ECOSYSTEM IMPLICATIONS OF THE RECENT SOUTHWARD SHIFT OF KEY COMPONENTS IN THE SOUTHERN BENGUELA

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DECLARATION

I know the meaning of plagiarism and declare that all of the work in this thesis, save for that which is properly acknowledged, is my own. This thesis has not been submitted in whole or in part for a degree at any other university.

Signature: ______________________

Date: ______________________

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Contents

ABSTRACT

Several ecologically and economically important species in the southern Benguela have undergone southward/eastward shifts in their distribution in recent decades, including sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* in the mid-1990s. This has affected prey availability to top predators such as seabirds, and the spatially-distinct nature of the system - the west coast characterised by seasonal, wind-driven upwelling, and the south coast with characteristics of both a shelf system and an upwelling system - means the location of a stock may have implications for its productivity. To investigate possible impacts of these shifts and their drivers on the ecosystem as a whole and on the south coast subsystem, now playing a more important role both commercially and biologically: i) the physical and biological characteristics of the west and south coasts (divided at Cape Agulhas) were comprehensively investigated using existing literature to better understand differences in structure and functioning; ii) distribution maps for before (1985 – 1991), during (1997-2000) and after (2003 – 2008) the shift in small pelagic fish were constructed for 14 key species using catch and survey data, and used to calculate spatial indicators (relative overlap in biomass and area, index of diversity, connectivity); iii) SST data previously used to link shifts in anchovy distribution and changes in cross-shelf SST gradient on the Agulhas Bank were reanalysed with refined and extended domains using a sequential t-test algorithm for detecting regime shifts (STARS) to re-evaluate this hypothesis; iv) results from the above were used to inform the design of a frame-based model (FBM). Sensitivity analyses and a series of model tests were performed, and the usefulness of this approach in the context of understanding spatial changes in sardine and anchovy explored. Results show that the south coast is more diverse than the west, and may be more constrained in terms of nutrient availability. For several species, previously unidentified increases in the proportion of biomass east of Cape Agulhas were shown to have occurred over the same period as that of small pelagic fish, although none to the same degree. On average overlap with small pelagic fish increased over time, but overall system connectivity was lowest in the intermediate period, possibly indicating a system under transition. Previously identified shifts in SST data were confirmed and additional undescribed shifts identified on the central Agulhas Bank and in the cross-shelf SST gradient on the western Agulhas Bank. A FBM approach appears to be useful within the context, allowing for the exploration of current thinking regarding drivers of distributional changes in small pelagic fish and the potential role of fishing, and for the development of an indicator of the capacity of the system to support top predators in terms of prey availability. The model was most sensitive to fishing parameters, and was not more sensitive than expected to alternate assumptions regarding the effects of the environmental driver used (ESI). Results suggest that the modelled productivity of the

sardine resource, and as a result the ability of the system to support top predators, is highly dependent on the spatial characteristics of fishing pressure. The role of anchovy within the model system has not yet been fully developed. Increasing our understanding of the relative suitability of environmental conditions on the west and south coasts, as well as the relationship between the two, is important if we are to increase our capacity to predict trends in abundance and distribution. In the context of the management of the small pelagic fishery, a FBM approach provides a useful alternative to a spatial model when attempting to better understand changes in sardine distribution.

CHAPTER ONE
INTRODUCTION

1.1. Introduction

Understanding the structure and functioning of a marine ecosystem is increasingly accepted as an important, if challenging, step towards understanding the consequences of environmental or human-induced change within the system and the effective management of human activities. This is particularly true given then changes we can expect to see as the impacts of climate change become more evident. Since the Reykjavík declaration of 2001 emphasized the importance of the use of an ecosystem approach to fisheries management (EAF) there has been a move towards applying EAF (FAO 2003) in the southern Benguela ecosystem, as discussed by Cochrane et al. (2004) and Shannon et al. (2006).

Variability in the environment has a strong influence on fish populations in terms of abundance, migration and distribution (Bakun 1996; Lehodey et al. 2006). As a result, climate change is expected to drive changes in latitudinal ranges in marine species as a response to local temperature changes, which has in some cases already been shown (e.g. Parmesan & Yohe 2003; Perry et al. 2005; Cheung et al. 2009; Brander 2010; Simpson et al. 2013). While potential impacts of future environmental change can be hypothesised, in reality the different life-history traits of each species means that a range of responses across species will result from any given change (Parmesan & Yohe 2003). This complexity in predicting system response to change only highlights the need for a greater understanding of ecosystem interactions and the nature of past system-level changes. An EAF is only likely to be successfully applied in inherently variable environments if these two conditions are addressed.

Given the increased importance of monitoring long term changes, both in the context of an EAF and of climate change, regime shifts have become an accepted concept in marine science. Here regime shifts are defined according to de Young et al. (2004) and as previously adopted in the context of the southern Benguela (Jarre et al. 2006) as ‘a rapid change from a quantifiable state, representing substantial restructuring of the ecosystem, acting over large spatial scales and persisting for long enough that a new quasi-equilibrium state can be observed’ (Jarre et al. 2006). Note that although patterns of alternating dominance in small pelagic fish in eastern boundary current systems, such as sardine and anchovy in the southern Benguela, have previously been termed ‘regime shifts’ (Schwartzlose et al. 1999), the term is now rather assumed to apply to ecosystem-level changes as described here (Shannon et al. 2006).

According to de Young et al. (2004) and Collie et al. (2004), the change from one stable state to another could take place in a number of distinct ways, for example: 1) as a gradual, steady change, which is most likely reversible; 2) as a more abrupt, but still steady and thus reversible, change, or lastly and with greater potential implications, 3) as an abrupt, discontinuous and irreversible change reflecting chaotic dynamics (Figure 1.1). Whether or not observed changes are widespread enough to be classified as a regime shift, and the potential for those changes to be reversed, has implications for the potential system-level effects of the change and the suitability of various management actions.

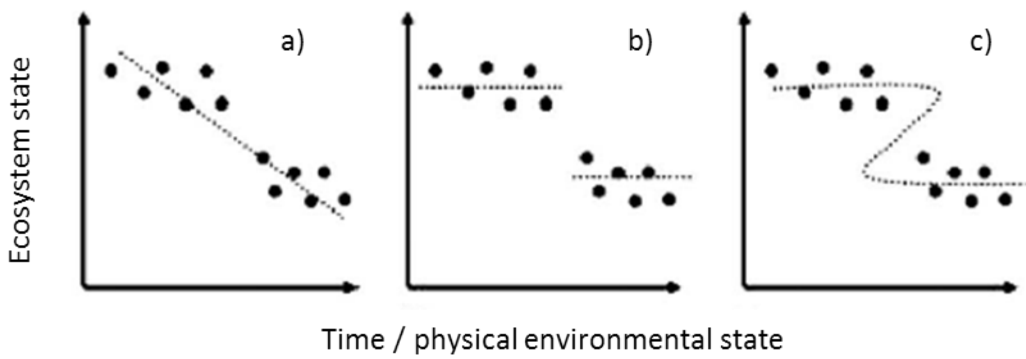


Figure 1.1: Illustrations of three possible models of change between two stable states: a) a smooth change; b) an abrupt change; c) a discontinuous change, thought to be irreversible (adapted from de Young et al. 2004).

Under the application of an EAF in the southern Benguela the monitoring of long-term ecosystem change has been recommended as a research priority (Shannon et al. 2006). van der Lingen et al. (2006) also highlight the need for an increased understanding of possible stable states, and the mechanisms behind changes. In this regard, Jarre et al. (2006) suggest the development of suitable indicators and testing of hypotheses regarding change and possible monitoring approaches.

When attempting to interpret any kind of change, one must remain aware that the spatial scale under consideration will inevitably affect one's approach and what factors or variables are considered as drivers or responses (Perry & Ommer 2003). For example, Hutchings & Nelson (1985) illustrate the interplay of different timescales involved in some of the driving processes in the southern Benguela (Figure 1.2). While small pelagic fish and plankton variability may operate on scales of days to months, often increased spatial scale implies a longer timescale (Perry & Ommer 2003). When considering ecosystem-level changes, years to decades are a more appropriate scale for meaningful observations of change. Combined with the longer term management objectives involved, this makes for a complex situation where the implications of the scale issues cannot be ignored.

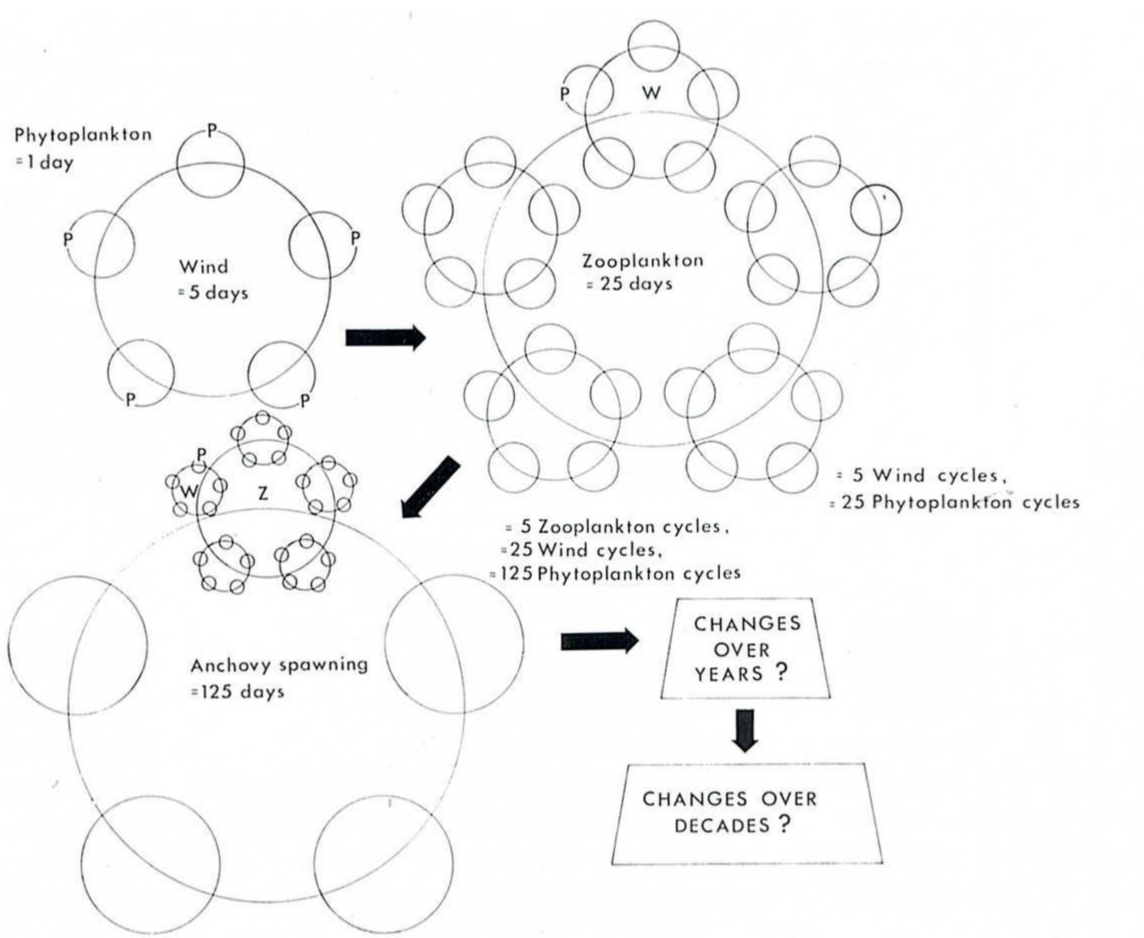


Figure 1.2: Various interacting timescales in the southern Benguela (Hutchings & Nelson 1985).

Given the levels of complexity and interdisciplinarity inherent in any attempt to apply an EAF, the use of models and indicators as means of increasing both our understanding and our ability to communicate system functioning and status, has become a vital and accepted practice (Garcia & Staples 2000; Degnbol & Jarre 2004; Starfield & Jarre 2011). Indicators have been and continue to be developed and used to evaluate various aspects of the southern Benguela (e.g. Cury et al. 2005; Yemane et al 2008; Shannon et al. 2009; Shin et al. 2010). These can in turn be used as inputs for various modelling techniques that allow for the distillation and clearer communication of findings to stakeholders and management alike (Paterson et al. 2007; Shin & Shannon 2010; McGregor 2015).

There is a huge range of modelling approaches and techniques that can be applied in the context of marine systems. Modelling of specific sectors of the ecosystem was once the most common approach, for example biogeochemical models such as NPZD-type models focused on the interaction between nutrients and plankton groups (Franks 2002; Heinle & Slawig 2013) or single or multi-species models of economically important higher trophic level species (e.g. Magnusson 1995). Increased understanding of the importance of an EAF and increased computing power has led to a proliferation of more complex whole-system, or end-to-end models, attempting to include all system process both biotic and abiotic (Travers et al. 2007; Fulton 2010). These include models constructed using modelling packages like Ecopath with Ecosim (Christensen et al. 2005), OSMOSE (Shin & Cury 2004) or Atlantis (Fulton et al. 2011).

Although extremely complex models including many interactions now exist, Fulton et al. (2003) have shown that increased complexity is not always desirable, and a 'humped' relationship exists between the complexity and the effectiveness of ecosystem models. An array of 'minimum-realistic' models is recommended as most effective to avoid the increasing uncertainty and difficulty in interpreting outputs arising from more complex modelling approaches (Fulton et al. 2003). One approach that has been suggested as suitable for the modelling of long-term system change is frame-based modelling, where a 'minimum-realistic' approach is taken with a particular objective in mind (Starfield & Jarre 2011). This is similar to the 'Models of Intermediate Complexity for Ecosystem assessments' (MICE) approach described by Plagányi et al. (2014), where a model somewhere between the complexity of a single-species model and an ecosystem model is developed to answer specific questions relating to management. Although without the complexity of some of the ecosystem models currently developed for the southern Benguela (Shannon et al. 2003; Shin et al. 2004; Shannon et al. 2008), the minimum realistic and MICE modelling paradigms do allow specific questions to be addressed with the minimum level of complexity, and thus investment of resources, necessary (Starfield et al. 1993).

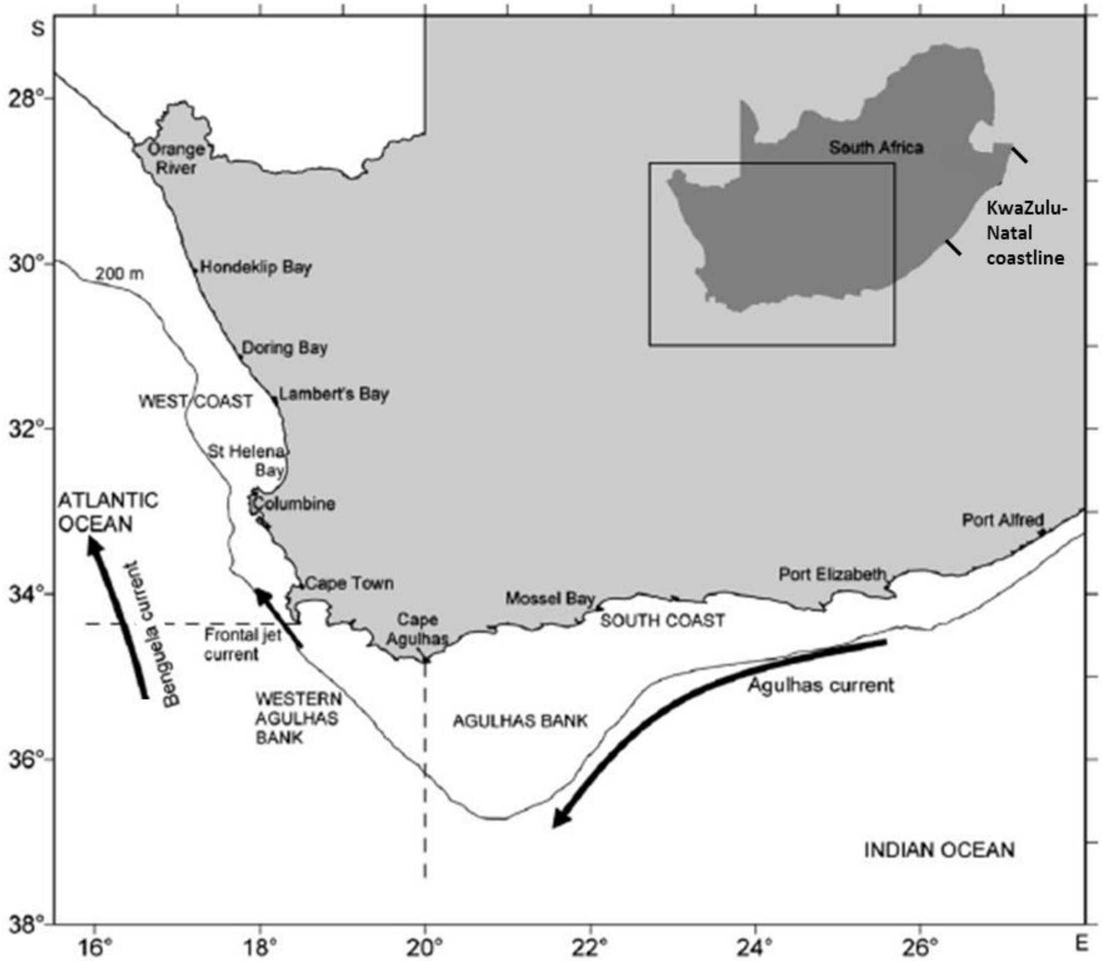


Figure 1.3: The southern Benguela and Agulhas and Benguela currents. The area east of Cape Agulhas is referred to as the south coast, and the area west and north of Cape Agulhas as the west coast (Coetzee et al. 2008a).

The southern Benguela has its northern boundary at 26°S at the Lüderitz upwelling cell, and stretches south and east around the coast to include the Agulhas Bank and reach its eastern boundary at East London (28°E). It includes within its extent two very different regions: the west coast, an area of wind-driven upwelling between Lüderitz in southern Namibia and Cape Agulhas (Figure 1.3) with upwelling increasingly seasonal towards the south; and the south coast, including the Agulhas Bank, which has both the characteristics of a seasonal shelf system and an upwelling system (Hutchings et al. 2009; Shannon 1985).

Although the established fisheries in the southern Benguela operate within both of these areas, historically the cold, nutrient-rich waters of the west coast have been more important with regards to productivity and landings by commercial fisheries (Crawford et al. 1987; Shannon 1985). Over recent decades, however, a number of commercially and ecologically important species (sardine, anchovy, rock lobster and horse mackerel) have undergone changes in their distributions, with relative or absolute increases in their abundances to the south and east recorded compared with the west coast (van der Lingen et al. 2006a; Cockcroft et al. 2008). The numerous known and countless unknown biological implications for trophically linked species, as well as the sometimes severe economic implications for the industries involved resulting from these changes, have drawn the focus of research effort. Our understanding of the repercussions is still far from complete, however, and the system-level effects in particular warrant further investigation.

1.2. Relevant species and observed changes

1.2.1. Sardine

The sardine *Sardinops sagax* is a small pelagic fish of great ecological and economic significance in the southern Benguela. Small pelagic fish as a group play an integral role in the trophodynamic structure of upwelling systems like the southern Benguela, influencing groups at both higher and lower trophic levels. This has been termed 'wasp-waist' trophic control over the ecosystem (Cury et al. 2000). Along with the anchovy *Engraulis encrasicolus,* sardine have also formed one of the mainstays of the South African pelagic purse seine fishery since its inception in the 1940s. Following sardine distribution patterns, the South African sardine fishery began at St Helena Bay on the west coast, where much of the industry's infrastructure was established and remains today. The pelagic fishery then expanded south and east through the 1960s and 1970s, extending to Cape Agulhas on the south coast and including the western Agulhas Bank (WAB) (Crawford 1981). Catches from the pelagic fishery peaked at ~ 400 000 t in 1962 but shortly afterwards in the mid-1960s the sardine stock collapsed as a result of increased effort and a southward expansion of the fishing grounds, coupled with inconsistent recruitment. Correspondingly lower yields from the fishery were recorded throughout the 1970s, 1980s and early 1990s (Crawford et al. 1987; Coetzee et al. 2008a). Subsequent conservative management strategies applied since the mid-1980s, coupled with favourable conditions on the west coast however, resulted in the recovery of the stock (Cochrane et al. 1998). Landings increased in the late 1990s, peaking in 2002 following unusually good recruitment from 2001-2003, but low levels of recruitment and a resultant decline in catches have been recorded in the years following (Coetzee et al. 2008a).

Sardine are distributed around the coast of South Africa according to size/age-group, as a result of both size-specific behavior and seasonal hydrological changes (Armstrong et al. 1987). When monitored over the period 1964-1976 and during the 1990s, spawning appears to have taken place predominantly during spring and late summer, over the Agulhas Bank (see Figure 1.3). Most 0-1yr old fish were found off the west coast from May to September while 2-4yr old fish were recorded predominantly on the spawning grounds over spring/ summer, migrating to the east in autumn (Crawford 1981; Barange et al. 1999; Beckley & van der Lingen 1999). Over the 1980s and 1990s the majority of sardine biomass was found west of Cape Agulhas (Barange et al. 1999). This is reflected in the centre of gravity (CoG) or mean location of sardine-directed landings for that period (Figure 1.4).

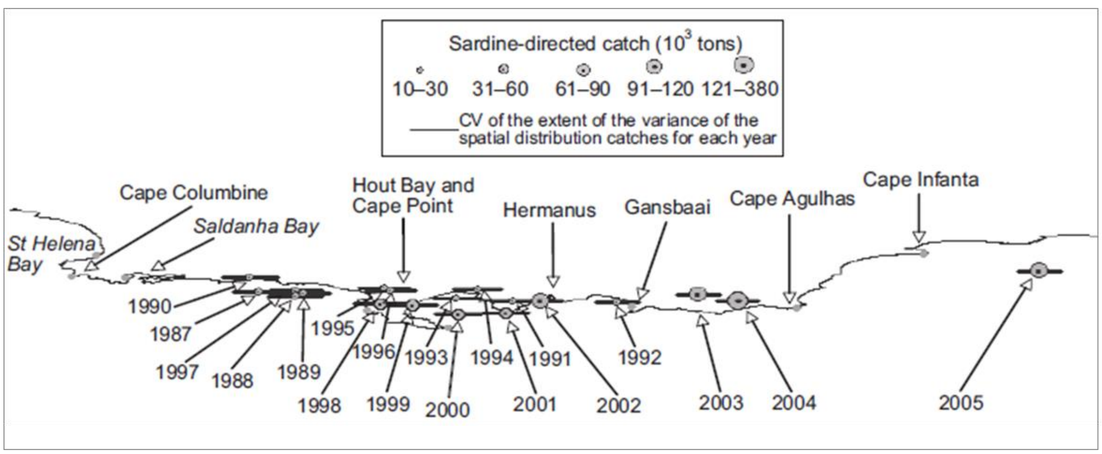


Figure 1. 4: Annual mean location of the sardine-directed catch along the linearised coast of South Africa from 1990 - 2005. Point size is proportional to catch (Fairweather et al. 2006a).

Since the late 1990s however, an apparent shift in sardine distribution or change in relative abundance has been observed by annual hydro-acoustic biomass surveys, ichthyoplankton sampling and the CoG of the catch: by 1999 the sardine biomass east of Cape Agulhas outweighed that to the west. Over the period 1997 – 2005, the CoG of catches showed an annual eastward movement (Figure 1.4), reflecting increased landings off the south coast and correspondingly lower catches off the west coast (van der Lingen et al. 2005; Fairweather et al. 2006a). Figure 1.5 shows that by 2004 sardine were found almost entirely east of Cape Agulhas, with the majority being as far as or further east than Mossel Bay (van der Lingen et al. 2005; Coetzee et al. 2008a). Apart from the implications for the pelagic fishery, now facing the costs of the separation of its processing infrastructure from its resource, the trophic importance of sardine within the system means this shift in distribution could have serious and not fully understood implications for the ecosystem as a whole. This is particularly of concern for the many groups which either prey on or compete with sardine (van der Lingen et al. 2005).

There are currently three hypotheses suggested to explain the mechanisms behind the shift, namely 1) differential fishing pressure, 2) environmental forcing, and 3) successful spawning on the south coast combined with natal homing of spawners (Coetzee et al. 2008a). The possibility of multiple sardine stocks, one on the west coast, one on the south coast, and a possible third on the KwaZulu-Natal east coast, is also currently being investigated. Biological data seem to suggest this may be the case (van der Lingen et al. 2013), but the hypothesis is so far not supported by genetic studies (Hampton 2014). The use of a two-stock recruitment model in the Operational management procedure (OMP) used to manage the small pelagic fishery is currently under consideration (de Moor & Butterworth, 2011;2013).

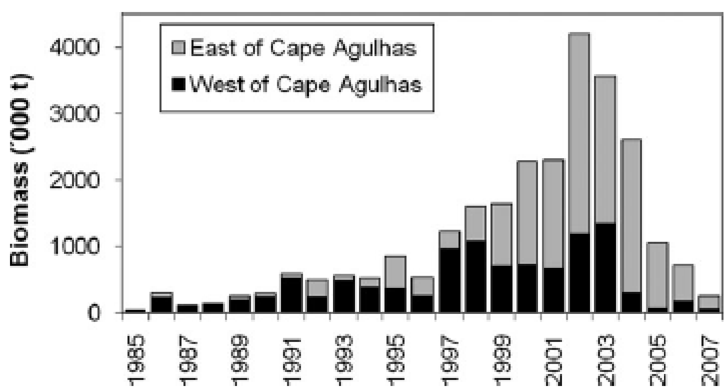


Figure 1.5: Biomass of sardine east and west of Cape Agulhas during the November acoustic surveys (Coetzee et al. 2008a).

1.2.2. Anchovy

Anchovy is another commercially and ecologically important small pelagic fish abundant in the southern Benguela. Like sardine, anchovy are important both as a prey species for larger fish and mammals and as a predator driving plankton abundance (Cury et al. 2000). Due to their short life-histories there is high interannual variability in sardine and anchovy abundance. As in other eastern-boundary systems the two species tended to show alternate dominance on a decadal scale until the late 1990s (Schwartzlose et al.

1999). A period of co-dominance has also occurred in the early 2000s when the abundance of both species was high (Fairweather et al. 2006a). Anchovy also experience high seasonal variability in distribution and abundance: after the peak summer spawning season on the Agulhas Bank, eggs and larvae are transported to west coast nursery grounds. By maturity at ~ 1yr, adult fish have migrated inshore and back to the Agulhas Bank (van der Lingen & Huggett 2003).

Similar to sardine, anchovy underwent a change in relative distribution in the mid-1990s: hydro-acoustic data for the period 1983-2005 reveal that the majority of anchovy spawner biomass shifted in 1996 from the western Agulhas Bank to the central and eastern Agulhas Bank (Figure 1.6), where it has remained since (van der Lingen et al. 2002; DAFF 2012) (although given their migratory lifecycle, anchovy juveniles are always found on the west coast for a portion of the year). This shift has been linked to changes in wind-driven upwelling and subsequent cooling on the south coast, suggesting a close association between environmental fluctuations and the biological functioning of the ecosystem (Roy et al. 2007).

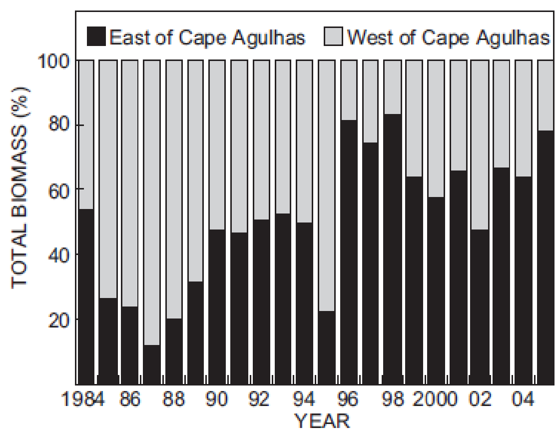


Figure 1.6: Proportion of anchovy spawner biomass found to the west and east of Cape Agulhas during November acoustic surveys from 1984 – 2005 (Roy et al. 2007).

1.2.3. West Coast rock lobster

In the inshore environment, the valuable commercial fishery for West Coast rock lobster *Jasus lalandii* has been operating in South Africa since the 1800s. Prior to the late 1980s the majority of landings were made on the west coast, but from this point landings on the west coast began to decline while those on the south coast increased until by the late 1990s the relative contribution by each coast to overall landings had been inverted. Since then the west coast has contributed <10% to total landings, reflecting a south and eastward shift in their distribution (Cockcroft et al. 2008). The decline on the west coast has been attributed to decreased productivity of rock lobsters on the west coast over the late 1980s and early 1990s as a result of decreases in somatic growth. When combined with an increased frequency of lobster walk-out events over the 1990s and consistently high fishing pressure (Cockcroft 2001; Cockcroft et al. 2008; van der Lingen et al. 2012) the stock could not recover. The increased walk-outs over the 1990s were the result of an increase in low oxygen events, caused when dense plankton bloom decay as a period of upwelling is followed by a period of calm. That this increase should occur concurrently with the less understood decrease in somatic growth, combined with the shifts in pelagic fish species described above, has however been suggested as evidence of some underlying system-level environmental forcing (Cockcroft et al. 2008). This is supported by positive shifts in upwelling variability and mean summer winds identified by Blamey et al. (2012) in the early – mid 1990s on the west and south-west coasts, concurrent with the shift in rock lobster distribution.

1.2.4. Horse mackerel

Another contributor to the pelagic fishery, as well as to the mid-water and demersal trawl fisheries, whose distribution may have shifted south and east since the 1990s is the Cape horse mackerel *Trachurus trachurus capensis*. Up until the 1980s landings were primarily made off the west coast, but large horse mackerel haven't been landed in significant quantities at St Helena Bay since the 1960s (Hutchings et al. 2012). Since the 1980s a possible south coast spawning ground has since been identified. Although juvenile horse mackerel are still prevalent on the west coast, the south coast now supports a far greater biomass of horse mackerel (combined juveniles and adults) than can be found on the west (Barange et al. 1998; Merkle & Coetzee 2007; Hutchings et al. 2012), hence horse mackerel currently plays a more important trophic role on the south coast than on the west coast.

1.2.5. Seabirds

Some of the more well-documented responses to changes in small pelagic fish and rock lobster distribution and abundance are in the seabirds preying on these species (Crawford 2013; Crawford et al. 2008a; Sherley et al. 2013; Cockcroft et al. 2008). Two species preying on sardine and anchovy and one feeding largely on rock lobster (African penguins *Spheniscus demersus,* Cape cormorants *Phalacrocorax capensis* and Bank cormorants *P. neglectus* respectively) have declined significantly since the 1990s (Crawford et al. 2007a; Crawford et al. 2008b; Crawford et al. 2011). Other species, generally those whose life histories allow for greater foraging range or flexibility in breeding site selection, have responded positively and have extended their ranges southwards and eastwards along with their prey species: Cape gannets *Morus capensis* and swift terns *Thalasseus bergii bergii* (Crawford et al. 2007b; Crawford 2009).

1.2.6. Ecosystem-level changes

In addition to the changes observed in the above species, a number of possible system-level shifts have been identified in the southern Benguela since the 1980s. Based on shifts in SST, upwelling and small pelagic fish abundance, Howard et al. (2007) identified an ecosystem-level shifts as having occurred in the early 2000s. Similarly, shifts in demersal fish assemblages have also been shown for the mid-1990s and the mid-2000s, although the latter may be due to changes in sampling (Atkinson et al. 2011a). Blamey et al. (2012) also identified shifts in the mid-1990s when examining wind and upwelling indices. These changes, together with those outlined above, seem to point to a degree of system-wide change with a greater potential influence on other aspects of ecosystem function and state than any individual species change could have.

1.3. Implications and questions

These distributional changes have had serious socio-economic and ecological implications. Biological consequences are inevitable, for example the increase in rock lobster abundance east of Cape Hangklip has also indirectly affected the abalone fishery by causing a decline in the abundance of sea urchins, which play important roles in abalone recruitment success (Tarr et al. 1996; Day & Branch 2002; Blamey et al. 2010). Widespread ecological impacts are likely to be felt by groups trophically linked to species undergoing changes in distribution, as has been illustrated in the case of pelagic fish and seabirds by Crawford et al. (2008a-c), ranging from changes in diet and reproductive success to shifts in distribution. The consequences of human-induced or environmentally driven changes or regime shifts are also not restricted to the biological subsystems, and are felt in the human social system as well via the fisheries and associated communities reliant on the various affected resources (Jarre et al. 2013).

The aim of this thesis is to investigate possible ecosystem-level impacts of distributional shifts of important component species in the southern Benguela, with a focus on small pelagic fish (sardine and anchovy). A combination of data-derived indicators and modelling will be used to better understand the processes affected and how this might influence ecosystem structure and function. Given the increased abundance of small pelagic fish now found east of Cape Agulhas, the south coast system is of particular interest in its now more important role both in terms of fisheries and ecological interactions within the southern Benguela.

In this thesis the following key questions are addressed:

a) Does the south coast function differently from the west coast, and if so, what are the implications for a large-scale change in the location of the majority of the biomass of small pelagic and other species affected?
b) Have the distributions of any other prominent species changed over a similar timeframe, and if so, what are the likely impacts?
c) How robust is the hypothesis that changes in anchovy distribution can be linked to changes in SST?
d) Can a frame-based modelling approach be useful in exploring our current understanding of the processes involved, and the relative importance of possible drivers?

As described further below, in the first three chapters the structure and functioning of the south coast and implications of shifts in small pelagic fish is investigated, distributions of other species are examined for concurrent changes, and a brief further investigation of sea surface temperature (SST) as a driver of change on the south coast is conducted. Finally the insights gained over the course of these earlier chapters inform the construction of a frame-based model of sardine and anchovy population distribution that is used to explore our current understanding of the processes involved. Work undertaken is in line with recommendations made by Shannon et al. (2006) for furthering the application of EAF in the southern Benguela.

1.4. Thesis structure

Chapter Two: Structure and functioning of the south coast system, with comparisons to the west.

Chapter Two outlines the trophic functioning of the south coast system as far as it is known, with some comparison with that of the west coast system. This mostly conceptual chapter provides an ecosystem perspective and a backdrop for what has been happening over recent decades, in more detail than introduced above. The south coast is expected to function differently from the west coast based on its shelf ecosystem characteristics and the greater species diversity present, e.g. a greater abundance of squid and cetaceans, and increased predation pressure on the Agulhas Bank. This would imply that different mean trophic linkages are in place on the south coast when compared with those on the west coast. This has implications for the structure and functioning of the south coast system as a whole and how these elements react to changes such as increased sardine and anchovy biomass.

Chapter Three: Spatial indicators and changes in distribution

Pecquerie et al. (2004) compiled a number of different data sources (acoustic and demersal surveys; pelagic, demersal including mid-water trawl, hake directed and tuna directed longline fisheries data) to create geographic information systems (GIS) distribution maps for 15 key species in the southern Benguela: anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax*, round herring *Etrumeus whiteheadi*, chub mackerel *Scomber japonicus*, horse mackerel *Trachurus trachurus capensis*, lanternfish *Lampanyctodes hectoris*, lightfish *Maurolicus muelleri*, albacore *Thunnus alalunga*, bigeye tuna *Thunnus obesus*, yellowfin tuna *Thunnus albacares*, silver kob *Argyrosomus inodorus*, snoek *Thyrsites atun*, Cape hake *Merluccius spp*., kingklip *Genypterus capensis* and chokka squid *Loligo vulgaris reynaudi*. These data were then used by Drapeau et al. (2004), to quantify spatial interactions between species using measures of overlap, and by Fréon et al. (2005a) to derive seven spatial indicators, two of which can be used to characterise the system and five to be used as an indication of fishing pressure.

A similar approach is used in Chapter Three, and distributions are plotted using updated time-series currently available from the Department of Agriculture, Forestry and Fisheries (DAFF) and other sources for the periods pre-, during-, and post shifts in small pelagic fish biomass (1985-1991; 1997 – 2000; 2003 - 2008). This allows for comparison of an inter-species overlap index over three time periods, to evaluate the null hypothesis that the spatial distributions of the main component species and fishing pressure have not changed from those reported in these earlier studies. Results should give further insight into possible changes to ecosystem structure and functioning over this period.

Chapter Four: Re-examining changes in SST on the Agulhas Bank as a driver of distributional change in small pelagic fish

SST has previously been implicated as a driver of the change in sardine distribution (Roy et al. 2007). In Chapter Four, this assertion is further examined by a more rigorous analysis of SST data for the Agulhas Bank using a sequential t-test algorithm for detecting regime shifts, or STARS method, developed by Rodionov (2004). This method has previously been demonstrated as useful in identifying long-term shifts in time-series for the southern Benguela (Howard et al. 2007; Blamey et al. 2012), and should clarify the presence of shifts and the previously hypothesised link to the change in anchovy distribution. The results of this chapter inform the switching rules for the frame-based model.

Chapter Five: Frame-based ecosystem modelling approach

Frame-based modelling is an ecosystem modelling approach that provides an alternative to the more detailed methodologies applied when using, for example, Ecopath with Ecosim or OSMOSE (Shin & Cury 2004; Christensen et al. 2005), for the purpose of assessing management strategies when applied to a changeable environment. Initially based on Westoby et al.'s (1989) State-and-Transition approach, frame-based modelling relies on the identification of the possible states, or 'frames', relevant to the objective of the investigation, representing specific characteristics of the ecosystem in different periods. During stochastic simulations run using these individual frame models, the likelihood of remaining in the current frame or switching to a different one that better describes the prevailing conditions is regularly evaluated using indicators. The advantages of this approach are that the development process is goal-oriented, and that while the model may be simple, it allows for exploration of the effects of management strategies on the system in a process-oriented modelling paradigm without the need for vast amounts of data, thus providing a practical tool for strategic management (Starfield et al. 1993; Starfield & Jarre 2011).

While previously used to describe the dynamics of terrestrial systems (Tester et al. 1997; Rupp et al. 2000), Smith & Jarre (2011) and subsequently Botha (2012) applied this technique as a means of modelling regime shifts in small pelagic fish in the southern Benguela, focusing on the west coast. In this project, frames are created to represent spatial shifts in distribution. The parameterisation of the south coast frame and the switching rules (i.e. the conditions under which a change of frame will occur) are informed by the results of previous chapters.

Chapter Six: Further model scenarios: effects of spatialised fishing pressure.

In Chapter Six, the model constructed in Chapter Five is used to explore possible implications of different management scenarios, exploring the hypothesis that the current fishing pressure is sustainable in the long term under 'reasonable' environmental variability. The possibility of the south coast frame favouring anchovy recruitment is also considered. The implications of all scenarios in terms of system state and suitability of each coast for top predators are examined.

Chapter Seven: Summary and conclusions

In this final chapter, results of the previous chapters are assimilated with respect to the key questions introduced above (section 1.3). Overall conclusions are drawn with regard to possible future directions and implications for strategic management advice.

CHAPTER TWO
STRUCTURE AND FUNCTIONING OF THE SOUTH COAST, WITH COMPARISONS TO THE WEST

2.1. Introduction

Previous models of trophic functioning of the southern Benguela have dealt with the entire ecosystem, from the Lüderitz upwelling cell in the north (26ºS) to East London (28ºE) (Shannon et al. 2003; Shin et al. 2004; Watermeyer et al. 2008; Travers & Shin 2010). The southern Benguela can however be divided into two physically and biologically distinct regions: the west coast, extending from the Orange River mouth in the north to Cape Point in the south; and the Agulhas Bank, extending east from Cape Point to East London (Hutchings et al. 2009). As discussed further below, although Cape Point is sometimes used as a break between the west coast and what is referred to as the south coast, in this project when referring to the west coast, the entire area west of Cape Agulhas including the western Agulhas Bank (WAB) is intended. The 'south coast' refers to the central and eastern Agulhas Bank. This chapter aims to outline possible implications of differing conditions in the two regions for the trophic structure and functioning in each via a structured review of available data, both qualitative and quantitative where possible. Information compiled in this chapter will be used both directly to inform the design of the model discussed in Chapters Five and Six, and indirectly to provide context for interpretation of results in the chapters that follow.

2.2. The south coast system with comparisons to the west

2.2.1. Physical characteristics:

Despite being part of the same upwelling system, the west and south coasts of the southern Benguela have quite different oceanographic characteristics:

The pulsed upwelling that characterizes the west coast is driven by prevailing southerly winds, strongest in summer and autumn (Shannon et al 1984; Hutchings et al. 2009). The resulting narrow but highly productive band of nutrient rich water along the coast is also associated with low bottom water temperatures and oxygen content.

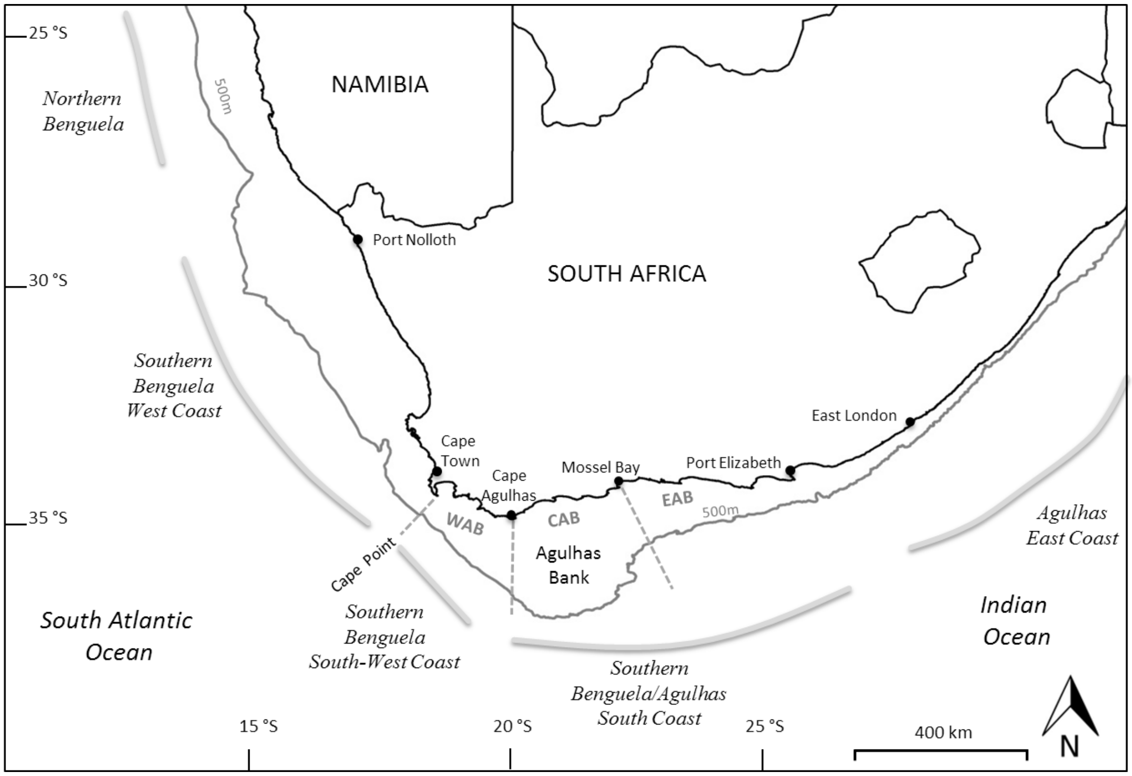


Figure 2.1: The major divisions of the southern Benguela: the west coast, including the western Agulhas Bank (indicated as the south-west coast/ WAB) and the south coast, which includes the central (CAB) and eastern Agulhas Bank (EAB). The shelf-edge is indicated by the 500m isobath (adapted from Blamey et al. 2014).

