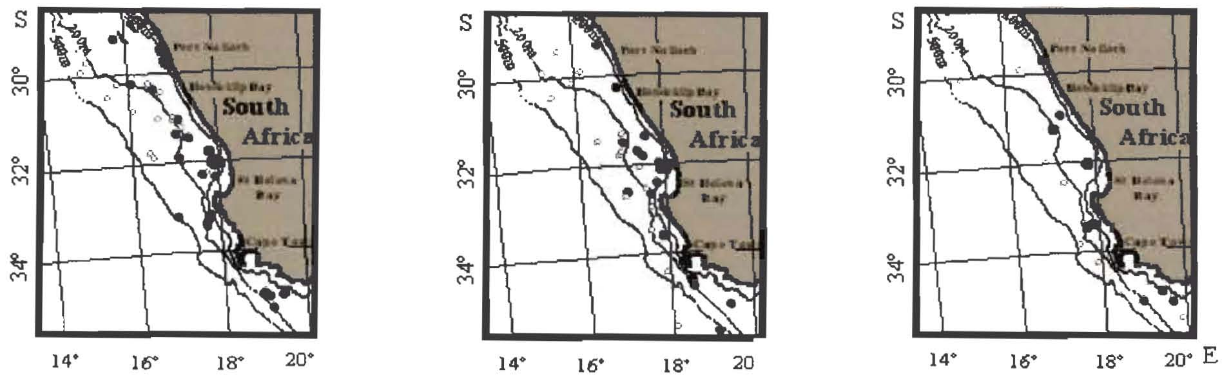
Figure A3 (cont.): Distribution of *M. paradoxus* adults for all survey months on the west coast of South Africa.



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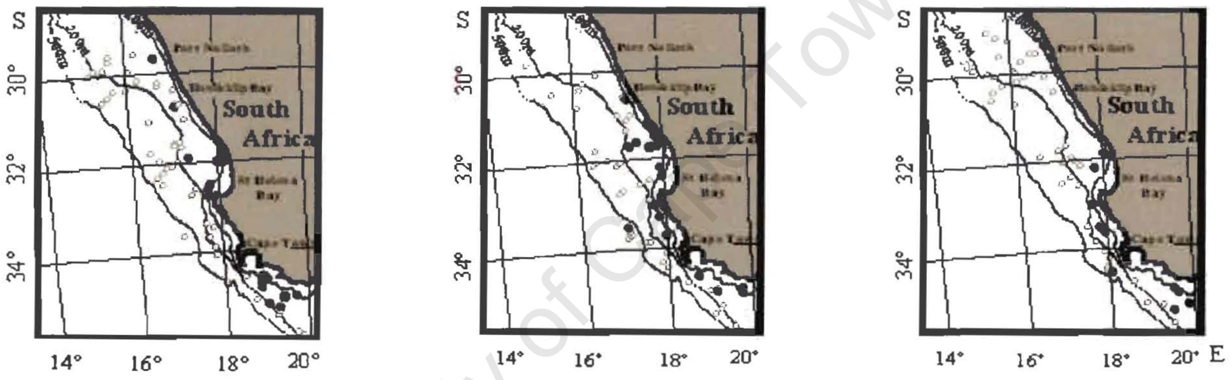

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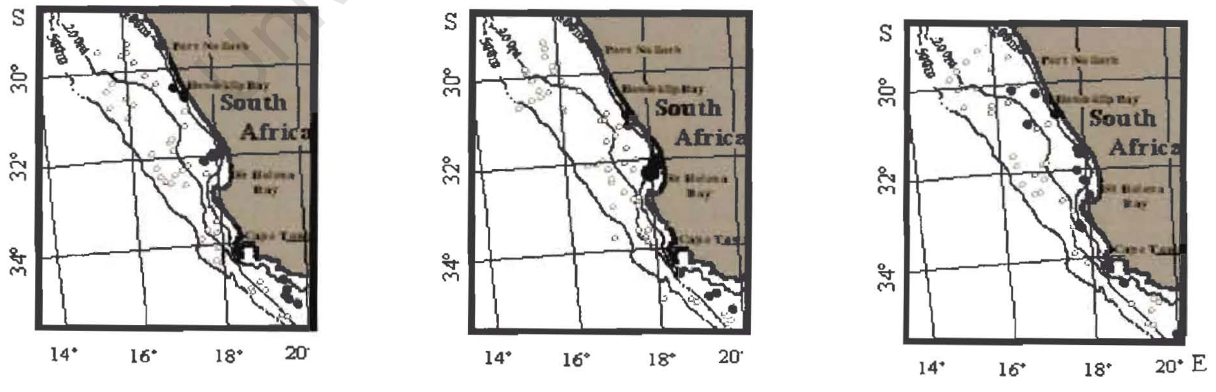

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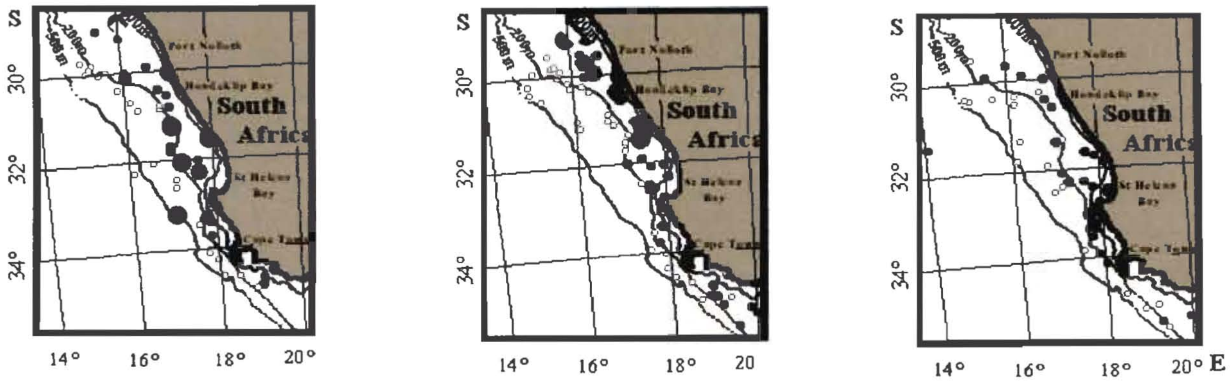
Figure A4: Distribution of *M. capensis* juveniles for all survey months on the west coast of South Africa (larger circles represent areas of higher fish density and smaller circles represent areas of lower fish density).



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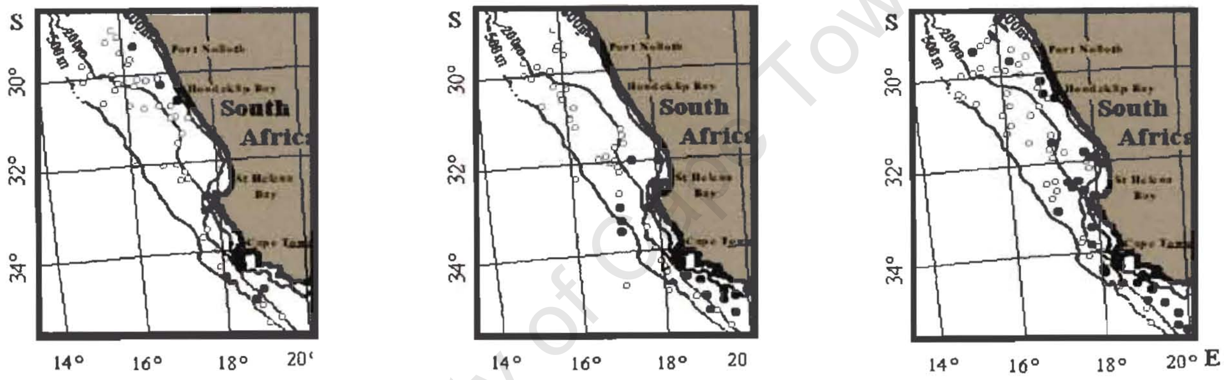

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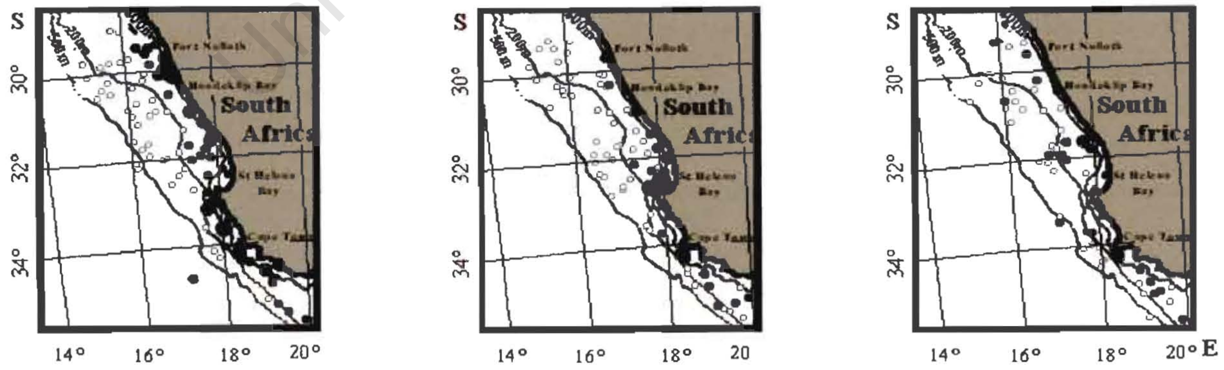

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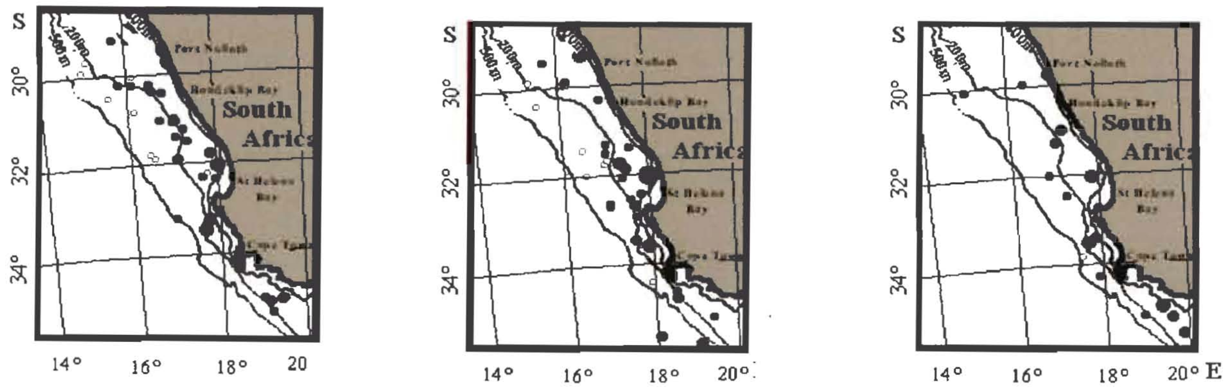
Figure A4 (cont.): Distribution of *M. capensis* juveniles for all survey months on the west coast of South Africa.