In contrast, the south coast, which includes the Agulhas Bank, has a relatively wider shelf and possesses characteristics of both temperate shelf and upwelling systems. The substrate is predominantly rocky compared with the muds that are more representative along the west coast shelf (Hutchings 1994; Sink et al. 2012). Both shelf-edge and wind-driven coastal upwelling occur, although less intensely than on the west coast, and high surface chlorophyll concentrations are relatively less common (Shannon et al. 1984; Boyd & Shillington 1994; Demarcq et al. 2007). Patterns of upper-mixed layer nutrients on the Agulhas Bank are strongly seasonal: the water column is subjected to deep-mixing during winter down to depths of 70-100m, especially on the western and central Agulhas Bank, in contrast to the west coast, while summer results in a far more stratified water column and a subsurface chlorophyll maximum, similar to the seasonal patterns of temperate shelf regions (Probyn et al. 1994; Lutjeharms et al. 1996).

Although nutrient concentrations in the surface layers increase during winter due to the mixing of nutrient-rich bottom water (Lutjeharms et al. 1996), the deep mixing results in light-limitation and low productivity during June-September. The possible exception is the eastern extent of the Agulhas Bank (Port Alfred), where persistent upwelling induced by the divergence of the Agulhas Current from the coast may facilitate perennial productivity (Verheye et al. 1994). Overall, there is a period of destratification from May-June (late autumn/ winter) as winter storms increase in frequency and intensity and insolation decreases, and conversely a period of stabilisation in October-November (Spring). These periods coincide with pelagic fish surveys, designed to cover peak anchovy spawning (Nov) and recruitment (May/ June) events. The south coast can also be distinguished from the west by its higher bottom water temperatures, particularly in winter, with higher dissolved oxygen concentrations (Roberts, 2005; Hutchings 1994).

Primary production on the south coast can be summarised as occurring via nine possible mechanisms (van der Lingen et al. 2006b):

a) the seasonal cycle characteristic of temperate zones;

b) intermittent mixing by high wind speeds, where turbulence introduces nutrients to the upper mixed layer resulting in increased production as the water column restabilises;

c) the subsurface chlorophyll maximum can be raised into the euphotic zone by internal waves resulting from transient low pressure systems and tidal movement (Largier & Swart 1987), temporarily increasing productivity;

d) wind-driven coastal upwelling;

e) upwelling resulting from divergence of the Agulhas Current from the shelf, generally between 26 and 28˚E;

f) shelf-edge upwelling;

g) increased divergence or convergence with the shelf, which can be caused by eddies in the Agulhas current, positively or negatively affecting production on the Agulhas Bank;

h) the semi-permanent cold-ridge feature described below; and

i) diffusion through the thermocline.

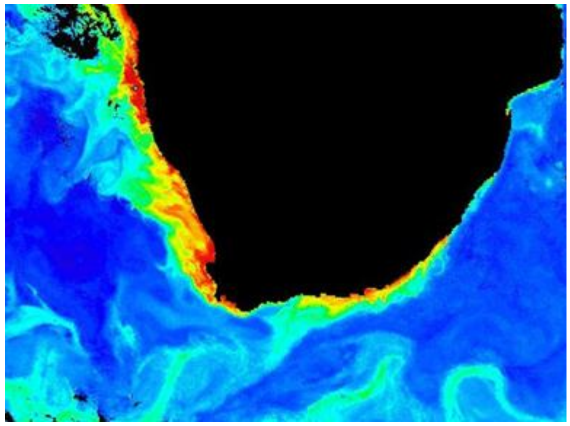


Figure 2.2: Primary productivity in the southern Benguela during summer (Feb) 2004 based on MODIS data. The higher productivity on the west coast when compared with the Agulhas Bank is clear.

The Agulhas Bank can be divided into three distinct regions based on hydrography, plankton, and forage fish patterns: the western (WAB), central (CAB) and eastern Agulhas Bank (EAB) (Figure 2.1). The WAB is similar to the west coast in that it is characterised by wind-driven coastal upwelling and the associated higher nutrient levels, particularly during late summer (Figure 2.2) (Hutchings 1994; Lutjeharms et al. 1996). The CAB and EAB experience relatively less coastal upwelling, occurring when it does largely in summer and autumn due to the seasonal increase in easterly winds. Enrichment along the shelf-break is also a typical feature of the CAB and EAB as a result of either shelf-edge upwelling from friction between the Agulhas Current and the shelf break, or eddies originating in the Agulhas Current and moving slowly SW along the shelf-break (L. Hutchings, pers. comm.).

This cool, upwelled water covers the entire shelf of the Agulhas Bank in summer on the bottom and, together with advection of Agulhas Current surface water and summer heating via insolation, significantly influences the development of the strong thermoclines in the region (Largier & Swart, 1987; Lutjeharms et al. 1996). A prominent feature of the south coast is a semi-permanent ridge of cold, productive water occurring around the 100m isobath from Mossel Bay to Cape St Francis, with peak productivity between March and June (Largier & Swart, 1987; van der Lingen et al. 2006). Because the Agulhas Current leaves the bank at the southern tip and approximately the widest point of the shelf at around 20^0 E, current-driven shelf-edge upwelling is not a feature of the WAB.

As previously mentioned, because the WAB has more physical characteristics in common with the west coast (namely episodic, seasonal and wind-driven upwelling) than with the rest of the Agulhas Bank (EAB and CAB), for the purposes of this thesis in the following chapters where a division between the west and south coast is discussed, the break between the two regions will be assumed to be Cape Agulhas (Figure 2.1), rather than Cape Point, which is sometimes used to divide the west coast from the Agulhas Bank. The WAB is thus included with the west coast in further discussions where possible unless otherwise stated, in line with regional oceanographic features as well as with assumptions currently made when considering spatial implications for the management of the sardine fishery (van der Lingen & van der Westhuizen 2013). Where possible, I will distinguish between west coast and western Agulhas Bank, and central and eastern Agulhas Bank. Where 'the Agulhas Bank 'is referred to, this implies the entire extent, including WAB, CAB and EAB.

2.2.2. Biological components

The biota of the south coast are outlined and compared with that of the west coast below, and summarized in Table 2.1.

2.2.2.1 Primary production

According to Probyn et al. (1994), phytoplankton concentration on the Agulhas Bank is on average lower than on the west coast (using Cape Point as a division), having an average chlorophyll concentration of 1.48mg.m^{-3} compared to 2.15 mg. m^{-3} on the west coast. Concentrations of > 3 mg.m^{-3} can however be found associated with the increased coastal upwelling on the WAB (Probyn et al. 1994), and 6-12mg. m^{-3} has been measured at times in the region between Plettenberg Bay and Algoa Bay (Shannon et al. 1984). More recently Demarcq et al. (2008) confirmed higher production on the west coast but estimated slightly lower rates of primary production as 1.6 g C.m^{-2}.d^{-1} for the west coast and WAB, and 1.2 g C.m^{-2}.d^{-1} for the CAB and EAB, using depth-integrated chlorophyll a distributions for the period 1997-2003. Brown et al. (1991) estimated total annual primary production as slightly higher on the south coast (79 x 10^6 tC.y^{-1}, or) than on the west (76.4 x 10^6 tC y^{-1}), based on limited data from the 1970s and 1980s. This still equates to higher primary productivity per unit area on the west coast (104 000 km^2) of 2.01 g C.m^{-2}.d^{-1} compared with 1.87 g C.m^{-2}.d^{-1} for the Agulhas Bank (116 000 km^2), particularly given that within the area of the west coast productivity is largely concentrated in a narrow belt along the coastline. Annual P/B has been estimated as higher on the Agulhas Bank: 153.y^{-1} versus 114.y^{-1} for the west coast, and similarly a slightly higher sedimentation rate of ~ 2 900 00 t C.y^{-1} for the south coast compared to 2 800 00 t C.y^{-1} for the west coast (Brown et al. 1991). These differences possibly result from variation in factors determining offshore transport or accumulation of phytoplankton on the two coasts. It should be noted that these rates were calculated as a function of primary production, and that the confidence limits were large (Brown et al. 1991).

2.2.2.2. Zooplankton

The zooplankton communities on the more diverse Agulhas Bank are structurally different from those on the west coast, although predictably the WAB does share some characteristics of the west coast, upwelling-driven community (Verheye et al. 1994). Heterotrophic zooplankton concentrations have however been modelled as substantially higher on the west coast (~100 $mg.m^{-3}$ vs ~30 $mg.m^{-3}$ on the Agulhas Bank) (Moloney et al. 1991). Seasonal variation in zooplankton is a common feature of the whole system, closely linked to upwelling and primary production summer maxima and winter minima. Although still present, seasonal variability is less clear on the west coast north of Cape Columbine, around St Helena Bay and on the WAB. Historically large biomasses of small pelagic fish have been present in these areas, juveniles during winter on the west coast and adults during summer on the south coast, and this may serve to obscure seasonal patterns in zooplankton abundance as a result of high predation rates (Verheye et al. 1992; Huggett et al. 2009). Zooplankton counts in the Mossel Bay region on the south coast have shown an approximately sevenfold decline since the 1980s (J. Huggett, unpublished data in DEA 2013). Different size classes of zooplankton play different trophic roles within the system, and so warrant individual attention:

Microzooplankton

Abundance of microzooplankton, important as a first prey for fish larvae, has been shown to be higher on the Agulhas Bank during summer, coincident with anchovy spawning (Verheye et al. 1994). Brown et al. (1991) estimated an average concentration of 6.3 $mg.m^{-3}$ for the west coast compared with 10.7$mg.m^{-3}$ on the Agulhas Bank (estimates are only available using Cape Point as a break between west coast and Agulhas Bank), which equates to 5.6 t C on the Agulhas Bank, compared with only 2.9 t C on the west coast.

Mesozooplankton

Mesozooplankton is the most prolific component of the south coast zooplankton community. Comprising largely copepods, this group makes up 90% of the standing stock biomass in terms of carbon on the Agulhas Bank, compared to only 60% on the west coast (Hutchings et al. 1991; Verheye et al. 1994), although estimates of standing stock concentrations in the 1980s on the Agulhas Bank (0.9 $gC.m^{-}$

^{2}) are only slightly higher than those for the west coast (0.8 $gC.m^{-2}$) and are highest towards the east in association with the cool ridge between Mossel Bay and Cape St Francis (Hutchings et al. 1991; Verheye et al. 1994). Huggett et al. (2009) estimated an average annual concentration of approximately 2.5 $gC.m^{-2}$ for the west coast, and only 1 $gC.m^{-2}$ for the WAB for the period 1988 - 2003, while concentrations of 1.34 $gC.m^{-2}$ were recorded in spring off Mossel Bay on the CAB for the 1990s, dropping to 0.5 $gC.m^{-2}$ during the 2000s (J. Huggett, unpublished data in DEA 2013). This may be as a result of increased predation by the high biomass of small pelagic fish on the south coast in that period, although the high degree of spatial and temporal variability in biomass indicates that copepod biomass is strongly influenced by local bottom-up as well as top-down trophic forcing (Verheye et al. 1992; Hutchings et al. 2006; Huggett et al. 2009).

On the Agulhas Bank the copepod *Calanus agulhensis* dominates the mesozooplankton community, particularly on the EAB where it may account for up to 85% of the copepod component (Verheye et al. 1994). It is replaced on the west coast by *Calanoides carinatus,* possibly as a result of differing responses to variability in food abundance, which is lower but more continuous on the Agulhas Bank (Huggett et al. 2007). Concentrations fluctuate seasonally with variation in upwelling-related winds and chlorophyll concentrations both on the Agulhas Bank and the west coast, and supporting seasonally different assemblages (Hutchings & Nelson 1985; Verheye et al. 1992; Verheye et al. 1994). Within the west coast and WAB however, seasonal differences in production have only been measured as significant on the central west coast, and winter production on the west coast and WAB contributed up to 39% of annual production (Huggett et al. 2009). As mentioned, the high copepod production on the Agulhas Bank sustains a relatively high biomass of pelagic fish, historically supporting large numbers of anchovy on the WAB, and seasonal fluctuations may also be masked by increased predation on the WAB during summer (Verheye et al. 1992; Hutchings et al. 2006) - the remainder of the Agulhas Bank was not included in that study and seasonal patterns on the CAB and EAB are not well studied (van der Lingen et al. 2006).

A P/B ratio of 20% and a diet of 50% phytoplankton, 50% microzooplankton were estimated for mesozooplankton on both the south and west coasts (Hutchings et al. 1991). If this assumption holds, copepods consume 15-25% of daily primary production on the Agulhas Bank, or 30-50% if phytoplankton constituted 100% of their diet (Verheye et al. 1994).

Macrozooplankton

Estimates for macrozooplankton are based on euphausiid abundance, as the primary constituent of this group in the southern Benguela, and suggest that concentrations are considerably higher off the west coast (1.16 g dry mass.m^{-2}) than on the Agulhas Bank (0.27 gC.m^{-2}) (Pillar et al. 1992). Estimates are only available using Cape Point as a break between west coast and Agulhas Bank, however biomass has been shown to be lower on the south west coast south of Cape Columbine, therefore concentrations on the WAB are likely to be lower and closer to those on the Agulhas Bank than to the higher west coast concentrations. P/B ratios for both coasts were estimated at 13% (Hutchings et al. 1991).

Phytoplankton are estimated to comprise 60% of the diet of macrozooplankton, although euphausiids are considered to be opportunistic feeders and become increasingly carnivorous if conditions allow (Hutchings et al. 1991; Pillar et al. 1992). Little seasonal variation in euphausiid biomass has been observed, possibly as a result of the resilience conferred by their longer lifespans (approximately 1 yr, vs 1 month for copepods) (Pillar et al. 1992). Although abundance varies, the permanent availability of euphausiids in the Benguela makes them an important prey item for a number of fish species, particularly anchovy, juvenile hake, sardine, redeye and horse mackerel (Pillar et al. 1992; Verheye et al. 1994). Although the relatively higher abundance of euphausiids makes them a more important prey item on the west coast, copepods and euphausiids combined have been shown to contribute between 40-100% to the diet of anchovy recruits on the west coast, compared with 80-100% for adults on the south coast (Verheye et al. 1994), where phytoplankton is a less important dietary component (Armstrong et al. 1991).

2.2.2.3 Small pelagic fish

The Agulhas Bank supports a relatively high fish biomass, particularly during summer when an increased biomass of small pelagic fish are present, estimated as 2 300 000 t for the period 1986-1992 (although this figure is believed to be an underestimate) (Japp 1994). Although this biomass is high in comparison to many systems, it is comparable with other eastern boundary upwelling systems around the world, characterised by high small pelagic biomass (Schwartzlose et al. 1999). Small pelagic fish are an important component of this community, exerting both top down and bottom up trophic control over other system components (Cury et al. 2000).

Sardine and anchovy

As previously mentioned, sardine and anchovy form the main component of small pelagic biomass and landings in the southern Benguela. Adults of both species migrate around the coast over the course of their lifecycle from the west coast feeding grounds to spawn on the Agulhas Bank during summer (peak upwelling season in the southern Benguela) (Crawford 1980). Although higher productivity on the south coast during summer does support spawning, energy reserves that have been built up on the west coast feeding grounds are also important for successful spawning, effectively subsidising energy requirements for small pelagic fish while on the south coast (Hutchings et al. 1998). Eggs and larvae are then transported back around Cape Point to the west coast via a fontal-jet current (Shelton & Hutchings 1982; Hutchings et al. 2002). After they recruit, both sardine and anchovy shift south and eastwards again with age and size, although some anchovy and sardine seem to move northwards as well as eastwards with age (Hampton 1987; Barange et al. 1999). There is a difference in length at maturity between sardine on the west and south coasts, with south coast sardine maturing at a larger size than those on the west (van der Lingen 2011).

There has been extensive variation in the primary spawning area of small pelagic fish in the southern Benguela (van der Lingen et al. 2006a): while anchovy spawned predominantly on the WAB during the 1980s, spawners were divided between the WAB and the CAB and EAB in the early 1990s, and subsequent years have seen the majority of spawners congregating on the south coast (van der Lingen et al. 2002). For sardine, tolerance for a wider range of spawning conditions, particularly for colder temperatures, has allowed for multi-year switches between chiefly west coast (late 1980s and 1990s) or south coast (early 1990s and 2000s) spawning (van der Lingen et al. 2006b).

As both sardine and anchovy biomass are highly variable on an annual and decadal scale however, it is difficult to provide an average for the Benguela as a whole, and consequentially for the west and south coasts, unless a specific time period is examined. Sardine spawners are generally found inshore of anchovy on the WAB, but tend to overlap further eastwards on the south coast. Both species have a positive relationship between spatial extent and stock size (Barange et al. 2009; Barange et al. 1999), and since the 1980s sardine have been consistently found on the WAB at all stock levels, expanding north, south and east as stocks increase (Coetzee et al. 2008a).

Based on data from the late 1980s Armstrong et al. (1991) estimated a higher average monthly biomass for anchovy (juveniles and adults) of 754 000 t (68%) on the Agulhas Bank, compared to 286 000t and an additional 66 000 t of pre-recruits on the west coast (32%) (it should be noted that as abundance for both sardine and anchovy is strongly seasonal, peaking in winter on the west coast and summer on the south coast/ Agulhas Bank, although a monthly or annual average is useful it may blur seasonally meaningful details). Since the late 1980s the proportion of the November anchovy spawner biomass found east of Cape Agulhas has increased from 15% to 63% in the 2000s (Roy et al. 2007; this study Chapter Four), with absolute biomass peaking in the early 2000s when more than 12 $\times 10^6$ t of sardine and anchovy were found on the Agulhas Bank during the November spawner biomass survey (Coetzee et al. 2008a; Hutchings et al. 2009). Based on data from the 1980s and 1990s anchovy found on the west coast are largely recruits, although in years of high anchovy biomass a low proportion of adults have been found there (Hampton 1987; Barange et al. 1999).

The proportion of sardine spawner biomass found east of Cape Agulhas began to outweigh that to the west from 1998 (Coetzee et al. 2008a). On average, this proportion has increased over the last decades, from 10% in the late 1980s, to 70% in the 2000s (this study Chapter Four). Similar to anchovy, sardine recruits are also found predominantly on the west coast, but a greater proportion of adult sardine have been also observed on the west coast during recruitment surveys than is the case for anchovy (Coetzee et al. 2008a). The high biomass of small pelagic fish in the early 2000s and the expected consequentially high levels of predation on eggs and larvae may partly explain the low proportion of recruits observed on the Agulhas Bank, particularly the central and eastern regions, when compared with the west coast (Hutchings et al. 2009). The possibility of multiple stocks within the southern Benguela is currently being assessed, based on a separation of sardine west and east of Cape Agulhas at medium and low biomass levels identified by Coetzee et al. (2008a). Two main stocks on the west and south coasts are hypothesised, with a small third stock off the KZN coast also suggested, although this has less bearing on management issues given the low proportion of total biomass and landings it contributes (van der Lingen 2011). Differences in various biological characteristics in sardine sampled west and east of Cape Agulhas support the existence of separate stocks on the west and south coasts, but with an unknown degree of mixing between the two (van der Lingen 2011). Whether or not this hypothesis is correct however would not change the observed patterns described here, but there would be potential implications for the suitability of various management strategies were that found to be the case (for example spatial management).

Armstrong et al. (1991a) estimated total consumption by pelagic and mesopelagic fish as 1 986 000 t and 1 604 000 t on the west coast and Agulhas Bank respectively, based on data from the 1980s when pelagic biomass on the south coast based on spring/summer acoustic survey data was of the order of 2-3 million tons – considerably lower than during the early 2000s. Over the same period, anchovy were calculated to have consumed only approximately half as much on the west coast (724 700 t dry mass) when compared with their consumption on the Agulhas Bank (1 552 200 t). Consumption rates were assumed the same on each coast, and it can be assumed that total consumption was substantially higher on the south coast in the 2000s due to both the higher proportion of biomass on the south coast and the higher absolute biomass during this period. Mean diet composition of anchovy differed on the two coasts, including a far larger proportion of phytoplankton on the west coast (pre- & post-recruits), 12.2%, compared to 1% on the south (post-recruits) (Peterson et al. 1992; Hutchings 1994). In contrast mesozooplankton dominated in the south coast diet (61.3% vs 49.8% on the west coast), where the copepod *Calanus agulhensis* predominates. On the WAB when anchovy stocks are high, particularly low concentrations of copepods have been recorded, implying a strong predation effect (Peterson et al. 1992; Hutchings 1994). Intense stratification resultantly deep thermoclines in this area in spring and summer may also result in lower copepod stocks, limiting anchovy feeding and leading to an increase in egg cannibalism in this region (Armstrong et al. 1991). Macrozooplankton accounted for approximately one third of the total diet of anchovy on each coast, again, based on the most recently available data, from the 1980s (Armstrong et al. 1991).

Like anchovy, sardine are omnivorous, although in contrast are primarily non-selective filter-feeders, consuming smaller plankton preferentially, their diet reflecting the local plankton environment (van der Lingen 2002; van der Lingen et al. 2006). Van der Lingen (2002) showed that although phytoplankton may account for a higher percentage of the diet in terms of frequency, large zooplankton and anchovy eggs contributed the most in terms of dietary carbon. In 1993 and 1994 anchovy eggs constituted on average 15% of dietary carbon, up to a maximum of 50%, although they were most important in sardine diet on the EAB. Valdés Szeinfeld (1991) found such high concentration of anchovy eggs in sardine stomachs in the late 1980s to suggest that they may be responsible for up to 56% of anchovy egg mortality. Although these findings have not been replicated, localized importance of eggs has been reported (van der Lingen 2002), and while spatial separation of sardine inshore from spawning anchovy further offshore may minimize egg predation under normal conditions (van der Lingen 2002; Barange et al. 1999), this seems to point to opportunistic and potentially heavy predation under suitable conditions. Based on previously published studies largely based on the west coast, Armstrong et al. (1991) gave diet composition for sardine in terms of weight as phytoplankton 67% (range 34-83%); mesozooplankton 30% (range 15-60%); macrozooplankton 3% (range 2-6%), and van der Lingen (2002) found that the majority of diet was composed of dinoflagellates, with copepods and crustacean eggs the most important zooplankton components. The high proportion of phytoplankton reported does not change the important role of zooplankton in the diet however, given the much higher proportion of both carbon and nitrogen provided by zooplankton when compared by volume with phytoplankton (van der Lingen 2002) Armstrong et al. (1991) estimated total consumption by sardine during the late 1980s as 40 x 10^3 $tC.y^{-1}$ on the west coast compared with 87 x 10^3 $tC.y^{-1}$ on the Agulhas Bank. As with anchovy, this can be assumed as substantially higher for the south coast during the 2000s. It is important to note however that the WAB was included in the Agulhas Bank when calculating these estimates.

Small pelagic fish in the southern Benguela have been intensively exploited by a purse-seine fishery since the 1940s. Catches were initially dominated by sardine, but after the fishery collapsed in the mid - 1960s, anchovy became the dominant small pelagic in terms of landings until the early 2000s when unusually good recruitment resulted in high catches of both species. Juvenile anchovy caught inshore on the west coast around St Helena Bay comprise the bulk of anchovy landings, and landings on both coasts are highest in winter (DAFF 2012). Before 1990 the majority of sardine were caught west of Cape Point (Hutchings et al. 2012), and all catches were taken west of Cape Agulhas. Catches on the WAB increased in the early 1990s however and from 1997 the mean location of sardine catches moved steadily eastwards until it was east of Cape Agulhas in 2005 (Fairweather et al. 2006b). The majority of the catch was taken from east of Cape Agulhas until 2008, after which 30-40% of landings continued to be made to the east and total landings also declined (van der Lingen & van der Westhuizen 2013). Sardine are generally caught further offshore than anchovy, on the south coast and southern west coast (Fairweather et al. 2006b).

Redeye

The third important small pelagic species in the southern Benguela, redeye (*Etrumeus whiteheadi*), spawns around the whole coastline, with a peak from August - October. Similar to sardine and anchovy, eggs and larvae are thought to be advected further inshore from spawning locations on the Agulhas Bank, or from the WAB to the west coast where juveniles aggregate inshore and, like anchovy, move southwards over autumn and winter. Larvae on the south coast (CAB and EAB), where the majority of adult redeye have been found (based on spring and summer surveys), are thought to remain there as juveniles, and move to deeper waters with age (Roel & Armstrong 1991).

The distribution of redeye extends throughout the southern Benguela, overlapping with that of sardine and anchovy but extending further offshore as far as the shelf break, with older fish favouring greater depths (Roel & Armstrong 1991). Based on data from the late 1990s/ 2000s, recruits of redeye are more abundant on the Agulhas Bank relative to sardine or anchovy recruits when compared with the west coast (van der Lingen et al. 2006b). According to Roel et al. (1994), redeye are found in deeper water along the shelf edge during winter when water column temperature is fairly uniform, but stratification and warming of offshore surface waters cause redeye to shift inshore to cooler waters (<20^{o} C) in summer. Based on data from the 1980s, older fish on the west coast tend to occupy deeper mid-shelf or shelf edge habitats, and hence have a lower degree of overlap on the west coast with anchovy particularly, and sardine to a lesser extent. In contrast on the south coast the three species overlap to a large degree and are often found in mixed schools, resulting in increased predation and competition interactions. As large schools of redeye are present on the WAB when anchovy are spawning, and have been recorded as consuming both anchovy eggs and larvae, this may impact on anchovy recruitment success (Roel & Armstrong 1991).

Based on summer acoustic survey data, biomass of redeye in the southern Benguela has increased from an annual average of 466 kt from the mid-1980s to -1990s to 1 357 kt over the late 1990s and 2000s (1999 – 2012) (Shabangu et al. 2012) – it should be noted however that the survey was initially designed to monitor anchovy and sardine abundance and not to cover the extent of the redeye distribution, making underestimation likely. In the late 1980s, biomass of redeye was estimated to be approximately seven times greater on the Agulhas Bank (with no distinction between WAB and south coast) than on the west coast, however this estimate is based on only two surveys, and the results of one are known to be an underestimate of west coast biomass (Roel & Armstrong 1991; Armstrong et al. 1991). For the period 2003 – 2009, however, Fairweather (2009) estimated on average only twice the biomass on the Agulhas Bank during autumn compared with the west coast during summer, although these results were based on demersal surveys. Summer acoustic spawner biomass surveys in 2012 however showed more than 70% of redeye biomass to be found east of Cape Agulhas, with the majority of the remainder located on the WAB (Shabangu et al. 2012).

Although both adult and juvenile redeye feed primarily on large copepods and euphausiids (Wallace-Fincham 1987; van der Lingen & Miller 2011), larvae of other fish species are likely consumed due to their similarity in appearance to euphausiids, rather than selective feeding (L. Hutchings, pers. comm.). results from stable isotope analysis suggest redeye have a higher trophic level than predicted from current knowledge of their diet, possibly reflecting a higher proportion of either fish or euphausiids consumed than previously reported (van der Lingen & Miller 2011). Based on estimates of production, copepod biomass on the WAB may be fully exploited by local anchovy stocks alone, thus anchovy in this area are likely to be particularly vulnerable to competition pressures imposed by redeye in the region (Roel & Armstrong 1991). Armstrong et al. (1991) estimated based on data for the late 1980s that redeye consumed five times as much food on the Agulhas Bank than on the west coast.

Redeye is also landed by the purse-seine fishery, although in smaller amounts than sardine and anchovy. Landings are made almost entirely on the WAB and west coast during late summer – autumn (Coetzee 2009). A limit of 100 kt has been set for redeye but has never been exceeded, and from a single species management perspective, redeye are assumed to be underexploited (Roel & Armstrong 1991; DAFF 2012).

2.2.2.4. Chokka

Chokka squid *Loligo vulgaris reynaudii* are an important component of the south coast system, where the majority of biomass is located, both economically and with regard to trophic linkages (Lipiński 1992). Like a number of species in the southern Benguela, the lifecycle of chokka squid is generally accepted to involve a migratory loop between spawning grounds and feeding grounds (Augustyn 1989; Augustyn et al. 1994). Spawning, peaking in summer (Augustyn et al. 1994), takes place inshore on the EAB between Plettenberg Bay and Port Alfred (Augustyn 1990; Roberts 2005), although there is evidence for additional if limited spawning further offshore and on the WAB (Olyott et al. 2007). Spawning on the west coast north of Cape Point is thought to be precluded by low oxygen concentration in bottom water. Similarly bottom dissolved oxygen levels on the WAB, although higher than on the west coast, appear unfavourable for spawning (Roberts 2005). Squid hatchlings are located primarily on the Agulhas Bank, predominantly in the more easterly regions (Augustyn et al. 1994), and juvenile squid are widespread inshore on the south coast year-round, between 30 and 150m depths. The highest concentrations of juveniles have been found between Cape St Francis and Nelson Mandela Bay (formerly Algoa Bay) on the EAB, and to the east of Cape Agulhas on the CAB (Augustyn et al. 1994; Olyott et al. 2007). Juvenile abundance is greatest during autumn when they dominate the size structure (Augustyn et al. 1994). On the Agulhas Bank, growth occurs in tandem with westward and offshore migration, and large adults are generally found in deeper waters > 100m depth, while small squid occupy inshore regions shallower than 100m (Augustyn et al. 1994). Although paralarvae were previously assumed to drift passively in westward currents to feeding grounds on the west coast, Roberts and van den Berg (2002) suggest that paralarvae from eggs spawned inshore, which are in the majority, are generally retained by a clockwise gyre and that only those spawned further offshore at greater depth would follow the suggested pattern of passive dispersal to the WAB and west coast. In either scenario, the majority of chokka found on the west coast and WAB are immature sub-adults which will return to spawning grounds on the Agulhas Bank as they mature (Augustyn et al. 1992). The distribution is uninterrupted from the Agulhas Bank around Cape Point until the region of Cape Columbine, where squid occur at greater depths than on the south coast, in waters up to 350m in depth, and subsequently becoming patchier further north (Augustyn 1991).

As described, chokka squid are found throughout the southern Benguela, but the majority of their biomass remains on the Agulhas Bank (Roberts 2005; Augustyn et al. 1992), with west coast biomass highest in summer (Augustyn 1991) and subject to a very high degree of variability (Augustyn et al. 1994). Estimates for the period 1986 - 1991 are 13 kt for the south coast and approximately 4.4 kt for the west coast, however as sampling was limited to trawlable areas, the catchability of the gear was unknown and migration effects not taken into account, estimates should not be taken as absolute (Augustyn et al. 1992). Biomass is dependent on spawning and recruitment success, which in turn are closely linked to environmental factors such as temperature, food availability, dissolved oxygen, transport (i.e. current strength), and as such is highly variable (Augustyn et al. 1992; Roberts 2005). Autumn survey data does however show an increase in biomass on the Agulhas Bank (WAB not distinguished) in the 2000s from 15.5 kt in 2004 to 31 kt in 2008 (DAFF 2012). Based on commercial catch data (this document Chapter Four), the estimated proportion of chokka squid found east of Cape Agulhas increased from 77% in the late 1980s to 91% in the 2004 - 2008, although van der Lingen et al. (2006) reported that no changes were observed in either catch or biomass of squid subsequent to the eastward shift of sardine and anchovy and their increased abundance on the Agulhas Bank.

During their initial passive planktonic phase of life, the paralarvae are particularly vulnerable to starvation (Augustyn et al. 1992), and feed primarily on copepods (Venter et al. 1999). The presence and strength of the cold ridge on the CAB and EAB, and the associated Agulhas Bank copepod maximum may be important in determining paralarval survival, in its role as a feeding ground (Roberts 2005). After 2-3months the now active paralarvae switch to euphausiids, amphipods and other macrozooplankton as prey (Augustyn et al. 1992). Late juveniles and adults are opportunistic predators and their prey spectrum expands with size. Generally an increasing proportion of fish, which provide an energetic advantage over crustacean prey, is consumed when older (Lipiński 1992; Augustyn et al. 1994). On the west coast, crustaceans become more important and fish less so in the diet during winter. Seasonal variability in diet is not distinct on the south coast (Augustyn et al. 1994). Frequency of occurrence of dietary components for chokka in the southern Benguela include macrozooplankton (6-13%); anchovy (10-32%); mesopelagic fish (3-5%); hakes (2-18%); cephalopods (1-45%) and other, non-commercial, fish (11 – 76%) (Lipiński 1992). Approximately 33% of diet on the feeding grounds (offshore on the south coast and the west coast) is estimated to consist of anchovy, with a high degree of variability, and cannibalism is primarily important on the spawning grounds and is less prevalent offshore (Augustyn et al. 1994).

Chokka squid are also prey to a number of fish species, all opportunistic predators. According to Lipiński et al. (1992), shallow water hake, kingklip, and, to a lesser degree, snoek all prey on chokka on the west coast, while on the south coast deep-water hake and monkfish also add chokka to their diets. Two species of hake are the most important predators of chokka squid. Consumption by *Merluccius paradoxus* occurs almost exclusively in spring, and for both species chokka consumption is primarily on the south coast, although other cephalopods are consumed on both coasts (Lipiński et al. 1992). Chokka comprised approximately 60-70% of mass of cephalopods in the diet of *M. capensis* on the south coast , vs 0% on the west coast, and < 5% by mass (although approximately 30% by frequency) of cephalopods in *M. paradoxus* diet on the south coast (Lipiński et al. 1992). Despite their importance as predators for chokka however, the total consumption of cephalopods by hake is not high, comprising on average < 5% of the diet by mass, except in the case of large *M. paradoxus* whose diet comprises up to 70% cephalopods. However, these are likely to consist of other large and more demersal cephalopod species. Squid on the spawning grounds in summer are less available to *M. capensis*, which prey more extensively on small adults on deeper feeding grounds in May (Lipiński et al. 1992). Cape fur seals also prey opportunistically on small chokka squid. This is presumed to occur in areas other than the chokka spawning grounds where the size of squid available is much larger (Lipiński 1992). Although cetaceans are assumed to consume some proportion of cephalopods (Shannon et al. 2003), knowledge of predation on chokka is limited and no reliable estimates are available (Augustyn et al. 1994)

From the 1960s – mid-1980s chokka squid was caught largely as bycatch by the demersal trawl fishery operating on the west coast and Agulhas Bank, but since the establishment of a squid jig fishery in the mid-1980s, jigging has been responsible for the majority of landings which are taken mostly from the south coast (Augustyn et al. 1992; DAFF 2012). Seasonality of peak catches varies, but catches tend to be higher during spring and summer (Augustyn et al. 1992). As of 2012 catches had remained steady over the 2000s and the stock was thought of as sustainably exploited (DAFF 2012; Cochrane et al. 2014).

2.2.2.5. Horse mackerel

Horse mackerel *Trachurus trachurus capensis* are found throughout the southern Benguela, but the majority of the southern Benguela stock is found on the south coast, where horse mackerel were estimated to constitute 14% of the total fish stocks over the late 1980s and early 1990s (Japp 1994). Spawning occurs on the Agulhas Bank in two peaks, one in summer and one in winter, with peaks occurring earlier on the EAB (June & November) than on the WAB (August & Feb) (Barange et al. 1998). A lifecycle proposed by Barange et al. (1998) suggests spawning predominantly on the EAB and CAB during summer and subsequent passive transport of reproductive products towards the rest of the Agulhas Bank and the west coast where recruits have been observed. 1-2yr old fish move into deeper water on the shelf-break, possibly moving inshore and south onto the south coast before winter spawning. This eastward movement continues with age, with oldest age classes found on the EAB.

Biomass on the south coast was reported as approximately five times that on the west coast in the 1990s, where almost exclusively recruits are found (Barange et al. 1998). More recently demersal survey trawl data estimating an annual average of approximately 50 kt on the west coast and 280 kt on the south coast between 2000 and 2009 (Fairweather 2009a), and November pelagic acoustic survey data from 1997 – 2009 estimating an annual average of approximately 6 kt on the west coast and 30 kt on the south coast, confirm this estimate. Biomass on the south coast is generally higher in spring than in autumn (Kerstan & Leslie 1994), and based on acoustic survey data from 1997 – 2006, predominantly comprised of larger adult fish, while horse mackerel on the west coast are more abundant in autumn and are largely recruits (Merkle & Coetzee 2007). Slower growth-rates for horse mackerel on the west coast have been observed than for those on the south coast (Hecht 1990).

Horse mackerel are opportunistic filter feeders (Kerstan & Leslie 1994), consuming mostly euphausiids and copepods (80-90% of diet), as well as a small proportion of largely pelagic fish (<10%) (Pillar & Barange 1998). Euphausiids and copepods are seasonally interchangeable in their contribution to the diet on the south coast, with euphausiids dominating in winter (~40%) and copepods dominating in spring (>40%). Both groups comprised a far greater proportion of diet on the south coast (~50%) than on the west coast (< 25%) (summer), where amphipods were more important and a large proportion of unidentifiable digested crustaceans (euphausiids, copepods and amphipods) have been recorded (Pillar & Barange 1998).

On the west coast the pelagic purse seine fishery began targeting adult horse mackerel in the 1940s, but landings declined rapidly after a peak in the 1950s. Exploitation on the south coast via the demersal trawl fishery began during the 1960s, but the contribution of horse mackerel to the catch declined in the early 1980s to approximately 20% of demersal landings on the south coast, after foreign vessels were withdrawn from the fishery. Subsequently a mid-water trawl fishery was initiated in the 1990s (Barange et al. 1998; Barange et al. 2005). Since the 1970s, landings have been as bycatch of the pelagic fishery targeting small pelagic fish (juveniles) and of the hake-directed demersal trawl fishery (adults), as well as from the mid-water trawl since the late 1990s (Barange et al. 1998; Hutchings et al. 2012). The mid-water trawl operates on the south coast and has recorded the majority of catches in the 2000s (DAFF 2012).

2.2.2.6. Mesopelagic fish

Previous biomass estimates for mesopelagic fish cover the west coast only (Armstrong et al. 1991; Armstrong & Prosch 1991), and very few records are evident in demersal trawl surveys on the south coast in the 2000s (DAFF, unpublished data). The group appears to be found almost entirely on the west coast (Hulley & Prosch 1987), and in the 1980s were largely absent from stomachs of pelagic fish (Smale 1986) and hake (Pillar & Wilkinson 1995) on the south coast. Lightfish (*Maurolicus Muelleri)* eggs have been found all over the west coast, but extend southward only along the south-western edge of the Agulhas Bank. Eggs were only found east of Cape Agulhas in some years (Armstrong & Prosch 1991). Based on trawl survey in the 1980s lanternfish *Lampanyctodes hectoris* are thought to be abundant north of Cape Columbine on the west coast, but largely absent southwards (Armstrong & Prosch 1991).

2.2.2.7. Hake

The Cape hakes are the most commercially important species on the south coast and together accounted for approximately 10% of total fish biomass on the Agulhas Bank during the 1980s and early 1990s (Japp 1994). Of the two species, shallow-water hake *M. capensis* dominates the shallower shelf environment of the CAB, while *M. paradoxus* is most prevalent in the deeper water on the western and southern shelf edges, with both species found progressively deeper with age (Badenhorst & Smale 1991). Both species spawn south of 32˚S (St Helena Bay on the west coast). The WAB has been identified as an important spawning ground (Grote et al. 2007; Stenevik et al. 2008), with eggs and larvae seemingly using a strategy similar to anchovy in which eggs and larvae are transported from spawning grounds on the southern west coast and WAB to feeding grounds on the west coast via the frontal jet current (Benguela jet) (Hutchings et al. 2002; Stenevik et al. 2008). Stenevik et al. (2008) identified spawning as occuring during spring and summer for both species, peaking in November-December, with a possible lesser peak for *M. paradoxus* in late summer/early autumn and potential year-round spawning on the Agulhas Bank. Grote et al. (2007) however found peak spawning to have occurred during winter-spring on the WAB over the period 1995 - 2003, and suggest that spawning occurs year-round with geographically-specific maxima.

On average since 1986, where estimates are available, the proportion of total hake biomass represented by each species on the south coast is approximately 70% *M. capensis* to 30% *M. paradoxus* (±10%), with the relationship approximately inverse on the west coast (±17%). Average annual biomass on the south coast is estimated to be approximately 134 kt *M. capensis* and 66 kt *M. paradoxus,* compared with 150 kt and 289 kt respectively on the west coast , which equates to approximately 30% of total hake biomass on the south coast (Fairweather 2009b; Rademeyer et al. 2008). No evidence of an eastward shift in response to the increased biomass of small pelagic fish east of Cape Agulhas during the 2000s has been observed for hake or other demersal fish species (van der Lingen et al. 2006b).

Hake are opportunistic predators, their diet in general reflecting the ambient food environment. Based on data from the west coast, Payne et al. (1987) calculated an index of relative importance (IRI) of prey items, a composite index derived from frequency of occurrence, numerical frequency, and contribution by mass. Crustaceans (euphausiids and amphipods) were shown to be the most important prey items for hake of both species < 50 cm (60-100% IRI), particularly for *M. paradoxus,* although in some areas hake of > 25cm have also been recorded consuming large proportion of small pelagic fish (~70% IRI), specifically anchovy, when availability allows. A small reliance (10-15% IRI) on mesopelagic fish was also commonly recorded. After a size of roughly 50cm depending on the area, diet diversifies to become predominantly piscivorous, including small pelagic fish, mesopelagic fish, hake, and other demersal and pelagic fish. Both species consuming more chokka in spring than autumn (Lipiński et al. 1992). According to Pillar and Wilkinson (1995), during the early 1990s teleost fish account for approximately 92% by mass of *M. capensis* diet over all size classes on the south coast. Of that, 52% were pelagic fish, 24% horse mackerel and 17% demersal. Anchovy are more important on the south coast, largely replacing the high proportion of crustaceans in the diet of small hake on the west coast, while redeye, pilchard and chub mackerel are important prey for mid-sized hake. As on the west coast, at approximately 50 cm, diet switches from primarily pelagic fish to mid-water and demersal prey (Pillar & Wilkinson 1995). Horse mackerel constitute up to 60% of the diet in large hake on the south coast, but is unimportant in the diet on the west coast, replaced by hake and other demersal fish. On the south coast, hake predation is largely cannibalistic, while on the west interspecific predation by *M. capensis* on *M. paradoxus* outweighs cannibalism. According to (Payne et al. 1987), cephalopods are not an important prey item for hake on the west coast, but are expected to be more so on the south coast where they are far more abundant. Pillar & Wilkinson (1995) however observed that cephalopods are more important for *M. capensis* on the west coast, along with mesopelagic fish, whose contribution to the diet of hake on the south coast is negligible. Lipiński et al. (1992) report similar frequencies of cephalopods in hake stomachs on both coasts (~6%), although chokka squid specifically was only found in stomachs sampled on the south coast. On the south coast over the late 1980s and early 1990s horse mackerel were more important prey for large *M. capensis* during spring, and crustaceans and cephalopods more important to small *M. capensis* during winter (Pillar & Wilkinson 1995).

The hake fishery is the most commercially valuable in South Africa, and the majority of catch is taken from the west coast by the deep-sea trawl sector (Fairweather et al. 2010), and *M. paradoxus* dominates landings from both coasts (Japp 1994; Glazer 2009).

2.2.2.8. Kingklip

Kingklip are a demersal species distributed along the west coast and as far as Port Elizabeth on the south coast. Uncertainty persists as to whether the south and west coast kingklip are a single stock or two separate stocks, making stock assessment difficult (Punt & Japp 1994; Brandão & Butterworth, 2008). Spawning aggregations are thought to occur on the south coast, particularly on the EAB, during late winter and spring, making these stocks particularly vulnerable to exploitation (Punt & Japp 1994). It is not known whether any spawning takes place on the west coast (Japp 1990).

Based on an Age-Structured Production model, spawner biomass has been estimated as lower on the south coast, at approximately 22 kt, compared with approximately 90 kt for the west coast from 2007 - 2012 (Brandão & Butterworth 2013). Biomass on the west coast was higher in summer than in winter while biomass on the south coast was higher in autumn than spring (Brandão & Butterworth 2013).

Kingklip has been a valuable by-catch of the hake-directed demersal trawl fishery since the 1930s. A directed longline fishery operated between 1983 and 1990, after which longline catches have only been taken as a bycatch in the hake longline fishery (Punt & Japp, 1994; Brandão & Butterworth, 2008). Between 1932 and the mid-1960s, 70-80% of kingklip landed was caught on the west coast, but increased effort on the south coast from the mid-1960s to the early 1980s, and exploitation of new fishing grounds, increased the contribution of the south coast to landings, although the west coast still dominated until the mid-1990s (Punt & Japp 1994). Subsequently landings on the south coast have outweighed those on the west due to the contribution of the trawl fishery, averaging 2520 t/y compared with 1420 t/y on the west coast. Longline landings remain higher on the west coast (Brandão & Butterworth 2008). Punt and Japp (1994) calculated that the stock on the west coast was overexploited by the 1970s (<50% of pristine stock) and by the 1980s on the south coast, and this was exacerbated by the longline fishery during the 1980s which specifically targetted spawning agreggations. The west coast stock has since recovered slightly, but increased trawl catches after the closure of the kingklip-directed longline fishery caused further declines in abundance (Brandão & Butterworth 2008). Since 2007 however the west and south coast stocks are thought to have undergone annual increases of 2% and 3% respectively (Brandão & Butterworth 2013).

2.2.2.9. Other pelagic & demersal predators

According to Smale (1992), although important pelagic prey species on the west and south coasts are to a degree the same (small pelagic fish and horse mackerel), the predator assemblages are different and are more diverse on the south coast. On the south coast these include yellowfin tuna, bigeye tuna, skipjack tuna, snoek, geelbek, and yellowtail, the latter being more abundant on the south coast and western Agulhas Bank than north of Cape Point (Smale 1992). Pelagic predators such as tuna appear to have responded positively to the increased abundance of small pelagic fish on the south coast, with yellowfin tuna abundance increasing, while abundance of Albacore tuna from the Atlantic on the west coast has declined (van der Lingen et al. 2006b). Trophic ecosystem models of the southern Benguela showed no significant change in biomass of large pelagic fish excluding snoek over the period from the 1980s to 2000s however (Osman 2010).

Atkinson et al.(2011) identified temperature and salinity as having the greatest influence on demersal fish assemblages on the west coast, which display temporal changes in the early 1990s and mid-2000s. These shifts in assemblage composition coincide with spatial changes in West Coast rock lobster and small pelagic fish distributions, and as such are thought to be linked to changes in the physical environment as well as the indirect effects of fishing (Atkinson et al. 2011b). The demersal community on the south coast has been shown to be more diverse compared to that of the west coast, and to have a greater chondrichthyan component, estimated as 176 876 t compared to 49 456 t on the west coast (Smale 1992). Yemane et al. (2010) have shown an increase in diversity of the demersal fish assemblage as a whole on the south coast, as well as a decline in dominance since the mid-1980s, a result of some combination of declines in dominant species and increases in those less abundant, probably related to differential exploitation rates. Diversity of demersal fish on the south coast however was significantly correlated with depth, a proxy for temperature, salinity and dissolved oxygen, which would indicate potential sensitivity to changes in the physical environment on the south coast. It is also hypothesised that greater visibility on the south coast as a result of increased stratification and lower nutrient levels may increase the efficiency of visual predators such as tuna, as well as many small cetacean species found in the region (L. Hutchings, pers. comm.).

2.2.2.10. Seabirds

Of the 91 seabird species occurring off southern Africa, 40 occur regularly, with 12 breeding in the region (Smale et al. 1994). African penguins *Spheniscus demersus,* Cape cormorants *Phalacrocorax capensis* and Cape gannets *Morus capensis* are the most prolific, and all three are currently classified as 'vulnerable' in terms of conservation status (Smale et al. 1994; Crawford 2013). Although other species have also exhibited changes over recent decades, given their abundance and hence increased role in trophic functioning of the system, these three species are focused on here.

Penguins in the southern Benguela breed largely at a number of localities within two areas – on the west coast (including WAB) between Lambert's Bay and Cape Agulhas (classified here as the west coast), and on the south coast in Algoa Bay in the Eastern Cape (Crawford et al. 2011). During the 1990s, the number of breeding pairs of penguins on the west and south coasts were similar. An increase in west coast populations in the early 2000s lead to an average of approximately 35 000 breeding pairs, around three times those found breeding on the south coast. By 2010 however populations on both coasts had declined again to similar levels of approximately 10 - 11 000 pairs in each area (Crawford et al. 2008a; Crawford et al. 2011).

Cape cormorants breeding on the west coast have declined from approximately 100 000 pairs in the 1980s and early 1990s to around 30 000 from 1994 – 2006. Very little breeding occurs on the south coast and only 253 pairs were recorded east of Cape Agulhas in the early 2000s (Crawford et al. 2007a).

Cape gannets breed at two locations on the west coast (Lambert's Bay and Malgas), and one on the south coast (Algoa Bay), where they are more abundant. The total number of gannets in the southern

Benguela has increased since the 1950s, however after fluctuating between 9000 and 12 000 pairs for the 1990s and early 2000s, breeding pairs at the western -/ northern- most location (Lambert's Bay) declined to zero from 2003 – 2005. Conversely breeding pairs in Algoa Bay increased from 55 – 65 000 in the 1990s to 98 000 pairs by 2005. Changes in colony sizes appear to mirror the changing availability of small pelagic fish as prey, and the increasing numbers on the south coast are thought to reflect the increase in small pelagic fish abundance east of Cape Agulhas since the late 1990s (Crawford et al. 2007b; Crawford et al. 2008a).

Overall consumption by seabirds during the early 1980s was only slightly higher on the Agulhas Bank (140 000 t wet mass) than the west coast (130 000 t) (Crawford et al. 1991). If the WAB is to be included in the west coast as it is in this project however, given the high number of seabirds found on the WAB – for example approximately half of the total population of Cape cormorants, the most important seabird consumers in the southern Benguela (Crawford et al. 1991), has been found on Dyer Island (Crawford et al. 2007a) – even given recent increases in some population on the south coast it can be assumed that consumption by seabirds is higher on the west coast than on the south. During the 1980s anchovy was the most important contributors to the diet of prolific seabirds, in addition to sardine, pelagic goby and hakes, with a higher proportion of sardine consumed on the south coast when compared with the west (Crawford et al. 1991). Consumption may also vary seasonally, for example breeding success of African penguins appears to be negatively affected when the proportion by mass of anchovy in their diet is below 75% during breeding season (Sherley et al. 2013).

2.2.2.11. Seals

The Cape fur seal *Arctocephalus pusillus pusillus* is the most abundant marine mammal in the Benguela (Smale et al. 1994), occurring throughout Namibia and on South Africa's west and to a lesser degree, south coasts: only two breeding colonies are located on the south coast, compared with 8 on the west coast and 14 in Namibia (Butterworth et al. 1995). Butterworth *et al.* (1995) estimated the population in 1993 to consist of approximately 2 million individuals, and this seemed little changed by the early 2000s, over which period approximately 33% of the population was located in the southern Benguela (Kirkman et al. 2007). Based on seal pup counts from the early 1990s and 2000s, less than 2% of those are found at the two south coast colonies (Kirkman et al. 2007). Although numbers on the west coast have increased since the 1990s, particularly in the region of St Helena Bay with the establishment and rapid growth of a colony at Vondeling Island, south coast colonies have remained relatively stable (Hutchings et al. 2012; Kirkman et al. 2013). Unlike a number of other species in the southern Benguela, seal distribution has not displayed an eastward shift over time in tandem with the shift in small pelagic fish, probably because available breeding space is already fully occupied along the south coast, constraining shifts in spatial distribution (Kirkman et al. 2007).

Smale et al. (1994) calculate annual consumption as foraging individual x daily ration of 3.76 kg x 365 days, and based on the conversion of pup count data to foragers (Smale et al. 1994; Kirkman et al. 2007), seals on the south coast can be estimated to have consumed approximately 5.4 kt y^{-1} during the early 2000s. In order of importance, anchovy, horse mackerel, hake, sardine and cephalopods constitute 84.2% of diet on the Agulhas Bank (David 1987). Dietary composition is known to vary according to local abundance of prey species however (Kirkman et al. 2007) - samples taken in the late 1990s – 2001 in the region of St Helena Bay on the west coast showed an increasing prevalence of sardine, concurrent with an its abundance at the time (Hutchings et al. 2012) – and given the change in small pelagic distribution in the mid-1990s it can be expected that small pelagic fish have contributed a greater proportion to the diet of seals on the south coast since.

2.2.2.12. Cetaceans

A number of dolphin and fewer whale species are found off the west coast, including Heaviside's *Cephalorynchus heavisidii*, dusky *Lagenorhynchus obscures* and long-beaked common dolphins *Delphinis capensis*, and Bryde's whales *Balaenoptera edeni* (Best & Folkens 2007). They are largely generalist feeders with the potential to range widely, and are therefore assumed to be relatively adaptable to changes in prey distribution (Best & Folkens 2007; Hutchings et al. 2012). Of the 32 cetaceans occurring off the south coast, four dolphin species and one baleen whale (Bryde's whale) have been observed frequently enough to be considered resident (Smale et al. 1994). There is no estimate for the Agulhas Bank specifically, but 80% of the sightings used by Best et al. (1984) to generate an estimate of total population of 582 Bryde's whales in the southern Benguela were made east of Cape Point, and estimated to consumed between 19 000 and 65 000 t of small pelagic fish in this region annually. In summer the majority of these are found east of Cape Agulhas (Best et al. 1984). A more recent estimate however, based on data from 2005 – 2008, suggests a smaller population of 130 – 250 individuals for the south coast (Penry 2010). Common (*Delphinus delphis)*, bottlenose (*Tursiops truncates)*, and humpback dolphins (*Sousa chinensis*) are all numerous in the region. The estimated 15 – 20 000 common dolphins on the south coast with a diet of roughly 66% fish and 33% cephalopods would consume 19 – 25 000 t annually (Cockcroft & Peddemors 1990; Smale et al. 1994). Consumption by the remaining dolphin species is in the order of thousands of tons, also comprised of fish and cephalopods (Smale et al. 1994), but no estimates of abundance are available.

2.2.3. Summary of biological components

2.2.3.1. Plankton

Although total primary productivity on the west coast is comparable with that on the Agulhas Bank, it is more concentrated on the west coast. Primary productivity on the WAB is more similar to the west coast and higher than on the south coast (CAB and EAB).

Zooplankton biomass is about three times greater on the west coast than on the Agulhas Bank, although based on data from the 1980s concentrations of microzooplankton are higher on the Agulhas Bank. Estimates for the WAB as distinct from the CAB and EAB are not available. Mesozooplankton are by far the main contributor to zooplankton biomass on the Agulhas Bank, although concentrations are estimated as similar as or somewhat lower than on the west coast. Zooplankton densities on the WAB are closer to those on the south coast than the west coast, although low concentrations here and on the CAB may be the result of heavy predation from small pelagic fish. Macrozooplankton are most abundant on the west coast north of Cape Columbine and concentrations are lower on the south west coast and Agulhas Bank.

2.2.3.2. Small pelagic fish and chokka squid

The majority of sardine and anchovy spawning takes place on the Agulhas Bank, alternating between the WAB (west coast) and CAB and EAB (south coast), while redeye spawn on both coasts. Sardine spawning peaks in spring and autumn, anchovy in summer and redeye in spring. Since the late 1990s the biomass of sardine and anchovy has been greater on the south coast than on the west coast and redeye have been shown to be more abundant on the Agulhas Bank in the 80s and specifically the south coast during the 2000s. Consumption by all species is greater on the Agulhas Bank, where it is important to note that the WAB is not distinguished in the majority of literature pre-2000. On the west coast, sardine and anchovy consume a greater proportion of phytoplankton, while predation and cannibalism on eggs is more of a feature of the Agulhas Bank. Anchovy and redeye are caught largely on the west coast and WAB, while sardine landings reflect distribution, taken mostly from the west coast prior to 2005, after which the majority or a large proportion were taken east of Cape Agulhas.

The majority, possibly up to 90% of chokka squid biomass is found on the south coast, where they spawn in summer on the EAB. There is dispersal to deeper waters on the Agulhas Bank and west coast with age before a return to spawning grounds at maturity. A number of opportunistic predators prey on chokka, particularly the two species of hake, which consume more on the south coast than the west. The majority of landings are made on the south coast.

2.2.3.3. Fish predators

Horse mackerel biomass is higher on the south coast, comprised of both adult and juvenile fish, while those on the west coast tend to be juveniles. Horse mackerel have slower growth rates on the west coast, where amphipods form a larger dietary component, whereas diet comprises euphausiids and copepods on the south coast. The majority of landings in the 2000s have been taken on the south coast by the mid-water trawl fishery.

The majority of hake biomass is located on the west coast which is dominated by *M. paradoxus*, unlike the south coast where *M. capensis* is more common. Mesopelagic fish and crustaceans in the diet of smaller hake on the west coast are replaced by small pelagic fish and horse mackerel on the south coast. *M. paradoxus* constitutes a greater proportion of hake catches, and landings are higher on the west coast. Kingklip are thought to spawn largely on the south coast, although biomass on the west coast is higher. Since the late 1990s landings from the deep-sea trawl sector have been higher on the south coast.

Mesopelagic fish appear largely absent from the south coast, however both pelagic and demersal predator communities are more diverse on the south coast, which also has a larger pelagic chondrichthyan component. The demersal community on the south coast has become more diverse since the 1980s probably as a result of high fishing pressure on historically abundant species over this period. Predation on the south coast may be more efficient for some predators due to increased visibility when compared with the west coast.

2.2.3.4. Top predators

Numbers of the most prolific seabird species are higher on the west coast than on the south coast (presuming the inclusion of the WAB in the west coast system, which is often not the case when seabird populations are considered), despite increases in some species on the south coast during the 2000s e.g. Cape gannets. The availability of small pelagic fish as prey appears important on both coasts and may have driven changes in seabird abundance since the 1990s. Consumption is assumed to be higher on the west coast. Almost all seals colonies in the southern Benguela are located on the west coast, where populations have increased since the 1990s. Seals are opportunistic and their diet reflects the relative abundance of local prey species. Cetacean populations are poorly known, but are thought to be adaptable to changes in prey distribution.

Table 2.1: Summary of the generalised differences in biological components of the southern Benguela between the west coast (in this project referring to the area west of Cape Agulhas) and the south coast (east of Cape Agulhas). Due to different data sources using Cape Point and Cape Agulhas interchangeably as the break between the west and south coasts, statements are colour-coded to match the area that they apply to: west coast = blue; south coast = green; west of Cape Point = red; east of Cape Point = yellow.

	West Coast		**South Coast**		
Biological Component	**West coast north of Cape Point**	**WAB**	**CAB**	**EAB**	**References**
Primary production	Higher concentration				Demarcq et al. 2008
Microzooplankton	Higher concentration				Brown et al. 1991
Mesozooplankton	Higher/similar concentration				Verheye et al. 94; Hugget et al. 2009; Verheye 2013.
Macrozooplankton	Higher concentration				Pillar et al. 1991
Anchovy		Spawning 1980s - mid-1990s.	Spawning mid-1990s - 2000s; majority biomass since mid-1990s-2008		van der Lingen et al. 2002
Sardine	Spawning late 1980s & 1990s.	Spawning early 1990s & 2000s; majority biomass on south coast mid-1990s-2007 & on WAB 2008 - 2010			van der Lingen et al. 2006b; de Moor et al. 2013
Redeye		Higher biomass & increased overlap with other spf's			Roel & Armstrong, 1991
Chokka			More abundant		Augustyn et al. 1992 & 1994
Horse mackerel			More abundant		Barange et al. 1998
Mesopelagic fish	Abundant	Mostly absent			Hulley & Prosch 1987
Hake	Higher biomass; *M. paradoxus* more abundant		*M. capensis* more abundant		Rademeyer et al. 2008; Fairweather 2009b
Kingklip	Higher biomass				Brandão & Butterworth, 2008
Other pelagic & demersal predators			More diverse; higher chondrichthyan biomass		Smale 1992
African penguins	Biomass similar to SC in 1990s; increased in early 2000s; declined		Biomass similar to WC in 1990s; declined to low levels over		Crawford et al. 2008; 2011
	low levels by 2010		the 2000s		
Cape cormorants	Almost all biomass; declined ~ 2/3 since 1990s				Crawford et al. 2007a
Cape gannets	Lower biomass; declined in early 2000s		Higher biomass; increased in early 2000s		Crawford et al. 2007b; Crawford et al. 2008
Seals	Almost all biomass				Kirkman et al. 2007
Cetaceans			Higher biomass but poorly known		Best et al. 1984; Smale et al. 1994

2.2.4. Synopsis

The differing physical characteristics of the south and west coasts in the southern Benguela translate into diverse systems. Due to the wider shelf on the south coast, the physical processes determining nutrient availability and water column characteristics are numerous and varied, and in many cases geographically distinct from other areas within the system. Less intense upwelling on the south coast allows for increased stratification of the water column, and warmer surface waters due to the influence of the warm Agulhas Current. Low oxygen bottom water is also less frequent, and the substrate on average more rocky.

The biological systems functioning within each region are consequentially inherently distinct (see Table 2.1 for summary). Primary production is greater on the west coast, but occurs in characteristic highly concentrated episodic blooms, which results in a lower degree of utilization than on the south coast. Both microzooplankton, an important food-source for recently hatched larvae, and mesozooplankton are more abundant on the south coast, while on the west coast macrozooplankton dominates the zooplankton community. Productivity on the south coast reaches a seasonal maximum during summer when the various drivers of primary productivity are enhanced, in contrast with winter when increased mixing and a decline in insolation result in light-limited conditions offshore and the resultant lower nutrient levels, driving abundant fish stocks inshore or to the west coast. It should be noted that much of the information available for plankton resources and small pelagic fish (below) is based on data collected in the 1980s, e.g. Armstrong et al. (1991), Hutchings et al. (1991), Roel & Armstrong (1991), Verheye et al. (1994) and has not been revisited on a system-scale since. That these data are representative of a system in which the majority of small pelagic fish biomass at the time was located on the west coast should be kept in mind.

In its role as spawning ground, the south coast supports a high biomass of small pelagic fish, particularly during summer. The majority of these are spawners that have spent the recruit phase of their life-cycle on the west coast feeding grounds, where phytoplankton constitutes a higher proportion of their diet, unlike on the south coast where mesozooplankton predation/cannibalism on anchovy eggs becomes far more important. Energy supplies built up on the west coast by small pelagic fish effectively subsidize activities on the south coast during summer, and together with the local nutrient levels on the south coast are important in determining the fitness of the spawning adult fish. Chokka squid also utilize the south coast as a spawning and feeding ground, adding to the pelagic biomass, with a dual trophic role as predator and prey.

For opportunistic predators such as Cape hake, prey profiles differ for each coast, with mesopelagic fish and crustaceans on the west coast replaced by anchovy, redeye and horse mackerel on the south coast. Conditions for growth and development appear to be more favourable on the south coast: species such as horse mackerel and kingklip have been shown to grow faster and larger on the south coast than on the west coast.

At all trophic levels, the communities on the south coast are more diverse, from zooplankton to predators. Lower nutrient levels are hypothesised to allow for greater visibility and thus increased efficiency for top predators such as tuna and dolphins. Seabirds also consume a significant amount of small pelagic fish on the south coast despite overall numbers being higher on the west coast (including the WAB) – Cape gannets in the 2000s for example are far more abundant on the south coast (Crawford et al. 2008a). The observed dependence of seabirds on the presence of small pelagic fish as prey, and recent shifts in the distribution of a number of species, it is likely that the degree of consumption on the south coast is may have increased since the eastward shift of sardine and anchovy in the 2000s. However, expansion of seabird populations on the south coast is limited by a lack of island habitats not already colonised. Seals consume more on the west coast, but as breeding localities are currently fully utilised, particularly on the south coast, this is not necessarily a reflection of food availability.

Overall, the higher consumer biomass and diversity on the south coast, in combination with a lower but more continuous supply of nutrients, implies a system where resources are more efficiently utilized and less is lost from the system in the form of sedimentation compared to on the west coast, although this remains to be tested through construction of trophic models. This can result in a more constrained system on the south coast in terms of potential for expansion of various populations, as resources are more easily fully exploited and there is a greater risk of food-limitation, particularly for lower trophic level consumers such as small pelagic fish, although the system is 'subsidised' by nutrients on the west coast feeding grounds which influence the condition of spawners on the south coast. The differences in mechanisms and trophic linkages between the two regions have implications for the potential impacts of system-level changes, particularly since many economically and trophically important species utilize both coasts at different stages of their life cycles. Differences between west and south coast structure and function need to be taken into account when considering ecosystem function in the southern Benguela as a whole, particularly in connection with regional changes in abundance. The functioning of the two sub-systems as described in this chapter will be used as a backdrop to the chapters ahead, both in the interpretation of results and in the design of the model described in Chapter Five. Although not all details described here are used directly, all contribute to overall understanding – for example, the information on the life-cycles and recruitment strategies of small pelagic fish species discussed here is important when the implications of the environmental signal (ESI) used in Chapter Five and Six and what it represents are considered.

CHAPTER THREE
SPATIAL CHANGES IN DISTRIBUTION AND OVERLAP

3.1. Introduction

An understanding of the functioning of an ecosystem is not achievable without knowledge of the interactions involved. This can be improved by observing any changes in the relative distributions of trophically linked species over time. Monitoring of past and current patterns becomes of even greater importance as climate change impacts become more apparent. Changes in migration and distribution ranges as well as distribution, all known to be strongly influenced by environmental fluctuations (Lehodey et al. 2006), have already been shown in multiple regions and species globally (Murawski 1993; Perry et al. 2005; Hiddink & ter Hofstede 2008; Rijnsdorp et al. 2009; Simpson et al. 2013).

Distribution maps for relevant key species in the southern Benguela have previously been constructed by Pecquerie et al. (2004) for the 1980s and 1990s and the overlaps between these used as a measure of spatial interaction between species, and for the calculation of indicators of ecosystem state (Drapeau et al. 2004; Fréon et al. 2005a). The eastward shift in sardine biomass is likely to have caused regional changes in the spatial interactions between trophically linked species, thus influencing the trophic functioning of the system. In this chapter, distribution maps of 14 key species in the Benguela were constructed for different time periods and analysed to identify possible changes in the level of interspecific interaction over time. Interactions on the east and west coasts were also compared.

3.2. Methods

3.2.1. Distributions

Data from scientific surveys and commercial catch records were used to plot the distribution maps. When distributions have been plotted previously (Pecquerie et al. 2004), all available data sources were combined into a single distribution map. This requires a number of assumptions to be made regarding the ability of various data sources to represent a particular species' distribution and the possible biases involved. For example given that both commercial catch data and survey data are by definition more representative of the species targeted by that fishery or for which the survey is designed and are likely to underrepresent other species, to combine the two data sources you would either need to assume equally accurate representation of the species in question by both, or decide on a weighting to the importance or representativeness of each. Because of this, and given that the aim is to detect change over time rather than the most accurate distribution map possible, for the purposes of this study it was decided that a single data source would be selected for each species rather as the most representative source, which would be best suited to reflecting temporal change for that species (see details below). Resultant distributions, while not assumed to be complete, are representative and appropriate given the aim of the study. 14 key species were examined: anchovy *Engraulis encrasicolus*; sardine *Sardinops sagax*; round herring *Etrumeus whiteheadi*; Cape hake *Merluccius capensis* and *M. paradoxus;* horse mackerel *Trachurus trachurus capensis*; chub mackerel *Scomber japonicus*; kingklip *Genypterus capensis;* chokka squid *Loligo vulgaris reynaudi;* snoek *Thyrsites atun;* silver kob *Argyrosomus inodorus;* yellowfin tuna *Thunnus albacares;* yellowtail *Seriola lalandi* and geelbek *Atractoscion aequidens.*

3.2.1.1. Survey data

Annual hydro-acoustic surveys of principal small pelagic fish species, comprising a summer (November) spawner biomass and a winter (May) recruitment survey, have produced reliable data for the southern Benguela since 1984 (Hampton 1992). Survey design and methods have been thoroughly described in Hampton (1992) and Barange et al. (1999). The abundance and biomass estimates from these surveys are an essential input into the management process, because they serve as a basis for total allowable catch (TAC) recommendations for sardine and anchovy stocks (Hampton 1992; de Moor et al. 2008), and are therefore very carefully designed and implemented. The area covered by the pelagic surveys initially extended from either the Orange River (May survey) or Hondeklip Bay (November survey) on the west coast to Port Alfred on the south coast (Figure 1.3), but in recent years has extended further east. The entire time series has recently been revised to take into account changes in survey equipment and an increased understanding of possible sources of error in earlier estimates (Coetzee et al. 2008b; de Moor et al. 2008). Pelagic survey data from both the May and November annual surveys (see below for details) were assumed as most representative of the distribution of the small pelagic sardine, anchovy and redeye, and hence were used to construct maps used in analysis for these species.

Demersal biomass surveys, as described by Badenhorst & Smale (1991), are also conducted around the coast of South Africa and are used in the estimation of hake biomass to inform the management of the hake-directed trawl fishery. Cruises have been conducted on the west coast (Orange River to Cape Agulhas) biannually from 1986 – 1990, after which the winter cruise was discontinued. On the south coast (Cape Agulhas to Port Alfred) surveys were conducted annually in spring from 1986-1990, and subsequently in both spring and autumn. Data from all available cruises up to 2008 were considered, and assumed to be the best descriptor of distribution for hakes, horse mackerel, and chub mackerel.

3.2.1.2. Commercial data

The inshore and offshore hake-directed trawl fishery has been operating off South Africa since the early 1900s (Lees 1969), and data are provided in the form of catch and duration of trawl per 20′x20′ grid cell. Data from these fisheries were taken as representative of kingklip, chokka and snoek distribution.

South Africa's line fishery is one of its oldest, operating around the whole coastline on the continental shelf (Griffiths 2000). Catch and effort data are available in the form of catch weight and catch days, and were obtained for years up to 2008. Line fishery data were used to produce maps for silver kob, yellowtail and geelbek.

The tuna longline fishery began in 1996, with boats reporting their catch and the number of hooks per set as well as the start and end positions of the line. Data from this fishery was used as the basis for the yellowfin tuna distribution used in analyses below.

3.2.1.3. Time periods

The average distribution during different periods was used as a means of examining change over time, based on the concept of regime shifts and on previously identified shifts in the biological and physical elements of the southern Benguela, the first in the early to mid-1990s and the second in the early 2000s (Howard et al. 2007; Roy et al. 2007; Atkinson et al. 2011b). Three time periods were chosen as representing different ecosystem states to be compared. Period 1 was therefore chosen as 1985-1991, representing the system before the increased abundance and eastward shift in sardine and anchovy; Period 2 as 1997-2000, an intermediate/transition phase, and Period 3 as 2003-2008, during which both sardine and anchovy were predominantly found east of Cape Agulhas. To create a clear snapshot of the specified periods and the ecosystem states they represent. The years between these selected periods (1992-1996 and 2001-2002) were omitted.

3.2.1.4. Constructing distributions

To choose the data source most representative of each species, a plot for each species during Period 3 (2003-2008) was constructed for each available data source (i.e. survey data and all commercial data). Based on these maps and discussions with scientists at UCT and DAFF, a single data source was then selected as most representative for each species and most likely to illustrate change over time. This was decided on the basis of which species a data source was either designed to represent or most likely to represent given the target species of the fishery concerned. For species that were not the primary target of a fishery or survey, the data source covering what was thought after discussion to be the largest proportion of their distribution was selected. Data sources used for each distribution and their units are listed in Table 3.1. To allow comparison between data sources that have different spatial scales, all data were joined to a 10′x10′ reference grid.

Positions of May and November pelagic survey intervals and their corresponding densities of sardine, anchovy and redeye, including zero values, were plotted using ArcGIS 9.3. The points were then joined to the reference grid and the average annual density per grid cell calculated for each period. Although May and November surveys estimate recruit numbers and spawner biomass respectively, and thus reflect different stages of the life cycle and the associated differing distributions, the data from surveys were combined. This investigation is to increase understanding of ecosystem function and how changes in distribution may have affected it, thus the interest lies in the availability of food to predators and hence both recruits and adult fish are to be considered. Data from both surveys were combined assuming an equal weighting. To avoid skewing the results due to the extension of sampling effort along the east coast during the more recent periods, an easterly limit on acceptable data points was set as the most easterly extent of surveys during Period 1.

Table 3.1: Data sources used to plot distributions for each species.

Species	Data source	Units
Sardine	Pelagic surveys*	g/m^2
Anchovy	Pelagic surveys	g/m^2
Redeye	Pelagic surveys	g/m^2
M. capensis	Demersal surveys**	kg/hr
M. paradoxus	Demersal surveys	kg/hr
Horse mackerel	Demersal surveys	kg/hr
Chub mackerel	Demersal surveys	kg/hr
Kingklip	Demersal commercial	kg/hr
Chokka	Demersal commercial	kg/hr
Snoek	Demersal commercial	kg/hr
Yellowfin tuna	Longline	kg/1000 hooks
Silver kob	Line fishery	kg/day
Yellowtail	Line fishery	kg/day
Geelbek	Line fishery	kg/day

* Both May and November surveys were included, see text.

** All available survey trawls were included, see text.

Demersal survey data were excluded where trawl duration was less than 15 minutes or north of the Orange River. Catches, including zero values, and minutes per trawl were converted to kg/hr. Catches and trawl duration were plotted and joined to the reference grid. The average annual catch in kg/hr per reference grid cell was then calculated for each period, including zero values.

To allow commercial inshore and offshore trawl data already assigned to a 20′x20′ grid to be displayed on the 10′x10′ reference grid, each reference grid cell was assigned one quarter of the catch of the 20′x20′ cell within which it was situated. The average annual catch in kg/hr per reference grid cell was then calculated.

Line fishery data are reported on a 5x5 minute grid. This grid was joined to the reference grid and the catch and number of catch days per grid cell summed and used to calculate the average annual catch per fishing day per cell during each period. Data for kob in the linefishery do not distinguish between species, however their distribution is limited to the area between Cape Point and the Kei River mouth (28.37 °E) on the southeastern coast of South Africa. Any records east of this point were excluded from analyses, and all those remaining were assumed to consist of primarily Silver Kob (Colin Attwood, Ma-RE UCT, pers. comm.).

Tuna longline data contains the start and end positions of the line set, as well as number of hooks deployed and the catch. Start positions were plotted and data points that were obviously incorrect were removed. The average annual catch in kg/1000 hooks for each reference grid cell during each period was then calculated.

For all data sources, any data points that fell obviously outside of possible sampling areas (i.e. on land/ far outside of known sampling area) were disregarded. To allow for uncertainty in areas of low density/ catch rate, cells representing the lowest 5% of all distributions in each period were removed, thus the final map used in analysis only represents the core 95% of the distribution.

3.2.2. Analysis

Maps were used to calculate the following indicators. Indicators i – iv relate to ecosystem state, whereas v is an indicator of pressure.

i) The proportion of biomass east and west of Cape Agulhas was calculated for each species in each period. To test for differences in the observed proportions in each period a beta regression model with a logit link function was fitted to the observed proportions, with period as an explanatory variable. This was done using the betareg package in R (Cribari-neto 2010).

ii) The relative overlapping areas and biomass (ROA and ROB) between species were calculated. $ROA_{a,j} = \frac{(A_{a,j} \cap A_{b,j})}{A_{a,j}}$

where a and b are the trophically related species, j is the period and ∩ symbolises the intersect between the two (Drapeau et al. 2004; Fréon et al. 2005a). Similarly, the proportion of total biomass overlapping was calculated (ROB). When calculating overlaps between species based on demersal survey data (hake, horse mackerel and chub mackerel) and small pelagics (based on pelagic survey data), only the November spawner biomass pelagic survey data were used for the overlaps. This was decided based on the timing of the surveys: since 1990, no winter demersal surveys have been conducted, so it was decided that a more accurate overlap could be obtained by excluding the winter pelagic survey from the analysis. All other species, based on year round commercial data, were overlapped with combined May and November pelagic survey data for small pelagics.

As in Fréon et al. (2005a), the averages of ROA and ROB between all species where a trophic relationship (predation or competition) exists (Table 3.2) were taken as a measure of overall ecosystem connectivity for that period. Although 'connectivity' is used in trophic models to refer to the degree of trophic linkage within the system, the term can also be applied to a range of factors relating to states of physical or trophic and literal or potential connectedness, or degree of interaction within systems or between components of those systems (e.g. With et al. 1997; Link 2002; Cadenasso et al. 2006). Here, 'connectivity' refers to the average degree of physical overlap between species and thus the potential for interaction (Fréon et al. 2005a).

Relationships were based on those identified by Drapeau et al. (2004), initially derived from trophic relationships in the southern Benguela (Shannon et al. 2003). Those for geelbek and yellowtail were added based on dietary literature (Nepgen 1982; Smale 1986; Griffiths & Hecht 1995) and discussion with DAFF scientists. All relationships involving yellowfin tuna were excluded from this calculation, as there are no data for this species during Period 1 (1985-1991). Differences in the degree of overlap over time was again tested using a beta regression model with a logit link function fitted to the observed proportions, with period as an explanatory variable (Cribari-neto 2010).

iii) An index of spatial biodiversity (ISB_j) was calculated for each period (j), based on mapped species only, and excluding yellowfin tuna as no data are available for this species for Period 1. Maps showing the number of species out of the possible 13 found in each cell for each period were also generated. ISB_j was calculated as the average proportion of total possible species *S* found in any grid cell during period j according to:

$$ISB_j = \sum_{g=1}^{n} (s_{g,j}/S) \times (100/n)$$

where *n* is the total number of cells with observations and *s* is the number of species in cell *g* (Fréon et al. 2005a). Differences in ISB between periods was again tested using a beta regression model with a logit link function fitted to the observed proportions and period as an explanatory variable (Cribari-neto 2010).

iv) The proportion of effort east and west of Cape Agulhas was calculated for each data source, in units of survey intervals (pelagic survey), trawl minutes (demersal survey), fishing hours (demersal commercial), hooks set (longline) and catch days (linefishery). These proportions averaged overall as well as for all commercial data and all survey data, for each period.

Table 3.2: Trophic relationships between species examined, updated from Drapeau et al. (2004). Strong predation (P) or competition (C) and moderate predation (p) and competition (c) are shown.

Prey\ predator		**Sd**	**An**	**Rd**	**Mc**	**Mp**	**Hm**	**Cm**	**Kk**	**Ck**	**Sk**	**Sn**	**Yf**	**Yt**	**Gb**
Sardine	**Sd**		C	C	pc	pc	pc	pc		pc	P	Pc		P	P
Anchovy	**An**	C		C	pc	pc	pc	pc		p	P	Pc		P	P
Redeye	**Rd**	C	C		pc	pc	pc	pc		p		Pc			
M. capensis	**Mc**	c	c	c	P	pc	c	c	Pc	Pc		pc	pc		
M. paradoxus	**Mp**	c	C	c	pc	P	c	c	Pc	Pc		pc	pc		
H. mackerel	**Hm**	c	C	c	Pc	Pc		c	P	p		pc	c	p	p
Chub mackerel	**Cm**	c	C	c	P	P	c					pc	c		
Kingklip	**Kk**				c	c	c	c				c	c		
Chokka	**Ck**	c			Pc	Pc				P		P	P	P	p
Silver kob	**Sk**													c	c
Snoek	**Sn**	c	C	c	c	c	c	c	c				pc	c	c
Yellowfin	**Yf**				c	c	c	c	c			c			
Yellowtail	**Yt**										c	c			C
Geelbek	**Gb**										c	c		C	

3.3. Results

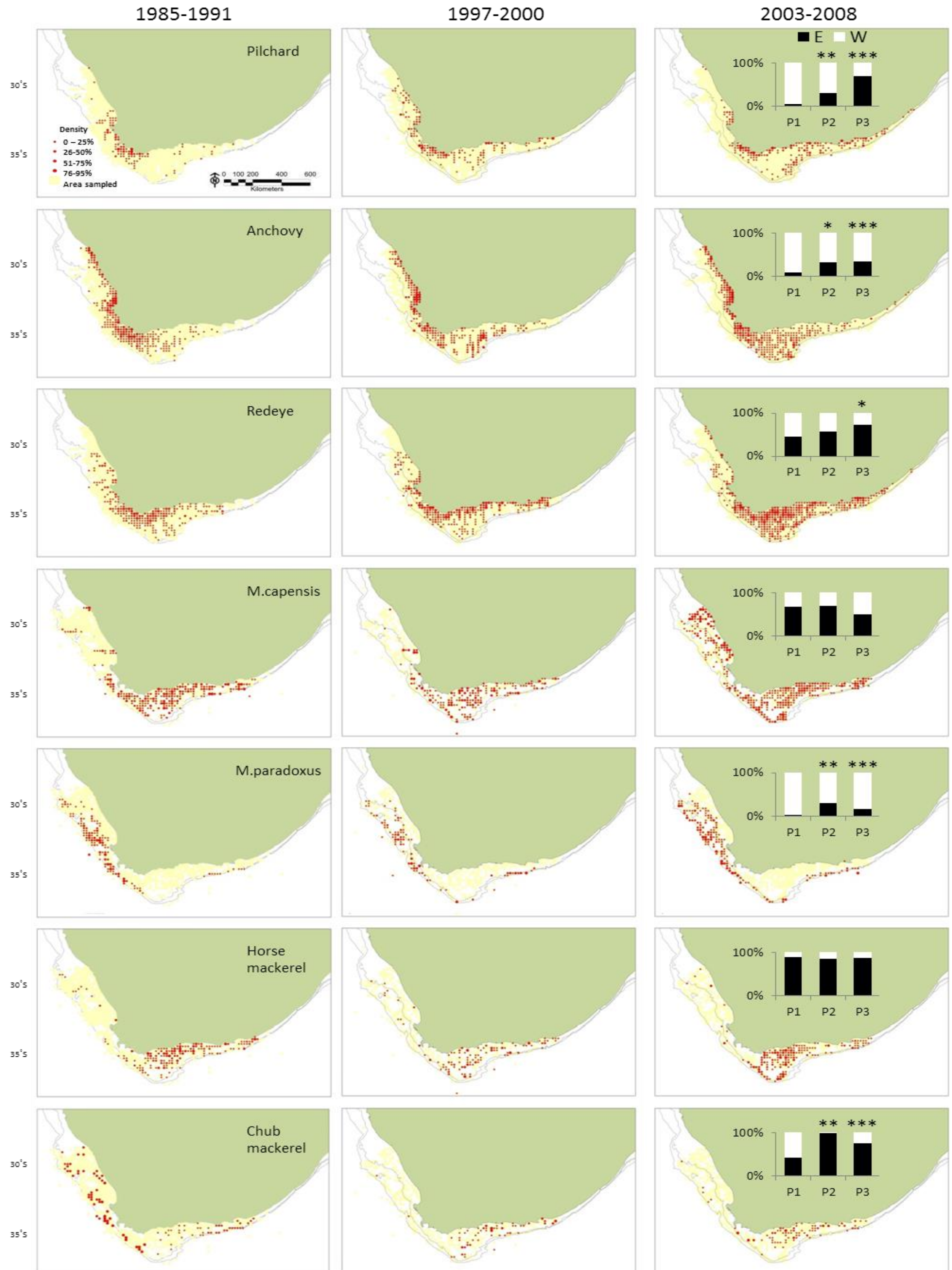


Figure 3.2a: Distribution maps for the 14 species investigated and proportion of biomass east and west of Cape Agulhas for each Period (P1, P2, P3). Asterisks indicate where a significant change from P1 was detected on further statistical analysis, results below. * = p < 0.05; ** = p < 0.01; *** = p< 0.001.

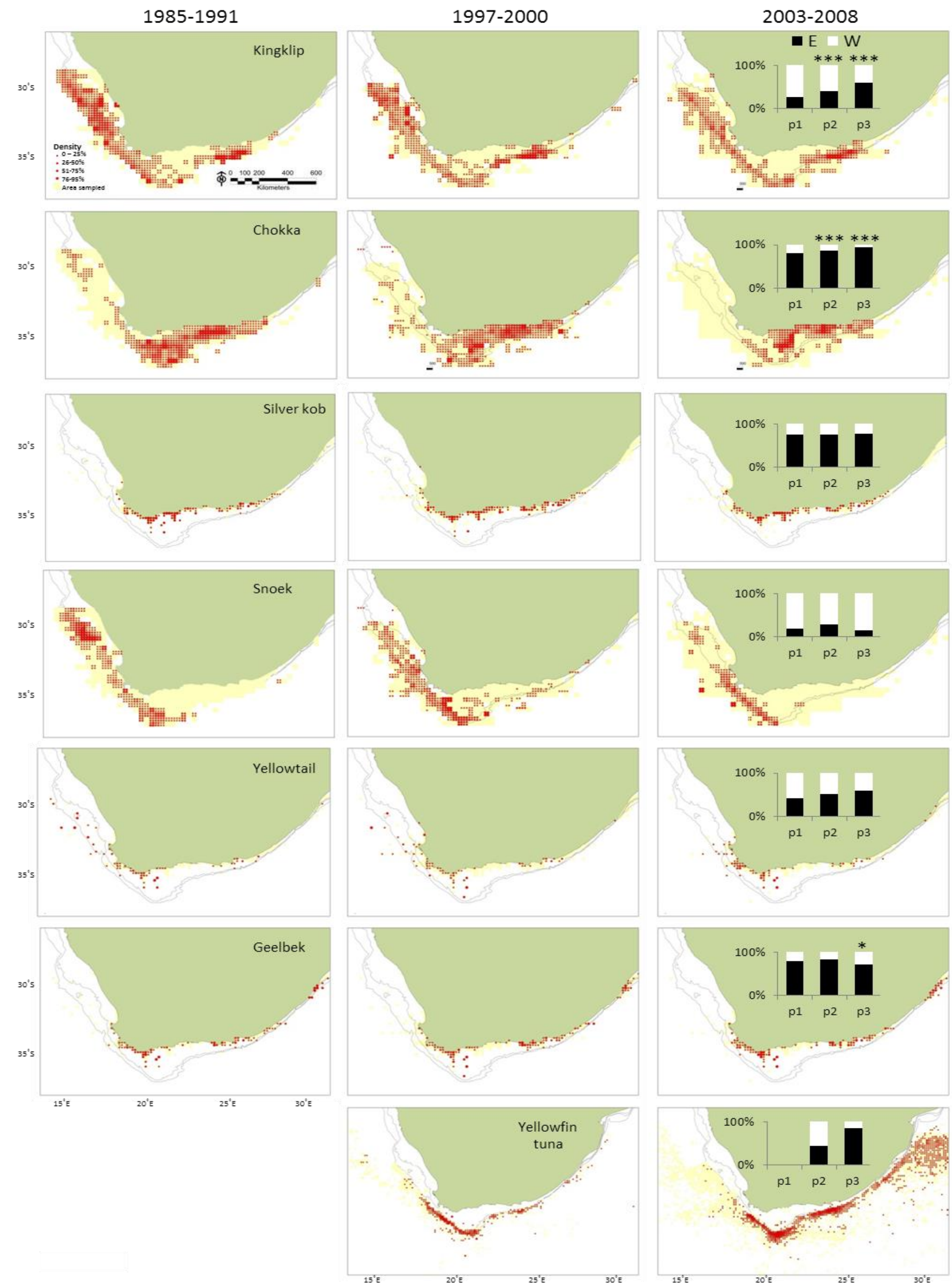


Figure 3.2b: Distribution maps (continued) and the proportion of biomass found E and W of Cape Agulhas for each period. Note there are no data for yellowfin tuna in Period 1 1985-1991. Asterisks indicate where a significant change from P1 was detected on further statistical analysis, results below. * = p < 0.05; ** = p < 0.01; *** = p< 0.001.