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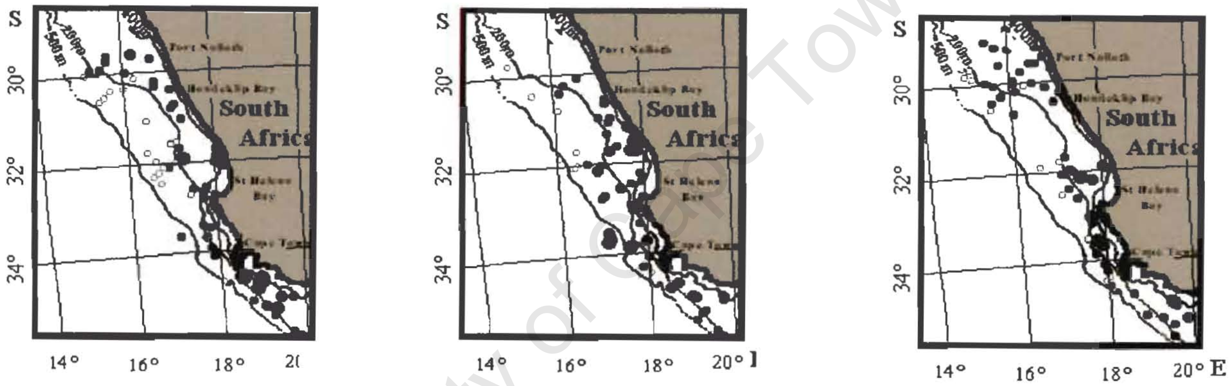

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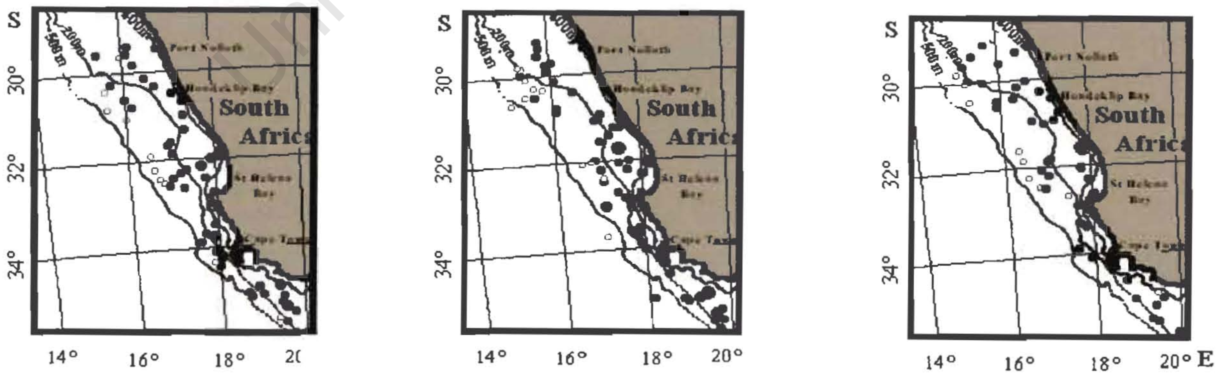

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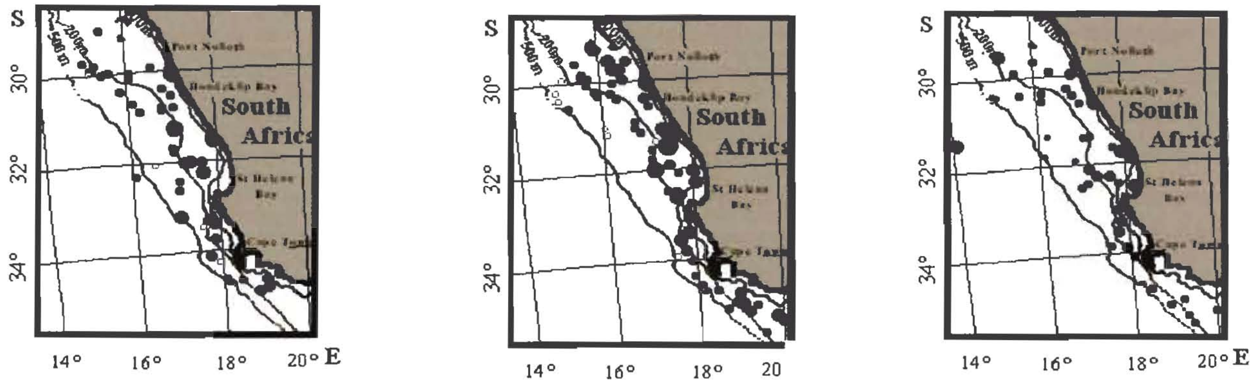
Figure A5: Distribution of *M. capensis* subadults for all survey months on the west coast of South Africa (larger circles represent areas of higher fish density and smaller circles represent areas of lower fish density).



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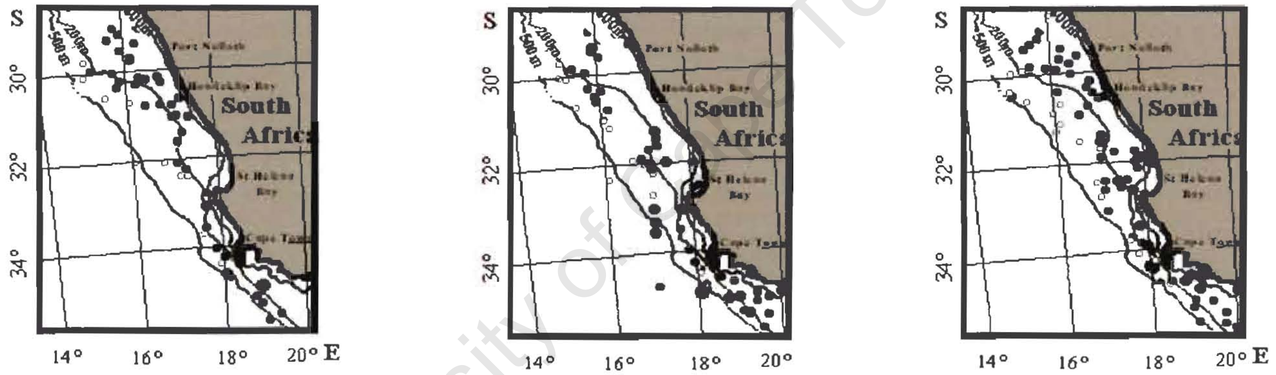

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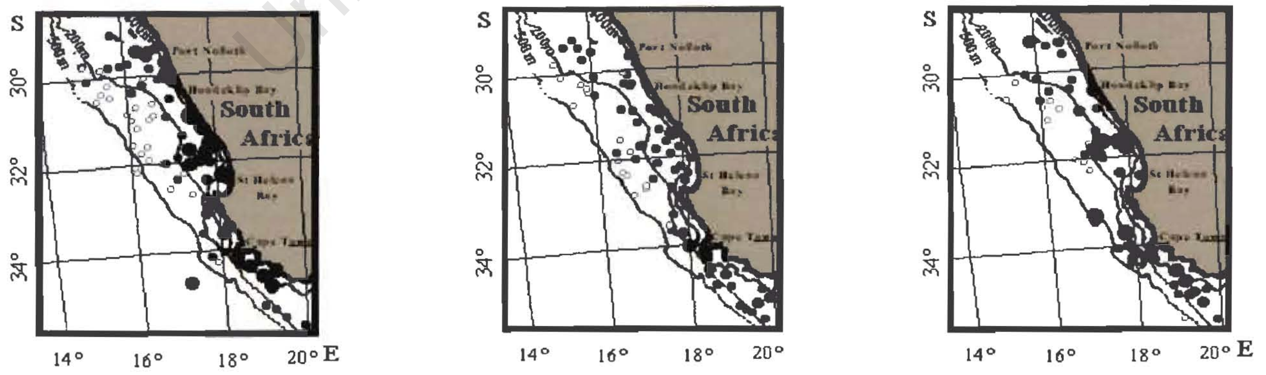

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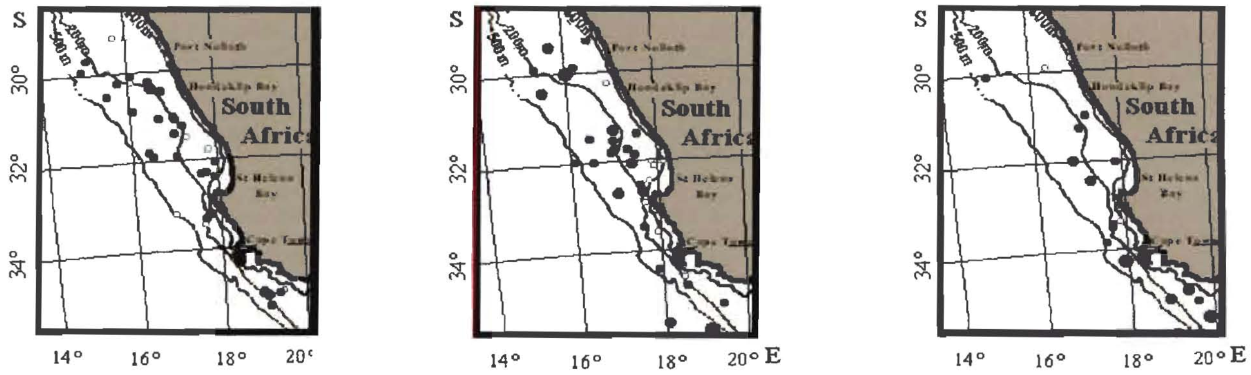

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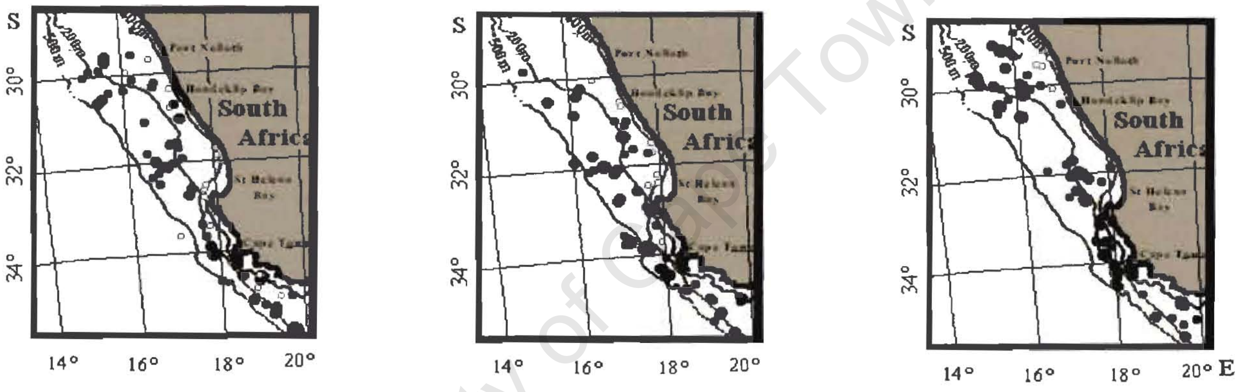

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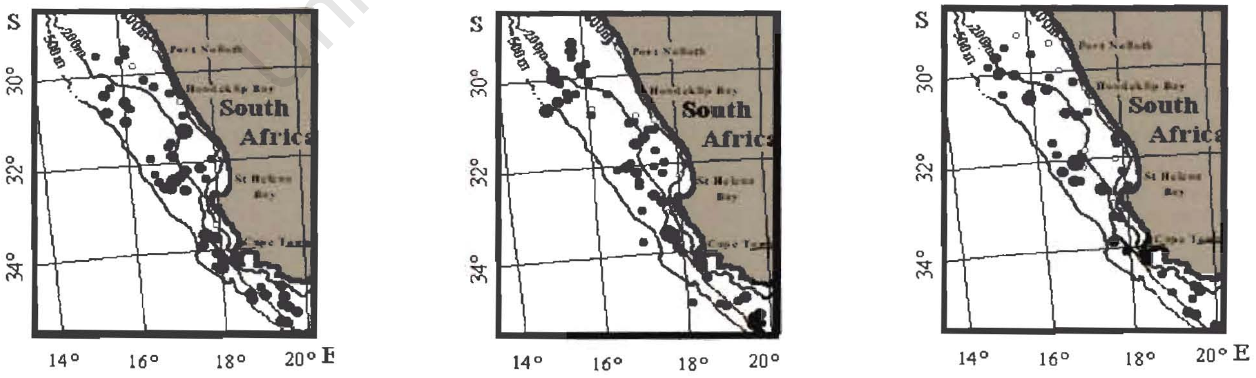

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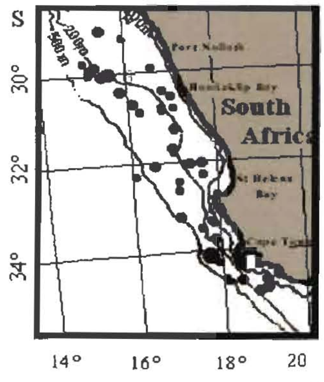
Figure A6: Distribution of *M. capensis* adults for all survey months on the west coast of South Africa (larger circles represent areas of higher fish density and smaller circles represent areas of lower fish density).



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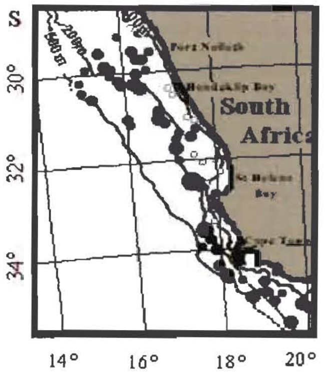

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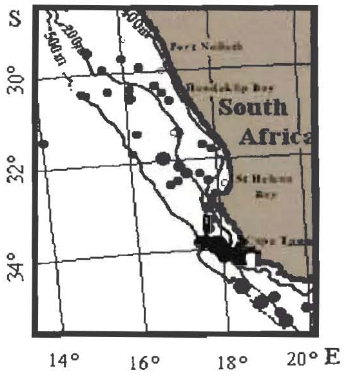

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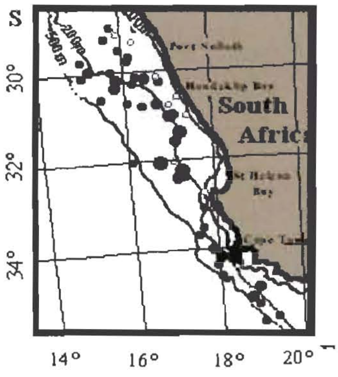

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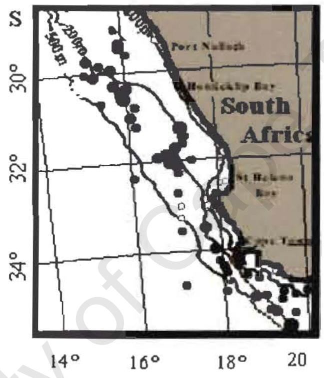

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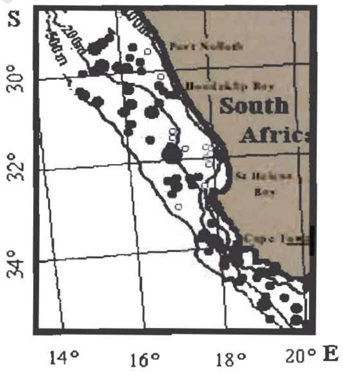

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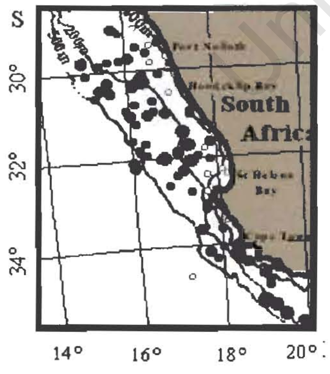

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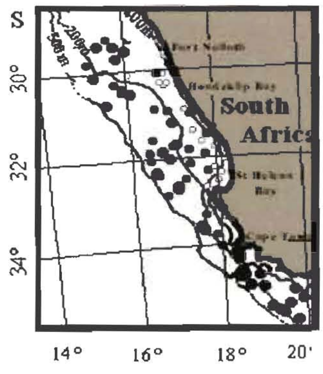

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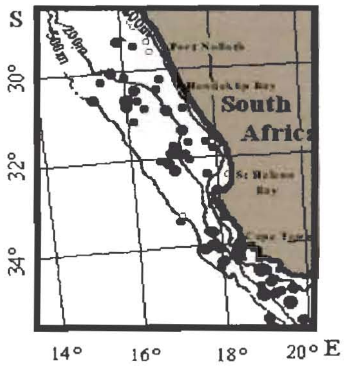

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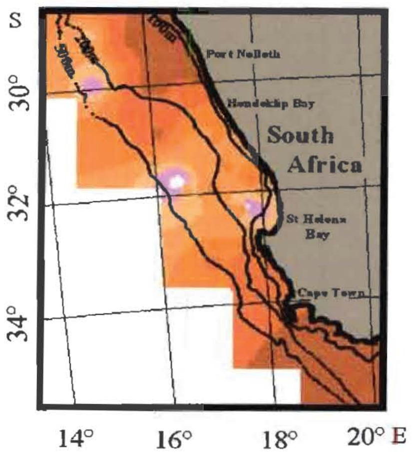
Figure A6 (cont.): Distribution of *M. capensis* adults for all survey months on the west coast of south Africa.



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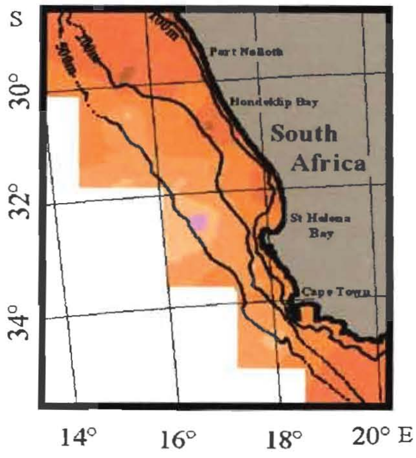
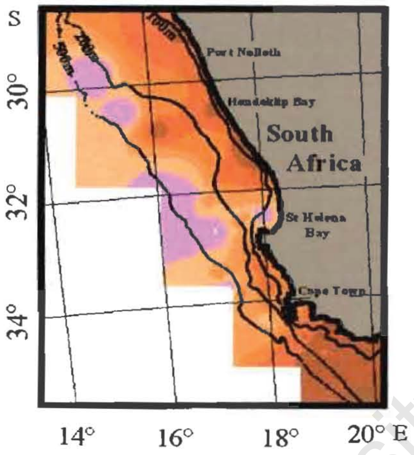
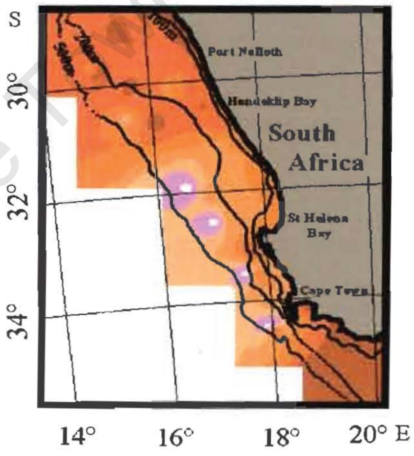