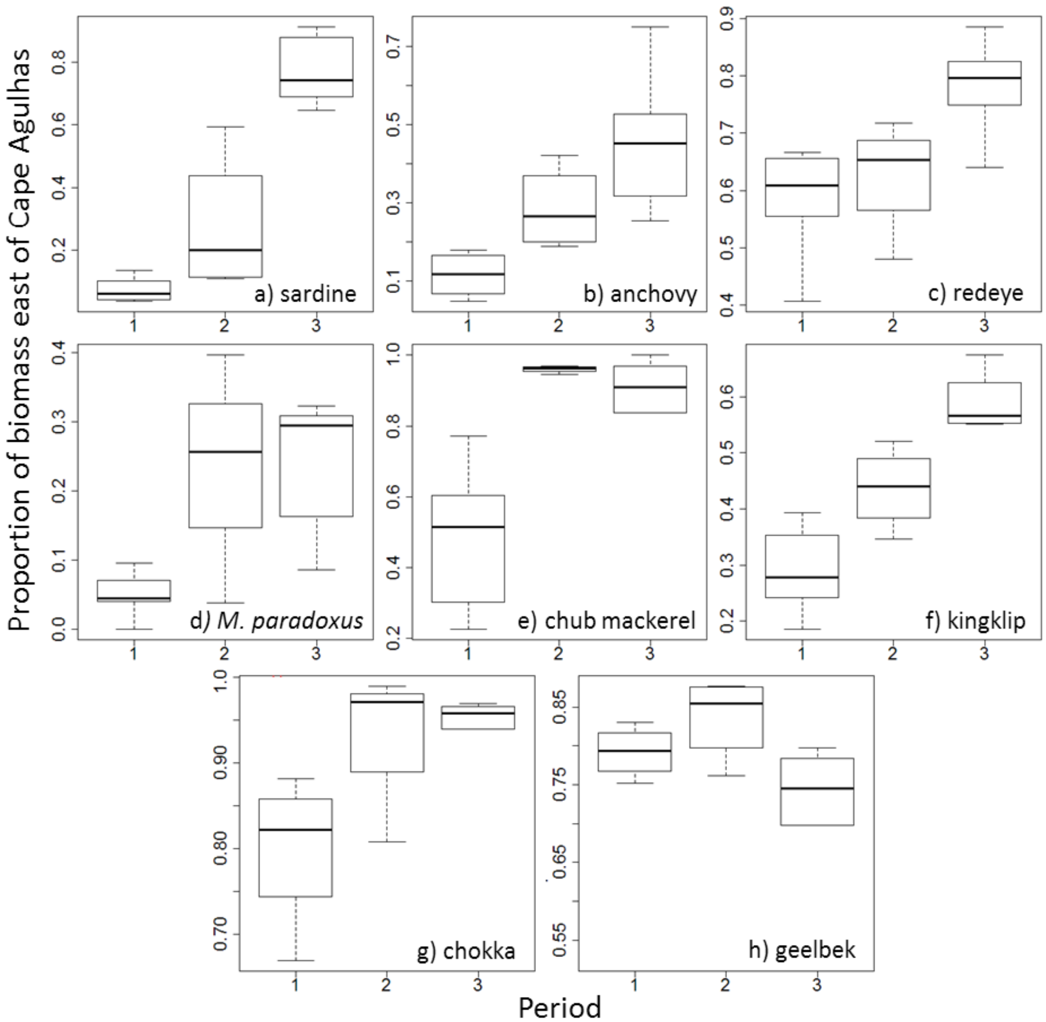


Figure 3.3: Estimated proportions of biomass east of Cape Agulhas in each period examined, for species where a significant change over time was found. Proportions were estimated using a beta regression model fitted to the observed proportions, with period as an explanatory variable. The median, upper quartile, lower quartile and interquartile range are shown.

Analyses and results from beta regression GLMs show number of species increased in proportion of biomass east of Cape Agulhas over the periods examined, although to a lesser degree than that shown for sardine here (P2: $p < 0.01$, P3: $p < 0.001$, pseudo $R^2 = 0.86$) and as previously illustrated by Coetzee et al. (2008a) and van der Lingen et al. (2005). Anchovy (P2: $p < 0.05$, P3: $p < 0.001$, pseudo $R^2 = 0.6$); redeye (P3: $p < 0.05$, pseudo $R^2 = 0.32$); *M. paradoxus* (P2: $p < 0.01$, P3: $p < 0.001$, pseudo $R^2 = 0.41$)*;* chub mackerel (P2: $p < 0.01$, P3: $p <0.001$, pseudo $R^2 = 0.26$); kingklip (P2: $p < 0.001$, P3: $p < 0.001$, pseudo $R^2 = 0.79$) and chokka (P2: $p < 0.001$, P3: $p < 0.001$, pseudo $R^2 = 0.\ 57$) all showed significant increases in proportion of biomass on the south coast relative to the west when compared with Period 1 (Figure 3.2 a and b and Figure 3.3). Not all changes over time were linear however. *M. paradoxus*, chub mackerel and snoek for example increased on the south coast from Period 1 to Period 2, and then declined again in Period 3, although *M. paradoxus* and chub mackerel both remained at significantly higher levels on the south coast in Period 3 than they had been during Period 1. The proportion of geelbek found east of Cape Agulhas was significantly lower in Period 3 compared to Period 1 ($p < 0.05$. pseudo $R^2 = 0.42$).

Horse mackerel, the linefish kob, snoek and geelbek, and chokka squid all showed similar proportions on the west and south coasts over all periods examined. Although effort in the tuna longline fishery expanded between periods 1 and 2, when evaluating Period 3 catches taken only within the area sampled during Period 2, there was still a far higher proportion on the south coast (77%) in the later period.

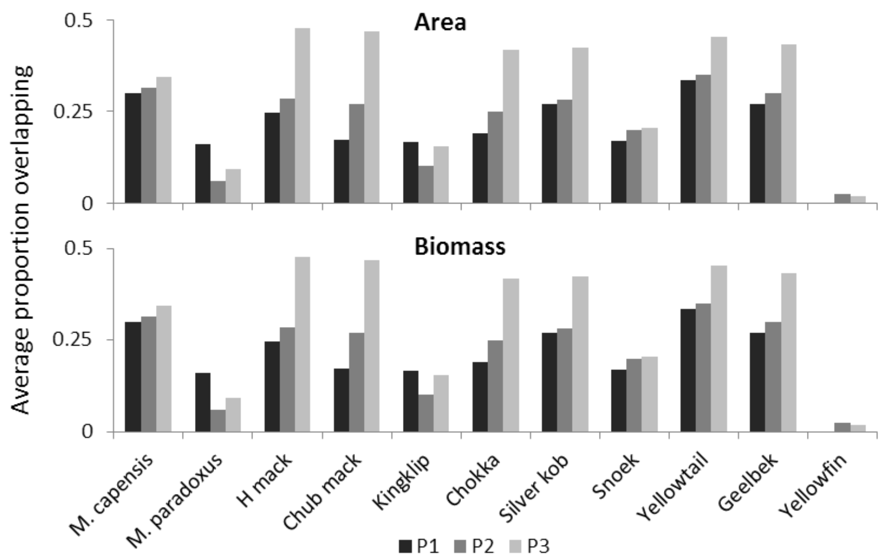


Figure 3.4: Overlap in area and biomass of all other species with small pelagic fish sardine, anchovy and redeye averaged for all three species for the three periods examined.

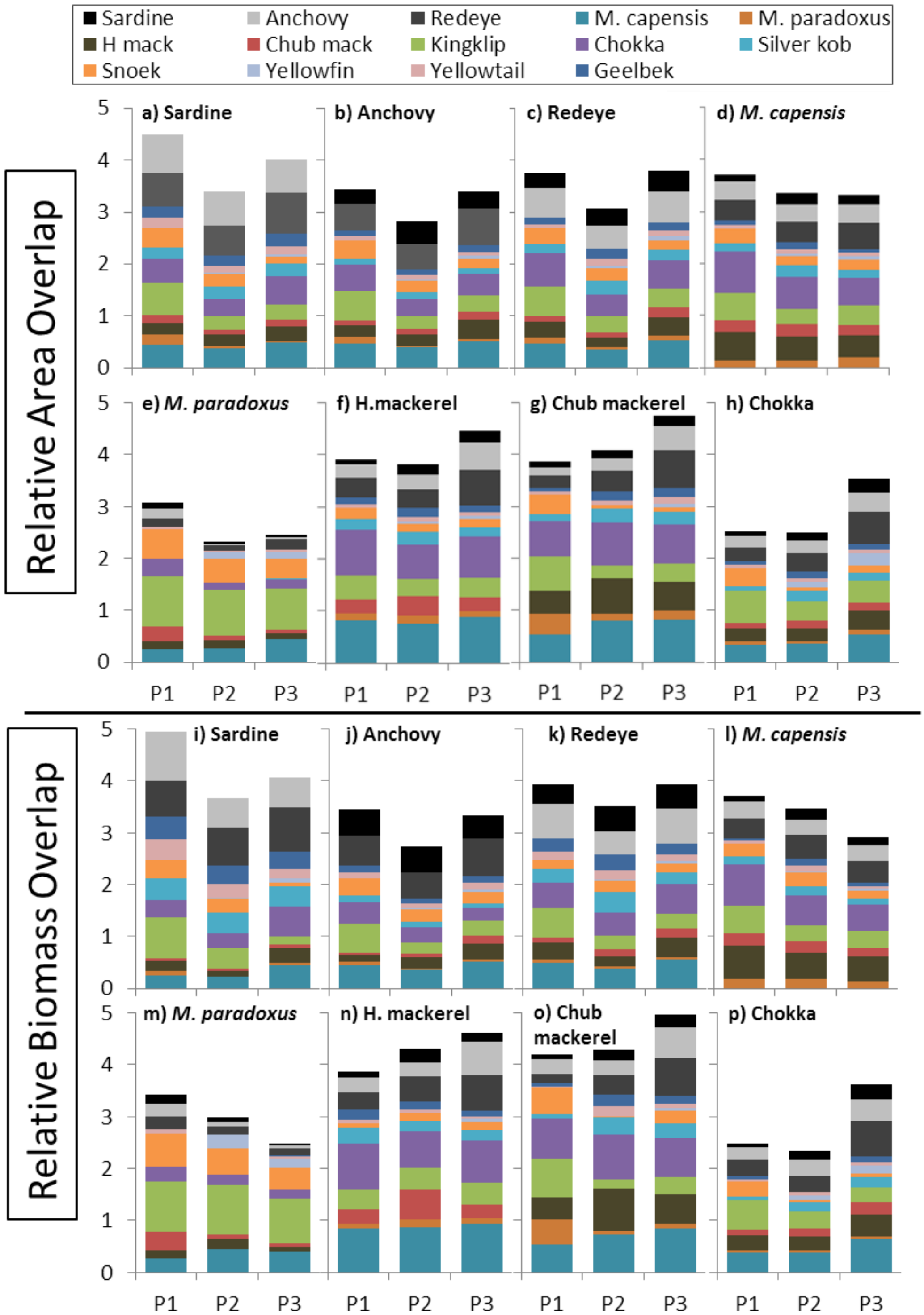


Figure 3.5 a - p: Relative overlap in area and biomass between selected species and all other species mapped, during each period, where 1 unit on the y-axis is equivalent to 100% overlap. For all overlaps by species and coast, see the Appendix.

Similar patterns were illustrated by ROA and ROB (Figures 3.4 and 3.5). There was an increasing overlap between small pelagics and horse mackerel, chub mackerel, chokka, the linefish kob, yellowtail and geelbek, and to a lesser extent *M. capensis* over all time periods (Figure 3.4). *M. paradoxus* although displaying a slight increase in overlap with redeye, overlapped less with sardine and anchovy over time. On closer examination of results, this is a reflection of a decrease in overlap with small pelagics on the west coast (see the Appendix), where the majority of *M. paradoxus* biomass is found (Figure 3.2a). Overlap of both biomass and area with small pelagics increased over time on the south coast however, but this is masked by the west coast trend.

In general overlaps were lower during Period 2, increasing again in Period 3, except in the case of the two hake species, which displayed similar levels in Periods 2 and 3 with regard to area overlap, while biomass overlaps declined over all three periods (Figure 3.5). All overlaps, separated for south and west coasts, are illustrated in the Appendix, displayed between each species and east and west of Cape Agulhas.

The pattern over time in system connectivity was similar based on area or biomass overlap, declining in Period 2 and increasing again in Period 3 (Figure 3.6a), although only overlap in area estimated by the fitted beta regression GLM during Period 2 was significantly different when compared with Period 1 ($p < 0.05$, pseudo $R^2 = 0.15$). Connectivity on each coast based on ROA and ROB (Figures 3.6 b & c) was initially lower east of Cape Agulhas in both cases, but in Period 2 declined in the west so that both coasts were similar. Modelled predicted overlap in area east of Cape Agulhas was however not significantly different in Periods 2 and 3 when compared with Period 1, but was significantly lower west of Cape Agulhas in Period 2 when compared with Period 1 ($p < 0.05$). The same is evident in overlap of biomass which was only significantly different from Period 1 on the west coast during Period 2 ($p < 0.05$), however both models had low explanatory power (pseudo $R^2 = 0.15$ and 0.09 respectively). Though connectivity on both coasts appears to have increased during Period 3, connectivity in the east remained higher than in the west.

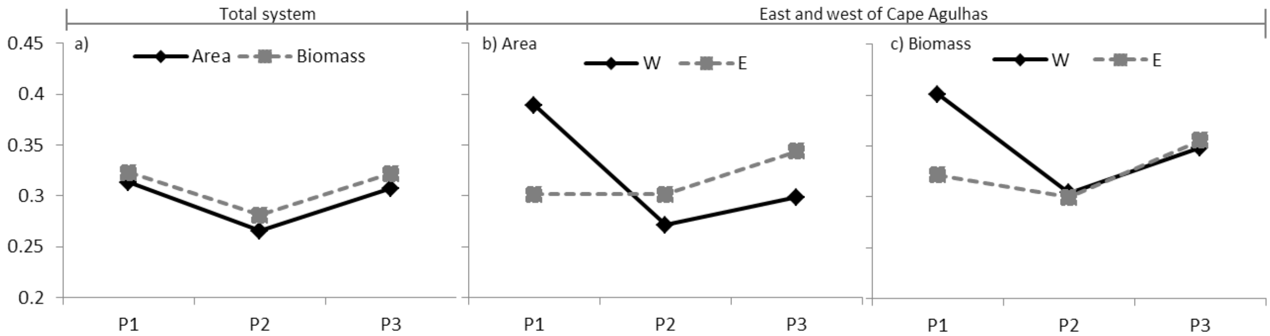


Figure 3.6 a-c: a) Overall system connectivity based on the average ROA (area) and ROB (biomass) between trophically related species (see Table 3.2 for relationships), and connectivity base on b) ROA and c) ROB on each coast.

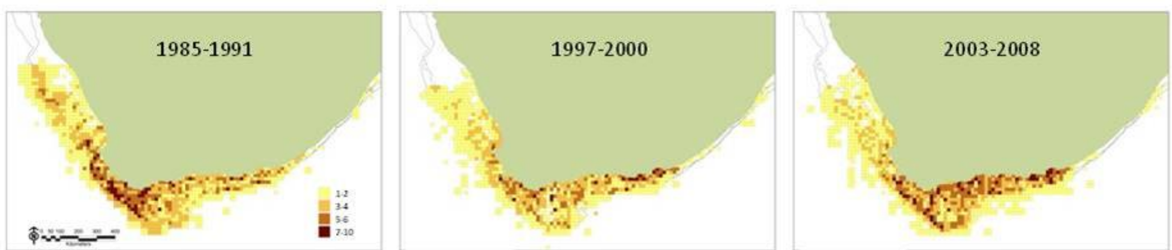


Figure 3.7: The number of 13 of the mapped species (yellowfin tuna was excluded) found per grid cell during each period.

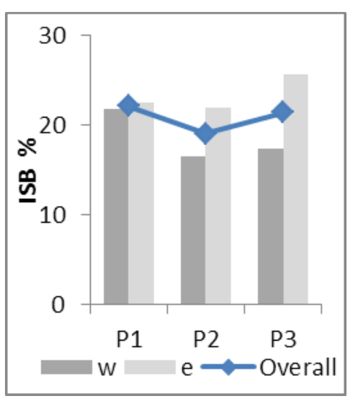


Figure 3.8: Index of species diversity (ISB) east and west of Cape Agulhas during each period.

Increasing ISB on to the east when compared with the west coast is illustrated both by the maps of the combined species distributions (excluding yellowfin tuna due to lack of data for Period 1) (Figure 3.7), and by the Index of Spatial Biodiversity, ISB. The index was similar around the coast during Period 1, but over time decreased in the west and increased in the east (Figure 3.8). When data were used to fit beta regression GLMs, overall ISB was significantly lower for both Period 2 ($p < 0.01$) and 3 ($p < 0.001$) when compared with Period 1, although the explanatory power of the model was low (pseudo $R^2 = 0.01$). The same results were true for the west coast as well (both $p < 0.001$, pseudo $R^2 = 0.04$). ISB east of Cape Agulhas was not significantly different in Periods 2 and 3, but the model had an even lower explanatory power (pseudo $R^2 = 0.007$).

As in Fréon et al. (2005a), ISB (ISB_{all}) was also calculated based on all common species identified by demersal surveys during each period (161 spp.) and compared to the above findings based on 13 species. As expected due to the large number of species included, overall ISB_{all} was much lower than when calculated based on the 13 mapped species included, being lowest in Period 1 (8.93%), increasing to approximately 11% in Periods 2 and 3. In all periods ISB_{all} was approximately 20% higher in the area east of Cape Agulhas than on the west coast.

Effort from all data sources increased on the east coast over time and decreased on the west (Figure 3.9). Due to the initial survey-driven bias towards the west coast, this has meant effort in the most recent period (3) is the most evenly distributed by coast of the periods examined. This difference is driven by increased survey effort rather than increasing commercial effort on the east coast (for example proportion of demersal commercial effort on the east coast in Period 1: Period 3 is 56:59%, while that for demersal survey is 33:62%).

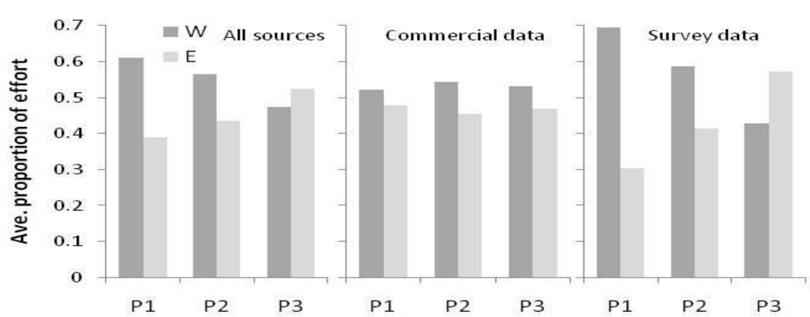


Figure 3.9: Proportion of effort east and west of Cape Agulhas averaged over commercial fisheries and survey cruises for P1: 1985 – 1991, P2: 1997 – 2000 and P3: 2003 – 2008.

3.4. Discussion

The pattern of eastward movement seems to be consistent throughout the small pelagic fish, and has already been illustrated for both sardine (van der Lingen et al. 2005; Coetzee et al. 2008a) and anchovy (van der Lingen et al. 2002; Roy et al. 2007), but was not consistently present in all higher trophic level species as one might expect. Although both hake species are strongly trophically linked to various other species that display increased abundance on the south coast over time (Table 3.2), e.g. small pelagic fish, horse mackerel and chokka, neither has followed the same pattern: the proportion of *M. capensis* on the south coast did not increase significantly in Period 2, and proceeded to decline in Period 3. The proportion of *M*. *paradoxus* on the other hand was significantly higher on the south coast during Periods 2 and 3. The relationship to changes in sardine was not linear however, with a decline in prevalence on the south coast between Periods 2 and 3. If prevalence of small pelagics, or chokka in diet is to be taken into account, horse mackerel, kob, geelbek and yellowtail would also have been expected to increase on the south and east coasts. Except for geelbek in Period 3, however, this was not the case. Yellowtail did display an increasing but non-significant trend. While kingklip did increase proportionally east of Cape Agulhas over time, it's possible that this is related to successful implementation of management actions in the region, rather than a shift in distribution.

Stocks of silver kob and geelbek, along with other species targeted by the line fishery, were heavily depleted by the late 1990s (Griffiths 2000). Despite a substantial reduction in effort in 2000, pressure from the line and inshore trawl fisheries remains relatively high given the low abundance of these species (DAFF 2012; Winker et al. 2012), and is likely to effect the ability of line fish species to respond to increases in prey abundance. Top predators were not included in this study, however observed trends in seabird abundance and distribution since the mid-1990s have already been linked to the concurrent changes in small pelagic fish distribution (Crawford et al. 2008a). Substantial declines in African penguins and gannet populations over the early 2000s for example have been related to the availability of small pelagics as prey, as has the increased abundance in Cape cormorants and swift terns on the south coast (Crawford et al. 2007; Crawford et al. 2008b; Crawford 2009; Crawford et al. 2011). Although the prevalence of sardine in the diet of Cape fur seals, opportunistic top predators, has been shown to reflect local availability, no change in population size or distribution to changes in small pelagic fish abundance or distribution has been recorded in South Africa (Kirkman et al. 2006). This is largely attributed to the lack of additional suitable breeding habitat limiting any potential expansion of the population however, and the decline and subsequent expansion of populations at the northern extent of their range in Namibia and Angola indicates that there is a direct effect on seals of changes in prey availability if space limitation is not a factor (Kirkman et al. 2013).

A number of species show peaks east of Cape Agulhas during Period 2, along with the documented shift in anchovy spawner biomass and eggs east of Cape Agulhas (van der Lingen et al. 2002). This abrupt change in distribution has been linked to environmental changes, possibly induced by increased coastal upwelling east of Cape Agulhas, and the resultant improvement of feeding conditions for anchovy spawners relative to those on the west coast (Roy et al. 2007). This may illustrate a bottom-up mechanism of trophic control in the ecosystems, where environmentally-mediated changes in primary production affect higher trophic level abundance and distribution (Cury et al. 2003). The above change in conditions to the east may then also have influenced the distribution of other species, such as chub mackerel, which also showed an increase on the south coast during Period 2. As the upwelling is restricted to coastal regions, it is unlikely to have effected the Period 2 increase in snoek east of Cape Agulhas, where records are largely further offshore.

Although plotting only 95% of the distribution has been suggested as too low a threshold (Drapeau et al. 2004; Pecquerie et al. 2004), in this context where a map based on a single data source was used to explore change over time, it was deemed a reasonable if conservative measure, allowing for meaningful interpretation of overlaps. As expected, where both species in the pair being examined for overlap exhibited an increase in proportion on the south coast, degree of overlap increased. That these are not always coupled predator and prey species seems to imply an outside driving force, or drivers, other than trophic interactions considered here, such as environmentally favourable conditions to the east as discussed by Roy et al. (2007) and in this project in Chapter Four. Increased overlap can also be seen in the case of chokka squid for example, which is more prevalent on the south coast and for which the degree of overlap with e.g. sardine is increased as this prey item shifts eastward. As in that example, there are numerous cases in which the trophic functioning of the system is likely to have been affected, as trophically related species (see Table 3.2) are not sharing the same proportions of their distributions as they were previously.

System connectivity (Figure 3.6) can give an indication of the ecosystems resilience and ability to withstand change, and the dip in Period 2 is not unexpected for this transitionary period. While the connectivity of the system as a whole does not appear to have changed dramatically (Figure 3.6a), figures 3.6 b & c illustrate the increased trophic importance of the south coast in Period 3 as more potential trophic interactions are located there than on the west coast, and a concomitant decrease in connectivity between Period 1 and Period 3 on the west coast. While in this study connectivity has been based on the interaction between only these 14 species, and is thus not truly a reflection of the whole ecosystem, it does in general include the most prevalent and commercially and trophically important species, and allows for comparison between time periods.

The ISBj indicator has some drawbacks, namely that different patterns can give the same overall average result, and it may not be suited to intersystem comparisons without consideration of the implications of the species used to calculate it (Fréon et al. 2005a). It does, however, allow for an exploration of possible ecosystem level change over time, and here seems to echo the increasing complexity on the south coast that has been suggested by increasing connectivity on that coast. The inclusion of a large number of less prevalent species in this calculation of ISB_{all} gives an overview of system state from a different perspective, but also explains the lack of agreement between the outcomes of the two ISB calculations (a dip in ISB_j in Period 2, and an increase in ISB_{all} from Period 1 to Periods 2 and 3).

The different data sources used have their own advantages and disadvantages. Survey data are by definition more suited to produce an accurate index of biomass, although it should be kept in mind that demersal surveys have been designed around hake and the pelagic surveys target sardine and anchovy, thus are not as representative for other species. Both redeye and chub mackerel for example are likely to have ranges extending further offshore than is captured by surveys. Horse mackerel have also been recorded by acoustic survey over the shelf-break area when demersal survey methods failed to detect them there (Barange et al. 1998). Commercial data on the other hand, while providing far greater sampling effort than surveys can, are unable to provide unbiased data as the effort is not random. Commercially viable concentrations of target species are actively sought out, and for example data for the pelagic fishery will reflect only those fish that are accessible in terms of port and processing facilities. Commercial data can potentially provide more accurate information and better coverage for species that are not the object of survey data collection, but the limitations must be kept in mind when assessing results. Unfortunately any single data source is very unlikely to represent the full extent of a species distribution. If this is kept in mind however, the method can still provide a useful means of comparing change over time, as has been done here.

Results could be improved if the disparate distributions and trophic roles of juveniles and adults of trophically important species, which were not considered separately for this study, could be taken into account. These data are only available at an ecologically satisfactory level of detail for sardine and anchovy, although data for redeye are also available. The decision to combine the May and November recruit and spawner biomass survey data for the small pelagic fish species was based on the goal of investigating ecosystem structure and functioning, and as such the need to understand the availability and distribution of small pelagic as potential food represented by all life-stages of a species within the ecosystem. However, the differences between the recruit and spawner distributions identified by each survey should be kept in mind. For example the eastward distributional shift in anchovy (van der Lingen et al. 2002) is evident only in the spawner biomass, while recruits remain almost entirely on the traditional west coast nursery grounds (data not shown here), with greater implications for the seasonality of prey availability to predators. On the other hand, sardine and redeye display very similar trends in both recruit and spawner biomass distributions, both found increasingly east of Cape Agulhas over time, with redeye recruits actually showing a more pronounced distributional trend towards the east than displayed by the redeye spawner biomass data (37% vs 18% increase in proportion found east of Cape Agulhas from Period 1 to Period 3). Thus while sardine and redeye seem to have undergone a distributional shift, anchovy have experienced rather a shift in spawning area, and this must be taken into consideration when interpreting results.

It appears that in many cases distributions and patterns of interaction have changed over time, and based on these and reported changes in top predators species such as seabirds, an understanding of trophic relationships is an important tool if potential system-wide changes are to be understood or anticipated. Changes identified were not particularly noticeable when considering the average state of the ecosystem as a whole, although previous studies based on ecosystem models have described changes to overall system functioning (Watermeyer et al. 2008; Osman 2010). Regional differences between the areas east and west of Cape Agulhas have occurred, with notable shifts in species distributions and the potential interactions between species (predators, prey and competition for common prey). During Period 1, a number of species displayed a far greater prevalence on the west coast compared to their Period 3 distributions. Connectivity was highest on the west coast during Period 1, and to the east in Period 3, with an overall dip during the intermediate Period 2. This pattern was largely echoed by the index of biodiversity. Although unfortunately beyond the scope of this thesis, future expansion of this work to investigate links with physical variables would be an important step in understanding system function. Spatio-temporal variations in biomass and structural complexity affect the structure and functioning of the system, and an understanding of these implications is important when attempting to appreciate the possible ecosystem impacts of current and future system-level change.

CHAPTER FOUR

RE-EXAMINING CHANGES IN SST ON THE AGULHAS BANK AS A DRIVER OF DISTRIBUTIONAL CHANGE IN SMALL PELAGIC FISH

4.1. Introduction

Understanding the impacts of expected climate change on our global fisheries, already evident in some cases (Finney et al. 2000; Pinsky & Fogarty 2012; Cheung et al. 2013), is of great importance given the potential ecological, social and economic effects. In ecological terms climate change could affect a system at many levels, from individual or species-level physiological or behavioural adaptation, to population structure, to system-level changes in trophic interaction and productivity (Pörtner & Peck 2010; Moloney et al. 2010). The mechanisms behind future or current changes are key to effective management of fisheries in systems undergoing change.

Although the impacts are widespread, the causes of the mid-late 1990s changes in small pelagic fish abundance and distribution are not clearly known. Environmental forcing has been suggested as responsible for the increasing proportion of anchovy east of Cape Agulhas since 1996 (Roy et al. 2007), while changes in sardine distribution, thought to be more affected by fishing pressure than anchovy, may be the result of a number of factors. As discussed, Coetzee et al. (2008) propose increased spawning success of sardines east of Cape Agulhas and natal homing of these easterly spawners, in combination with the traditional west coast focus of the fishing pressure despite the increased proportion of biomass to the east.

To try and clarify possible drivers or pressures that may have been involved, it is useful to examine available data series as possible indicators of change in system state, or of the possible impacts of change, and a number of studies have already used this approach for detecting long-term change in the southern Benguela. Roy et al. (2007) used decadal averages for cross-shelf SST gradient on the central (CAB) and eastern Agulhas Bank, and atmospheric surface pressure and zonal wind speed at a point on the EAB, to infer possible shifts in these data series in the mid-1990s. As these shifts would have coincided with the sudden increase in the proportion of anchovy spawners found east of Cape Agulhas from 1996, it was hypothesised that wind-driven coastal upwelling increased on the Agulhas Bank in the mid-1990s and enhanced the spawning conditions for anchovy in the region.

In recent decades, as long-term datasets have become available, changes at an ecosystem level such as those above have more frequently been thought of in terms of 'regime shifts' (de Young et al. 2004), a term characterised by a sudden, large-scale and persistent move by an ecosystem from one measurable state to another, that requires adjustment of the ecosystem structure to its new state (de Young et al. 2004; Jarre et al. 2006). Rodionov (2004) developed a sequential t-test algorithm for detecting regime shifts, or STARS. STARS method has some advantages over those previously available in that being sequential allows for the detection of regime shifts without an a priori hypothesis of when a shift may have occurred. The method may also be applied to relatively short time series, still reliably detecting shifts at the end of the series. STARS has been used successfully in a number of studies, including analysis of the Pacific decadal oscillation (PDO) dataset, and on datasets from North Pacific, Bering Sea and Gulf of Alaska amongst others (Rodionov & Overland 2005; Litzow 2006). More recently it has been applied to multiple physical and biological time-series in the southern Benguela (Howard et al. 2007; Blamey et al. 2012).

Howard et al. (2007) statistically examined a number of physical (SST, upwelling anomaly) and biological time series for shifts that could indicate changes in state, and identified a long-term, ecosystem-level change as occurring in the late 1990s/ early 2000s based on shifts in SST and upwelling at points on the west coast, and positive shifts in small pelagic fish abundance over this period. Shifts in the demersal fish assemblages in the southern Benguela have also been identified by Atkinson et al. (2011 and 2012) in the early-mid 1990s and the mid-2000s, although the latter shift coincides with a change in survey gear so may not signify a real shift. In the inshore region, Blamey et al. (2012) have investigated multiple data series, and identified an increase in the in-situ measurements of the summer southerly wind component at Cape point in the mid-1990s (1994), as well as an increase in remotely-sensed upwelling at Cape Point, Hangklip and Cape Agulhas in the mid-1990s. Shifts in upwelling variability at Cape Hangklip and Cape Agulhas were also detected in 2007. While no individual variable gives a clear idea of system functioning, by examining multiple time series, the timing of system-level changes and possible implications of future change can be better understood.

Although Roy et al. (2007) linked shifts in anchovy abundance to concurrent changes in decadal cross-shelf SST gradient, these shifts were identified by examining decadal means. By subjecting the same dataset to more rigorous analysis using the STARS method, and in light of more recent analysis of regime shifts in the southern Benguela (Howard et al. 2007; Blamey et al. 2012), a greater understanding of the processes involved should be gained.

4.2. Methods

4.2.1. Data

Data analysed were extracted from the optimally interpolated SST (OISST) data-set (Reynolds et al. 2002), previously used in Rouault et al. (2009 and 2010) and described in more detail by Rouault et al. (2010), and by NOAA (http://www.ncdc.noaa.gov/sst/). The data resolution is 1° x 1°, and monthly means were extracted for the domains selected for this analysis for the period 1982 – 2010. The domains used here were extended from those used by Roy et al. (2007) to include an additional offshore domain for the CAB (domain 5 in Figure 4.1), offshore domains on the WAB and EAB (domains 2 and 8) and a second domain inshore on the EAB (domain 7). All domains used are shown in Figure 4.1, representing inshore and offshore regions for the western (WAB), central (CAB) and eastern Agulhas Banks (EAB). Where possible, on the CAB and the EAB inshore, data from two 1° x 1° blocks were aggregated to make for more robust results.

4.2.2. Analyses

Annual, early summer, late summer, and autumn-winter SST anomalies over the period 1982 -2010 were calculated for specific sub-domains, as was the gradient between inshore and offshore SST on the WAB, CAB and EAB. The domains selected to represent each area were refined from those used by Roy et al. (2007), and on the EAB the cross-shelf gradient was calculated between domains 6 and 8 (Figure 4.1), rather than using the aggregated inshore domain. Early summer was assumed as October – December, late summer as January – March of the following year, and autumn – winter as April – September. Cross-shelf gradients were calculated by subtracting mean inshore SST from offshore, so that a positive shift in gradient would result from some combination of warming offshore and cooling inshore that left the inshore relatively cooler than previously.

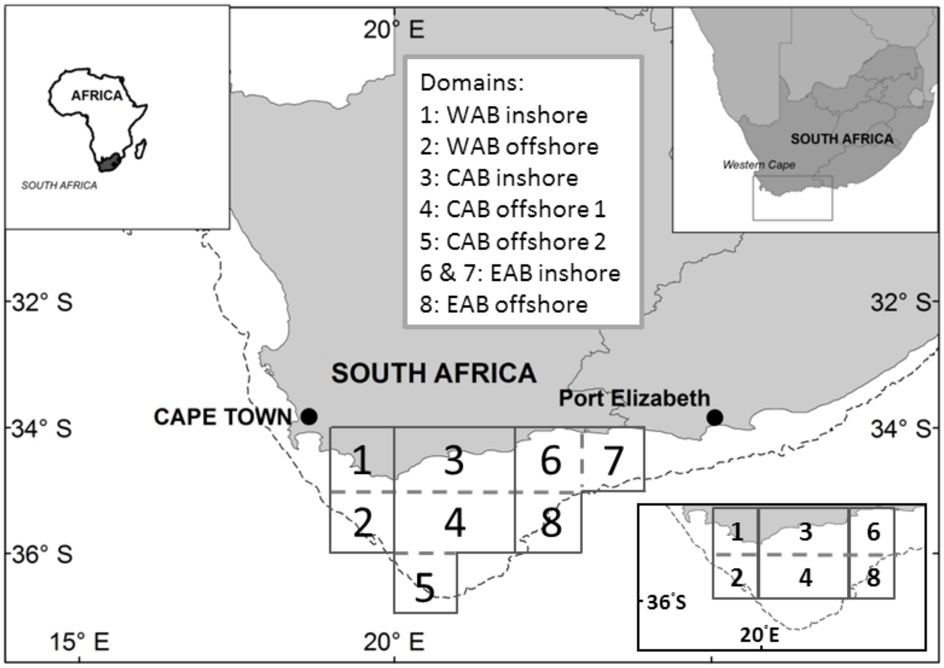


Figure 4.1: Location of the domains for which data were extracted. Domains 1 and 2 represent the WAB, 3, 4 and 5 the CAB, and 6, 7 and 8 the EAB. The map inset at bottom right show the domains used to calculate cross-shelf SST gradient.

Data were analysed using STARS, the algorithm for which is described in Rodionov (2004) and uses seven steps to decide at each observation whether to accept or reject *Ho* - that a shift has not occurred, comparing each observation to the current mean by way of a Student's t-test. If a significant difference in the current observation from the previous mean is determined and confirmed by analysis of subsequent observation, a regime shift is marked as occurring, and its magnitude and direction determined, represented by the regime shift index (RSI) output. See Rodionov (2004) for a full description of this method.

The sensitivity of the model to three possible input parameters was tested using the same methods described by Howard et al. (2007) and Blamey et al. (2012): cut-off length *l*, which prescribes the minimum regime length; Huber weight parameter *H*, which determines the weighting given to outliers; and significance level α, setting the level at which the difference between two possible regime means is considered significant, was tested by varying the values of each over 10 iterations, as applied by Howard et al. (2007). Default analyses were run using $H = 1$, $l = 10$, $\alpha = 0.1$, with further sensitivity testing varying the settings to $H = 3$ or 6, $l = 5$, 7 or 13 and $\alpha = 0.05$.

To account for the assumption of no autocorrelation made by the STARS method, a second set of sensitivity analyses were run using the same input parameters but first removing autocorrelation in the data by a built-in ‘pre-whitening’ method within the STARS program. This method was developed and described by Rodionov (2006) to remove potential autocorrelation from the data before the data are analysed As in previous studies (Blamey et al. 2012), the IP4 (Inverse Proportionality with 4 corrections) built-in method was used to estimate the first order autoregressive model (AR1) required to model red noise in the data set, and thus remove autocorrelation (Rodionov 2006).

As in previous applications of the STARS method, based on sensitivity analyses shifts detected were considered ‘robust’ when detected in the same year under 70% or more of the model settings during both the initial ‘straight’ and the second ‘pre-whitened’ analyses. Shifts detected under ≥ 70 % of model settings only during the ‘straight’ analyses are termed ‘possible’ shifts, and only during the ‘pre-whitened’ analyses referred to as ‘pre-whitened’ shifts.

4.3. Results

4.3.1. Western Agulhas Bank

Inshore (Figure 4.2a), a pre-whitened shift in annual SST anomaly was detected in 2008 but in seasonal anomalies the only shift detected was in 2009 during early summer. No shifts were detected in the offshore WAB, however positive shifts in cross-shelf gradient (Figure 4.2c) were evident in autumn-winter 1995 and annual and early- summer season in 1996.