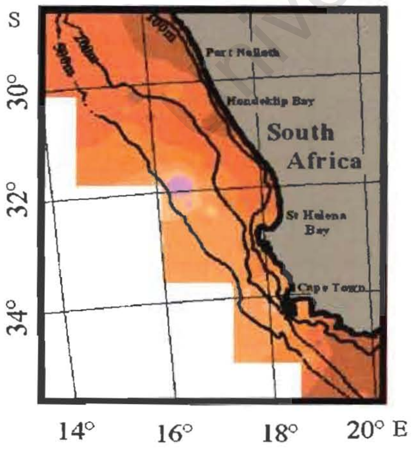
January 1986



July 1986



January 1987



July 1987

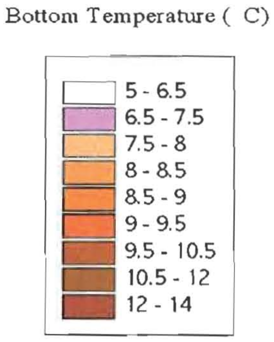
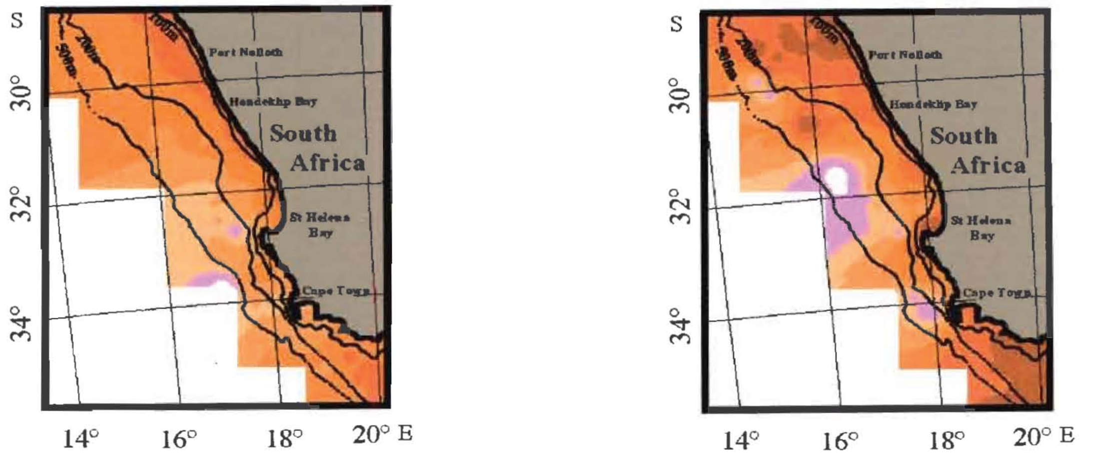
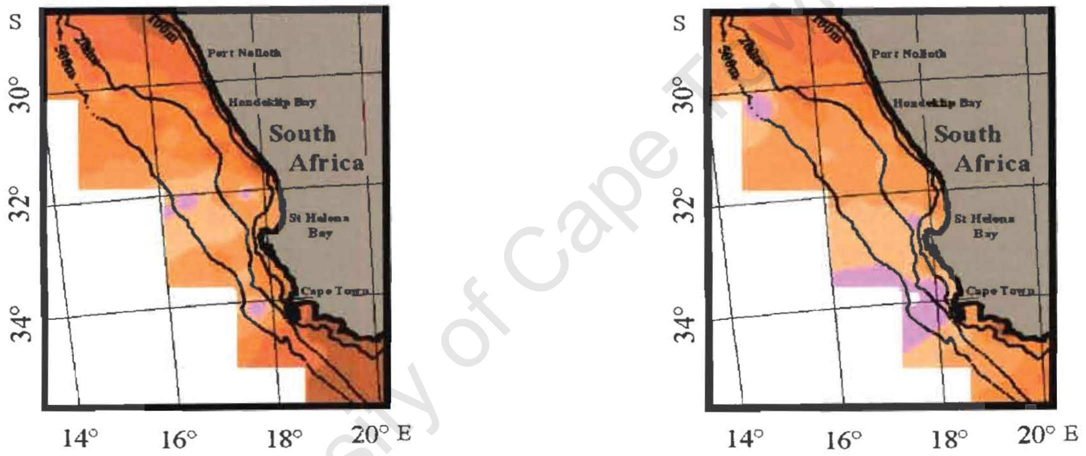


Figure A7: Bottom temperatures off the west coast of South Africa for each survey month.



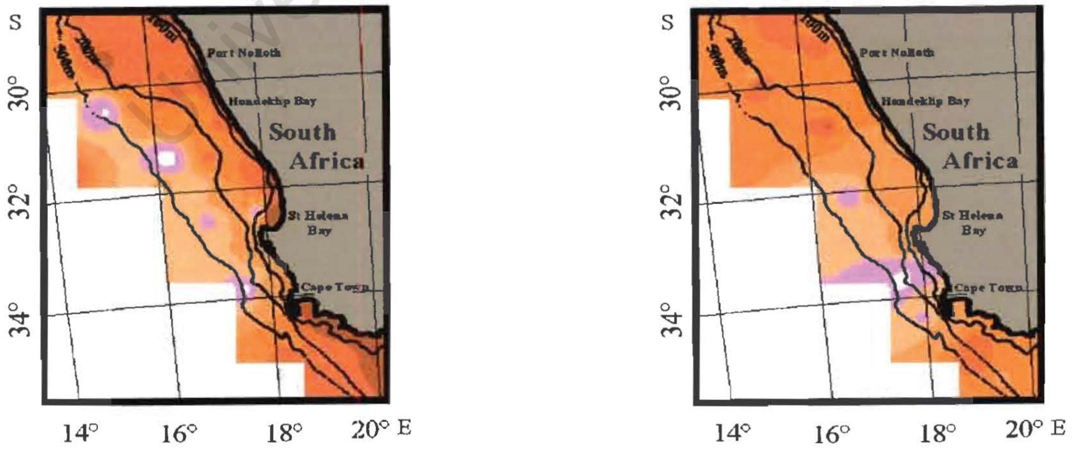
February 1988

August 1988



July 1989

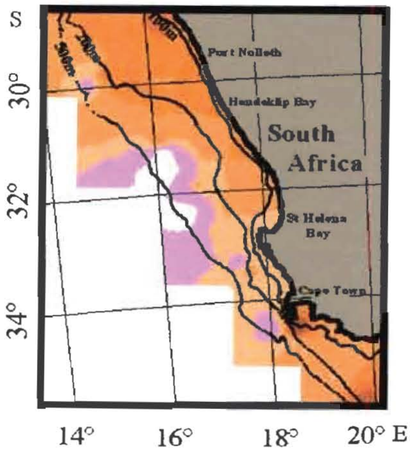
January 1990



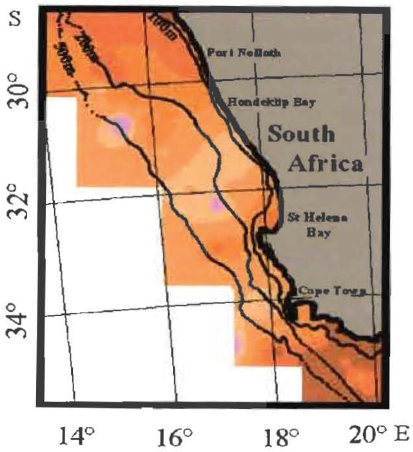
July 1990

January 1991

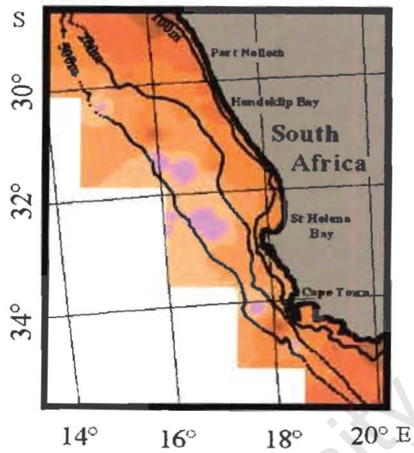
Figure A7 (cont.): Bottom temperatures off the west coast of South Africa for each survey month.



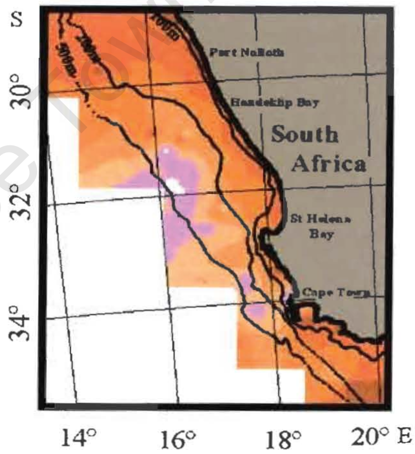
February 1992



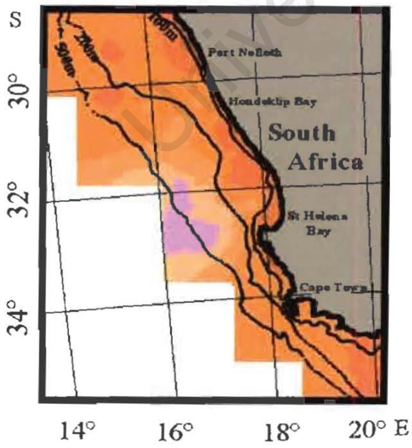
January 1993



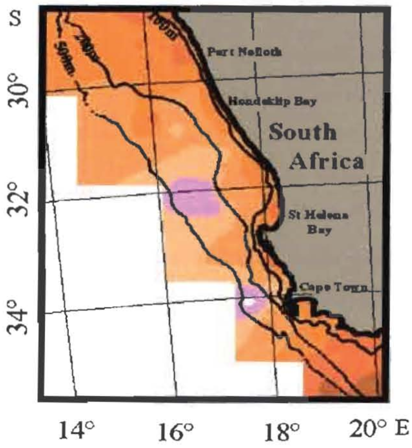
January 1994



January 1995

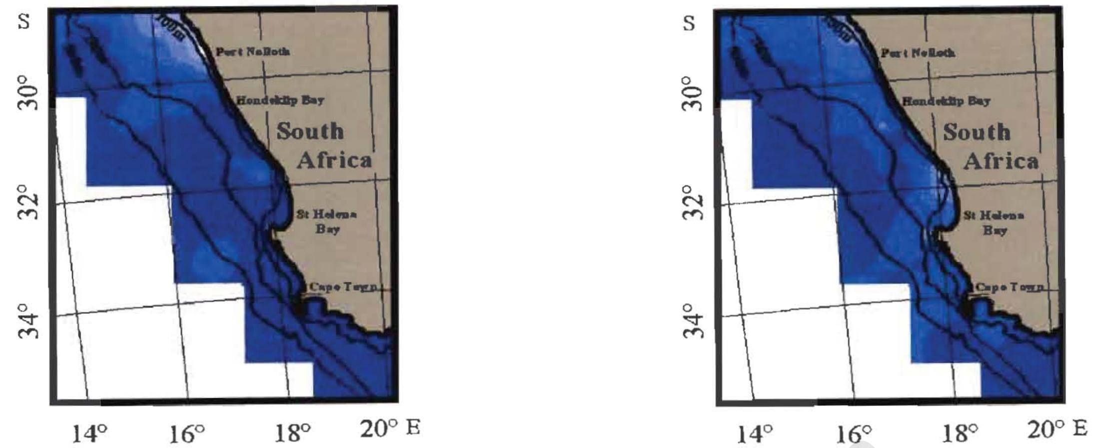


January 1996



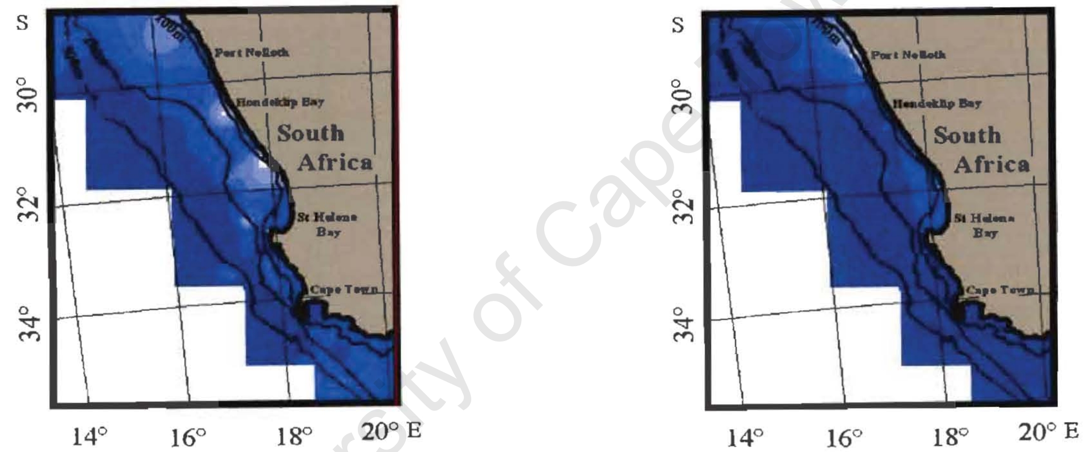
January 1997

Figure A7 (cont.): Bottom temperatures off the west coast of South Africa for each survey month.



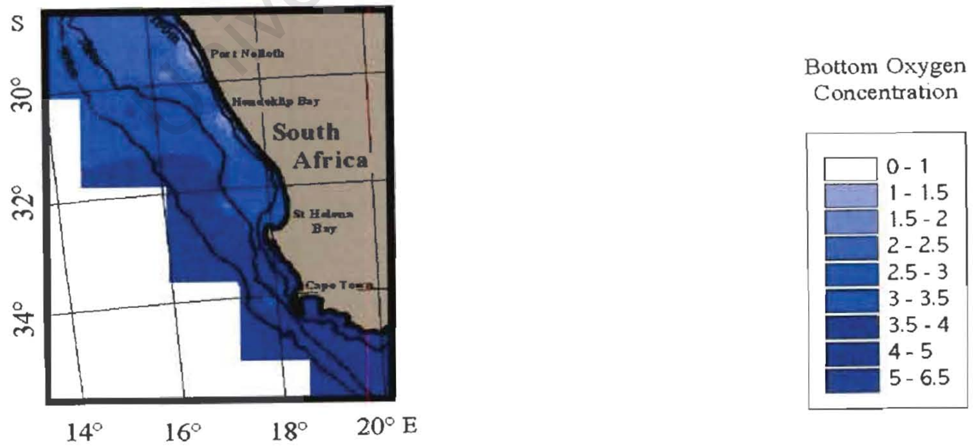
June 1984

January 1986



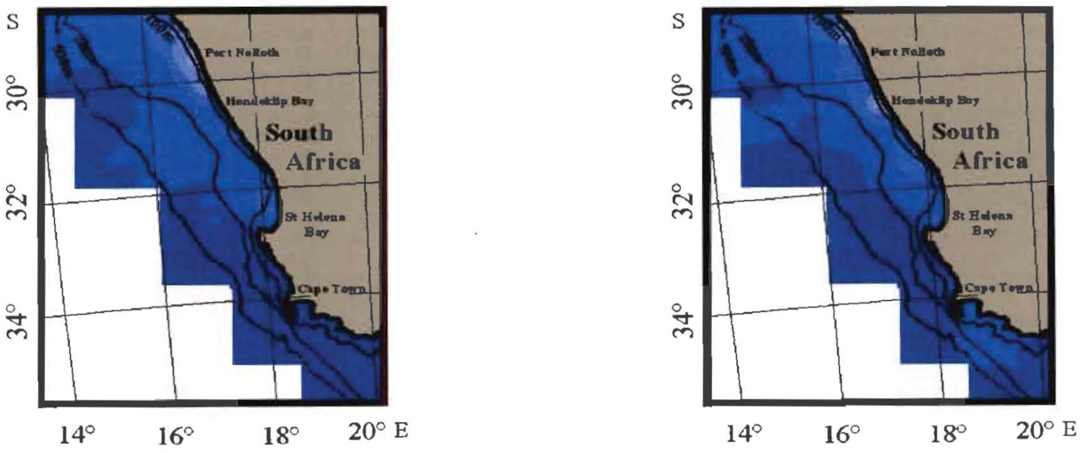
July 1986

January 1987



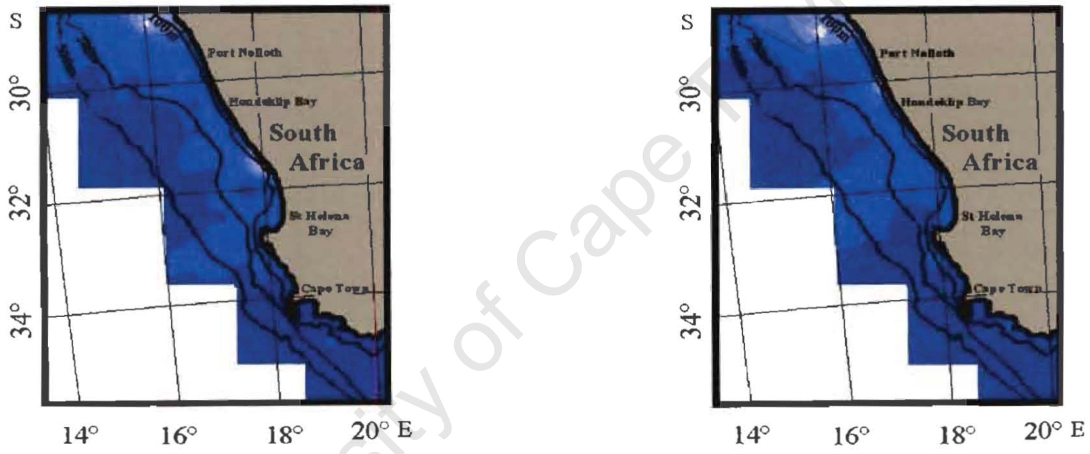
July 1987

Figure A8: Bottom oxygen concentrations off the west coast of south Africa for each survey month.



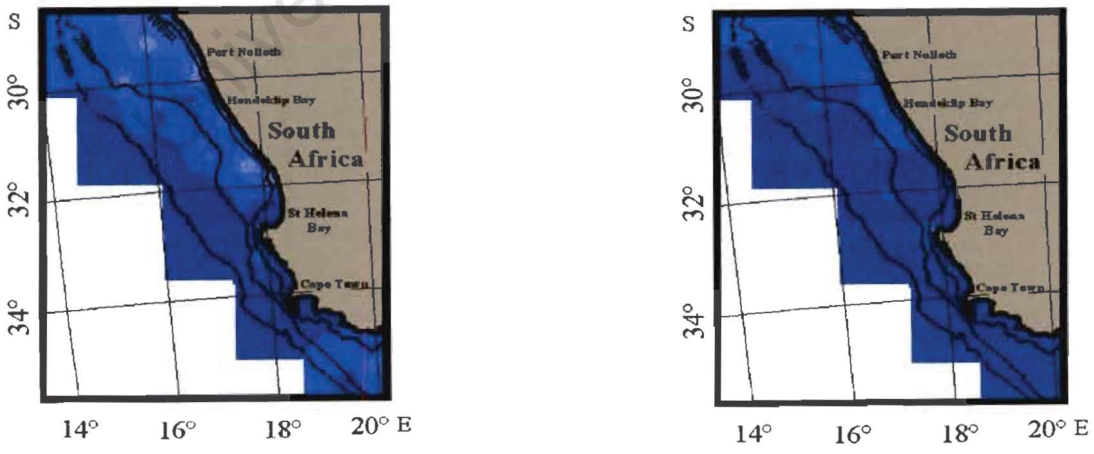
February 1988

August 1988



July 1989

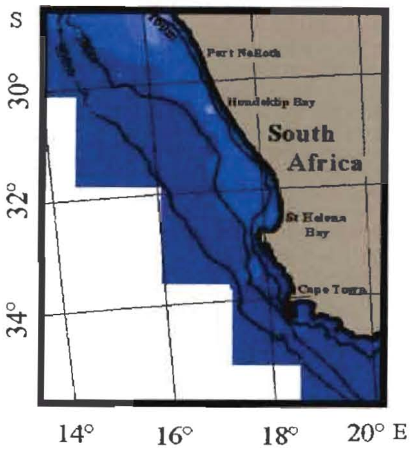
January 1990



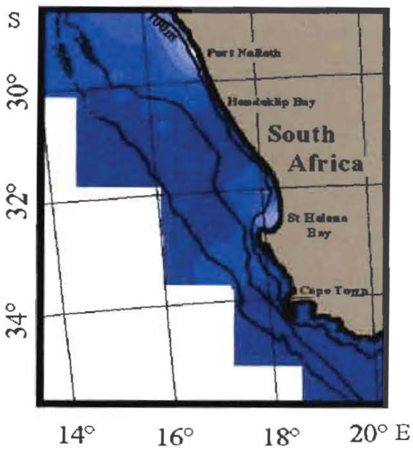
July 1990

January 1991

Figure A8 (cont.): Bottom oxygen concentrations off the west coast of South Africa for each survey month.