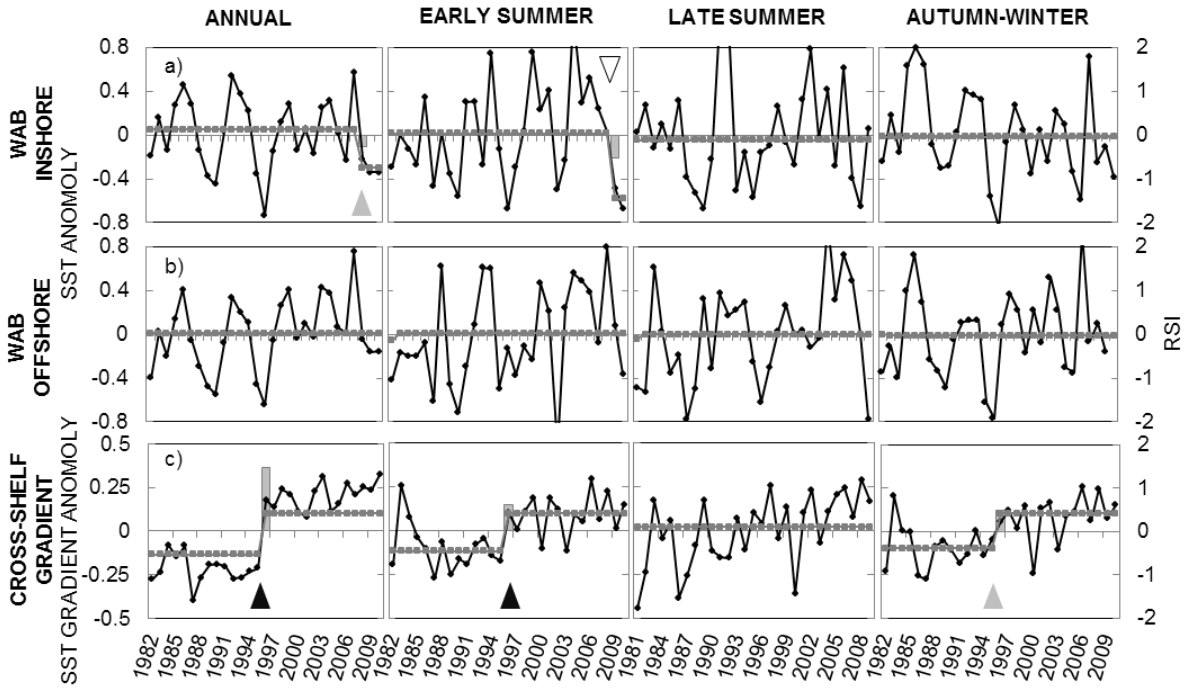
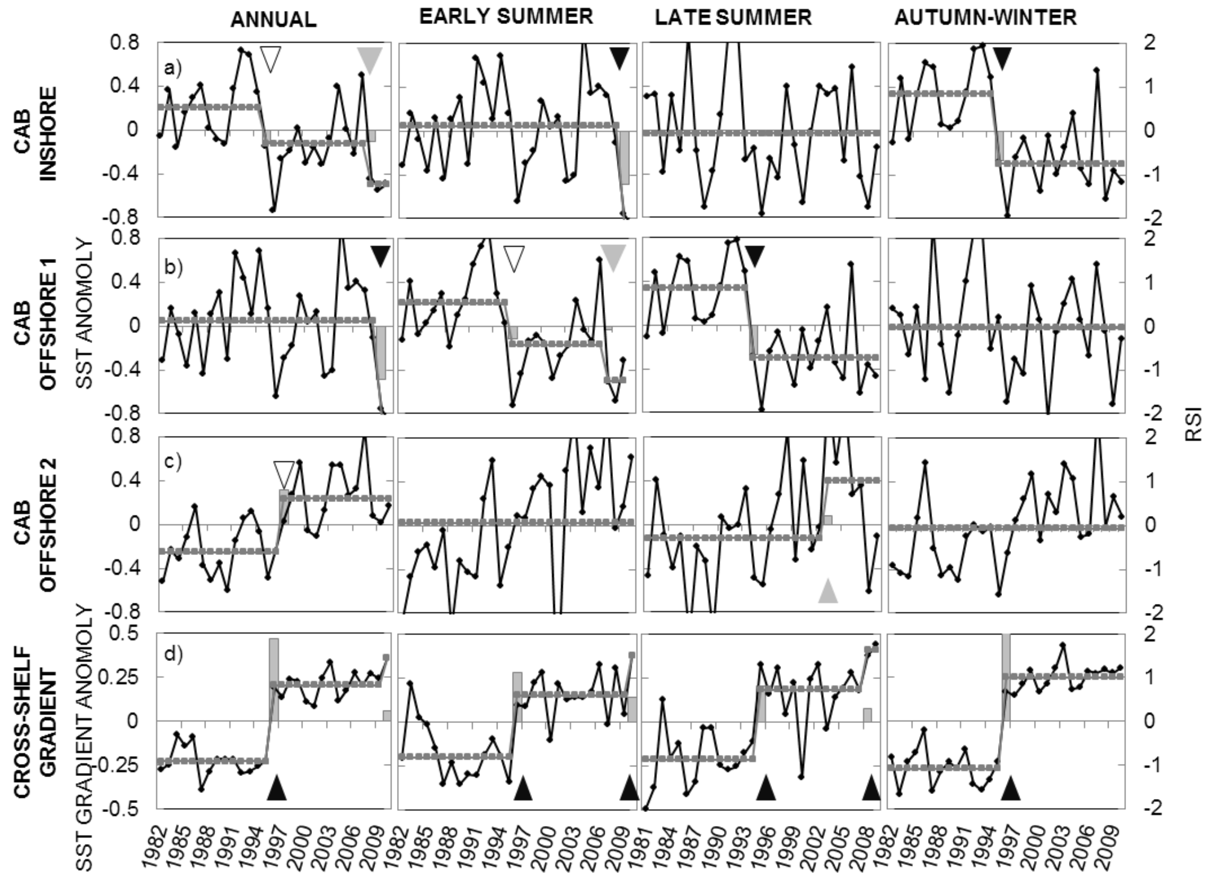


Figure 4.2 a-c: SST anomaly, regime shift index (RSI) and weighted regime mean on the WAB for a) subdomain 1 inshore, b) subdomain 2 offshore, and c) the cross-shelf gradient. ▼ indicates a robust shift, ▼ a pre-whitened shift, and ▽ a possible shift.

4.3.2. Central Agulhas Bank

On the CAB inshore (Figure 4.3a) negative shifts in the mid-1990s (1995) were only detected in the annual and winter anomalies, the annual and early summer anomalies also displaying negative shifts in 2008 and 2009 respectively. In offshore 1 domain (Figure 4.3b) mid-1990s shifts were this time evident in the summer timeseries, with robust shifts detected in 2009 and in late summer 1994. Early summer showed possible and pre-whitened shifts in 1996 and 2008 respectively, with none in winter. In offshore domain 2 (Figure 4.3c), a positive possible shift is evident in annual SST anomaly in 1997 and a positive, pre-whitened shift in late summer 2003. When the cross-shelf gradient between the inshore domain and offshore 1 domain was examined robust positive shifts were detected in the late summer 1995 and in 1996 in the annual, winter and early summer anomalies (Figure 4.3d). Robust shifts were again detected in late summer 2008 and in 2010 for the annual and early summer anomalies.



Figures 4.3 a-d: SST anomaly, regime shift index (RSI) and weighted regime mean on the CAB for a) inshore, b) offshore 1/ domain 4, c) offshore 2/ domain 5, and d) the cross-shelf gradient. ▼ indicates a robust shift, ▼ a pre-whitened shift, and ▽ a possible shift.

4.3.3. Eastern Agulhas Bank

On the EAB inshore (Figure 4.4a), possible and pre-whitened shifts were detected in the annual SST anomaly in 1996 and 2008 respectively. Robust shifts were detected in early summer 2008 and a pre-whitened shift in autumn-winter 1995. Offshore, analyses only detected one negative, pre-whitened shift in 2008 in the annual data. The cross-shelf gradient however exhibited robust shifts in the mid-1990s across all seasons: late summer 1995 and 1996 for the annual, autumn-winter and early summer datasets. Further robust shifts appeared in the annual and early summer 2010 anomalies.

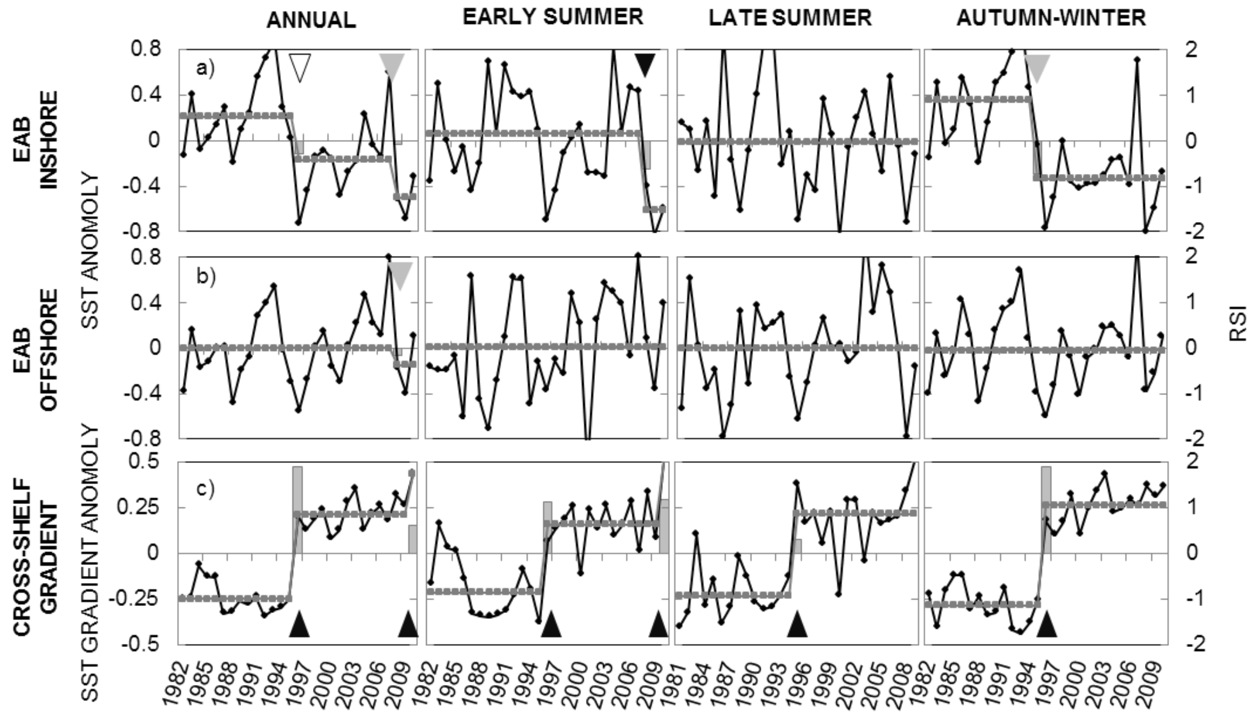


Figure 4.4 a-c: SST anomaly, regime shift index (RSI) and weighted regime mean on the EAB for a) inshore, b) offshore, and c) cross-shelf gradient. ▼ indicates a robust shift, ▼ a pre-whitened shift, and ▽ a possible shift.

4.3.4. Sensitivity Analyses

Results from sensitivity analyses are not presented here, as they reflect the responses expected from altering the parameters concerned and mirror the results of the same tests performed by Howard et al. (2007) and Blamey et al. (2012): analyses were not sensitive to changes in Huber parameter and very little difference across input values (1, 3, 6) was observed; on average more shifts were detected at shorter than at longer cut-off lengths; and analyses were somewhat sensitive to significance level, with either the same amount or fewer shifts being detected at 5% significance than at 10%.

4.4. Discussion

The shifts identified here in the mid-1990s (the majority in 1995 and 1996) using STARS analysis on the whole confirm the findings of Roy et al. (2007), who describes a shift in 1996 in the cross-shelf SST gradient over the central and eastern Agulhas Bank using the same time series but using only decadal means and somewhat different domains. Rouault et al. (2010) also identify 1996 (amongst others) as a year during which a cooling event was experienced on both the west and south coasts after a warm period that lasted approximately three years. When the data used here were previously examined by Roy et al. (2007) however, no changes were identified in the mid-1990s in the WAB or CAB offshore SST (corresponding to the CAB offshore domain 1 here), and very little difference was found between pre- and post-1996 SST gradient between the WAB inshore domain with the CAB offshore domain. Similarly in this study no shifts were detected in either in- or offshore WAB subdomains SST, however, shifts were detected in 1995/96 in the SST gradient across the two, indicating that environmental changes were not restricted to the region east of Cape Agulhas as previously suggested. Additional shifts offshore on the CAB were also evident in the current analyses, but otherwise results for the CAB and EAB do reflect similar patterns to those identified by Roy et al. (2007), with robust shifts in the cross-shelf gradient apparent on the EAB and CAB in 1995/96. The proximity of the Agulhas Current to the coast on the EAB must be kept in mind however, as cross-shelf gradients are consequentially likely to be less meaningful in this region than they are further to the west.

The negative shifts detected in the annual SST signal in 2008/2009 for a number of subdomains (1, 3, 4, 6/7, and 8), and the robust negative shifts in the early spring-summer SST anomalies in the same years for some of those subdomains in the inshore (3 and 6/7), seem to indicate possible increased upwelling. Although negative shifts were also detected offshore (domains 4 & 8), these shifts were smaller than those inshore, and as a result positive shifts in the cross-shelf temperature gradient were still apparent in 2008 on the CAB and EAB. When Blamey et al. (2012) investigated upwelling indices along the south coast using a number of methods (including STARS) to detect regime shifts, shifts were detected in upwelling variability at Cape Hangklip and Cape Agulhas in 2007, which may be linked to the cooling identified here. It also appears that winter winds, with northerly and westerly components, declined since 2007/2008 at Cape Point and along the south coast, and over the same period winter upwelling increased on the west and south coasts (Blamey et al. 2012; DEA 2011).

Roy et al. (2007) proposed that the 1996 increase in the easterly distribution of anchovy was environmentally driven, given concurrent and statistically significant changes in zonal wind speed and annual atmospheric surface pressure on the EAB, and cross-shelf SST gradient and an unpublished increase in retention on the Agulhas Bank east of Cape Agulhas that also reportedly took place in 1996 (Roy et al. 2007). It was suggested that the changes in SST gradient may also have been symptomatic of ecosystem-level changes that lead to the reversal of the long term (1950 – mid 1990s) positive trend in zooplankton abundance in St Helena Bay (Verheye et al. 1998), although this negative trend has also been linked to a simultaneous increase in abundance of anchovy recruits (Hutchings et al. 2006).

Because environmental changes were restricted to the coastal zone, it was concluded that the change in SST gradient on the CAB and EAB was likely driven by increased coastal wind-driven upwelling, rather than by the influence of the Agulhas Current. The findings of Blamey et al. (2012) seem to support this theory, having detected an increase in upwelling at Cape Columbine and along the south coast also in the early- to mid-1990s. As 1996 was a La Niña year the characteristic stronger summer winds and cooler SST's relative to previous years were to be expected (Rouault et al. 2010). However although peak concentrations of surface chlorophyll on the south coast (March-April and October) do coincide with temperature minima at the Tsitsikamma underwater temperature recorder (deployed at a depth of 10m), they do not match up with peaks in wind-driven upwelling or the easterly winds responsible, which are strongest over the spring and summer months (DEA 2011). Similarly, shifts in the inshore region during the mid-1990s on the CAB and EAB inshore detected here appear to be a result of cooling during the winter months, out of sync with peaks in upwelling favourable wind during summer. Cooling in SST on the south coast over the period 1982 - 2009 described by Rouault et al. (2010) was also predominantly a feature of winter. Warming of the Agulhas Current system over the same period, due to intensification of the Agulhas Current, is thought to have led to intensification of the dynamic upwelling cell at Port Alfred and may explaining some of the cooling on the EAB observed here better than the hypothesised increase in summer coastal upwelling.

This cooling was even more prominent when trends around the coast of South Africa were examined by Rouault et al. (2009) using AVHRR Pathfinder SST. Subsequent comparison of this dataset against MODIS SST and in situ data however have shown that for versions prior to Pathfinder version 5.2, there was a warm bias in Pathfinder SST of 3 – 5 ^{o} C in monthly summer SST data for nearshore areas in the southern Benguela and other eastern boundary systems (Dufois et al. 2012). In version 5.2 this bias is improved, and reanalysis of trends around South Africa using this version show the cooling trends on the west and south coasts identified by Rouault et al. (2009) are no longer evident except in the vicinity of the Cape Peninsula. In contrast to changes in nearshore results, the previously identified long-term warming of the Agulhas system is still evident (Rouault et al. 2009; Blamey et al. 2014)

The warming in the Agulhas current system and localised cooling observed on the west coast as a result of increases in upwelling-favourable winds seem to be features of the winter and late summer months, with little change occurring during the early summer (Rouault et al. 2010). This, however, is not entirely reflected in the results presented here, where changes during summer were generally apparent during both early and late summer months. A significant, positive correlation has been demonstrated though between SST anomalies on the west coast describing this cooling and those for the inshore region of the south coast using the warm-biased dataset (Rouault et al. 2010). This can be attributed to large-scale weather systems concurrently influencing these regions, although these findings need to be updated using SST from version 5.2. Changes in conditions on the west coast may also influence those on the south by way of Kelvin waves propagating around the coastline from west to east (Rouault et al. 2010), and it follows that changes in the physical environment on the south coast should not be considered in isolation.

Increased cross-shelf SST gradients would theoretically mean a better food environment for small pelagic fish, with increased upwelling during both summer and winter. However, less mixing in winter would also allow fish remaining on the Agulhas Bank to be relatively more successful in terms of condition and hence potential future spawning success. As both sardine and anchovy east of Cape Agulhas have previously been shown to be in better condition than those to the west (van der Lingen et al. 2002; van der Lingen et al. 2006), this may have greater implications for spawning and recruitment success than an improved food environment on the west coast might have. Anchovy have displayed a preference for a spawning temperature envelope of 16 - 19 degrees (Richardson et al. 1998), and a relatively stronger cross-shelf gradient would presumably mean a contraction of the area suitable for spawning, particularly on the narrow WAB, which again may have resulted in greater success for anchovy further to the east on the CAB and EAB post 1996. Another potential compounding factor is the tendency in both anchovy and sardine for older fish, with a generally greater likelihood of spawning success, to be found further to the east (Barange et al. 1999; Hampton 1987). Although an increased cross-shelf gradient might also mean more efficient transport back to the west coast where the majority of recruits are found, eggs and larvae being transported over the Agulhas Bank from further east would be subject to a high degree of predation/ cannibalism by adult fish, possibly resulting in a lower proportion reaching the WAB or west coast.

Given the bias in datasets from Pathfinder prior to version 5.2., reanalysis using a revised dataset is recommended, however results presented here represent the understanding at the time of undertaking this study. Although the limitations of the data analysed here in describing mesoscale features accurately, given the relatively low-resolution and interpolation methods used, should be kept in mind, it does seem that a regime shift occurred in the mid-1990s on the south coast, driven at least in part by some combination of increasing wind-driven upwelling and the intensification of the Agulhas Current since the 1980s (Rouault et al. 2009; Blamey et al. 2012). The resultant cooling in the inshore region and an increase in the cross-shelf temperature gradient over the Agulhas Bank year-round could have improved spawning and feeding conditions for small pelagic fish on the Agulhas Bank, leading to the increased proportion of sardine and anchovy found east of Cape Agulhas from the late 1990s. The more rigorous reanalysis and refined spatial resolution here of the data used by Roy et al. (2007) to link changes in anchovy distribution to SST using the STARS method has identified previously unrecognised shifts in the temperature gradient on the western Agulhas Bank, an area playing a vital and not completely understood role in the life history of small pelagic fish. Understanding interactions in this region in particular becomes even more important given the changes in distribution of both sardine and anchovy since the 1990s, and the implications of possible separate sardine stocks or substocks on the west and south coasts, with mixing between the two occurring in this region.

CHAPTER FIVE
A FRAME-BASED MODELLING APPROACH TO UNDERSTANDING CHANGES IN THE DISTRIBUTION AND ABUNDANCE OF SARDINE AND ANCHOVY IN THE SOUTHERN BENGUELA

5.1. Introduction

5.1.1. Biology

As in most eastern boundary current systems, small pelagic fish in the southern Benguela play an important role in ecosystem function, acting as a trophic stepping stone between plankton and higher trophic level species such as predatory fish and seabirds. A system operating under this model of trophic function is described as 'wasp-waisted', with small pelagic fish exerting both top-down control on zooplankton populations as well as bottom-up influence on predatory groups. The southern Benguela is thought to operate in this manner (Cury et al. 2000), and the structure was generally supported when modelled data were fitted to observed data time-series (Shannon et al. 2008). As discussed, in addition to their role in ecosystem function, sardine and anchovy have also formed the bulk of South Africa's commercially valuable purse-seine fishery since the 1940s (Crawford et al. 1987, Fairweather et al. 2006). As a result of their ecological and commercial importance, the dynamics of sardine and anchovy populations are of particular interest from an ecosystem research and fisheries management perspective in the southern Benguela. Historically both research and management have focused on a target resource – oriented, two species approach, but more recently with the increasing emphasis on the application of an ecosystem approach to fisheries management, increasing effort is being made to better understand the role of sardine and anchovy within the system as a whole.

Sardine and anchovy populations around the world have been observed as highly variable on an interannual and decadal scale, with decadal-scale dominance shifts between the two species (Schwartzlose et al. 1999, Cury & Shannon 2004). This holds true for populations of sardine and anchovy in the southern Benguela, where one species has been dominant for a period (on a decadal scale), followed by a change in the community structure and dominance of the other species. The southern Benguela has also seen a period of high abundance of both species during the early 2000s, as a consequence of an ecosystem regime shift (Howard et al. 2007; Blamey et al. 2012).

As has been discussed in Chapter Four, recent decades have seen the concept of regime shifts in marine systems become a more common approach to describing long-term changes at an ecosystem level (de Young et al. 2004). To recap, here we are defining a regime shift as a sudden change from one quantifiable state to another, occurring at a large spatial scale (de Young et al. 2004; Jarre et al. 2006). As discussed in previous chapters, shifts in a number of physical and biological time series for the southern Benguela, including in the distribution of sardine and anchovy, have been detected in the late 1990s – early 2000s (Roy et al. 2007; Howard et al. 2007; Blamey et al. 2012; Atkinson et al. 2012, Chapter Four): as discussed previously, since the late 1990s the majority of small pelagic fish has been found east of Cape Agulhas, where historically biomass was located largely on the west coast, (van der Lingen et al. 2002; van der Lingen et al. 2005).

The mechanisms behind these shifts in sardine and anchovy distribution are not well understood. Fishing pressure and environmental shifts, in combination with possible natal homing of those sardine spawned further east are thought to be the main drivers behind the changes in distribution (Cury 1994; Coetzee et al. 2008a). Coetzee et al. (2008) outline the role that maintaining high fishing pressure on the west coast while the stock had shifted south and east may have played. The sardine fishery is managed using an Operational Management Procedure (OMP) that assumes a single stock and with no allowances for spatial elements. As a consequence, during the late 1990s and 2000s when the majority of biomass has been on the south coast, fishing effort remained largely where it had been focused for the previous 50 years – on the west coast. The resulting high fishing pressure exerted on the diminished biomass of sardine on the west coast may have contributed to the continued lower abundance. As a result, spatial management of the sardine fishery is now under consideration (de Moor et al. 2013; de Moor et al. 2014). In the case of anchovy, Roy et al. (2007) suggest links between changes in anchovy distribution and shifts in SST on the Agulhas Bank.

More recently there has also been some debate as to whether sardine in the southern Benguela are in fact made up of two separate stocks, one on the west coast and one on the south coast, with some mixing between them (Coetzee et al. 2008a). The possibility of a small third stock on the KZN south coast had also been hypothesised (van der Lingen et al. 2010; Chapter One). Differences in biological characteristics between sardine found on the west and south coasts, and a separation of distributions and spawning areas at medium to low biomass levels do appear to support the hypothesis of functionally separate stocks (van der Lingen 2011; de Moor & Butterworth 2011). Investigation using genetic markers though has so far shown that while the southern Benguela sardine stock has complicated structure, it is well-mixed and the existence of genetically differentiated west and south coast stocks was not supported (Hampton 2014). Although investigations are ongoing, based on biological data (morphometrics, meristics, some life-history traits) there is still currently a recommendation to explore the incorporation of a two-stock approach into the management of the sardine fishery in South Africa (de Moor & Butterworth 2012; van der Lingen 2011; de Moor et al. 2014). Further genetic studies and investigation using parasites as a means of estimating possible mixing (van der Lingen et al. 2013; van der Lingen & Hendricks 2014) are currently underway to clarify this matter.

Given the uncertainty regarding the drivers of these shifts and the potential implications for management, the construction of a model to represent the important processes as we understand them would be a useful next step. A thoughtfully constructed model could assist in examining our current understanding of the mechanisms behind the shifts, and in gaining some insight into possible outcomes of strategic management decisions regarding spatial direction of fishing pressure.

Because ecosystems consist of many complicated interactions at multiple levels of complexity, models to address specific objectives are often employed by ecologists in the application of an ecosystem approach to fisheries management (EAF) (Cury & Christensen 2005; Plagányi 2007; Starfield & Jarre 2011). A model can allow for the simplification of a concept to explore a specific problem or interaction based on only relevant and available knowledge. Although complex ecosystem models that attempt to represent all interactions within a system as accurately as possible are useful for increasing our understanding of ecosystem function, insights can also be gained from models constructed by distilling complexity down to the minimum needed to meet a particular modelling objective (Fulton et al. 2003; Starfield & Jarre 2011; Plagányi et al. 2014). This approach, in line with the 'Models of Intermediate Complexity for Ecosystem assessments' or MICE, discussed by Plagányi et al. (2014) and in Chapter One of this thesis, is adopted here. Starting with a very simple structure, complexity is only added where needed to better meet the objective. Although this approach will not (and does not aim to) perfectly represent all aspects of the real-world system, an objective-driven approach allows the exploration of relevant interactions of interest in a way that can feed back directly to questions of strategic input, without becoming entangled in the multiple layers of uncertainty that are of necessity inherent in more complex ecosystem models.

Two modelling approaches were considered here: a frame-based model (FBM) based on the idea of a single stock that shifts its main distribution around the coast, as is assumed under current management procedures, and a spatial model incorporating the thinking behind the two-stock hypothesis. For a spatial approach, populations on each coast would be modelled separately with a degree of mixing (van der Lingen 2011). Whether or not the system operates in this manner is still not conclusively shown though, and genetic data show a well-mixed, if complicated, stock structure (Hampton 2014). A frame-based approach - where possible stable states are identified and rules for switching between them constructed - would assume the single stock shifts between a west frame and a south frame, i.e. periods during which the majority of biomass is found on the west or south coast respectively. This is expanded below.

Both approaches have advantages and disadvantages, assumptions that must be made, or parameters that are currently unknown and must be estimated. A FBM requires an assumption to be made as to what proportion constitutes 'the majority' of biomass, and if relative fishing pressure in the two areas is to be calculated, an estimate of the biomass found on the other coast during any particular year must be made (e.g. biomass on the south coast when the majority is on the west). The nature of long term changes in small pelagic fish biomass and distribution in the southern Benguela do however lend themselves particularly well to this modelling format, in that available data show long periods of relative stability followed by relatively rapid changes to another persistent state, i.e. regime shifts.

A spatial model, while incorporating the hypothesis of two separate stocks with mixing, has its own drawbacks. The existence of separate stocks with mixing is still to be conclusively shown, and the drivers and processes involved in mixing between the two hypothesised stocks are not understood to the point that this mixing can be estimated. Assigning some degree of mixing between the stocks would therefore be a speculative exercise.

Notwithstanding benefits and limitations in both modelling approaches, FBM was selected for the following key reasons: it is possible to base the estimate of 'other' coast biomass on historical abundance on the non-dominant coast; the suitability of the approach given the nature of change in small pelagic fish (regime shifts); and the fact that FBM has already been shown to be a useful alternative when modelling sardine and anchovy abundance shifts in the southern Benguela (Smith & Jarre 2011). In keeping with the principles of rapid prototyping (Starfield & Jarre 2011) a FBM approach also allows for the ready addition of alternate frames at a later stage – an advantage in view of the expected future ocean climate change.

The thinking behind the frame-based model described below is thus that the majority of the population is on one coast, while at least a small nucleus remains on the other. Unless conditions on the 'other' coast are conducive, this nucleus won't grow (i.e. a shift from one frame to another will not occur). Sardine on the more favourable coast do better in terms of recruitment, and thus that population expands.

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5.1.2. Frame-based modelling

In keeping with a minimum-realistic and objective oriented approach, Starfield et al. (1993) proposed a frame-based modelling paradigm. This approach is suitable when dynamic ecosystem functioning can be divided into distinct states or 'frames', as has been shown to be the case for small pelagics in the southern Benguela. A simple model for each frame is constructed that represents only the processes relevant to the objective of the model. Only one frame is operational at any time, and rules must be developed for when the model should switch to a different frame. This approach lends itself to the technique of rapid prototyping, which allows for the simplest possible model to be developed quickly, tested, and adapted or complexity added in the next iteration if necessary (Starfield & Jarre 2011). This has the advantage of allowing results of testing and feedback on the current generation model to inform developments in the next version, making the final version more useful than if it had been developed from scratch to a high level of complexity. Rapid prototyping also means that fully functional versions of the model are available at increasing levels of complexity, allowing hypotheses to be addressed before the final version of the model has been reached, which is of value for time-sensitive projects (Staples 1997), as well as demonstrating effective use of limited funding (Starfield & Jarre 2011).

A FBM approach has been used to model shifting vegetation patterns in terrestrial ecosystems (Starfield et al. 1993; Rupp et al. 2000), but more recently it has also been applied to the southern Benguela to explore regime shifts in the dominance patterns between sardine and anchovy by Smith & Jarre (2011). A further iteration of this model for the southern Benguela has since been produced by Botha (2012), updated to include an age-structured sardine population model. In these previous versions single stocks of anchovy and sardine that migrate around the coastline have been assumed, in line with current assessment practice, with the frames representing high or low population levels.

While the previous work has aimed to model abundance, here a spatial element is added with the aim of modelling distribution shifts in addition to abundance. Adding the concept of an ecosystem regime shift / spatial dynamics on top of the population dominance shifts should allow for realistic simulation of patterns of movement and fluctuations in populations size. The two regions to be included, the west and south coasts (east of Cape Agulhas), are functionally quite different due to different physical environments and ecosystem structures. The west coast is characterised by high but episodic wind-induced productivity, while the south coast has lower concentration but more continuous availability of nutrients and a higher biomass of consumers / predators (see Chapter Two). As a result, the population dynamics of small pelagic fish have been shown to be quite different on each coast, with recruitment being poorer on the south coast (van der Lingen 2011; de Moor & Butterworth 2012). The formulation of an additional regime shift between west and south coast modes within the model should therefore allow for better representation of the system dynamics than previous model versions (which simulated shifts between high and low population levels but were implemented for a 'west coast' scenario only).

The aim of this chapter is thus to use a frame-based model to describe ecosystem dynamics in connection with the regime shifts between a west coast upwelling system and a south coast shelf system as observed in the late 1990s in small pelagic fish. Modelled outcomes under possible strategic management options are also explored via the development and testing of spatial fishing strategies within the model.

5.2. Model design

5.2.1. Model outline

The details of the model and the design process are given below, but to allow the reader some context a basic outline of the model is provided here. The steps outlined by Starfield et al. (1993) for constructing a frame-based model are used (numbered 1 - 6 below). Where applicable, model elements were based on those used in the previous prototype of the southern Benguela frame-based model which focused on fluctuations in sardine and anchovy abundance (Botha 2012). Where necessary these were adapted to better address the focus of this current version - regime shift between upwelling (west coast) and shelf (south coast) dominated system.

1. Identify the model objectives:

    Although the mechanisms behind the west/ south shifts are not fully understood, as discussed, fishing pressure and environmental changes are thought to be the primary drivers (Coetzee et al. 2008, this thesis Chapter One and Chapter Five section 5.1). If the current understanding of the processes involved is sound, and is used as the basis for a model of the system shifts, the model results should reflect similar patterns to those observed in the real world. The model would then allow for exploration of the implications of the various assumptions made during construction on model outputs, and the testing of alternate hypotheses regarding the drivers of shifts and the responses to these drivers. The model objective is thus to investigate whether our current understanding of the drivers of the west/ south shifts in small pelagic fish can roughly reproduce the observed dynamics. If that is the case, further testing of possible strategic management options will then be performed and evaluated on performance in terms of catch, stability and a food base for the ecosystem. The robustness of model results under alternate management strategies, and sensitivity of outputs to uncertainties in our understanding of the relevant dynamics, will also be explored.

2. Identify variables that will drive the model:

   As in the previous, non-spatial iterations of this model, there are two variables driving shifts:

   - Environment, represented by the Environmental Suitability Index (ESI), which serves as a proxy for physical variables affecting sardine and anchovy populations.
   - Fishing pressure.

   The focus of scientific effort and the small pelagic fishing industry has been on sardine during recent years (Shannon et al. 2006; Hutchings et al. 2012). Because of this and the historically conservative management and highly variable recruitment of anchovy, in this model and previous versions (Smith & Jarre 2011; Botha 2012) a very simple anchovy model is used, where only environment (and not fishing) affects the population. Anchovy are fished within the model, but only to allow for calculation of the bycatch of juvenile sardine taken in the anchovy-directed catch (see Chapter Two section 2.2.2.3 for a description of the pelagic fishery). The sardine population is affected by both environment and fishing pressure.

   Note that although food web processes such as predation are known to play a large role, for the purposes of this model a roughly constant mortality is assumed. Possible increased predation effects on the south coast are incorporated via lower recruitment success when in a south frame (discussed in section 5.2.2.1 below).

3. Choose frames:

   The four possible frames used previously to representing abundance (all combinations of sardine and anchovy high or low) will still be present, but an element identifying the current location of the majority of the stock is added; west or south coast. These represent upwelling or shelf system regimes respectively. This results in 16 possible frames when all combinations of sardine and anchovy abundance and location (high/ low and west/south) are considered. Because both abundance and location of sardine and anchovy in the model will be largely independent of each other (with the exception of the 'school' trap' effect, discussed below), for the purposes of describing the frames and shifting rules, the two species will be dealt with separately. Four frames are possible per species (Figure 5.1):

   I. The majority of biomass located on the west coast, or 'west coast mode'; population levels are high
   II. West coast mode; population levels are low
   III. South coast mode; population levels are high
   IV. South coast mode; population levels are low

   Based on oceanographic characteristics and in line with assumptions being made when considering spatial implications for fisheries management (van der Lingen & van der Westhuizen 2013), Cape Agulhas, rather than Cape Point, is assumed as the break between west and south (discussed in Chapter Two). This has implications for seabirds in particular and must be kept in mind when interpreting results.

4. Identify the relevant variables in each frame based on your objectives and chosen frames:

   The relevant variables in the population models within each frame are those relating to recruitment of each species. For sardine, because the stock is modelled using an age-structured model, driven by a hockey-stick stock-recruitment (SR) relationship curve (de Oliveira 2002, de Moor & Butterworth 2009), the important parameters are those determining the shape of the SR curve. For details of the initial implementation of this age-structured model in the previous model prototype (for the west coast) see Botha (2012). In this prototype, it is implemented for a south frame as well.

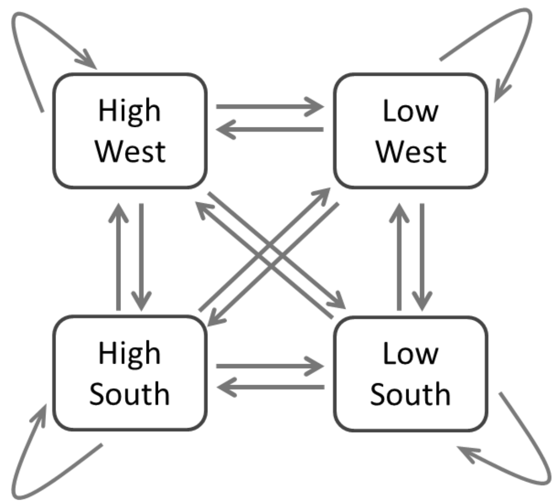


Figure 5.1: Possible frames and the possible shifts between them for each species, including the possibility of remaining in the current frame. 16 frames are possible when the two species are combined in the model.

As in all previous model versions, anchovy is modelled very simply by stochastic dynamics around a mid-point. This point and the degree of variance around it are determined by the current frame.

For both sardine and anchovy, the assumption is made that recruitment is less successful when in a south frame, and recruitment parameters are adjusted to reflect this within each frame (see section 5.2.2.1: 'Anchovy population model' below for further discussion).

5. Set out the rules for when to switch between the frames:

   An independent agent within the model software, known as a 'daemon', monitors relevant parameters and determines when to switch from one frame to another. As in previous versions, both sardine and anchovy daemons monitor population levels to 'decide' whether the species is in a high or low frame.

   To determine whether a population is in a west or a south frame, both daemons monitor the ESI, and the sardine daemon also monitors the fishing pressure.

6. Construct the dynamic model for each frame:

   Each frame contains a population model for sardine and another for anchovy, parameterised according to the frame.

The model was based on the most current previous model version (Botha 2012), however the changes described here required comprehensive restructuring and expansion of the model and code. Whereas the concept and design of the model, based on the understanding of the ecological processes involved, were my own, core model code was implemented in collaboration with Patrick Mulumba, PhD candidate, Dept. of Computer Science, UCT. The model was developed using C# in the Microsoft .Net framework.

5.2.2. Model elements

5.2.2.1. Population models

The sardine and anchovy population models comprise the dynamic model that runs within each frame, each parameterised according to that frame.

Sardine population model:

The first iteration of this model used a very simple sardine population model (Smith & Jarre 2011), which was updated by Botha (2012) to the age-structured model used in the assessment of the sardine stock in the Operational Management Procedure 02 (OMP02) (de Oliveira 2002). It is this age-structured version that is built on in this current model iteration. The full implementation of the age-structured model within the frame-based system is described in Botha (2012), but the model structure will be described briefly below. The age-structured population model is based on the following:

$$N_{y+1,1} = (N_{y,0}e^{-M_{ju}/2} - \frac{C_{y,0}}{\bar{\omega}_{0c}})e^{-M_{ju}/2}$$

$$N_{y+1,a+1} = (N_{y,a}e^{-M_{ad}/2} - \frac{C_{y,a}}{\bar{\omega}_{ac}})e^{-M_{ad}/2}$$

where

$N_{y,a}$ is the number of sardines (billions) at age *a* at the start of year *y*, and *a* has values 1 – 4 and sardine die after age 5.

$C_{y,a}$ is the mass in kilotons of sardine of age *a* caught in year *y*,

M_{ju} and M_a are the natural mortalities of juvenile and adult sardine respectively, and

$\bar{\omega}_{\text{ac}}$ is the mean mass in grams of sardine in catch $C_{y,a}$.

Recruitment:

Recruitment is modelled around a hockey-stick (HS) stock-recruit (SR) curve, the shape of which is adjusted according to the current frame (west or south and high or low) and the favourability of the environment (see below). Although the HS stock – recruit relationship is only one of a number considered during stock assessments for the sardine in the southern Benguela and is not currently selected as the most representative, it has been previously, and is still used when running alternate scenarios (e.g. de Moor & Butterworth 2012).

$N_{y,0}$ is log-normally distributed around the curve according to the following:

$$N_{y,0} = f(B_y)e^{\varepsilon_y \sigma_r}$$

where

$$\varepsilon_y = S_{cor}\varepsilon_{y-1} + \sqrt{1-(S_{cor})^2}\,.\,\omega_y$$

σ_r is the standard deviation of the residuals around the log of the SR relationship,

ω_y is drawn from the standard normal distribution ($\mu = 0$, $\sigma^2 = 1$), and

S_{cor} is the serial recruitment correlation.

Recruitment variability:

σ_r and S_{cor} are used to introduce variability into recruitment around the SR curve. The residual standard deviation σ_r defines the 'spread' of the variability in residuals around the SR curve – increasing σ_r will on average increase the variability. Recruitment serial correlation S_{cor} specifies the degree to which recruitment differs from that of the previous year. A value closer to 0 is more likely to return recruitment that is different from the previous year, while complete autocorrelation will mean that recruitment is proportional to biomass every year. As in the previous version, in this model σ_r is set to 0.499 and S_{cor} is 0.374, both as per de Oliveira (2002). Note that while these values have been updated in OMP-04 and -08, as the model was not very sensitive to these parameters in the frame-based model previously (Botha 2012), and because a population model representing reality exactly is less important here than one that behaves realistically within the model context, values have been left the same in this version. The same applies to other variables such as mean mass at age.

Stock-recruit (SR) curve:

The shape of the SR curve is defined by the parameters for its inflection point *b, a*, where *b* represents the biomass (kt) and *a* the base recruitment level (billions), according to:

$$f(B_y) = \begin{cases} a & , \text{ if } B_y \geq b \\ \dfrac{a\, B_y}{b} & , \text{ if } B_y < b \end{cases}$$

where B_y is the November spawner biomass as determined by

$$B_y = \sum_{a=1}^{5} N_{y,a}\, \overline{\omega}_a$$

$\overline{\omega}_a$ is the mean mass in grams at age *a*, values used as per Botha (2012) after de Oliveira (2002) using average values for 1989 -2000, with $\overline{\omega}_1$ = 34.326, $\overline{\omega}_2$ = 69.537, $\overline{\omega}_3$ = 86.538, $\overline{\omega}_4$ = 98.706 and $\overline{\omega}_5$ = 111.525. Although these values have changed over time, this dataset remains representative with minor variation from estimates currently available (de Moor & Butterworth 2009) and was retained allow for comparison with results from the previous model version.

The shape of the SR curve is adjusted depending on the current frame to reflect:

a) lower recruitment success within a south frame, by varying the inflection point *b, a*: (Figure 5.2)

b) a density dependent effect in a high frame by varying the slope of the curve (see below); and

c) an environmental effect driven by the environmental suitability index (ESI) of the current frame (see below).

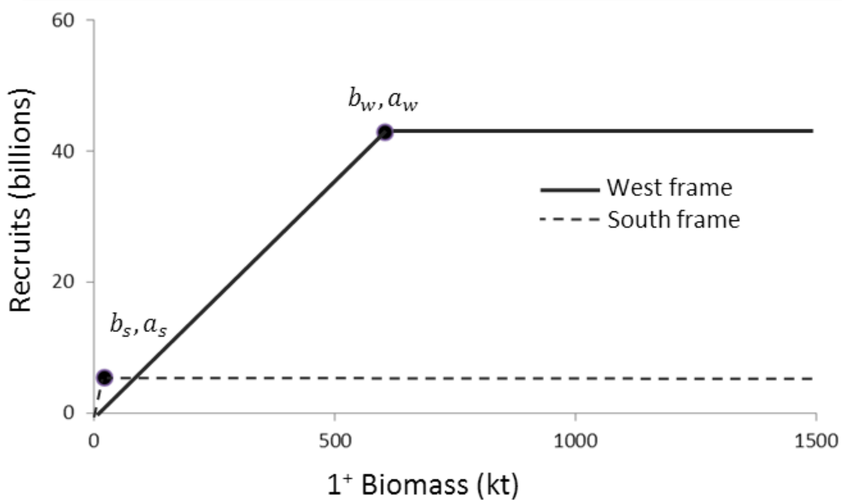


Figure 5.2: Stock-recruit curves used in the model. b_w, a_w represents the inflection point of the curve used for the west frame (Botha 2012; Cochrane et al. 1998) and b_s, a_s the inflection point of the south frame curve (de Moor & Butterworth 2012). Curves are further adjusted according to high/low frame and the environmental suitability index as discussed below.

Density dependent effect:

The Allee effect (Allee 1931) predicts that recruitment is inversely related to density until a population drops below a certain point, after which density is so low that successful spawning becomes less likely. This is implemented as follows: when sardine are in a high frame, the slope of the SR curve is decreased on a sliding scale from S_{max} as biomass increases until biomass B_{max} is reached (Figure 5.3). As in the previous version (Botha 2012), B_{max} is set to 2000 and S_{max} in a west coast frame is set to 0.0357 based on the OMP-04 values for *b,a* (de Moor & Butterworth 2009), and in a south coast frame S_{max} = 0.1256 based on the values used for the south coast stock in de Moor & Butterworth (2013). S_{min} is equal to S_{max} /2.

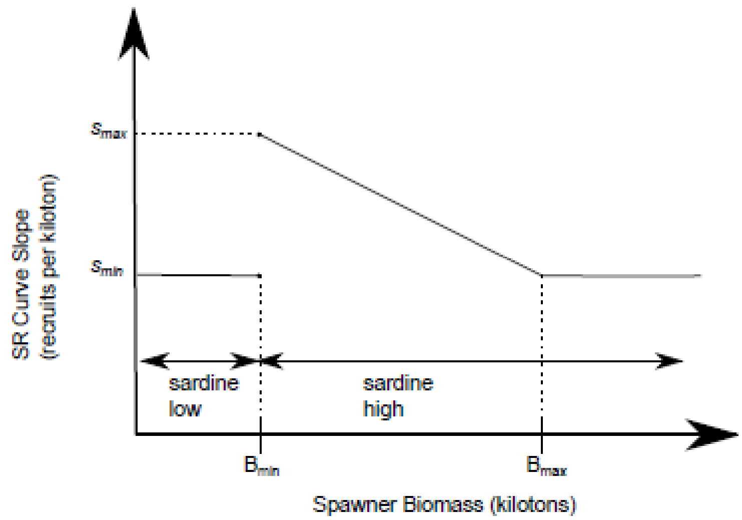


Figure 5.3: SR-curve adjustments under the density dependent effect (Botha 2012)

The 'other' coast population:

One of the assumptions of this model is that the explicitly modelled population represents only the *majority* of that total possible population. For example if sardine are in a west frame, the west coast is assumed to be the location of the majority of the population, representing anything from 60 – 100% of the total population, with the remainder being on the other, non-explicitly modelled frame – the south coast in this case.