February 1992



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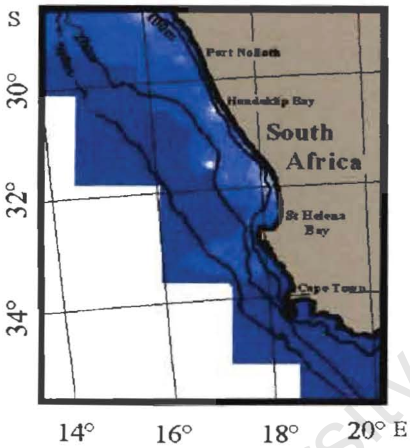
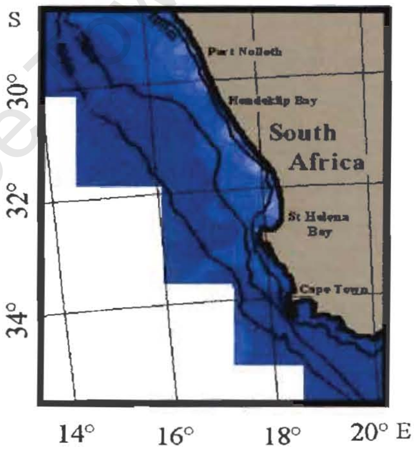
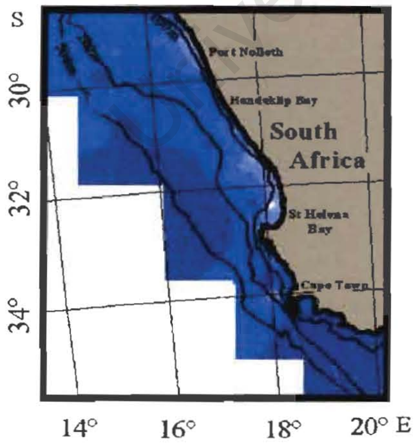


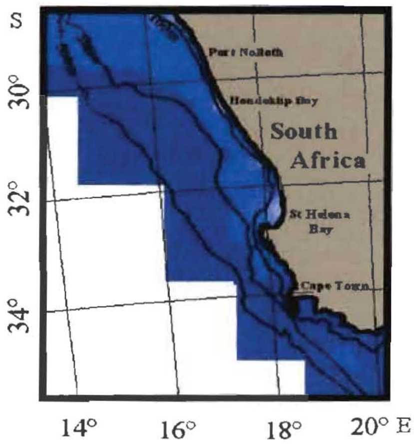
January 1994



January 1995

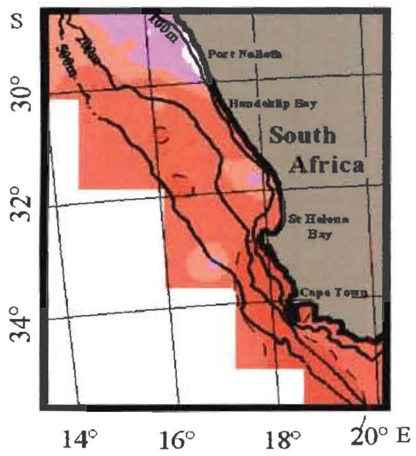


January 1996

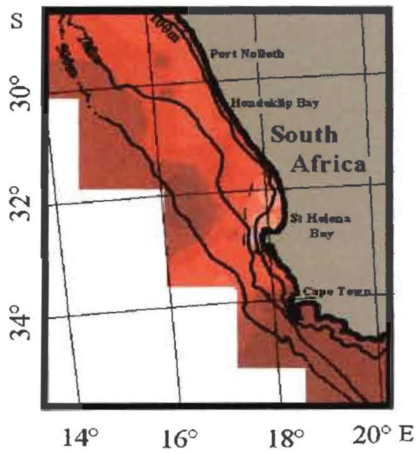


January 1997

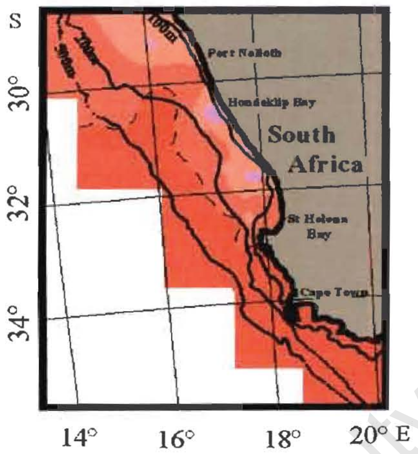
Figure A8 (cont.): Bottom oxygen concentrations off the west coast of South Africa for each survey month.



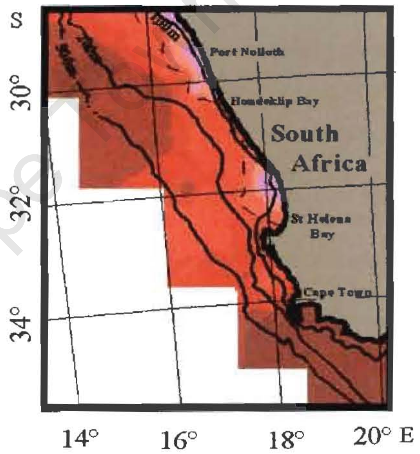
June 1984



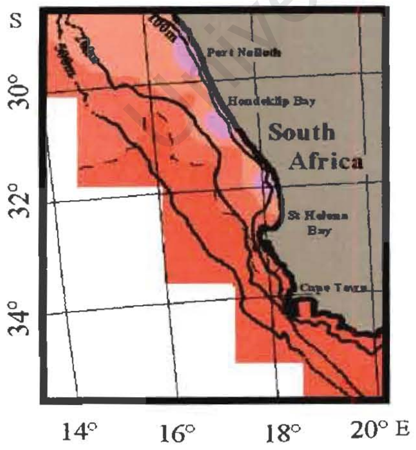
January 1986



July 1986



January 1987

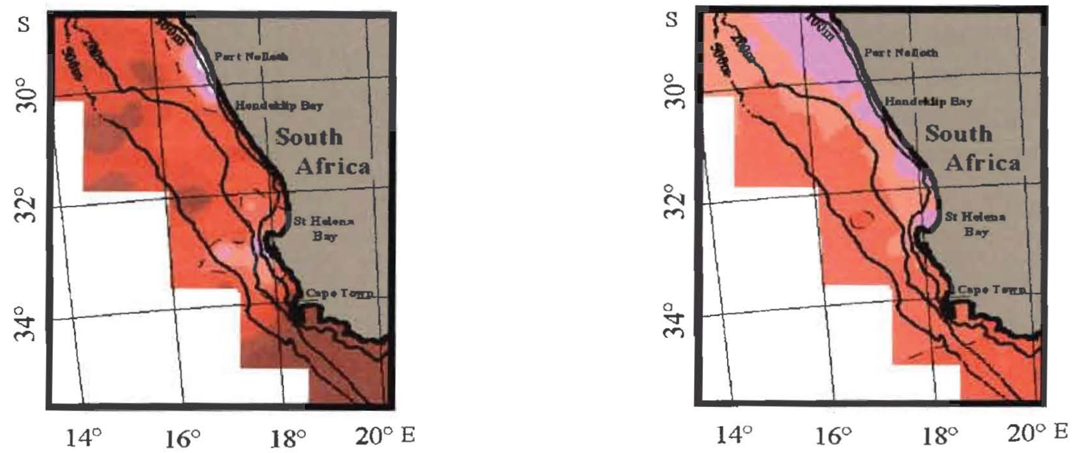


July 1987

Sea Surface
Temperature (C)

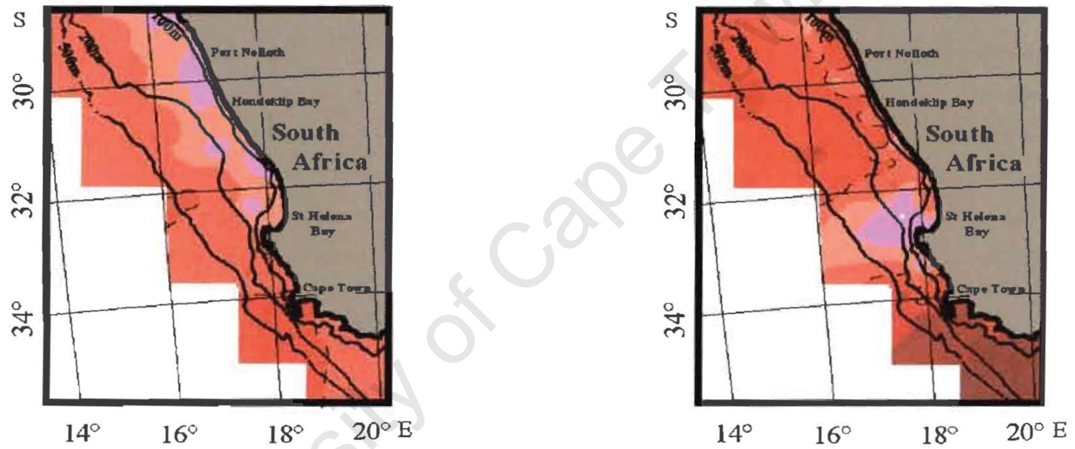
☐	10 - 12
■	12 - 14
■	14 - 15
■	15 - 16
■	16 - 17
■	17 - 18
■	18 - 19
■	19 - 20
■	20 - 22
■	22 - 24

Figure A9: Sea surface temperatures off the west coast of South Africa for each survey month.