Because a shift between frames (west-south) is dictated by ESI and fishing pressure, for the sardine daemon to evaluate the decision of whether to switch or not the daemon needs to be able to evaluate the level of fishing pressure on the 'other' coast relative to the current location. To make this possible, a number needs to be assigned to the proportion of the total population on the 'other' coast. This means that while the current coast sardine population is modelled as above, the other coast population is estimated as follows:

The proportion of the total population that may be on the 'other' coast at any time is assumed to be anything from 0 – 40%. Correspondingly a random number between 0 and 40 is drawn and used to calculate a biomass for the 'other' coast for the current year. Interannual variability is constrained to be less than 20%. This value is then fed to the sardine daemon to calculate whether fishing pressure on the coast as set by the user is relatively high or low and used to inform the shifting decision.

Anchovy population model:

The anchovy population is modelled simply as stochastically variable around a midpoint, with both the mid-point and the variability dependent on the current frame (Smith & Jarre 2011, Botha 2012). When referring to a west or south frame for anchovy, this refers to their spawning location. Their annual life cycle means that juvenile anchovy will always feed on the west coast, but in the model west or south frame distinguishes between whether they migrate to spawn on the west coast and western Agulhas Bank (west frame), or move further south/ east and spawn on the central and eastern Agulhas Bank (south frame). Unlike sardine, the anchovy population is not modelled explicitly but rather is determined entirely by the current frame, which is based on an environmental signal (ESI, below) and not affected at all by fishing as discussed above.

Anchovy parameters for the west coast frame were updated based on the revised biomass estimates in de Moor et al. (2008). When adding south coast frame parameters, increased recruitment variability for anchovy when on the south coast was assumed (van der Lingen et al. 2002), as well as increased mortality. This is represented in the model as lower recruitment when in a south frame: although recruitment was initially shown to be higher after the change in anchovy distribution southward and eastward in 1996 (van der Lingen et al. 2002), at the time of model construction recruit biomass had been measured as three times lower than the long-term average (Twatwa et al. 2011a). Although anchovy recruitment has since bounced back, given this bad year and the fact that heavier predation is expected on the south coast (Chapter Two; Hutchings et al. 2009; Osman 2010), a negative influence of the south coast on recruitment of anchovy was assumed within the model. This assumption is however tested in Chapter Six of this thesis, addressing the possibility of a positive effect of the south coast frame on anchovy. To represent increased mortality and recruitment variability, the midpoint for the south frame is 1/3 less than for the west frame, effectively increasing relative variability at the same time. Parameters used are tabulated (Table 5.1).

Table 5.1: Anchovy population model parameters for recruitment in kilotons.

Anchovy Frame	Midpoint	Variability
West coast High	3000	± 1500
West coast Low	1500	± 750
South coast High	2000	± 1500
South coast Low	1000	+ 1500; - 1000

5.2.2.2. Environmental Suitability index

The suitability of the environment for spawning, recruitment and feeding are known to be important determinants of the population size of both sardine and anchovy (Hutchings et al. 1998; Shannon 1998). Although the physical characteristics of their preferred spawning environments per species have been well investigated (van der Lingen et al. 2001; Twatwa et al. 2005; Twatwa et al. 2011), here the ESI represents physical conditions resulting in good recruitment (rather than spawning) due to the recruitment-based population models used.

Recruitment is influenced by a number of factors, from current speeds and the transport of eggs and larvae from spawning grounds to nursery grounds, the degree of retention on the shelf, to the suitability of the food environment for all stages of growth (Miller et al. 2006; Huggett et al. 2003). Feeding conditions are particularly important in driving fluctuations in population levels as they determine the condition of the spawning fish as well as the survival of larvae and recruits (van der Lingen et al. 2006c). Because sardine and anchovy favour different methods of feeding however, optimal feeding conditions are not the same for both: sardine mainly filter-feed on small zooplankton and phytoplankton, while anchovy are generally particulate feeders better suited to large zooplankton (van der Lingen et al. 2006c). Because the environment strongly influences the structure of the zooplankton community, the prevailing physical conditions indirectly determine which species is favoured by the food environment. Stronger upwelling results in suitable conditions for larger zooplankton, generally favourable for anchovy recruitment success, and more stable conditions and weaker upwelling promoting the growth of smaller plankton and are thus more suitable for sardine (van der Lingen et al. 2006c). Because of this the ESI used to drive the model is designed as a proxy for the physical variables affecting the food environment, representing intensity of upwelling, wind stress, current strength, salinity, SST etc.

Mean upwelling strength and SST have been shown to vary on a decadal scale in the southern Benguela (Roy et al. 2007; Howard et al. 2007; Blamey et al. 2012). As such, in previous models representing the west coast system (Smith & Jarre 2011; Botha 2012) the ESI was set to fluctuate between favourable and unfavourable every 10 years, as a 20 year cycle.

In addition to changes in the mean conditions however, shifts in the degree of variability of physical variables have also been detected in the southern Benguela, although over longer timescales (20 – 30 years) when compared with changes in the mean (Blamey et al. 2012). These changes in variability might also be assumed to have some impact on species in the system; perhaps this is not the case for the food-limited south coast, where variable productivity is still more beneficial than low productivity, but the value of including this longer timescale fluctuation in the west coast ESI signal was explored: When the shifts in upwelling variability on the west coast, which increased in 1990 and again in the 2000s at Hondeklip Bay and Cape Columbine (Blamey et al. 2012), are compared with zooplankton and recruit data over this period, there does not appear to be a discernible effect, although this has not been tested. Although autumn zooplankton biomass in the early 1990s on the west coast was high (Verheye et al. 1998), anchovy spawner biomass did decline from the early- to mid- 1990s. Small pelagic biomass increased from the mid-1990s, whereas upwelling variability remained high and a further positive shift has been detected in the 2000s (Blamey et al. 2012). There also does not appear to be any decreasing trend in anchovy recruitment after 1990, despite the increase in physical variability at the time (Miller & Field 2002). Based on this, we assume in the model that changes in the degree of variability of the environment do not have a strong effect on recruitment, or the effect is not distinguishable from that of changes in the mean. The ESI was therefore taken to reflect only changes in the mean conditions.

In this model we hypothesise a slightly longer timescale for environmental variability on the south coast. Results presented in Blamey et al. (2012), and Howard et al. (2007) and Shannon et al. (2010), show what appears to be a lower incidence of regime shifts on the south coast: shifts have been detected for the west coast in the early 1970s, 1990s and 2000s, while for the south coast similar shifts are only evident from 1996 onwards. To represent a longer timescale of changes in the south coast physical environment, the ESI period for the south coast has been set to 30 years in this model, while the west coast ESI period remains 20 years. The effect of alternate assumptions regarding ESI period for the south frame was examined in the model testing phase.

Implementation of ESI:

In Botha (2012) and Smith & Jarre (2011) ESI was modelled as a sine function with a 20 year period operating as a mid-point around which random integers were drawn from a defined range. This simulates decadal-scale variation and introduces stochasticity. In this prototype, to allow daemons within the model framework to 'decide' where the majority of the population would be (i.e. in a west or south coast frame) based on the relative suitability of each coastal environment, ESI's representing the ambient environmental conditions were run for each coast, instead of just one ESI for the west coast as in the previous two studies. Based on the above, ESI in the model was structured as follows:

1. Two ESI signals running simultaneously, one representing the conditions on each coast. As in previous models, ESI is modelled around a sinusoidal function centred around 50 with amplitude of 60 (note the units are arbitrary and created purely for modelling purposes). The ESI for the current year is set randomly within +- 10 from the sine function value for that year. As introduced above, as in previous versions a 20 year period is used for the west coast function, but a longer 30 year period is used for the south coast.
2. For the west coast, as before and based on the difference in trophodynamics between the two species and hence their suitable food environments (van der Lingen et al. 2006c), on the west coast what is 'good' for one species is assumed to be 'bad' for the other, thus the ESI has opposing effects on the two species. On the south coast however, because it is known to be a more food-poor environment, any increase in nutrients is thought to benefit both species. As such the ESI has the same effect on both species – i.e. what is 'good' for one is 'good' for the other.
3. As in previous model prototypes, to establish whether the environment is 'good' or bad' for each species on each coast, the ESI is evaluated based on a running total: each year's ESI value is added to the previous total unless the annual value is < 40. If so, the running total is reset to the current year's ESI value: see example in Table 5.2. The values at which the running total evaluates as 'good' or 'bad' for sardine and anchovy are shown in Table 5.3. For both species in both frames (west and south), if the running total is between 40 and 150 there is no change to the previous year's ESI evaluation – i.e. if it previously evaluated to have been 'good' it maintains that classification.

Table 5.2: Example of how the ESI running total (ERT) is calculated based on the current ESI. The ERT is reset to the current ESI value when that value is < 40.

Current ESI	90	84	79	57	57	42	29	21
ERT	90	174	253	310	367	409	29	21

Table 5.3: Thresholds for evaluating the favourability of the ESI for each species within each frame (west or south). ERT is the ESI running total.

	Sardine		Anchovy	
ERT	**West**	**South**	**West**	**South**
< 40	Good	Bad	Bad	Bad
40 - 150	No change from previous	No change	No change	No change
> 150	Bad	Good	Good	Good

4. For both species a favourable ESI will mean increased survival of early life stages and hence increased recruitment. The influence of ESI is greater for anchovy, which are thought to be more sensitive to environmental conditions (Twatwa et al. 2005) and unlike sardine are not affected by fishing pressure within the model.
5. Effect on sardine population model:
   There are two mechanisms by which ESI affects sardine recruitment depending on whether sardine are in a high or low frame (Figure 5.1). In a high frame, the ESI effect is implemented the same way as in the previous version: by altering *a* in SR curve inflection point *b,a*. If ESI is favourable and evaluates to 'good', $a = a_2$. When ESI evaluates to bad, $a = a_1$. Botha (2012) however found that this approach meant the ESI had no effect when sardine where in a low frame, as the low frame population was by definition < b_1 and so unaffected by changes in *a.* To address this and allow for an increased recruitment or rate of recovery in the low frame or when the biomass of age 1^+ sardine is < b_1, in this model version when ESI favours sardine and the population is < b1 the slope of the SR curve is adjusted (rather than *a)* and is increased from S_{min} to S_{max} (values as for the density dependent effect, see above) (Figure 5.4).

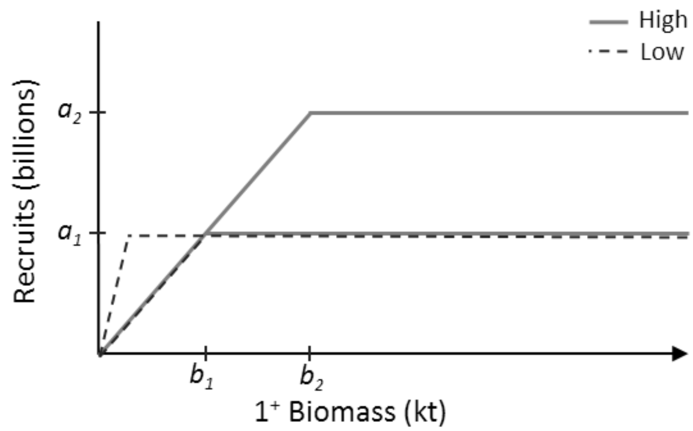


Figure 5.4: parameters altered to implement the ESI effect on the sardine SR-curve during high and low frames, adapted from Botha (2012). The slope of the 'Low' curve is set to S_{max} and the slope of the 'High' curve to S_{min}.

5.2.2.3. Fishing

In reality, both sardine and anchovy fisheries are managed by controlled catches via an Operational Management Procedure (OMP) designed to limit the risk of stock depletion. Based on the OMP annual total allowable catches (TACs) for sardine and anchovy separately are recommended, based on the results of biannual acoustic surveys (de Oliveira & Butterworth 2004). In the model TACs are set as follows:

Sardine fishing

The sardine fishery targets only adult, age 1^+ fish, and is implemented by the user with three possible fishing strategies available: 1) a set TAC for each species for the whole run ('Individual'); 2) TACs reset by the user repeatedly throughout the run after some user-defined number of years ('Active'); and 3) automatic management, structured in a similar manner to the OMP but at several levels of severity, re-evaluating the TAC every year based on the 1^+ biomass ('Automanage'). Fishing mortality is applied to the sardine population model as described in Botha (2012), using the selectivity at age from OMP-02 to split the TAC among the age classes.

1. Individual TACs:

   This strategy allows the user to set a fixed sardine TAC for the duration of the run for each species. In previous models this took the form of a value in kilotons. For this version it was decided that a more realistic approach would be to use a percentage of total biomass as a TAC. With the addition of the spatial element, the user can also now specify a further spatial fishing strategy for sardine; fishing may be focused on the west coast ('max. west coast') or south coast ('max. south coast'), or the TAC can be split between the coasts based on the proportion of total biomass on each coast each year ('dynamic tracking'). If either of the first two options is chosen, the model will catch the maximum TAC possible on the chosen coast, even if this means fishing sardine on that coast to zero, and redirect the remainder of the TAC from the other coast.

2. Active management:

   This strategy is the same as in previous versions, allowing the user to reset the TAC every three years as a default, enabling the user to explore various reactive management options over a run.

3. Automanage:

   In previous models, automanage was set up as a sliding scale from conservative to severe. The population size was evaluated based on pre-set thresholds, and a sardine TAC in kilotons assigned based on whether the population was identified as low, moderate or high. Although theoretically this approach could allow for a more nuanced evaluation of fishing effects, in reality the results tended to be fairly stable up to a 'tipping point' (e.g. results for 0 – 40% severity were quite similar, but differed from results for 50 – 80%) (J. Botha, pers. comm.), and when used for model testing generally only one of three settings was applied (0%, 50% or 100% severity). As such, when developing the current model the sliding-scale was replaced with three discrete options with minimal loss of meaningful detail: conservative; moderate and severe. Like the individual fishing strategy, TAC was also now set proportional to biomass, rather than as a set value as before. To give more realistic results, the previous approach of a fixed TAC based on population level category is revised in this version to use a strategy similar to that used in the OMP for sardine: below a lower population threshold the TAC is set to zero; between this and an upper threshold the TAC is constant and set to a minimum TAC specific to that level of fishing pressure; above the upper threshold the TAC is proportional to biomass with the slope again related to the chosen severity (Figure 5.5). Minimum TAC and TAC slope increase with increasing severity and the lower threshold is reduced.

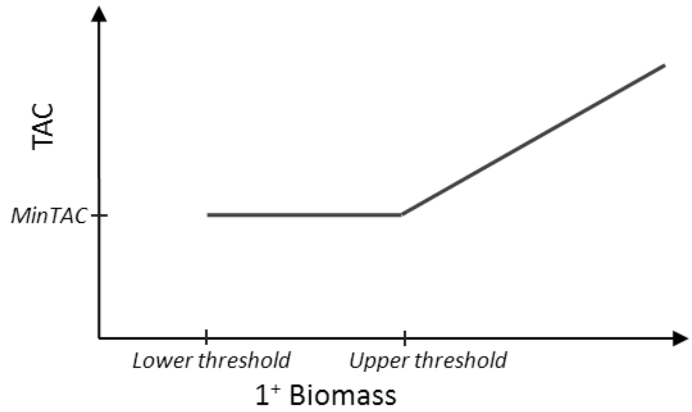


Figure 5.5: Relevant parameters used by the automanage fishing strategy to set the sardine TAC as a proportion of 1^+ biomass.

Parameters were set based on the assumptions from previous (west frame) models that conservative fishing results in zero probability of the sardine population crashing (where a crash is defined as biomass < 10 kt), severe in 60% probability of crashing, and in this model moderate fishing results in a 30% probability of crash. Starting values for each parameter were based on those used in previous models and the values used in OMP-08 TAC – biomass curve, but were tuned to the previous assumptions re. the probability of crash in a west coast frame so as to be comparable with previous versions. Parameters used in the model are given in Table 5.4.

Table 5.4: Parameters used under the automanage fishing strategy to set sardine TAC at conservative, moderate and severe fishing pressure. Threshold and min TAC values are in kt.

Parameter:	Conservative	Moderate	Severe
Lower threshold	250	150	150
Upper threshold	900	621.5	422
MinTAC	90	124.3	126.5
TAC slope	10%	20%	30%

The model is very sensitive to the minimum TAC and lower threshold parameters, as was the case in the previous model version, where the sardine population only began to crash as the sliding scale approached 'severe'. As a result, there is not a very big difference in the parameters for 'moderate' and severe' (Table 5.4), as a small change produced a large change in outputs. Because the assigned values do result in the required probability of crashing the population however (30% and 60% respectively), the two categories were kept as a useful tool in the model despite having similar parameters. Further exploration of this sensitivity should be incorporated into any following model iterations.

School trap effect:

At low levels of abundance small pelagic fish are known to school together. This disadvantages the less abundant species as the school feeding behaviour will be that of the more abundant species – an effect known as the 'school trap' (Cury et al. 2000). In the southern Benguela this also means that when the sardine population is low and juvenile sardine school with anchovy, they are taken as a bycatch with anchovy catches.

As in previous models the school trap effect is taken into account in the model by assuming proportional mortality of juvenile sardines based on anchovy catch when the sardine population is in a low frame. In this model the effect only occurs when sardine are in a west frame, or west coast mode, both because school behaviour is less important on the south coast (C. van der Lingen, DAFF, pers. comm.), and because the commercial anchovy catch is taken almost entirely on the west coast, during their annual migration from feeding to spawning grounds.

Sardine bycatch is calculated as a proportion of juveniles based on anchovy catches, scaled by the school trap factor - a measure of the proportion of sardine juveniles thought to be schooling with anchovy. When sardine are in a low frame and anchovy are in a high frame and likelihood of mixed schools is highest, the school trap factor is set to 0.4; when both sardine and anchovy are both low it is set to 0.2; when sardine are in a high frame the school trap factor, and thus bycatch, is equal to zero.

Anchovy fishing:

As in previous versions anchovy fishing is included to allow for calculation of juvenile sardine bycatch via the school trap effect when sardine are in a west frame. Because regardless of spawning area (west or south) the lifecycle of anchovy takes them to the west coast annually as larvae and recruits to feed before returning to the spawning grounds on the Agulhas Bank,– i.e. whether they're classified as spawning west or south, a portion of the stock will always be present on the west coast over autumn/ winter (Hutchings et al. 1998). Because as previously mentioned the majority of the anchovy catch is take on the west coast as the fish return from the west coast to their spawning grounds, within the model anchovy catch is taken regardless of whether anchovy are in a west or south frame (to recap, this refers to spawning location).

The three fishing strategies outlined above can also be applied to anchovy with the following alterations: under the 'Individual' fishing strategy, because anchovy are caught only on the west coast in the model the user is not able to specify a TAC for the west and the south, as for sardine, but rather sets a single TAC; unlike for sardine, the 'automanage' option sets anchovy TACs as a proportion of biomass based on whether the population is high or low and on the fishing severity selected (see Table 5.5).

Table 5.5: Proportions of biomass used to set anchovy TACS using the 'automanage' fishing strategy.

Severity/ Frame	Low	High
Conservative	0.2	0.4
Moderate	0.25	0.5
Severe	0.3	0.6

Note that this approach is simpler than that applied in reality via the OMP, which sets TACs for both species and aims to maximise sardine and anchovy catches without exceeding pre-defined limits of acceptable risk of either stock declining below acceptable levels (de Moor et al. 2011). As previously discussed, in this model the emphasis has been placed on the sardine-directed fishery. Further model iterations however may explore this approach of setting the two TACs based on a trade-off curve.

5.2.2.4 Daemons & frame shifting rules

The sardine and anchovy daemons monitor population levels, ESI and fishing, and based on these variables 'decide' whether to stay in the current frame or whether to shift into a new frame, If a shift occurs, the daemons then determine which frame to shift to. Rules for shifting between frames are shown in Figure 5.6, and discussed below.

Sardine daemon

High – low frame switching:

The rules for switching between high and low frames are driven by adult sardine biomass: the sum of the 1^+ biomass over three years is evaluated and sardine shift to low if this value is ≤ 1800 kt, to high if ≥ 2400 kt, or otherwise remains in the current frame (Figure 5.7, Botha (2012).

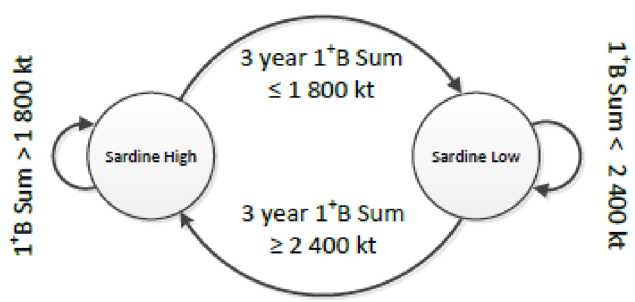


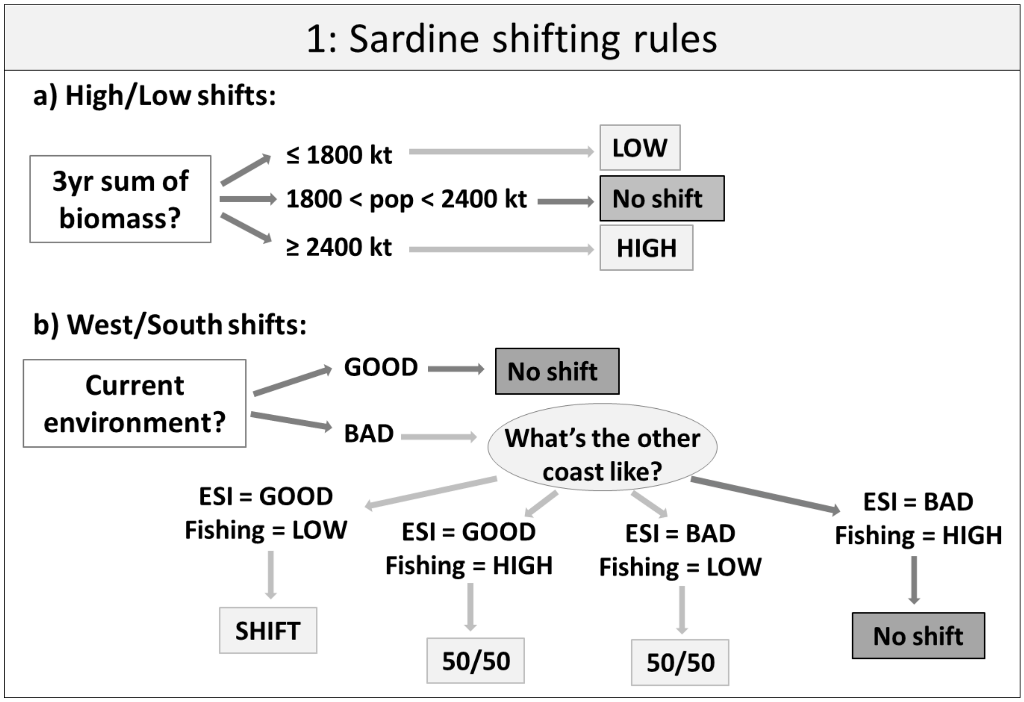
Figure 5.7: Sardine daemon high – low frame switching thresholds (Botha 2012).

West – south frame switching:

Based on the hypothesis that the change in sardine distribution in the late 1990s can be linked to environmental changes and fishing pressure (Coetzee et al. 2008a), spatial frame switching is decided based primarily on the ESI of the current coast, and then secondarily on the ESI and fishing pressure on the other coast. If the current coast's ESI is favourable, a shift is rejected and sardine remain in their current frame. If the current coast's ESI is unfavourable, the daemon considers the conditions on the 'other' coast when deciding whether or not to shift: if both ESI and fishing are favourable, sardine shift to a new frame – the ‘other’ coast; if both are unfavourable, sardine remain in their current coast frame; if one parameter is favourable and the other is not, there is a 50% probability that a shift will occur. Note that it is assumed that population level does not affect west – south shifts: population size on the west coast did not decline before the late 1990s shift occurred and was actually quite high, so this is assumed not to be a driver of frame dynamics.

Fishing pressure is evaluated using the fishing mortality (F), calculated as catch/ biomass. Patterson (1992) suggests that at an exploitation rate (E) > 0.4, where E = F/Z, a population is likely to decline. Assuming $Z = 1.2.y^{-1}$ for sardine in the southern Benguela, in the model fishing pressure is considered low/ favourable if F < 0.48, and high/ unfavourable if E > 0.48. As previously discussed, ESI is evaluated according to Table 5.3.

To avoid unrealistic rapid shifting from one coast to another that can occur under these rules in years when the 50/50 probability of a shift rule is invoked for consecutive years, west – south frame shifts for both sardine and anchovy are constrained to a minimum number of years between shifts. Data on changes in spawning location for sardine over time suggests shifts on the timescale of 3 - 7 years (van der Lingen et al. 2006a), which equates to roughly a full life-cycle. This may support the hypothesis of natal homing (Cury 1994), with recruits returning to the areas where they were spawned. Based on this, both sardine and anchovy daemons are constrained to shift a maximum of once every three years.



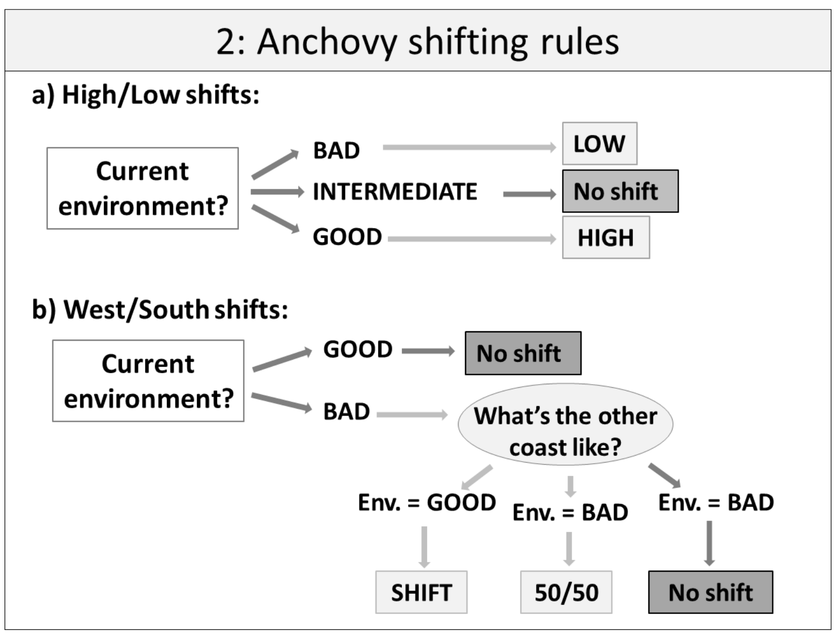


Figure 5.6: Rules for sardine (1a&b) and anchovy (2a&b) shifting between high and low, and west and south frames. Sardine shifts depend on current population size, environment (ESI) and fishing pressure, while anchovy is driven only by the ESI.

Anchovy daemon

High – low frame switching:

Anchovy high or low frame depends on the ESI. If the ESI running total > 150, anchovy shift to high, between 40 and 150 there is no shift and anchovy maintain their current frame, and if the running total is < 40 anchovy shift to a low frame (see Table 5.3).

West – south frame switching:

As previously discussed, unlike the sardine daemon the anchovy daemon bases the west –south frame decision purely on ESI and fishing pressure is not considered: if the current coast's ESI is favourable, a shift is rejected and anchovy remain in their current frame (Figure 5.6). If the current coast's ESI is unfavourable, the daemon considers the conditions on the 'other' coasts ESI. If it's favourable, anchovy shift to a new frame; if not, there is a 50% probability that a shift will occur. As for sardine, frame shifts are restricted to a minimum three year interval.

5.2.2.5. Additional outputs: system state

As mentioned in the motivation for constructing this model, small pelagic fish are of interest because of their impact on other trophic levels within the system. Model outcomes here have implications for the functioning of the system as a whole, and in this version an indicator of system state has also been included in the model outputs.

Cury et al. (2012) have shown over multiple systems that if forage fish biomass in a marine ecosystem falls below approximately 1/3 of their maximum long-term abundance, seabird breeding success is likely to be negatively affected, providing a useful (if generalised) link between patterns in small pelagic abundance to top level predators. This is particularly topical in the southern Benguela, where fluctuations, and in the case of the African penguin, serious declines, in seabird populations have been strongly linked to small pelagic fish abundance and distribution (Crawford et al. 2008a; Crawford 2013; Crawford et al. 2008c; Ludynia et al. 2010; Sherley et al. 2013; Weller et al. 2014). Although this is a generalised indicator

In addition to the two bars on the model output display showing the current frames (high/low and west/south), a third bar has been added giving an indication of whether the system as a whole is in ‘west coast mode’ or ‘south coast mode’, or whether the conditions as a whole are unfavourable for predators (small pelagic biomass is < 1/3 of its long-term maximum). The system is assumed to be in west or south coast mode when the majority of small pelagic biomass is located on that coast, based on the current frame for each species. For example if sardine and anchovy are on opposite coasts and one species is at a high biomass level and the other low, the coast with the high population is set as the current mode.

Sardine have a higher calorific value than anchovy based on an average of reported calorific values (Balmelli & Wickens 1994; Pichegru et al. 2010), and the seasonal transience of anchovy makes them less accessible as prey. Consequentially if species are on opposite coasts and are both high or both low, the system mode is biased towards sardine and the system mode is set to that of sardine. For example if sardine are in a high west frame, and anchovy high south, the system registers as being in west coast mode.

The system state is flagged as unfavourable for predators, or ‘bad’, when the total (combined) biomass of both species falls below 1/3 of the long-term maximum within the model (based on the average max 100 year run biomass of sardine and anchovy over 100 runs), as suggested as a threshold by Cury et al. (2012).

Table 5.6: Descriptions of the variables and parameters used in the model.

	Parameter	Description
Sardine population model	$N_{y,a}$	the number of sardines (billions) at age a at the start of year y, and a has values 1 – 4 and sardine die after age 5.
	$C_{y,a}$	the mass in kilotons of sardine of age a caught in year y
	M_{ju}	the natural mortality of juvenile sardine
	M_a	the natural mortality of adult sardine
	$\bar{\omega}_{ac}$	the mean mass in grams of sardine in catch $C_{y,a}$.
	σ_r	the standard deviation of the residuals around the log of the SR relationship
	S_{cor}	the serial recruitment correlation
	ω_y	a random sample drawn from the standard normal distribution
	B_y	the November spawner biomass
	$\bar{\omega}_a$	the mean mass in grams at age a
Stock - recruit curve	b	biomass value (kilotons) of the SR curve inflection point
	a_1	base recruitment level (billions) for a west frame
	a_2	base recruitment level (billions) for a south frame
	S_{max}	maximum slope of the SR curve
	S_{min}	minimum slope of the SR curve
	B_{max}	biomass above which density dependent effect no longer comes into effect
ESI	ESI	Environmental Suitability Index
	ERT	ESI running total
Automanage	MinTAC	the TAC set between the upper and lower thresholds
	TAC slope	slope determining the proporrtion of biomass set as the TAC
	Lower threshold	biomass below which TAC is set to zero
	Upper threshold	biomass above which TAC set as proportional to biomass, according to the TAC slope
	V_{IA}	the interannual variability in the sardine catch

Table 5.7: Values used for key sardine parameters in the model.

Parameter	Value used
$\bar{\omega}_1$	34.326
$\bar{\omega}_2$	69.537
$\bar{\omega}_3$	86.538
$\bar{\omega}_4$	98.706
$\bar{\omega}_5$	111.525
M_{ju}	0.8
M_a	0.4
σ_r	0.499
S_{cor}	0.374
$a_{1,w}$	21.64
$a_{2,w}$	14.42
$a_{1,s}$	5.4
$a_{2,w}$	3.6
$S_{max,w}$	0.0357
$S_{min,w}$	0.01785
$S_{max,s}$	0.1256
$S_{min,s}$	0.0628
B_{max}	2000

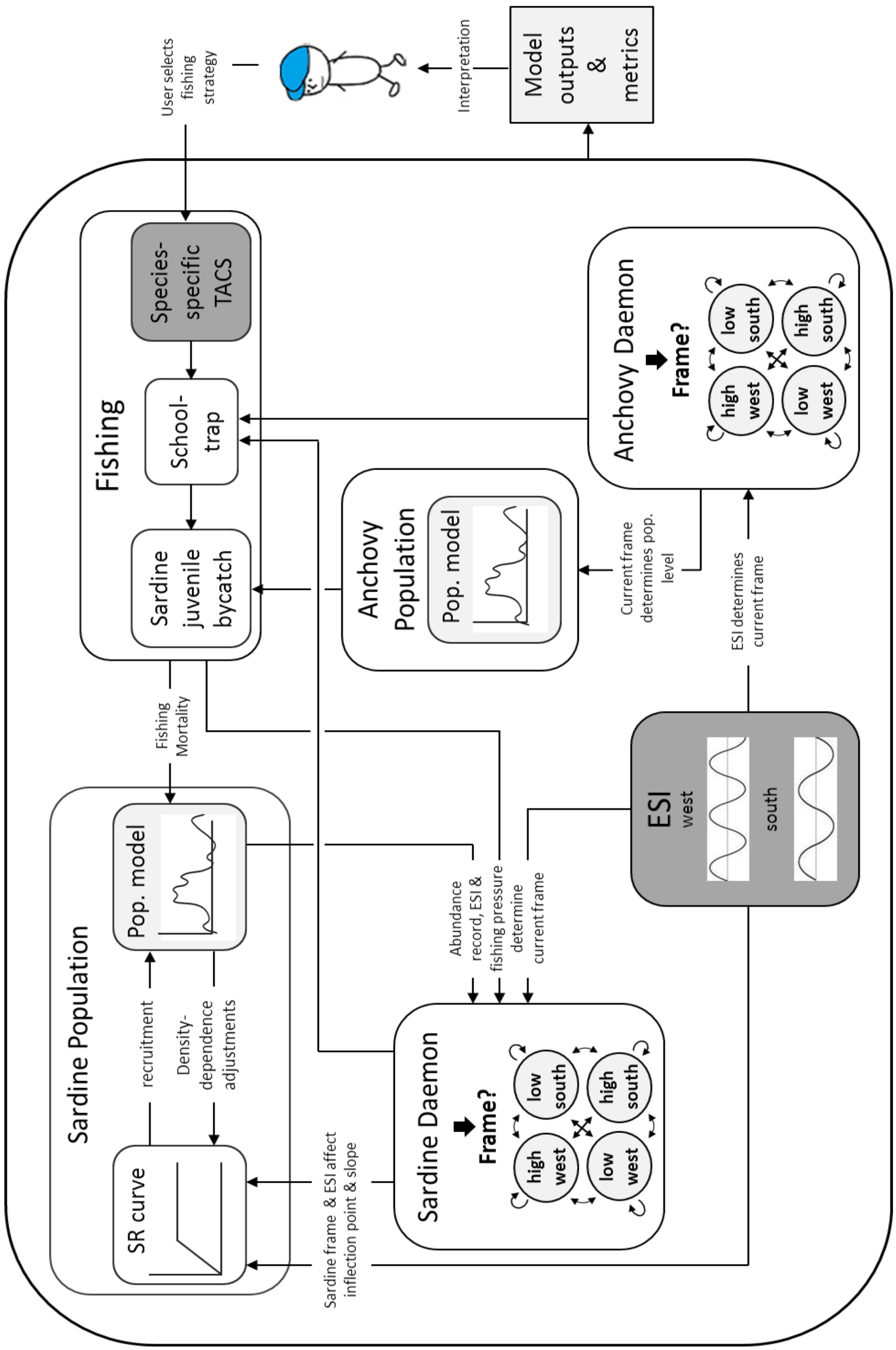


Figure 5.8: Model structure diagram. Model outputs, such as population timeseries, are shown in pale grey, and forcing components, such as Environmental Suitability Index (ESI) in dark grey.

5.3. Testing and analyses

The assumptions necessary in the construction of any model and the uncertainty inherent in its inputs, whether based on quantitative data or estimated qualitatively from available information, need to be tested to establish whether the model is working as it should. Sensitivity of outputs to the inputs used must also be tested. Below are discussed:

1. General model tests, run to test whether the model is working as it should, and to illustrate how it functions;
2. Tests to see how the addition of a south coast frame has affected model functioning by running recovery from Low frame duration tests. Results were compared with those from similar tests run on previous versions of the model. (Testing the hypothesis that recovery of sardine is not affected by the addition of a south coast frame);
3. Sensitivity analyses, testing the degree to which inputs are affecting the model outputs. Because our objective is explore our understanding of spatial dynamics and their implications for management decisions, analyses will be focused around sensitivities of the model to the additional inputs used for functioning in the south coast frame, and the rules governing switching between west and south coast frames to better understand model sensitivity to additional parameters used;
4. Exploration of model outcomes and testing some alternative climate scenarios.

5.3.1. General model tests

5.3.1.1. Does ESI affect recruitment and is this effect evident in all frames?

a) Does sardine recruitment increase during periods when the ESI is favourable for them?

Because anchovy recruitment depends entirely on ESI, it is possible to identify these periods by observing the anchovy biomass. On the west coast, what is favourable for sardine is unfavourable for anchovy. On the south coast, what is favourable for one is favourable for the other. During a normal model run (for the purposes of this analysis a model run length is equal to 50 years) even when no fishing pressure is applied, the stochasticity inherent in the population models and the ESI, as well as frequent switching between west and south frames, makes it difficult to test the model functioning (Figure 5.9). As a result, the test was run with no fishing, stochasticity set to zero and autocorrelation to

1 so that recruitment is proportional to spawner biomass. Because the ESI signals on the two coasts are not in phase, to allow for clear observation of the effect of the ESI, two model runs were completed in which sardine and anchovy in the model were both forced to either the west or south frame for the duration of the run. In all tests, the west coast frame run was expected to mirror the results as the previous version of the model (Botha 2012), as that version was essentially a west coast model.

Expected result: sardine should recruit at lower levels when the environment is unfavourable.

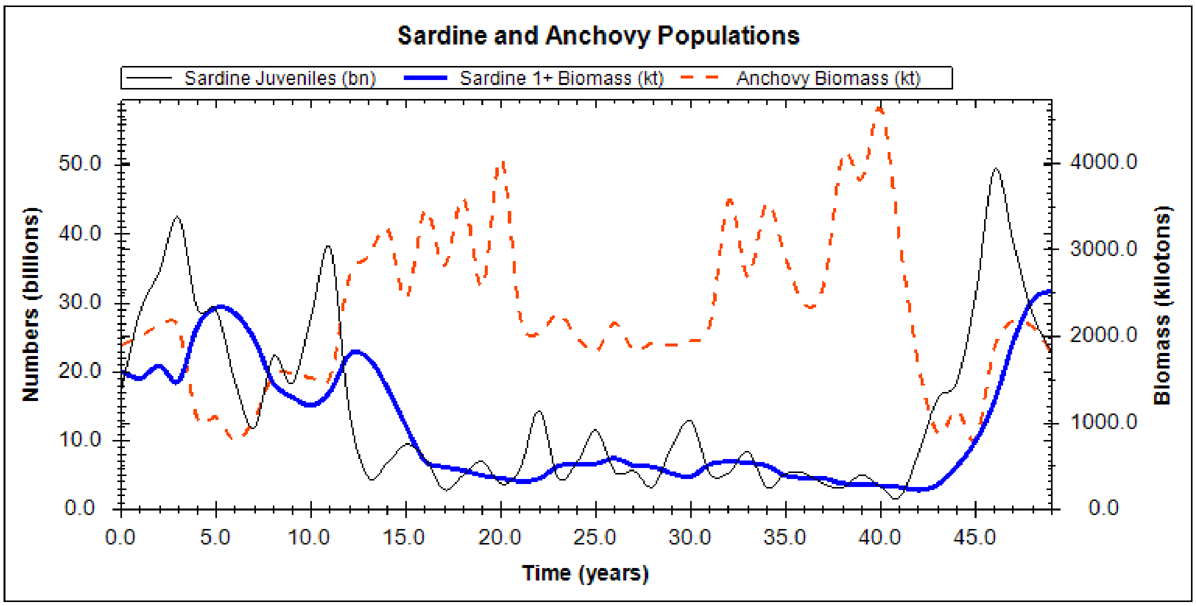


Figure 5.9: A standard model run, with stochasticity enabled and no fishing. Note lag time of approximately three years between recruitment and 1^+ biomass levels.

Results:

Both west and south coast runs performed as expected and reflect higher recruitment during phases of favourable ESI at the levels set by the a_1 and a_2 inputs to the SR curve set for each coast (Figures 5.10 and 5.11). The different periods set for the ESI on each coast were also visible, with 20 year cycles in biomass on the west coast and 30 year cycles on the south. Note the opposite effect of ESI on sardine vs. anchovy on the west coast, compared with the direct and equal effect on the south coast, where what is good for one species is assumed to be good for the other. When forced to a south frame, under test conditions without stochasticity and with serial autocorrelation set to 1 (Figure 5.11), the sardine population did not exceed 500 000t except during the first couple of years, where it is stabilising after starting up in the high frame.

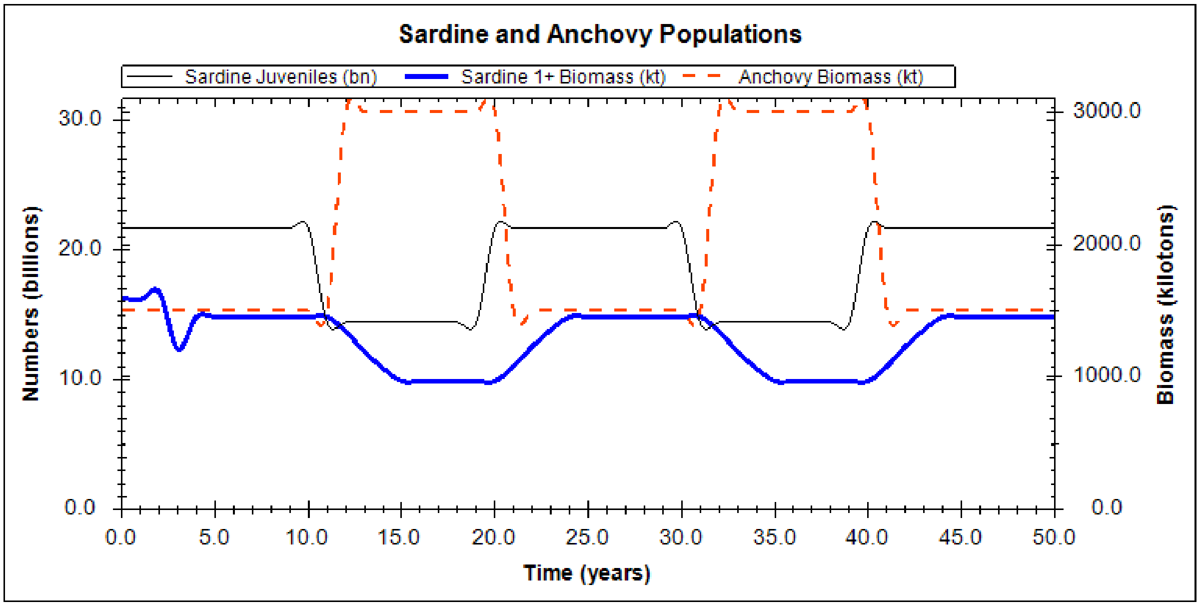


Figure 5.10: Model run in the west coast frame, with no fishing or stochasticity. Sardine are in the high frame throughout, while anchovy alternates between high and low.

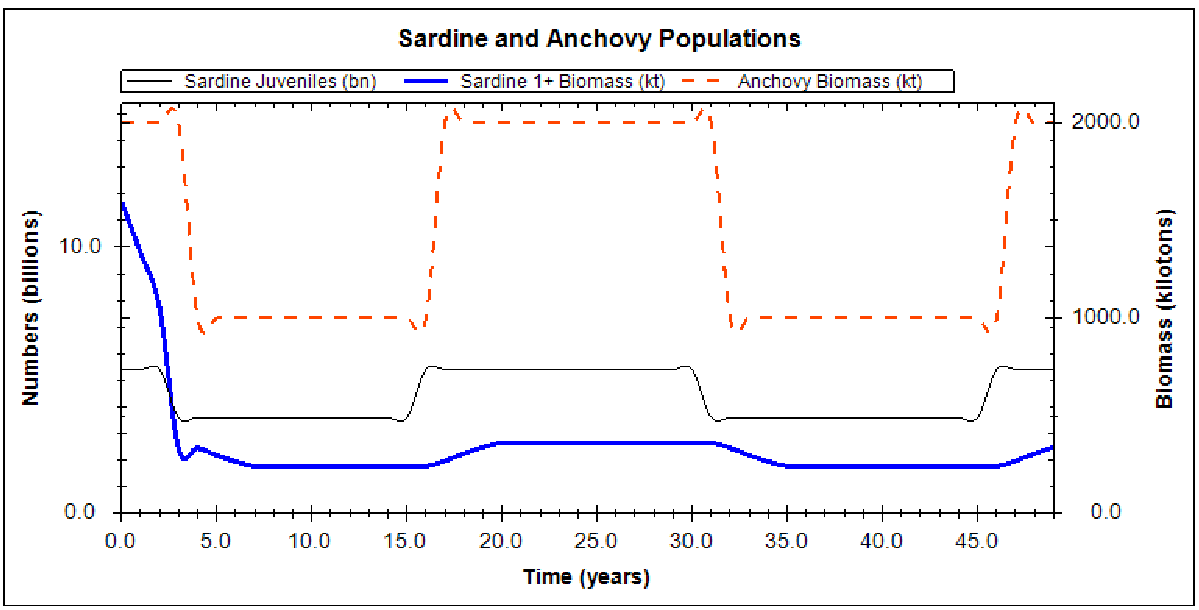
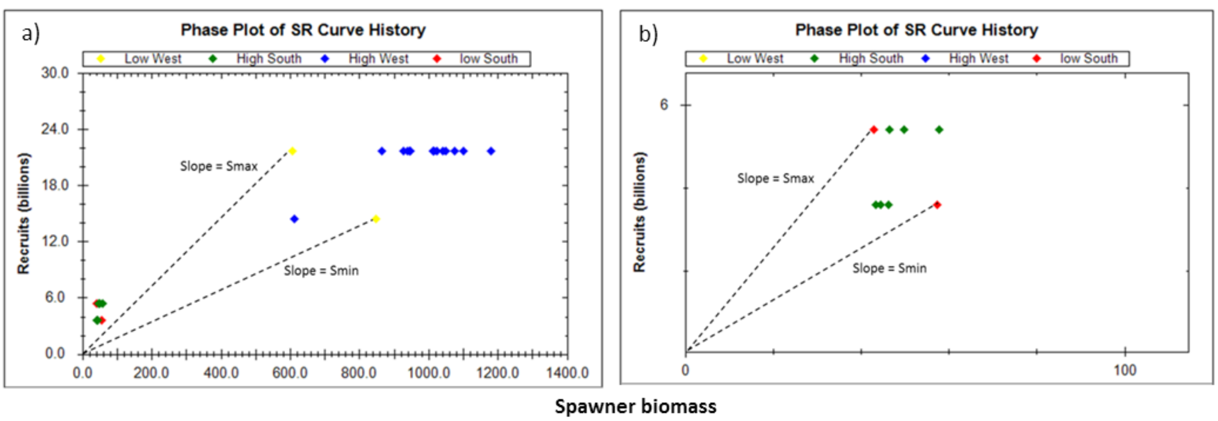


Figure 5.11: Model run in the south coast frame, with no fishing or stochasticity. Sardine are in the low frame for the majority of the run, while anchovy alternates between high and low.

b) Does ESI affect recruitment in the low frame?

As discussed, in the previous version of the model it was discovered that ESI did not have an effect when sardine were in the low frame: because the implementation of this effect (altering the y-component of the SR inflection point *a*) relied on the biomass being greater than the x-component of the inflection point, b (Figure 5.4). Because this is almost never the case in the low frame, the effect of ESI on recruitment was effectively not implemented. In this version of the model, in addition to altering *a*, the influence of the ESI is implemented in the low frame by changing the slope of the SR curve between S_{max} and S_{min} to reflect a favourable or unfavourable ESI (see section 2.2.2 this chapter). To test if this implementation is working, single model runs were completed with fishing set to zero and the phase plots of the SR curve inflection points used during the runs were examined.

Expected result: If the ESI effect is functioning in a low frame, the slope of the curve in the low frame should vary between the relevant S_{min} or S_{max} of the current coast frame. If it is not, the slope should be roughly equal to S_{min} in all years.



Figures 5.12 a & b: inflection points of the SR curve when sardine are in a) a west coast frame, and b) a south coast frame, illustrating the changes in slope when in a low frame due to the effect of ESI. Note y-axis scales are different.

Results:

Phase plots confirm that when in a low frame, the slope of the SR curve varies between S_{max} and S_{min} (Figures 5.12 a and b).

5.3.1.2. Does the coast frame affect recruitment?

Based on model inputs, sardine in a south coast frame should recruit less well than when in a west coast frame. This result can be observed in Figures 5.10 & 5.11 above, where sardine biomass and recruitment when running in a south coast frame never exceed 1000 kt after initial stabilising years. In a west coast frame however (Figure 5.10), biomass and recruitment are either equal to or greater than 1000 kt. The phase plots above in Figures 5.12 a and b also show much lower inflection points for the SR curve in south coast frames, all showing that the coastal frame does affect recruitment.

5.3.1.3. Does density affect sardine recruitment on the south coast?

Because the density dependent effect has already been tested for the west coast in the development of the previous model version, only the south coast is tested here. Single model runs were completed with fishing set to zero and phase plots of the SR curve inflection points used examined.

Expected result: if the density dependent effect is functioning and allowing the slope to vary in a high frame, the slope of the curve should be variable between S_{min} and S_{max} in the high frame. If not, the slope should be roughly equal to $S_{max.}$

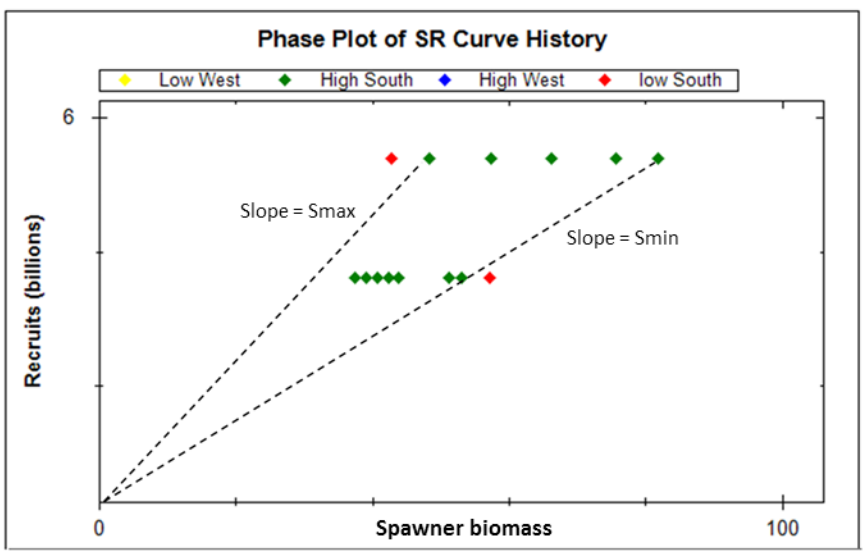


Figure 5.13: Phase plot of sardine SR curve inflection points during a run of the model forced to the south coast, confirming that the slope of the curve varies between S_{min} and S_{max} in a high frame.

Results:

The phase plot in Figure 5.13 show that the slope of the curve varies with S_{min} and S_{max} (the slopes of the two low south frame points in the figure) as outside limits, thus confirming that there is a density dependent effect is operational when sardine are in a high frame on the south coast.

5.3.1.4. Does sardine directed fishing mortality have an effect in a south coast frame?

Because this has already been tested for a west coast frame in the previous version of the model, only the south coast frame will be examined here. Initially the same method was applied here as used by Botha (2012) when testing the previous version of the model (west coast model): heavy fishing was applied for 3 years using the active fishing strategy, and decreased over the next six years, after which sardine were allowed to recover. The changes to the SR curve on the south coast however mean that the biomass during a run when sardine has been forced to the south coast is significantly lower than on the west coast (as shown in test 5.3.1.2 above). Because of this, the levels at which sardine are fished for had to be adjusted (lowered) in this test, and TAC was set at 100kt for the first 3 yrs, 50 kt for the next and 30 for the next, before allowing the population to continue unfished. Although this does impact the biomass over the run, because of the generally low biomass levels in a south frame and the inherent stochasticity in the model, the effects of the fishing are not as obviously evident when looking at the population graph output as on the west coast. As a result, in addition to the above test, individual fishing strategy was used, which allows for multiple runs to be performed, making results clearer. Figures 5.14 a and b show 5 runs with no fishing and 5 runs using individual fishing set at 40% of total biomass with maximum catch taken on the south coast, in a model where sardine and anchovy were both forced to the south coast.

Expected result: During runs when fishing pressure is applied, the level of sardine biomass should be depressed.

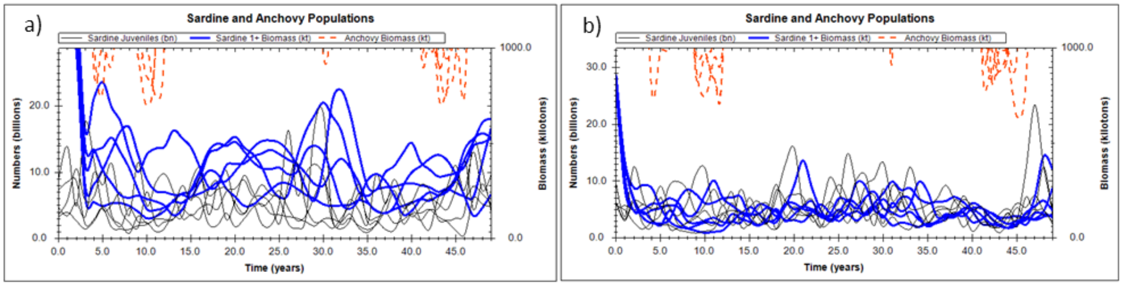


Figure 5.14: 5 runs with no fishing (a), and 5 runs with individual fishing set at 40% 'max. south coast' (b). All runs are forced to a south frame only.

Results:

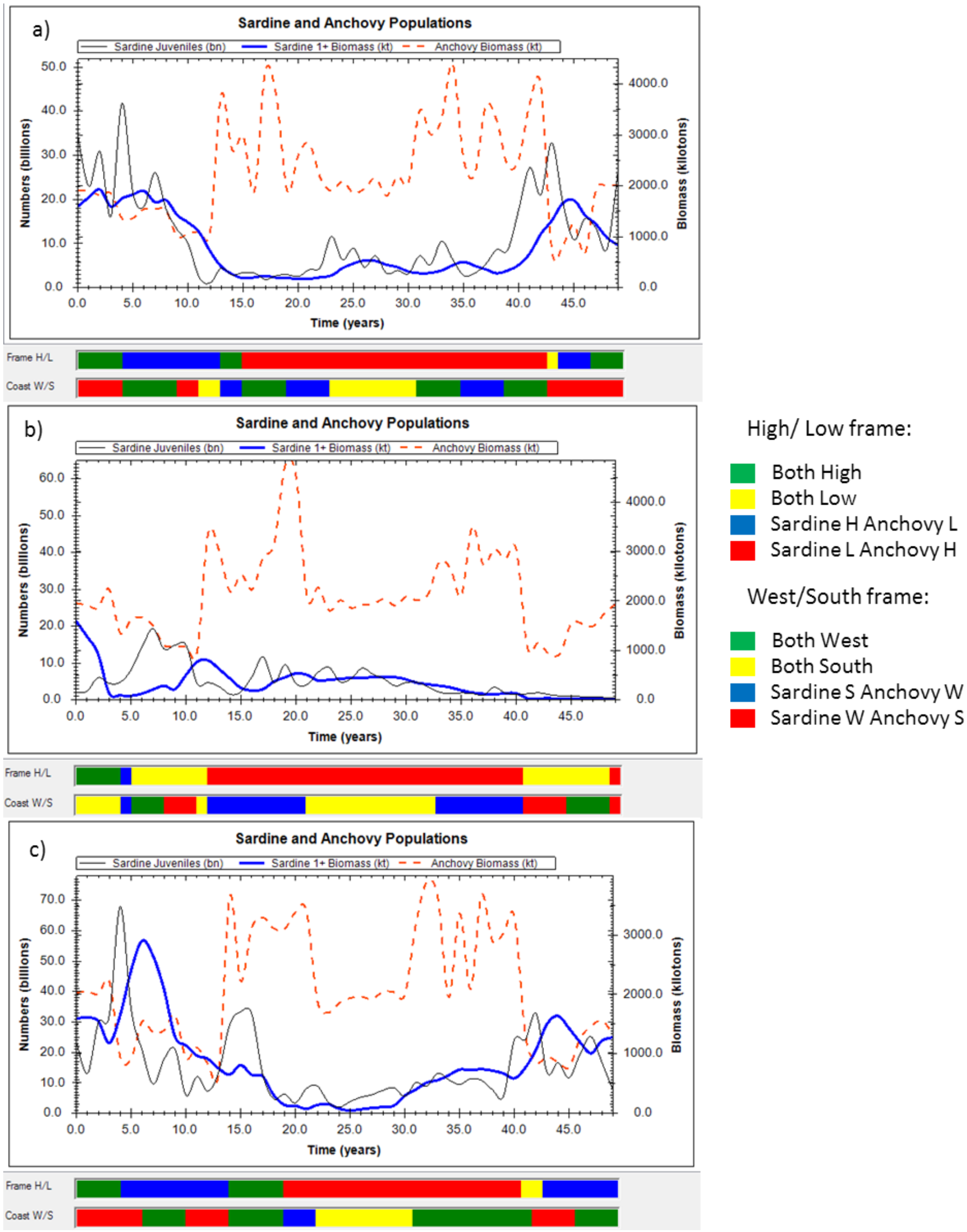
Figure 5.14b shows lower overall biomass during all runs, seldom exceeding 250 kt, unlike the unfished runs which vary between about 600 kt and 250 kt (Figure 5.14 a). This confirms that when in a south coast frame, sardine responds as expected to directed fishing pressure and have on average lower biomass than when no fishing takes place.

NOTE: there is no anchovy fishing on the south coast, hence the bycatch of juvenile sardine in a south coast frame is not tested. Functionality was tested for a west frame by Botha (2012).

5.3.1.5. Does fishing pressure affect the sardine west/south frame shifts?

The switching rules for sardine location (west and south frames) are driven by ESI and fishing. Here the effect of increased fishing on one coast on shifting behaviour of sardine were tested. The automanage fishing routine was used for this test. First severe fishing pressure was applied to the west coast, and zero fishing pressure to the south. The pressure was then reversed between the coasts. Stochasticity was enabled.

Expected result: Although the ESI is the primary determinant of location for sardine, if the local ESI is unfavourable, the fishing pressure on both coasts is evaluated. As a result, sardine should favour the coast where fishing pressure is lowest/ conservative, and increased pressure on one coast should result in increased time spent on the other coast by sardine.



Figures 5.15 a – c: Representative model runs with a) no fishing, b), fishing on the west and c) south coasts. Bars below the population plot represent residence time in high/low and west/south frames.

Results:

Figure 5.15a shows a representative run with no fishing on either coast. The west/ south frame is indicated by the second colour bar below, and shows a relatively even split in time spent in the west frame vs south frame by sardine (duration west:south 57.5% : 42.5%). Figures 5.15 b and c show representative runs where severe fishing pressure is applied to the west and then south coasts, and shows a higher residence time for sardine in the unfished coast/frame in each example. Where fishing pressure was applied to the west coast, sardine show a preference for the south (figure 5.15 b duration west:south 28.5% : 71.5%), and vice versa (figure 5.15 c duration west:south 74% : 26%). Note that the runs illustrated here are only representative runs: due to the stochasticity in the system the full spectrum of results vary from sardine being located entirely on the unfished coast to slightly higher residency on the fished coast than shown above. The illustrated runs do, however, represent the most common outcome, and the test does confirm that fishing pressure affects the location of sardine and that they ‘favour’ the coast where fishing pressure is lower.

5.3.2 Sensitivity analyses

Models can be sensitive to their inputs either in that variability in a sensitive input may account for a large proportion of output variability, or if model outputs are strongly associated with an input to the point that small changes in that input result in larger changes in the output (Hamby 1994). To test the degree to which model outputs are affected by the selected input parameters, a sensitivity analysis must be performed. Because the model objective is to describe spatial dynamics and explore their possible implications for management decisions, analyses will be focused around sensitivities of the model to the additional inputs (compared with previous model versions which are equivalent to a west coast only model) used for functioning in the south coast frame, and the rules governing switching between west and south coast frames. The model constructed by Botha (2012) was effectively a west coast version of the current model. As such, model parameters have already been tested for this previous model, and thus the west coast frame. With the addition of a differently structured south coast frame, it is important to establish any additional or different sensitivities of the model when running under these new conditions. As such, the tests below are run on a version of the model that has been forced to run exclusively in the south coast frame, unless otherwise stated. Where applicable, results from these previous analyses performed on the west coast frame, described by Botha (2012), will be referred to for comparison between west and south coast results. Sensitivity analyses aim to identify additional functionality achieved by the addition of a south coast frame and the sensitivity of the model to additional parameters used in the switching rules for the shift between west and south coast frames. Note that although baseline tests of model function and sensitivity are described in this chapter, further testing of alternate scenarios, e.g. alternate climate scenarios and shifting rules, are found later in this chapter (sections 5.3.3. and 5.3.4.) and tests using spatial fishing are described in Chapter 6

5.3.2.1 Inputs tested

Model sensitivity to the following inputs was tested:

1) Sardine SR curve parameters: various inputs determine the shape of the curve and are used to implement the effects of density dependence and ESI on the sardine population. Parameters tested are: the high and low y-intercepts a1 and a2, used to implement the ESI effect when sardine are in a high frame; and the slope of the curve S_{max} and the inflection point B_{max}, used to implement the density dependent effect when sardine are in a high frame and the ESI effect when sardine are in a low frame. Because S_{min} is equivalent to 50% of $S_{max,}$ it was not explicitly tested. Sardine recruitment variability parameters S_{cor} and σ_r were also tested.
2) Sardine juvenile and adult natural mortality.
3) Automanager settings: the lower threshold below which TAC is set to 0; the upper threshold above which TAC is set proportional to biomass using the TAC slope; the TAC slope; and min. TAC applied between the upper and lower thresholds.
4) Sardine daemon switching thresholds: the biomass thresholds below which and above which the sardine daemon switched from a high frame to a low and a low to a high frame respectively.
5) Sardine daemon fishing pressure threshold: threshold exploitation level above which fishing pressure is classified as 'high', used by the sardine daemon when selecting coastal frame.
6) ESI: variance and period of the ESI on each coast.
7) 'Other coast' population estimate parameters: maximum proportion of total biomass assumed to be on the 'other' coast, maximum interannual variability in the proportion of biomass assumed to be on the other coast

5.3.2.2 Output metrics

Metrics used in previous sensitivity analyses were reused here to allow for comparison and are as follows:

1. Average biomass of sardine and anchovy
2. Average catches
3. Interannual variability in sardine catch (V_{IA}):

   The interannual variability of the sardine catch is of concern to the small pelagic fishing industry, because high year-on-year variability in TACs is not conducive to industry stability and therefore undesirable. Constraints on the degree of change from the previous year's TACs are in place in the OMP used to manage the resource to minimise variability, however these constraints have not been applied to the TAC in this model, and so it is useful to monitor the sensitivity of catch variability to changing input parameters as well as the response of this output to various management strategies applied to the model. As in Botha (2012), an indicator is used to quantify variability in the landings of adult sardine, (V_{IA}), and is calculated as the sum of the interannual variation from the previous year's TAC, over the model run (equation below). To allow the metric to be expressed as a percentage, it is scaled by the maximum possible V_{IA} that can be produced by automanager over a run (V_{IA} max), which is equivalent to a run during which TAC alternates between the minimum (0) and the maximum TAC automanager may set, according to the following equation (Botha 2012):

   $$V_{IA} = \frac{\sum_{y=1}^{k} \sqrt{\left(TAC_y - TAC_{y-1}\right)^2}}{V_{IA}max}$$

4. Frame duration:

   As in the previous model, the amount of time spent by sardine in the high frame is reported, and an additional output monitoring west or south frame behaviour, west frame duration, has been added. The frame duration outputs are both calculated as described in Botha (2012), by calculating the average number of years spent in that frame over the model run. The duration of the last frame the model is in for any particular run is excluded, because there is no way of knowing whether it would have had long or short duration. For example if the west / south frame sequence runs WWWWWSSSWWWWSS, the last sequence, SS, will be excluded from the calculation, unless it is > 10% of the model run length. Only sardine frame duration is monitored because the anchovy frame essentially tracks the ESI signals, but also because anchovy abundance does not appear to have been as affected by the southward shift we are attempting to understand using this model.

Output metrics are presented as the mean over all runs performed, however the median and standard deviation of each were also calculated. Mean and median of all outputs were compared over 1000 runs with automanager set to conservative fishing, to test whether or not any of the output metrics were non-normally/ -unimodally distributed and therefore perhaps not well represented by the mean (Table 5.8). Most were normally or unimodally distributed, although sardine juvenile bycatch, sardine high frame and west frame duration all appear to be slightly skewed to the right. Although differences were small, distributions for the outputs were plotted to verify the use of the mean as representative (Figure 16). All outputs were normally distributed and as such the mean was used as representative for all outputs.

Table 5.8: Differences of the mean from the median of sensitivity analyses outputs, used as a measure of distribution.

	Population		Sardine catch			Anchovy catch		Frame duration	
Output	Sardine	Anchovy	West	South	V/A	Catch	Bycatch*	High	West
mean	598.33	2122.76	101.16	75.75	1714.02	618.23	0.15	0.38	0.57
median	587.45	2121.94	98.59	75.72	1677.88	617.82	0.13	0.35	0.54
% difference	-1.82	-0.04	-2.54	-0.04	-2.11	-0.07	-11.93	-9.51	-4.93

*denotes bycatch of juvenile sardine in anchovy-directed catch

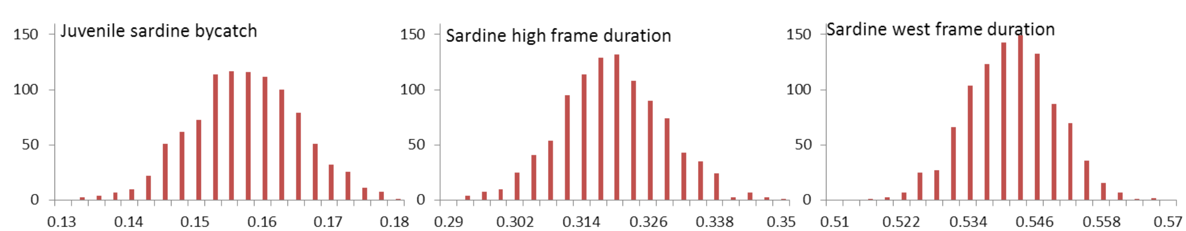


Figure 5.16: frequency distributions for bycatch, high, and west frame duration over 1000 runs.

5.3.2.3 Stochasticity

To take into account the stochasticity built into the model and allow for robust interpretation of outputs, results for analyses are averaged over multiple runs. Before sensitivity analyses were begun a test of the variability of outputs over multiple numbers of runs was performed (Table 5.9). Tests were run using the automanage function set to moderate, and the mean and standard deviation of outputs to be used in sensitivity tests recorded for 10 replicates at 50, 100, 500 and 1000 runs.

Table 5.9: Variability of selected model outputs (percentage runs crashed, sardine high duration, and west frame duration, over increasing numbers of model runs.

Output	**No. runs:**	**50**	**100**	**500**	**1000**
% crash	mean	29.80	34.80	29.54	31.05
	stdev	6.00	3.36	1.91	1.55
Sardine High duration	mean	0.37	0.36	0.38	0.38
	stdev	0.05	0.02	0.01	0.00
Sardine West duration	mean	0.57	0.56	0.57	0.57
	stdev	0.02	0.01	0.00	0.00

The standard deviation of outputs decreases substantially between 100 and 500 runs, and even further by 1000 runs, in some cases to zero. Based on these results we can safely assume that, averaged over 500 or more runs, the effect of the built-in stochasticity has a low impact on the outputs. To eliminate the effects on sensitivity analyses results, the outputs for tests were averaged for 1000 runs.

5.3.2.4 Model set-up for testing

Parameters tested were varied from – 50% to +50% of the baseline value used in the model in steps of 10% of the baseline value. Output metrics were averaged for each individual run and those values averaged over all the repetitions (referred to as reps from here on) performed at that input parameter setting. As discussed above, tests 1 – 4 were run on a model forced to run in the south frame only, to test the functioning of the added model parameters used for the model when in that frame. West coast frame parameters have been previously tested (see Botha, 2012). Tests 5 and 6, dealing with parameters involved with switching rules, were run on the full model with sardine and anchovy switching between west and south frames. Test 7 involving the period and variance parameters of the ESI, was run twice, once on a model forced to the west coast while west coast ESI parameters were altered, and again on a model forced to the south coast while south coast ESI parameters were altered. All tests were run using automanager to implement fishing, set to conservative.

The sensitivity of the model to run length was tested prior to the sensitivity analyses, by altering run length from 25 to 75 years in 5 year increments. Models using a run length of 100 and 125 years were also tested. Using the same criteria as for the sensitivity tests above, the model was only slightly sensitive to changes in run length except when the length was set to 55 (sensitive) and 60 years (moderately sensitive). Because the degree of influence of the ESI period is to some degree determined by the length of a model run, this is to be expected and shows that the model is not sensitive except when the run length is close to, but not more than, twice the length of the ESI period. For runs of shorter length, the two ESI's have not had a chance to become out of sync due to their different periods, so outputs don't vary greatly, and for longer runs the effects of ESI period are smoothed by averaging. Because the purpose of this model is to explore changes in a short-lived species using decadal-scale forcing functions, general model tests and sensitivity analyses are all still run over 50 years, but based on these results any test involving the changing of ESI period was run over 100 years (the longest ESI period tested is 40 years). All tests were run using 1000 replicates.

5.3.2.5 Results

Output metrics were ranked in degree of sensitivity to input parameters from negligible to extremely sensitive. Note that the outputs are ranked based on a sensitivity index calculated as the relative change in output compared with that in the variable being tested - an output categorised as 'negligible effect' or 'slightly sensitive' is still responding to the change in input, but not outside the expected bounds. See Table 5.10 for details of categories. For tests run on a model forced to the south coast frame only, west coast catch, sardine juvenile bycatch (taken in the anchovy fishery, which operates in the west frame only) and west frame duration are not applicable. An overview of the results from sensitivity testing is shown in Table 5.11, and specific results are presented in tables at the end of this section.

Table 5.10: Thresholds for categorising sensitivity of outputs to inputs tested. The sensitivity index is a measure of proportional change in output relative to the change in input, where 1 represents equal change in both.

Category	Sensitivity Index
Negligible effect	< 0.001
Slightly sensitive	0.001 – 0.49
Moderately sensitive	0.5 – 0.99
Sensitive	1 – 1.49
Extremely sensitive	>1.5

Table 5.11: Overview of sensitivity analysis results. Sensitivity to the following inputs was tested in six sets of tests: 1) sardine SR curve parameters - high and low y-intercepts a1 and a2, the slope of the curve S_{max}, the inflection point B_{max}, and recruitment variability S_{cor} and σ_r; 2) sardine juvenile and adult mortality (Juv. and Ad. Mort.); 3) automanage fishing settings including values used for conservative (C), moderate (M) and severe (S) levels of fishing pressure - lower threshold, upper threshold, min. TAC and TAC slope; 4) sardine daemon high-low frame shift thresholds (L-H and H-L); 5) sardine daemon fishing pressure threshold, tested at all fishing intensity levels (C, M and S); and 6) ESI period and variance for each frame (west/south). Model version refers to whether the model was forced to run in only a west or south frame, or whether the full model with shifting between the two was used. Note that bycatch represents juvenile sardine caught in the anchovy-directed catch.

	Parameter tested	Model version	Ave. population		Sardine catch			Anchovy catch		Frame duration	
			Sardine	Anchovy	WC	SC	V_{IA}	WC	Bycatch	H	W
SR curve	a_1	SC	Slightly sens.	Negligible	N/A	Moderately sens.	Moderately sens.	Negligible	N/A	Slightly sens.	N/A
	a_2	SC	Slightly sens.	Negligible	N/A	Moderately sens.	Moderately sens.	Negligible	N/A	Slightly sens.	N/A
	B_{max}	SC	Slightly sens.	Negligible	N/A	Slightly sens.	Slightly sens.	Slightly sens.	N/A	Slightly sens.	N/A
	S_{max}	SC	Slightly sens.	Negligible	N/A	Slightly sens.	Slightly sens.	Slightly sens.	N/A	Slightly sens.	N/A
	S_{cor}	SC	Slightly sens.	Negligible	N/A	Slightly sens.	Slightly sens.	Slightly sens.	N/A	Slightly sens.	N/A
	σ_r	SC	Slightly sens.	Negligible	N/A	Slightly sens.	Moderately sens.	Negligible	N/A	Slightly sens.	N/A
Mort.	Juv.	SC	Moderately sens.	Negligible	N/A	Moderately sens.	Sensitive	Negligible	N/A	Slightly sens.	N/A
	Ad.	SC	Moderately sens.	Negligible	N/A	Slightly sens.	Moderately sens.	Negligible	N/A	Moderately sens.	N/A
Automanager thresholds	Low C	SC	Extremely sens.	Extremely sens.	N/A	Extremely sens.	Extremely sens.	Extremely sens.	N/A	Extremely sens.	N/A
	Low M	SC	Extremely sens.	Extremely sens.	N/A	Extremely sens.	Extremely sens.	Extremely sens.	N/A	Extremely sens.	N/A
	Low S	SC	Extremely sens.	Extremely sens.	N/A	Extremely sens.	Extremely sens.	Extremely sens.	N/A	Extremely sens.	N/A
	Upper C	SC	Slightly sens.	Negligible	N/A	Slightly sens.	Slightly sens.	Negligible	N/A	Slightly sens.	N/A
	Upper M	SC	Slightly sens.	Negligible	N/A	Slightly sens.	Slightly sens.	Negligible	N/A	Slightly sens.	N/A
	Upper S	SC	Slightly sens.	Negligible	N/A	Slightly sens.	Slightly sens.	Slightly sens.	N/A	Slightly sens.	N/A
Automanager TAC	MinTAC C	SC	Slightly sens.	Negligible	N/A	Moderately sens.	Extremely sens.	Negligible	N/A	Slightly sens.	N/A
	MinTAC M	SC	Extremely sens.	Extremely sens.	N/A	Extremely sens.	Extremely sens.	Extremely sens.	N/A	Extremely sens.	N/A
	MinTAC S	SC	Extremely sens.	Extremely sens.	N/A	Extremely sens.	Extremely sens.	Extremely sens.	N/A	Extremely sens.	N/A
	TAC slope C	SC	Slightly sens.	Negligible	N/A	Slightly sens.	Slightly sens.	Slightly sens.	N/A	Slightly sens.	N/A
	TAC slope M	SC	Slightly sens.	Negligible	N/A	Slightly sens.	Slightly sens.	Slightly sens.	N/A	Slightly sens.	N/A
	TAC slope S	SC	Slightly sens.	Negligible	N/A	Slightly sens.	Slightly sens.	Slightly sens.	N/A	Moderately sens.	N/A
Shifting threshold	L-H	SC	Slightly sens.	Negligible	N/A	Slightly sens.	Slightly sens.	Negligible	N/A	Moderately sens.	N/A
	H-L	SC	Slightly sens.	Negligible	N/A	Slightly sens.	Slightly sens.	Slightly sens.	N/A	Moderately sens.	N/A
Fishing pressure threshold	C	FULL	Slightly sens.	Negligible	Slightly sens.	Slightly sens.	Slightly sens.	Negligible	Slightly sens.	Slightly sens.	Slightly sens.
	M	FULL	Slightly sens.	Negligible	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.
	S	FULL	Slightly sens.	Negligible	Slightly sens.	Slightly sens.	Slightly sens.	Negligible	Moderately sens.	Slightly sens.	Slightly sens.
ESI	Variance	WC	Negligible	Negligible	Negligible	N/A	Negligible	Negligible	Negligible	Negligible	N/A
	Period	WC	Slightly sens.	Slightly sens.	Slightly sens.	N/A	Slightly sens.	Slightly sens.	Moderately sens.	Slightly sens.	N/A
	Variance	SC	Slightly sens.	Slightly sens.	N/A	Slightly sens.	Slightly sens.	Negligible	N/A	Slightly sens.	N/A
	Period	SC	Slightly sens.	Slightly sens.	N/A	Slightly sens.	Slightly sens.	Slightly sens.	N/A	Moderately sens.	N/A
'Other coast' pop.	Max. prop	FULL	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.
	Var.	FULL	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.

Negligible | Slightly sens. | Moderately sens. | Sensitive | Extremely sens. | N/A

Test 1: Sardine SR curve parameters:

a. High and low y-intercepts, a1 and a2 (Figures 5.17 a and b):

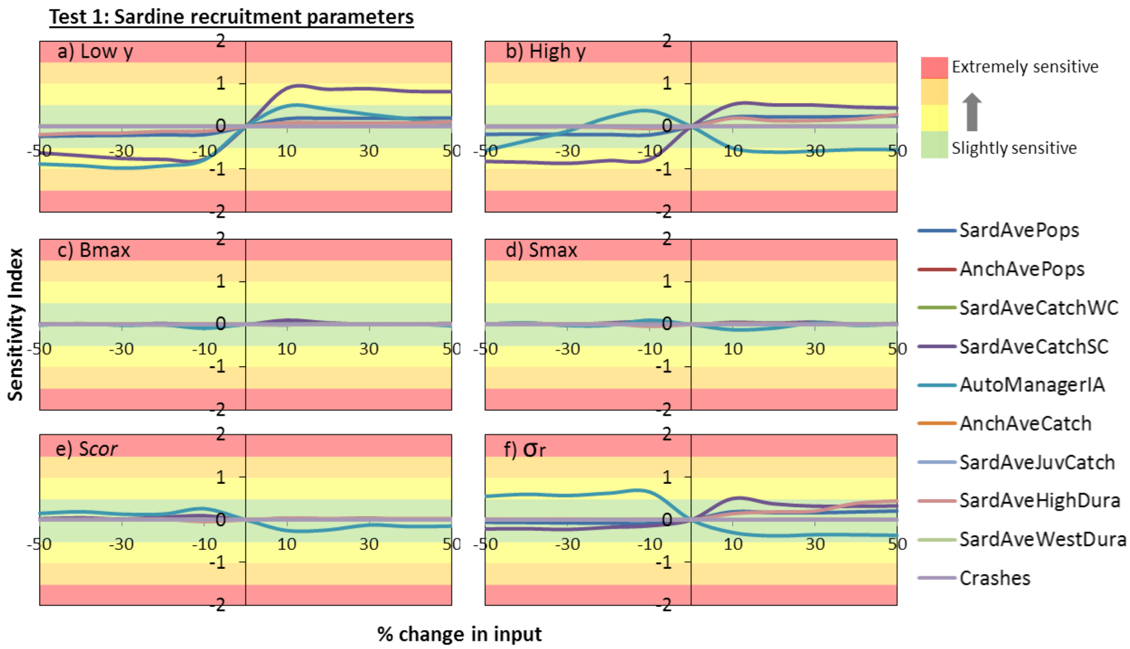
   The model is not particularly sensitive to y-intercept of the SR curve. Sardine catch and catch variability are the most affected because changing the a1 or a2 value results in the sardine population moving further above or below automanager's lower threshold below which TAC is set to 0. This means a higher or lower TAC as you increase or decrease a, and increasingly frequent years in which the TAC alternates between 0 and minTAC, increasing the interannual variability.

b. Slope of the curve S_{max} and the inflection point B_{max} (Figures 5.17 c and d):

   The model is not very sensitive to these parameters, especially when compared to the model in a west coast frame (Botha 2012). This is a result of the shape of the SR curve used for the south coast frame. Because the inflection point of the curve, b, is much lower than in the west frame (14 vs 606), the sardine biomass is > b for the majority of any run in the south frame, limiting the influence of the slope of the curve.

Table 5.12: Abbreviations used for sensitivity test outputs as plotted in Figured 5.17 -21 below.

Abbreviation	Output
SardAvePops	Average sardine biomass
AnchAvePops	Average anchovy biomass
SardAveCatchWC	Average sardine catch on the west coast
SardAveCatchSC	Average sardine catch on the south coast
AutoManagerIA	Interannual variability in sardine catch
AnchAveCatch	Average anchovy catch
SardAveJuvCatch	Average bycatch of juvenile sardine
SardAveHighDura	Years spent by sardine in a high frame
SardAveWestDura	Years spent by sardine in a west frame
Crashes	Proportion of runs in which the sardine population crashed



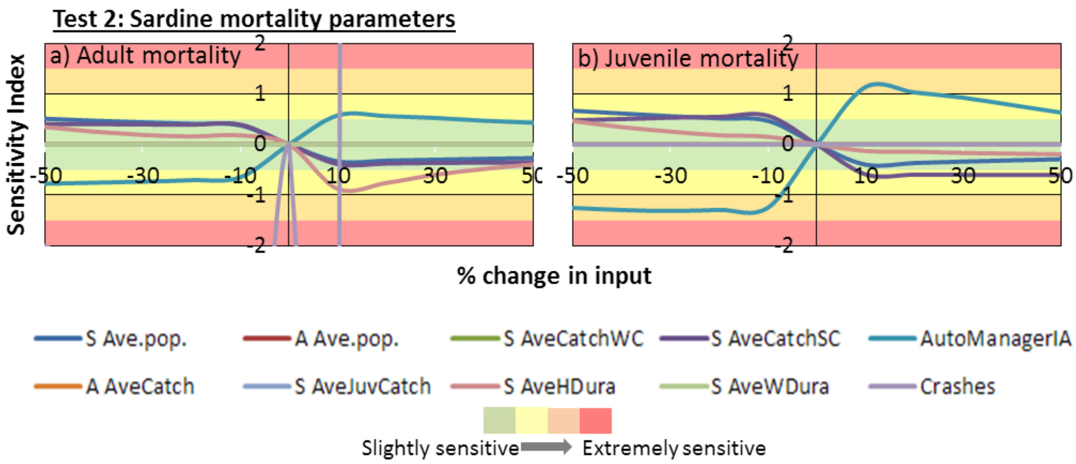
Figures 5.17 a - e: Results of sensitivity analyses of sardine SR curve parameters, where the sensitivity index is a measure of change in output relative to the change in input. Change in parameter tested is shown on the x-axis. See Table 5.12 for key to abbreviations used for plotted outputs.

c. Sardine recruitment variability parameters Scor and σ_r (Figures 5.17 e and f) :

The model is not particularly sensitive to these parameters. V_{IA} shows moderate sensitivity as a result of lower recruitment variability resulting in lower biomass, and increased fluctuation around the lower automanager threshold and a TAC of either 0 or MinTAC, so greater catch variability. The south coast frame is more susceptible to this effect (Botha 2012 show the model is not sensitive in the west frame) as the biomass is on average lower than when in a west frame.

Test 2: Sardine juvenile and adult natural mortality:

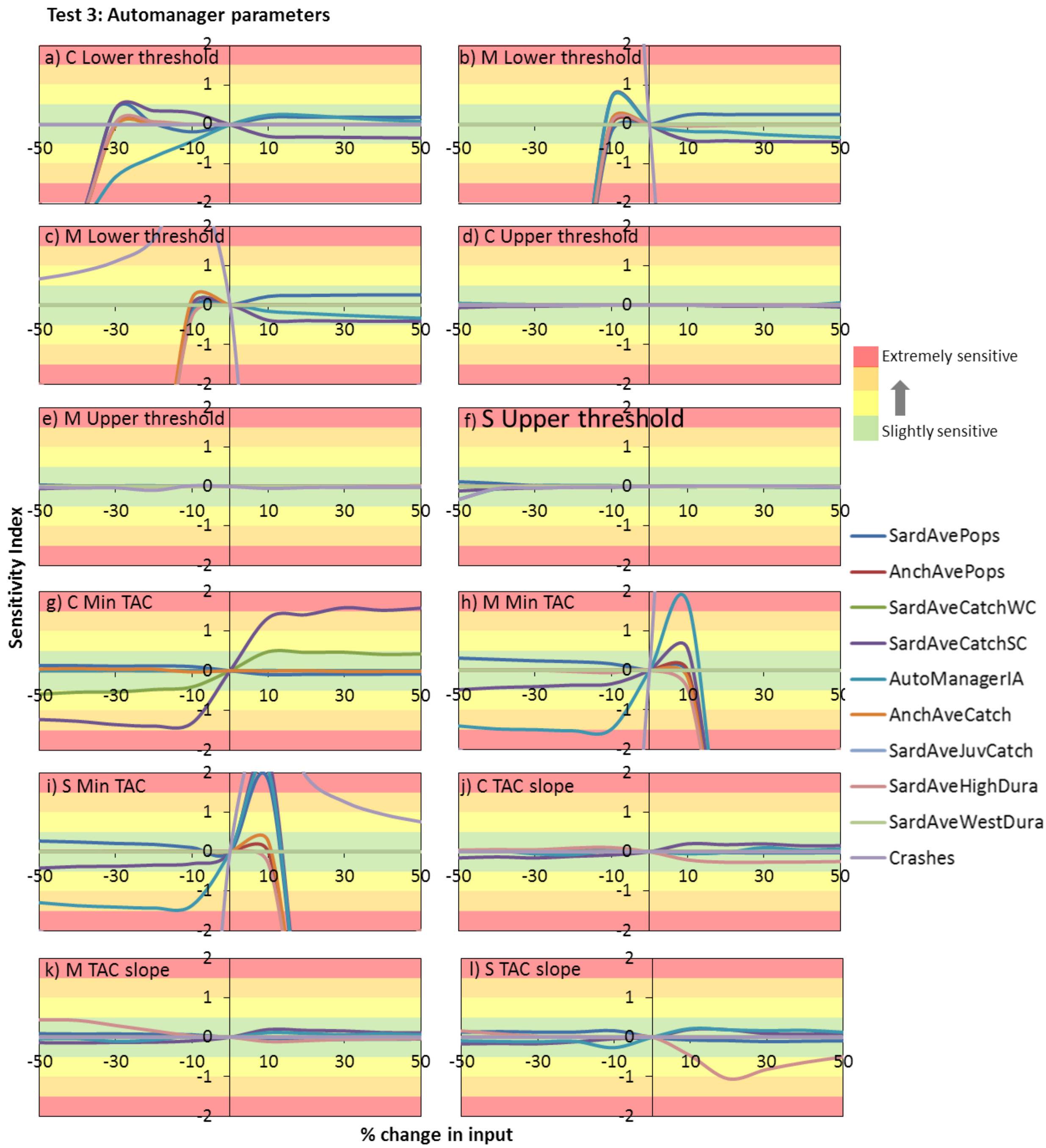
As expected, the model is relatively sensitive to the mortality parameters used. Sensitivity is higher at low values for parameters, except in the case of crash rate which is extremely sensitive to increased levels of adult mortality (Figure 5.18).