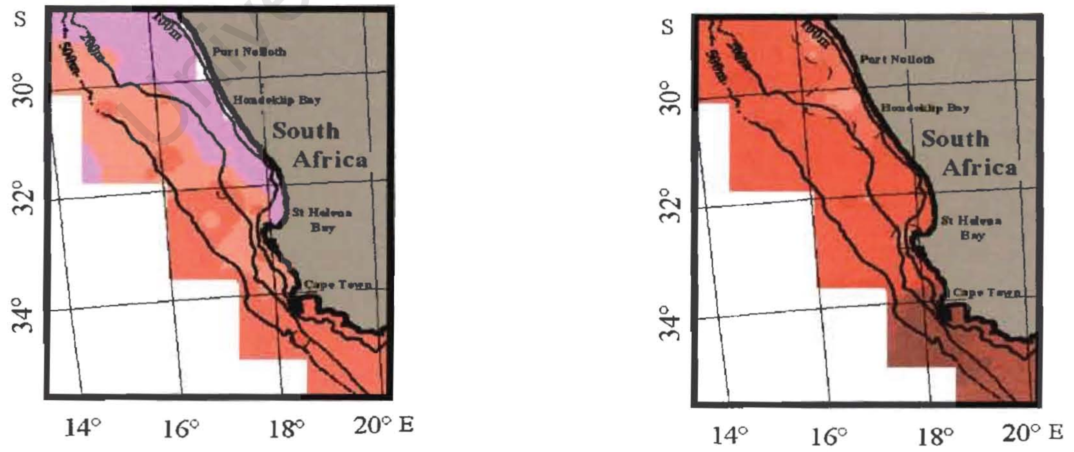
February 1988

August 1988



July 1989

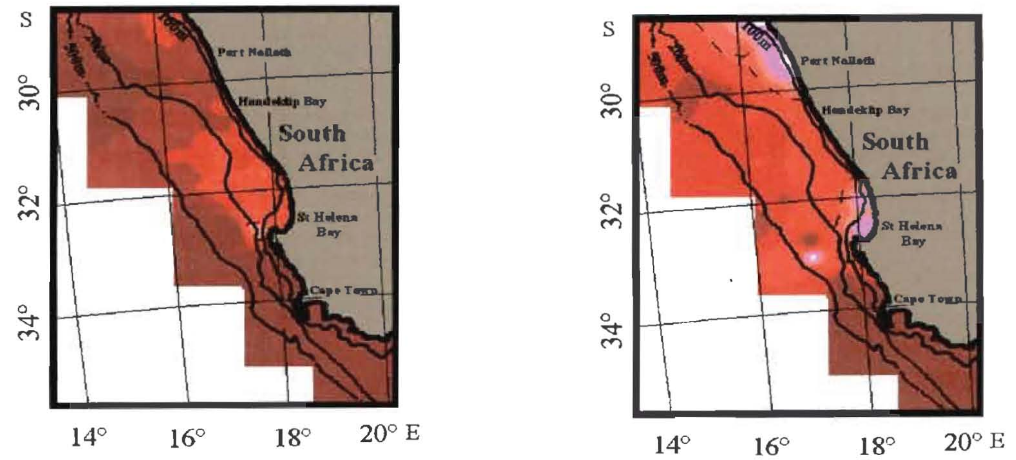
January 1990



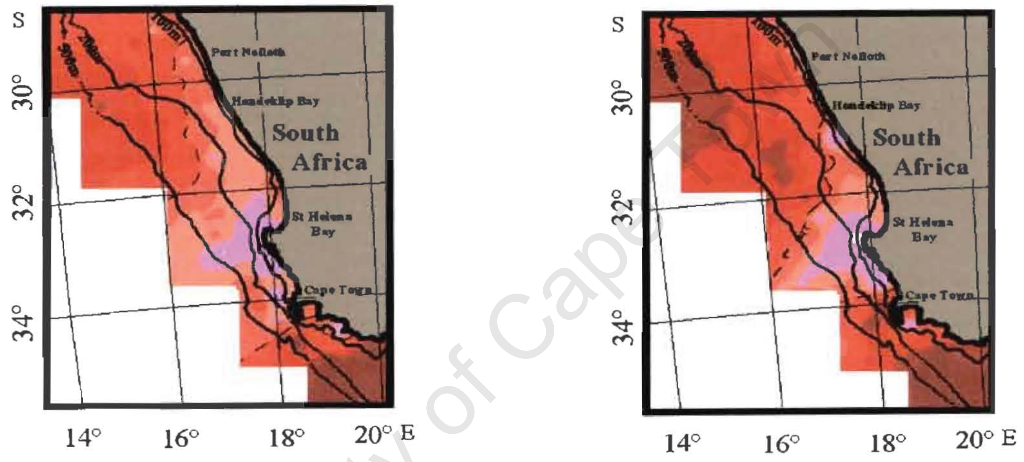
July 1990

January 1991

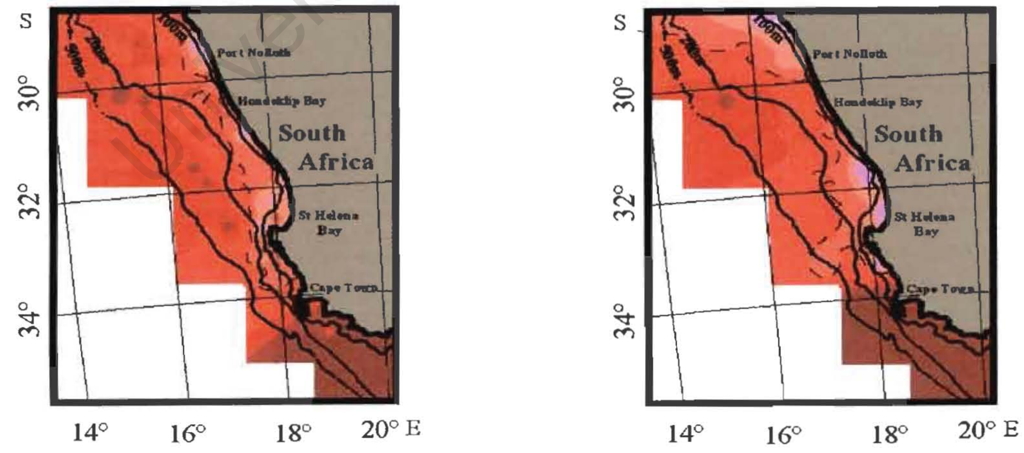
Figure A9 (cont.): sea surface temperatures off the west coast of South Africa for each survey month.



January 1992 January 1993

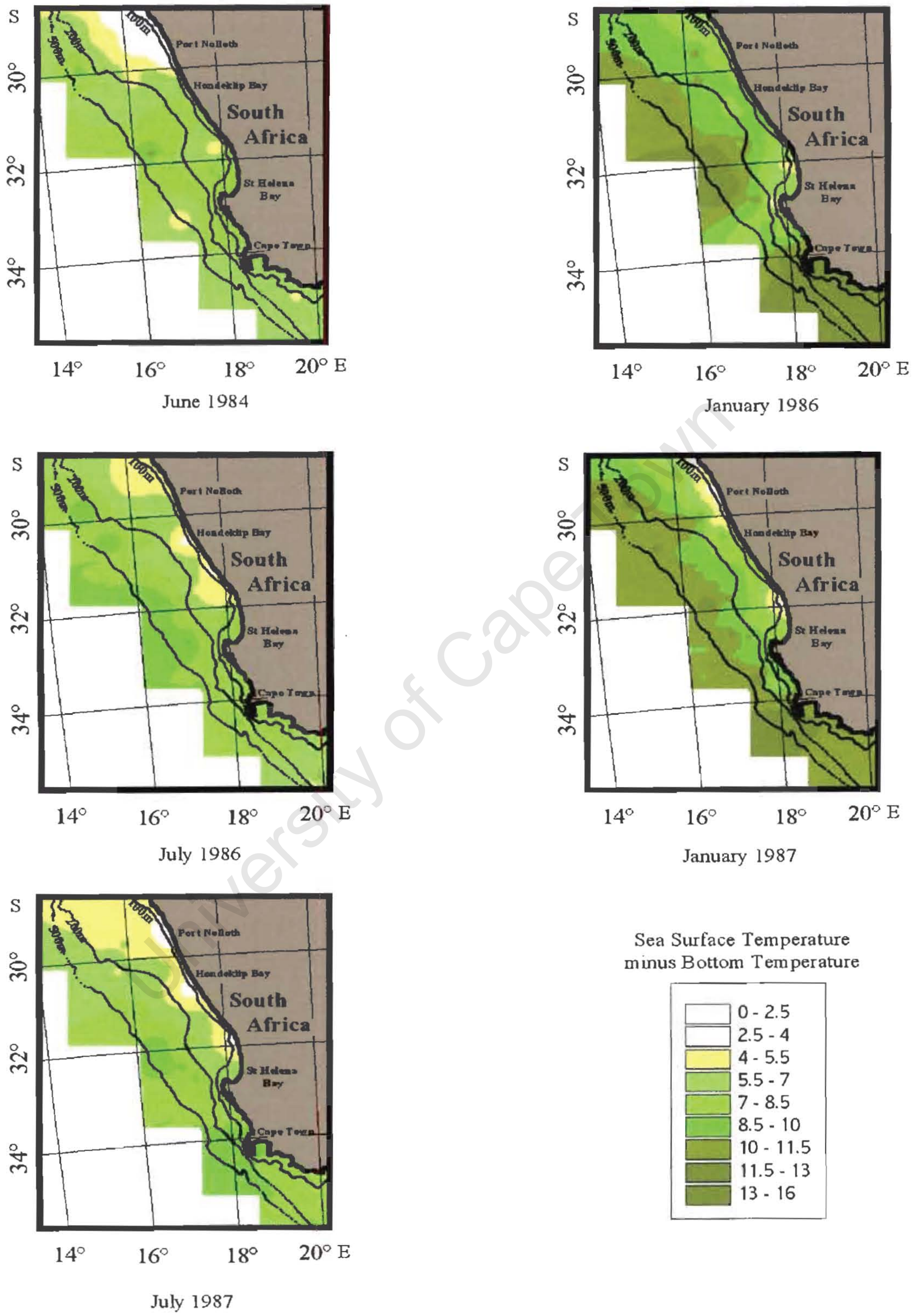


January 1994 January 1995



January 1996 January 1997

Figure A9 (cont.): Sea surface temperatures off the west coast of South Africa for each survey month.



June 1984

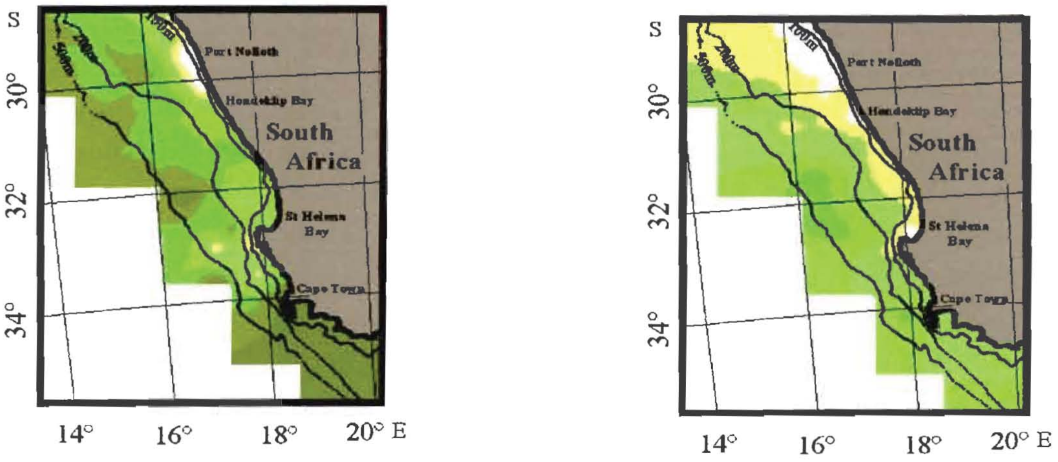
January 1986

July 1986

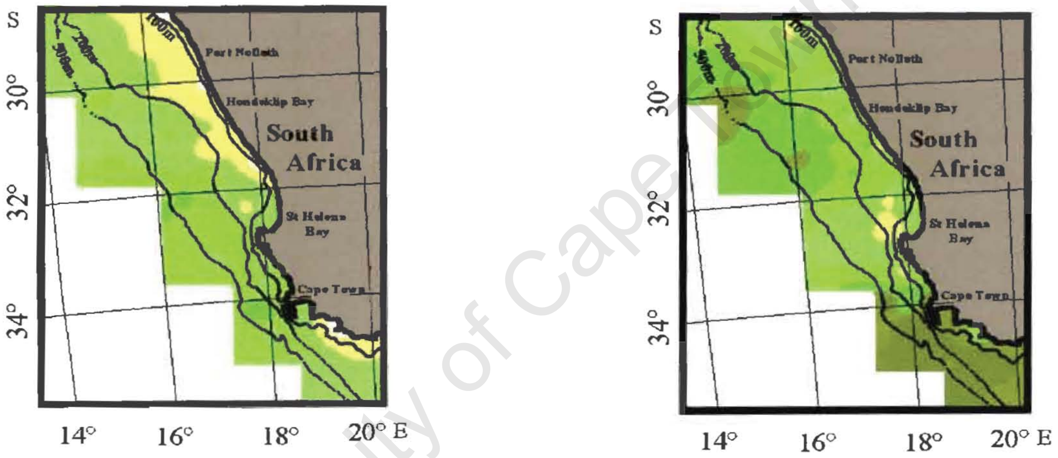
January 1987

July 1987

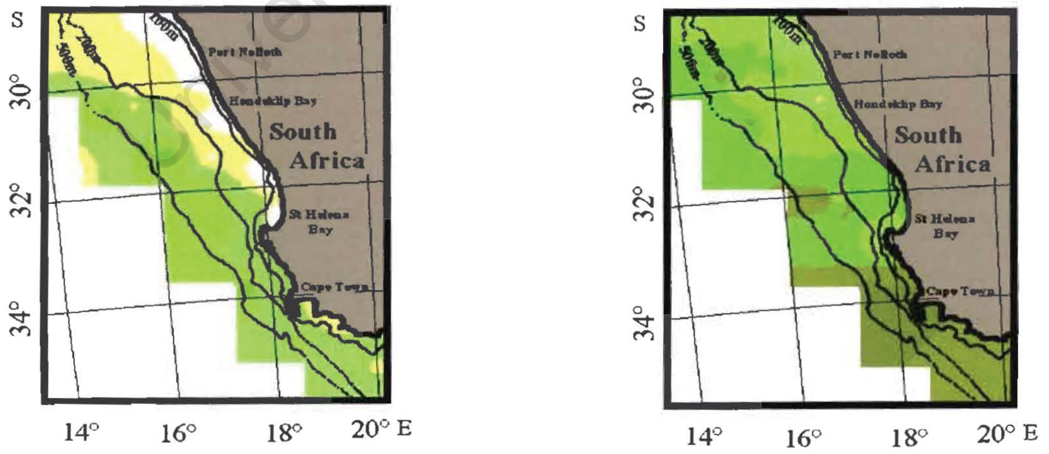
Figure A10: SST-BT off the west coast of South Africa for each survey month.



February 1988 August 1988

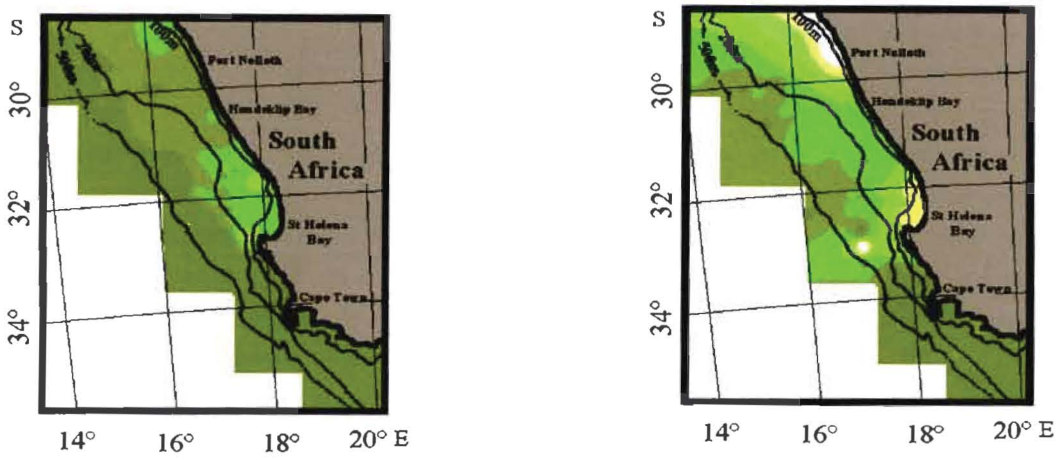


July 1989 January 1990

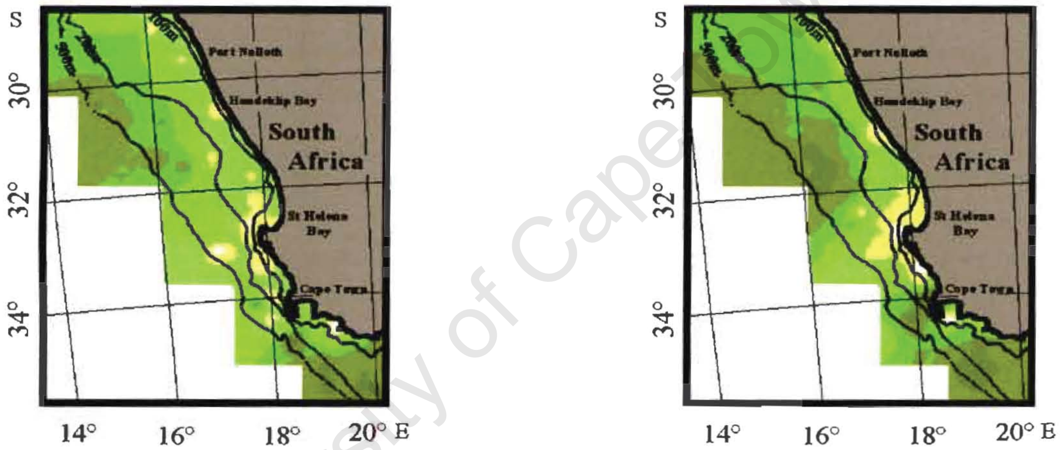


July 1990 January 1991

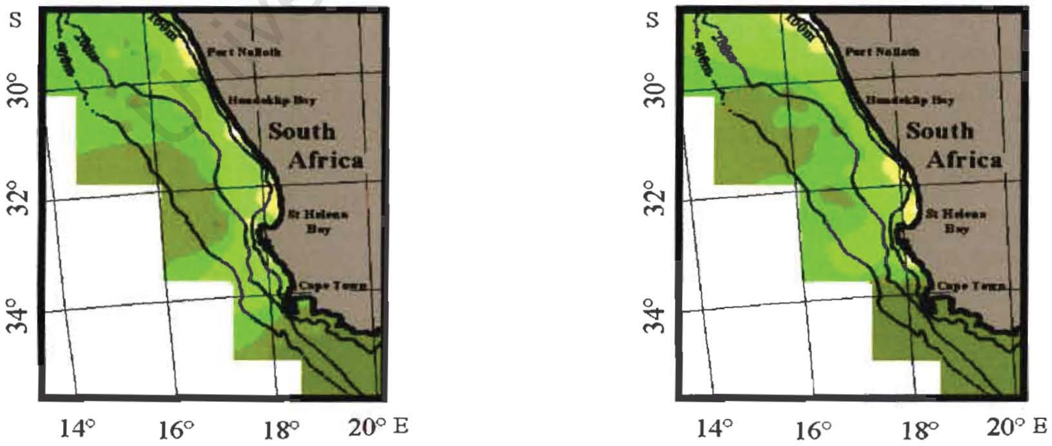
Figure A10 (cont.): SST-BT off the west coast of South Africa for each survey month



February 1992 January 1993



January 1994 January 1995



January 1996 January 1997

Figure A10 (cont.): SST-BT off the west coast of South Africa for each survey month.