Figures 5.18 a and b: Results of sensitivity analyses for sardine mortality parameters. See Table 5.12 for key to abbreviations used for plotted outputs.

Test 3: Automanager settings:

The model is very sensitive to the lower threshold and Min TAC (Figure 5.19 a-c and f-h) and not very sensitive to the upper threshold and TAC slope (Figure 5.19 d-f and j-l). This is because the min TAC and lower threshold are fairly close together; for example for severe fishing, min TAC is 126.5 kt and the lower threshold is 150kt. If the lower threshold or min TAC are decreased or increased respectively at all, it is possible for the TAC to be greater than the population, and sardine will crash very easily. Because the upper threshold and TAC slope are only applied when the population is relatively high, even as their values are changed ±50%, a situation where it becomes possible to fish out the whole population is never created. As expected, for all automanage parameters, sensitivity of outputs increased as the severity of fishing increased from conservative to moderate.

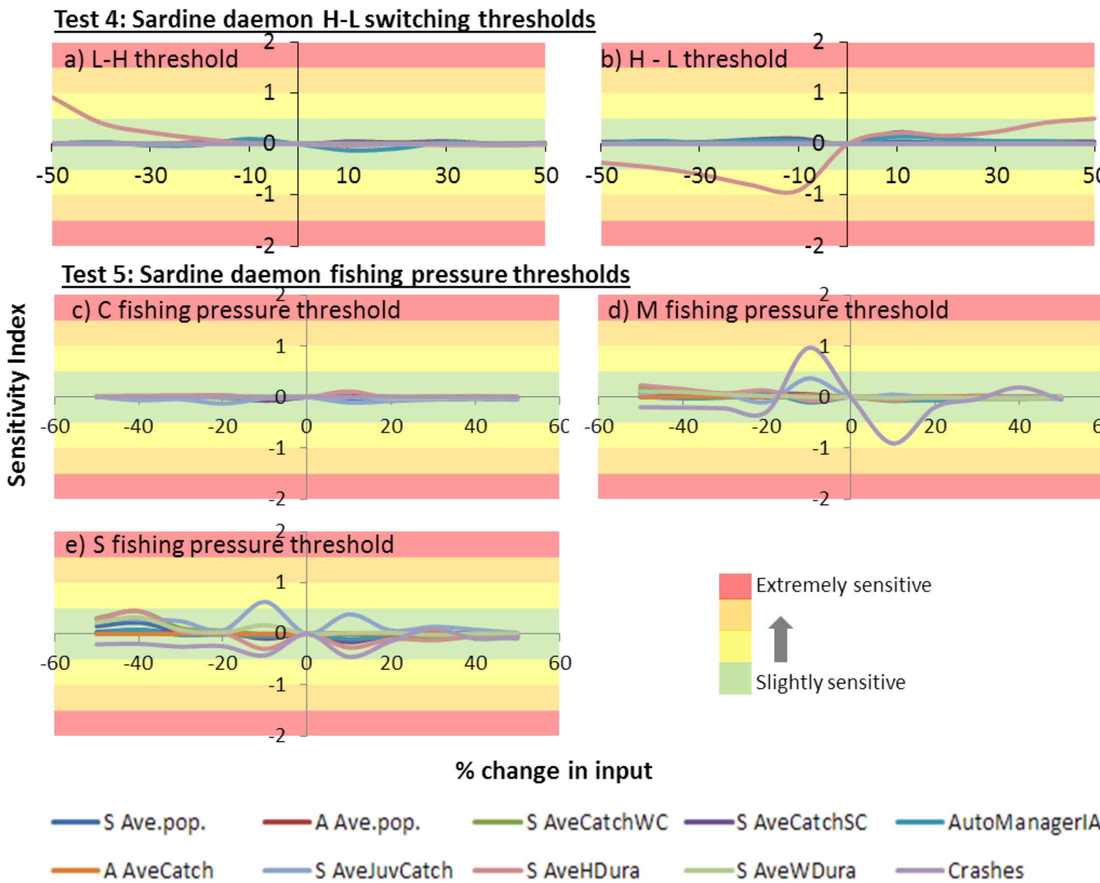


Figures 5.19 a - l: Results of sensitivity analyses for the automanage fishing strategy parameters.

See Table 5.12 for key to abbreviations used for plotted outputs.

Test 4: Sardine daemon switching thresholds:

Changes to these parameters do not have a particularly large effect, with the directly affected output, high frame, being the most sensitive (Figures 5.20 a and b).



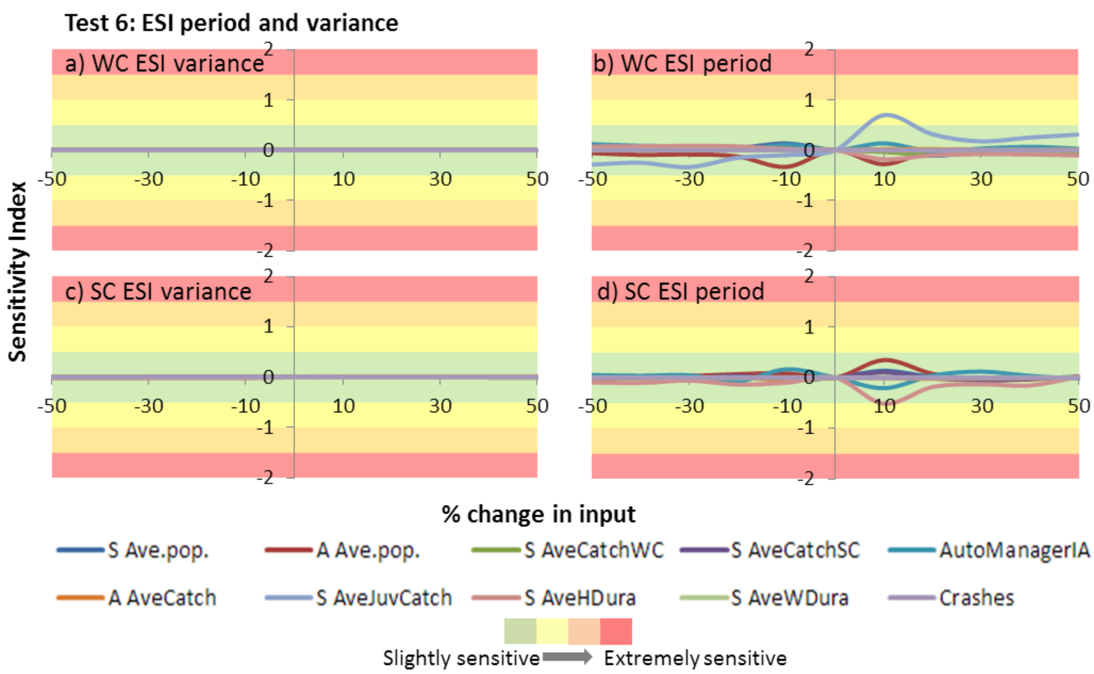
Figures 5.20 a - e: Results of sensitivity analyses for the sardine daemon high – low frame shifting and fishing pressure threshold parameters. See Table 5.12 for key to abbreviations used for plotted outputs.

Test 5: Sardine daemon fishing pressure threshold:

The model is not very sensitive to this parameter (Figures 5.20 c – e). The moderate sensitivity of sardine bycatch is a result of an amplification of the positive effect on west frame duration.

Test 6: ESI variance and period on each coast:

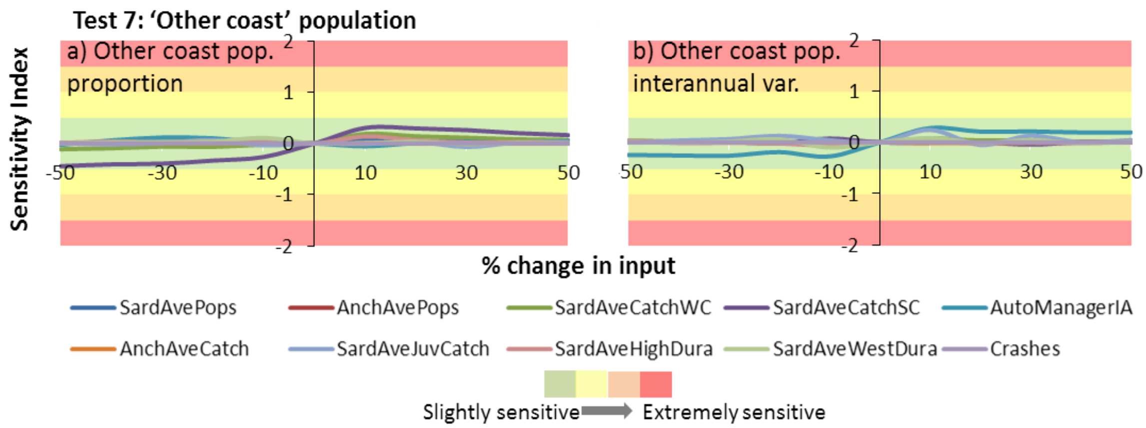
The model is not more sensitive than expected to the ESI parameters (Figures 5.21 a – d). The response of sardine bycatch (S AveJuvCatch in the figure) to period in the west frame is the result of the ESI effect on anchovy, increasing its biomass at a period of baseline + 10% and thus increasing bycatch. Increased sardine biomass also at period baseline + 10% in the south frame caused increased and moderately sensitive high frame duration.



Figures 5.21 a - d: Results of sensitivity analyses for the ESI parameters. See Table 5.12 for key to abbreviations used for plotted outputs.

Test 7: 'Other coast' population parameters:

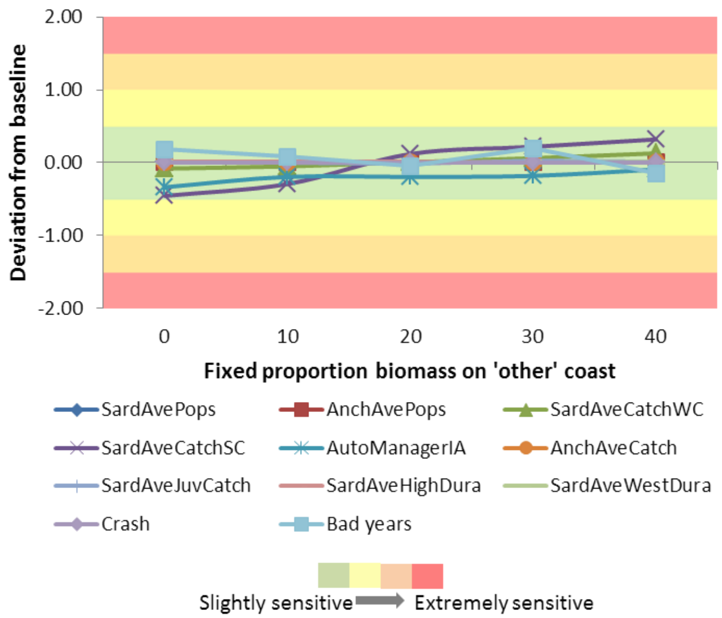
The model was only slightly sensitive to changes in the 'other coast population' parameters, and although parameters were estimated, the values used did not greatly impact model outputs.



Figures 5.22 a - b: Results of sensitivity analyses for the 'other coast' population parameters. See Table 5.12 for key to abbreviations used for plotted outputs.

To further explore the implications of the value used for the proportion of biomass assumed for the 'other' coast (tested in a) above), additional tests were run whereby the proportion of sardine biomass on the 'other' coast was fixed for the duration of a run (i.e. zero interannual variability) and increased in 10% increments from 0% - 40% and the outputs used in sensitivity analyses recorded (Figure 5.23).

The model was not particularly sensitive to changes in the proportion of biomass for the 'other' coast, with the most sensitive parameters being sardine catch on the south coast (SardAveCatchSC) and then interannual catch variability (AutoManagerIA). In both cases the runs using "0%" of biomass for the 'other' coast showed the greatest deviation from the baseline outputs. The changes from baseline values are consistent with the slight increase in proportion of run spent in a west frame at increasing levels of 'other' coast biomass and the fact that over all tests sardine were in a west frame for the majority of the run (~55 – 60%), thus 'SardAveCatchSC' would have been relatively more dependent on the proportion of biomass on the 'other' coast than west coast landings. This variable requires further testing however: because the automanage fishing routine used in this test very seldom results in fishing pressure on either coast being classified as 'high' by the sardine frame-switching daemon, the proportion of biomass on the ‘other’ coast will not greatly affect switching and thus outputs. Effects of alternate proportion on this ‘other coast’ needs to be tested under more variable and higher fishing pressure, and this is described in the following chapter using spatial fishing scenarios, see Chapter Six , scenario 3



Figures 5.23: Change in outputs from baseline values under alternate fixed proportions of biomass on ‘other’ coast.

5.3.3 Testing alternate climate scenarios

The climate function (ESI) used in the model assumes that the periodicity on the south coast is longer than on the west (30 compared to 20 year cycles), and that the effects of the ESI are different on each coast/ in each frame: in the west coast frame, ESI conditions that favour sardine do not favour anchovy, and vice versa; in the south coast frame, conditions that favour one species favour the other as well. These assumptions are based on what has been observed in measured data, but are assumptions none the less. Testing alternate scenarios for how the climate signal on each coast is generated and its influence on the two species will give a better idea of the importance of these assumptions, both in the model and in reality. All tests were run for 100 years for 1000 replicates, using the automanage fishing strategy set to conservative. The following tests were performed:

Test 1: Does the relative starting phase of the ESI's for each coastal frame influence results?

In a normal model run, ESI signals start out in phase with each other, and slowly become out of phase due to the longer period of the south frame ESI (30 years compared to 20 years for the west coast). To test the effect of this on the model, four alternate scenarios were run: west frame ESI was offset by 10% and 50%, while the south frame ESI offset was kept at 0, and then vice versa. This would be expected to influence model outputs, because the relationship between the two ESI's affects the frame transition between west and south, and the ESI on the current coast affects the high / low frame transition.

Results:

As predicted, outputs are affected by starting phase because of the resultant changes is frame duration (Table 5.13). Both sardine high and west frame duration were moderately sensitive, affecting the sardine catch for the west coast and also the bycatch of juvenile sardine, which was extremely sensitive, but only for the test that offset the west coast phase by 10%.

Table 5.13: Sensitivity of the model to changes in relative ESI phase.

% Offset		Ave population		Sardine catch			Anchovy catch		Frame duration	
WC	SC	Sardine	Anchovy	WC	SC	V_{IA}	WC	Bycatch*	H	W
0	10	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Moderately sens.	Slightly sens.
0	50	Slightly sens.	Slightly sens.	Moderately sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Moderately sens.	Slightly sens.
10	0	Slightly sens.	Slightly sens.	Moderately sens.	Slightly sens.	Slightly sens.	Slightly sens.	Extremely sens.	Moderately sens.	Moderately sens.
50	0	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Moderately sens.	Slightly sens.	Slightly sens.

Negligible Slightly sens. Moderately sens. Sensitive Extremely sens.

* represents juvenile sardine caught in the anchovy-directed catch.

Test 2: Does the starting coast for each species during a run affect model outputs?

We assume that both sardine and anchovy start in a west frame in the model, to mimic conditions in the southern Benguela during the 1960s. The effect of alternate assumptions regarding start coast was tested. Changes to start coast would be expected to affect frame duration, given that sardine and anchovy in a west frame are parameterised to be more productive, and that both species will start the model run affected by different ESI conditions than in the baseline model.

Results:

The only output affected was sardine catch interannual variability (Table 5.14), which was moderately sensitive when sardine were started in a south frame. This is in response to the lower population levels that result from increased time spent in a south frame, which place the sardine population close to the lower threshold of the automanager TAC curve. This results in an increased probability of successive years in which the TAC can alternatively be set to the min TAC or 0, hence increased year-on-year variability.

Table 5.14: Sensitivity of model outputs to alternate start coasts for each species.

Start coast		Ave population		Sardine catch			Anchovy catch		Frame duration	
Sardine	Anchovy	Sardine	Anchovy	WC	SC	V_{IA}	WC	Bycatch*	H	W
W	S	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Negligible	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.
S	S	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Moderately sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.
S	W	Slightly sens.	Negligible	Slightly sens.	Slightly sens.	Moderately sens.	Negligible	Slightly sens.	Slightly sens.	Slightly sens.

Negligible Slightly sens. Moderately sens. Sensitive Extremely sens.

* represents juvenile sardine caught in the anchovy-directed catch.

Test 3: Does the period of the ESI for each coast affect the outputs?

Although we are assuming that the period of the west coast ESI is shorter than that of the south coast (20 years compared to 30 years) based on recorded changes in the mean of physical variables (see section 5.2.2.2), it is possible, given the relatively short data series available, that these values will not always reflect conditions in reality. This assumption was tested for both coasts by first setting the periods to 20 years for both, and then increasing one coast's ESI period from 20 to 30 and 40 years while keeping the other constant. Note that the base condition against which outputs are tested for sensitivity is a period of 20 years for the west ESI and 30 years for the south, as used in the model and in all other tests.

Results:

The model was largely insensitive to changes in period, but sardine high frame duration and bycatch/ catch were moderately affected when both periods were set to 20 years, and when the west ESI period was increased to 40 years, respectively (Table 5.15). These are all a result of increased west frame duration during these tests; although the change was not great enough to register as sensitive, it would have resulted in increases in all of the sensitive parameters as well.

Table 5.15: Effects of alternate ESI period combinations.

ESI period		Ave population		Sardine catch			Anchovy catch		Frame duration	
WC	SC	Sardine	Anchovy	WC	SC	V_{IA}	WC	Bycatch*	H	W
20	20	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Moderately sens.	Moderately sens.	Slightly sens.
20	40	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.
30	20	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.
40	20	Slightly sens.	Negligible	Moderately sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Moderately sens.	Slightly sens.

Negligible Slightly sens. Moderately sens. Sensitive Extremely sens.

* represents juvenile sardine caught in the anchovy-directed catch.

Test 4: Relative influence of ESI on fish populations

The impact on model outputs of different assumptions of the relative influence of ESI on sardine and anchovy in each frame were also tested. We assume that opposite conditions are favourable for each on the west coast, but that the same conditions favour both on the south coast. Alternate scenarios were tested in which the same conditions favoured both species, or the opposite conditions favoured each, in various combinations for the two coasts. This assumption should impact the daemons when 'deciding' to which frame to switch, and also the degree to which both species are found in the same frame.

Results:

Changing the ESI effects does impact frame duration as expected, but not to the degree that it registers as sensitive (Table 5:16). Sardine bycatch is moderately sensitive when the effects on both coasts are set to equal however, as a result of the positive change in sardine west frame duration during this test.

Table 5.16: Alternate ESI effects on sardine and anchovy for each coast.

ESI effects		Ave population		Sardine catch			Anchovy catch		Frame duration	
WC	SC	Sardine	Anchovy	WC	SC	V_{IA}	WC	Bycatch*	H	W
same	same	Slightly sens.	Negligible	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Moderately sens.	Slightly sens.	Slightly sens.
same	opposite	Slightly sens.	Negligible	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.
opposite	opposite	Slightly sens.	Negligible	Slightly sens.	Slightly sens.	Negligible	Slightly sens.	Slightly sens.	Slightly sens.	Slightly sens.

Negligible Slightly sens. Moderately sens. Sensitive Extremely sens.

* represents juvenile sardine caught in the anchovy-directed catch.

5.3.4 Alternate shifting scenarios

The model is highly dependent on the rules dictating when the model shifts (or does not) from one frame to another. In the interests of further exploring the implications of the current shifting rules, a number of alternate rule scenarios (within the bounds of the assumed drivers, fishing pressure and environment) were tested.

Test 1: What effect do alternate shifting rules have on model outputs?

West/ south frame shifting rules for sardine within the model operate as follows:

The environmental suitability index (ESI) of the current coast is first evaluated by the daemon. If it is 'good', there is no shift, if it is 'bad', both the ESI and the fishing pressure on the other coast are evaluated. If both are favourable, a shift occurs. If neither is, no shift occurs. If one variable is favourable and the other is not, there is a 50/50 probability of a shift occurring. Here alternate rules for when a shift between a west and a south frame occurs for sardine were tested:

I. Only fishing pressure is considered

II. Only ESI is considered

In both of the above cases, the current coast was first evaluated. If it was found favourable, no shift occurred. If not, the other coast was evaluated and either a shift occurred if it was favourable, or there was a 50/50 probability of a shift occurring if not.

III. Under conditions when a probability of a shift occurring is the outcome, the probability is high (80/20)

IV. Under conditions when a probability of a shift occurring is the outcome, the probability is low (20/80)

Results:

The model was not sensitive to the alternate shifting rules under test conditions except for the rules using only fishing pressure to determine a shift (Figure 5.24) – in this case sardine biomass, sardine catch on the west coast, years 'bad' for predators, and high and west frame duration all registered as moderately sensitive – sensitive. This is to be expected, because under the automanage fishing scenario used for tests, the way in which TAC is calculated means that fishing pressure very seldom registers as 'high', particularly at conservative fishing levels, and thus ESI is expected to be the main influence over shifts in the baseline model. As a result the 'fishing only' rule set resulted in zero shifts occurring (100% residence in a west frame over runs). Further testing of alternate rules under increasing fishing pressure needs to be carried out, and this is done in the following chapter where spatial fishing scenarios are tested (see Chapter Six, scenario four). The probability of shift rules only comes into play when the 'other' coast is classified as either combinations of a suitable ESI and high fishing pressure, or an unsuitable ESI and low fishing pressure. Thus for the same reasons this decision is taken less often under automanage fishing given that fishing pressure is seldom high. As a result changes to the probabilities used to determine a shift (i.e. 'likely' – 80/20 or 'unlikely' – 20/80 vs the 50/50 used in the baseline model) did not have strong effects on model outputs under these conditions.

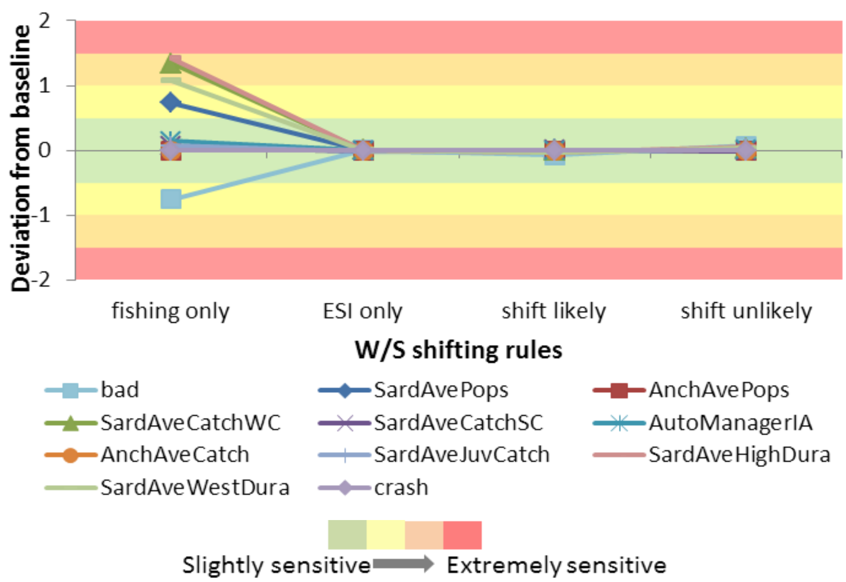


Figure 5.24: Change in outputs from baseline values for alternate west/ south frame shifting rules: only fishing pressure influences shifts; only environmental signal (ESI) influences shifts; where a probability of a shift occurs, a shift is likely; and where a probability of a shift occurs, a shift is unlikely.

Test 2: What effect do alternate minimum years between shifts have on model outputs?

Currently the model is restricted in the maximum frequency of shifts with a minimum of 3 years between shifts. This is to deal with the possibility of unrealistic rapid shifting that can occur under these rules in years when the 50/50 probability of a shift rule is invoked for consecutive years. The decision to restrict shifting in this manner was based on data on changes in spawning location for sardine over time which suggest shifts on the timescale of 3 - 7 years (van der Lingen et al. 2006a), which equates to roughly one to two generations. The implications of this decision to set a minimum time between shifts were tested as follows: minimum years between shifts were set to 0, 5, 7 and 10 years, and outputs compared to those for a 3 year minimum (baseline value used in model).

Results:

The model was not particularly sensitive to alternate minimum years between shifts, and changes in outputs were greatest at increased years between (highest under the 7 year restriction) and show the detrimental effects on sardine of being forced to remain in an unfavourable frame (Figure 5.25): increased bad years for predators (total biomass < 1/3 of long term maximum biomass) and a decrease in catches under the 5 – 10 year restrictions were the strongest responses. No restriction on switching (i.e. '0' years) resulted in similar outputs to the baseline model (3 year restriction), strengthening the case for use of this restriction which prevents unrealistic year to year switching but doesn't have a significant impact on outputs. This test is further explored in Chapter Six, scenario five, under increasing fishing pressure and spatial fishing scenarios.

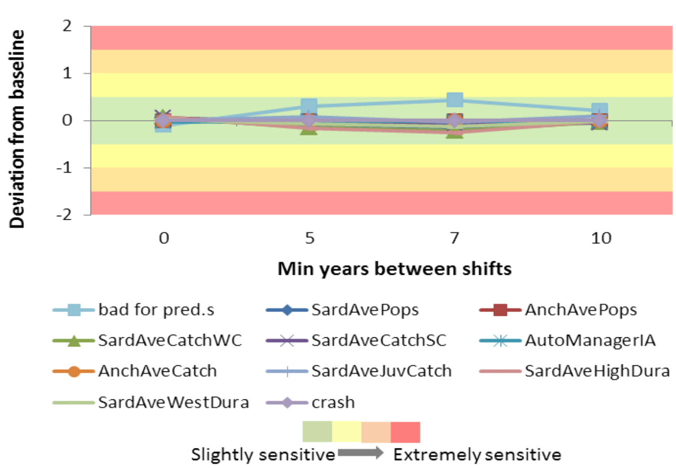


Figure 5.25: Change in outputs from baseline values under alternate minimum years between shifts.

5.4. Summary

The model appears to function as expected within the specifications laid out during construction. Sensitivity analyses show that model function is sensitive to the addition of a south coast frame and to changes in the switching rules for the shift between west and south frames. Sardine recruitment is affected by ESI in all frames, and both sardine recruitment and anchovy population levels are affected by changes between west and south frames. Effects implemented for sardine in a south frame (density dependence and fishing mortality) have the expected impact on outputs, and fishing pressure does drive shifts between west and south frames.

In a south frame, the model was not particularly sensitive to sardine recruitment parameters, but does show sensitivity to mortality parameters. The highest degree of sensitivity to parameters tested was to automanage fishing strategy parameters, specifically to the lower threshold and MinTAC values. There was a low degree of sensitivity to high – low switching thresholds and fishing pressure thresholds for sardine. Sensitivity was also low to most ESI parameters, although the model was moderately sensitive to the *periods* of ESI used to represent the long-term variability on west and south coasts.

This moderate sensitivity to the periods, and hence relative phase of the ESI signals for each coast, occurs because of the implications for frame duration. Some moderate sensitivity to the start coast used for each species and the period used for the west and south ESIs was also shown, but assuming different implications for sardine and anchovy in terms of ESI (i.e. conditions are 'good' for both species or have opposite effects on each) had little effect in terms of model sensitivity. It needs to be remembered that there is an effect when these parameters are changed, but according to the criteria adopted in section 5.3.2.5 the change does not classify as 'sensitive', i.e. it not highly non-linear. This lack of sensitivity is likely also due to a general lack of sensitivity of the very simple anchovy population model used to changes within the model as a whole, as shown in the alternative climate scenarios in this chapter, and explained further in Chapter Six.

The assumptions made regarding the proportion of biomass assumed to be found on the 'other' coast in any year and the interannual variability in this proportion (Figures 1 and 2) did not influence model outputs to any large degree (never classified as more than 'slightly' sensitive), and are accepted as reasonable for the purposes of this model.

The decision to limit switching between west and south frames to a maximum of once every three years was based on the observed frequency of shifts in the spawning location of sardine in the southern Benguela (van der Lingen et al. 2006a), and is also a way of incorporating a degree of natal homing effect, also suspected of playing a role in the eastward shift in the late 1990s (Coetzee et al. 2008a). While the model was sensitive to the increased the minimum number of years between shifts, it was not sensitive when shifting was not restricted (i.e. the min. years set to 0). The use of a 3 year limit to shifting in the baseline model is thus defensible in that it results in a more realistic representation of shifting by preventing year on year shifting back and forth, without unduly influencing outputs.

Exploration of alternate switching rules is an important step given the degree to which these rules determine model functionality. The incorporation of an environmental signal and then fishing pressure as drivers fits with the current understanding of the mechanisms behind observed shifts (Coetzee et al. 2008a), albeit in a simplified structure in keeping with the minimum realistic approach. Neither ESI nor fishing alone can be (nor are they) assumed to drive frame shifts alone. The alternate rule scenarios tested here (Figures 5 and 6) affirm that the current rule set provides satisfactory results within the constraints of the model and given current understanding of processes involved: fishing pressure alone as a driver does not result in realistic model behaviour. Given that fishing pressure was not and is not always likely to be what was classified here as 'conservative', further testing of rules under alternate fishing scenarios is necessary, and is reported in the following chapter. Nonetheless this rule set (using fishing pressure alone as a driver) is rejected as far as functioning of the baseline model goes.

The 'ESI only' rule set, as well as the alternate probabilities of shift sets, produced results very similar to that of the baseline model. This raises the question as to whether the inclusion of fishing pressure in the rules adds anything to the model. Again, this is related to the "conservative" fishing routine applied, which seldom triggers the rules relating to fishing pressure. Further testing of alternate rules under increased fishing pressure and spatial fishing, where outputs under the 'ESI only' rule set would then be expected to deviate more if the inclusion of fishing pressure in the switching rules is of significance, is described in the following chapter.

A frame-based modelling approach is potentially useful when applied to the situation of changing distributions of small pelagic fish. Overall, results from alternate climate scenario tests seem to indicate that the relative environmental conditions on the two coasts have an important effect on the spatial distribution of sardine. The incorporation of environment via a simplified proxy such as ESI remains an adequate solution, keeping model complexity relatively low while remaining a reasonable representation of physical forcing. If the link between small pelagic variability and environment becomes better understood in the future, this proxy could be easily adjusted to incorporate new information. Sensitivity analyses and model testing suggest that future research should focus on this area. Increasing our understanding and ability to monitor these conditions is important if we are to increase our potential to predict shifts or impacts of previous shifts. This is particularly true of our understanding of the effects of relative conditions on both coasts, if we are to begin to understand potential future changes in distribution and system dynamics.

While this chapter focuses on the construction of the model and its functionality, the ability of the model to describe and explore the dynamics of sardine and anchovy is further explored and discussed in Chapter Six.

CHAPTER SIX
FURTHER MODEL SCENARIOS - EFFECTS OF SPATIALISED FISHING PRESSURE

6.1. Introduction

Chapter Five describes various levels of testing applied to the model as a check of functionality and behaviour, as well as of model sensitivity to inputs. Here some scenarios are run to exercise the model and test the model outcomes under various 'what if?' questions, selected based on their relevance to topics in the generation of current management advice.

One of the consequences of the change in sardine distribution and increased biomass on the south coast versus the west is highlighted by Coetzee et al. (2008): Given the role the fishery may have played in the initial change in distribution, and the persistence of sardine on the south coast since, two pertinent questions are: what may the effects of a spatialised fishing strategy have been prior to the late 1990s when sardine were largely on the west coast, or in west coast mode, and how might those effects differ now that the majority of the biomass is on the south coast/ in south coast mode? These questions are addressed within the model during the first two scenarios examined below.

Despite the large contributions anchovy make to the fish biomass in the southern Benguela and to the landings of the small pelagic fishery, their role in structuring the ecosystem is still not fully understood. Although single species models are used with some success under the OMP's designed for the management of sardine and anchovy directed fishery in the southern Benguela (de Oliveira & Butterworth 2004; de Moor et al. 2011), the influence of environmental variability and the implications of the previously unobserved high biomasses on the south coast are not known to the degree that they can be included in these models. Increased biomass of anchovy may mean increased predation on sardine eggs, influencing sardine biomass recovery, as well as increased prey availability for species such as redeye. In light of their continued high biomass since 2000 (Shabangu et al. 2012), it has become even more important to better understand the potential influence of anchovy on the system. As discussed in Chapter Five, it was assumed when constructing this model that conditions on the south coast were less favourable to both sardine and anchovy. Since the change in 1996 to a more easterly distribution however, anchovy biomass has increased and remained high, and it seems possible that the south coast may actually provide favourable conditions for adult anchovy. This possibility is explored within the model environment under Scenario three below.

The ‘Individual’ fishing strategy developed in this thesis and built into the model was structured specifically to try to address some of the more pressing questions relating to spatialised fishing in the management of the sardine-directed fishery at the moment in the context of the model. By allowing the user to select via a ‘spatial strategy’ whether fishing pressure is directed at the west or south coast (‘max. west’ or ‘max south’), or rather to split the TAC according to the current distribution of sardine (‘dynamic tracking’), the implications of each fishing strategy can be explored in the model environment. To recap (for initial description see Chapter Five section 5.2.2.3), under the ‘max. west’ strategy for example, the maximum possible proportion of the assigned TAC is taken from the west coast. This means that when sardine are in a west frame (and thus the majority of the biomass is on the west coast), 100% of the TAC is taken from the west coast. If sardine are in a south frame, as much of the TAC as possible is still taken from the west coast (now represented by the ‘other coast’ population, see Chapter Five section 5.2.2.1), and any remainder of the TAC is taken from the south coast. The ‘max. south’ strategy operates in the same way but directs the TAC preferentially to the south coast. The ‘dynamic tracking’ strategy splits the TAC according to the current distribution of biomass, for example if sardine are in a west frame with 90% of the total biomass on the west and the remaining 10% on the south (represented by the estimated ‘other coast’ population), 90% of the TAC will be directed towards the west coast and 10% to the south.

Given that spatial management is a possibility for the sardine-directed fishery, testing the effects of each fishing strategy in the scenarios mentioned above may provide some useful insight into the potential implications of applying (or not applying) a spatial approach. At the least, the model should be a useful tool for illustrating some potential outcomes given the various assumptions used to construct the model.

6.2. Methods

Scenario 1: Effects of spatial fishing in the model

The first scenario is to explore what effect the different spatial strategies have on model outputs. Assuming, as suggested by Coetzee et al. (2008a), that increased pressure on the west coast contributed to the relative increase in biomass on the south coast in the late 1990s and since, and given the design of the rules governing switching for sardine, the 'max. west' and 'max. south' strategies should result in increased residency of sardine in south and west frames respectively, which would in turn affect model outputs such as total population based on the differences in productivity of sardine on each coast. The 'dynamic tracking' strategy should have little to no effect on west and south frame residency which should be driven rather by ESI because the dynamic strategy should not result in high fishing pressure on either coast. All scenarios are run over 100 years, to avoid any potential influence of ESI fluctuations. The individual fishing strategy was used, and model outputs over different spatial strategies and levels of fishing pressure compared. A TAC of 10%, 20% and 30% of total biomass was applied to both sardine and anchovy in three separate tests, and the outputs for each were averaged over 1000 runs.

Scenario 2: Effects of spatial fishing when sardine are in a south frame

Sardine do not appear to be as productive on the south coast as they are on the west, given the low recruitment observed since the early 2000s when biomass has been primarily located on the south coast (de Moor & Butterworth 2012; Shabangu et al. 2012). As a result, and given that fishing is thought to play a role in their distribution (Coetzee et al. 2008a) there is some concern as to whether any particular fishing strategy would be more or less likely to result in an increased biomass on the more productive west coast. In this scenario the effects of the possible fishing strategies in the model were tested with sardine starting out in a south frame and the strategies resulting in the most rapid return to a west frame identified. Given the shifting rules and that high fishing pressure on the south coast is most likely to arise during the 'max. south' strategy, this strategy would be expected to result in the quickest or most frequent shifting of sardine back into a west frame. This scenario was tested using a model configuration in which sardine are forced into a south frame for the first 15 years of a 100 year run.

Scenario 3: Alternate fixed proportions of biomass on the 'other' coast under spatial fishing scenarios and increasing fishing pressure

In an expansion of test 7 in section 5.2.3.5., the alternate fixed proportions of biomass on the 'other' coast described there are further tested under the spatial fishing scenarios used in scenarios 1 and 2 here. All scenarios are run over 100 years, to avoid any potential of ESI fluctuations. The individual fishing strategy was used, and model outputs over different spatial strategies and levels of fishing pressure compared. A TAC of 10%, 20% and 30% of total biomass was applied to both sardine and anchovy in three separate tests, and the outputs for each were averaged over 1000 runs. Model outputs are expected to be sensitive to changes under spatial fishing, as lower or higher biomasses on the 'other' coast will affect whether the sardine daemon evaluates fishing pressure on that coast as 'low' or 'high' and thus is likely to affect shifting.

Scenario 4: Alternate shifting rules under spatial fishing scenarios and increasing fishing pressure

In an expansion of test 1 in section 5.2.4., the alternate shifting rules described there are further tested under the spatial fishing scenarios used in scenarios 1 and 2 here. As described above, all scenarios are run over 100 years and the individual fishing strategy was used at TACs of 10%, 20% and 30% and using dynamic tracking, max. west and max. south spatial fishing strategies. As in section 5.2.4., the alternate rules tested were as follows:

I. Only fishing pressure is considered
II. Only ESI is considered

   In both of the above cases, the current coast was first evaluated. If it was found favourable, no shift occurred. If not, the other coast was evaluated and either a shift occurred if it was favourable, or there was a 50/50 probability of a shift occurring if not.

III. Under conditions when a probability of a shift occurring is the outcome, the probability is high (80/20)
IV. Under conditions when a probability of a shift occurring is the outcome, the probability is low (20/80)

Scenario 5: Alternate minimum years between shifts under spatial fishing scenarios and increasing fishing pressure

As in scenario 3, test 2 in section 5.2.4. addressing alternate minimum number of years between shifts, is expanded here. The min. years between shifts was set to 0, 5, 7 and 10 and model outputs under the spatial fishing scenarios used in the scenarios above compared with those of the baseline model.

Scenario 6: Positive effect of a south frame on anchovy

Based on previous observations and theory on the structure and functioning of the south coast / shelf-based system, as has been discussed it was predicted that both sardine and anchovy would be less productive there than when on the west coast. This however may not be the case, given that anchovy biomass is currently higher than it was before the 1996 change in proportional abundance. This scenario tests the implications of increased production for anchovy in a south frame, rather than lower productivity as previously assumed, for model outputs. Tests were run on a model version parameterised to allow increased recruitment success for anchovy in a south frame. Recruitment parameters used are shown in Table 6.1. The assumption that variability is higher in a south frame is retained, and as in the standard model, variability is set at half of the high frame mid-point.

Table 6.1: Recruitment parameters for anchovy used for each frame, with the altered parameters used during Scenario 3 in the south frame below in grey.

	Anchovy Frame	**Midpoint**	**Variability**
Standard	West coast High	3000	± 1500
Standard	West coast Low	1500	± 750
Standard	South coast High	2000	± 1500
Standard	South coast Low	1000	± 1500
Scen. 3	South coast High	3000	± 2000
Scen. 3	South coast Low	1500	± 1500

As for Scenario 1 low, medium and high TACs (10%, 20 % and 30% of total biomass) were applied to both sardine and anchovy for each spatial fishing strategy (dynamic, max. west and max. south), and the outputs for each were averaged over 1000 runs of 100 years. Results were compared with those from the standard model in Scenario 1.

6.3. Results

Scenario 1

As expected, Scenario 1 tests show that the spatial strategy chosen does affect model outputs. Figures 6.1 and 6.3 show example runs under the 'max. west' and 'max. south' fishing strategies, where sardine have shifted away from the coast that is experiencing the higher fishing pressure: for example under 'max. west' fishing, sardine spend the majority of the run in a south frame, with implications for productivity. Change in selected outputs for each strategy over the different fishing pressures are shown in figures 6.3 a - g. Somewhat counterintuitively from a historic fisheries management perspective, 'max. south' appears to be the strategy that resulted in increased residency time in west and high frames, maximising both the biomass and catch of sardine as a result (discussed further in section 6.4 below). Note that under this strategy although the majority of the catch is taken from the south coast, some is still taken from the west, and this proportion increases with increasing pressure (see WC catch, Figure 6.3 a). Crash rate under this strategy also benefits and remains close to zero even at high levels of fishing pressure. The interannual variability of the catch is the highest under this strategy however (figure 6.3 g). Surprisingly, the 'dynamic tracking' strategy, where the TAC is split according to the division of biomass west and south, performed the worst both in terms of total yield and sustainability, resulting in relatively high crash rates at 30% TAC (151/1000). Predictably this strategy did not affect west/ south frame residency, however high frame duration did decline over time. Although the 'max. west' strategy appears more sustainable than the dynamic tracking approach, with fewer crashes under high fishing pressure, it resulted in the lowest population levels and total catch due to low catch returns on the south coast, and increased time spent in a south frame (Figure 6.3). Catch variability under dynamic tracking and 'max. west' strategies was similar.

With regards to testing the use of low fish biomass as an indicator of food availability to top predators, the system state indicator fell below the threshold of 1/3 of the longterm maximum increasingly with increasing fishing pressure under all strategies (Figure 6.3h). Under both 'max. west' and 'max. south' strategies, the difference in number of bad years per run was greatest from low to medium pressure, when compared with medium – high pressure. Under the ‘max. west’ strategy particularly, the number of ‘bad’ years per run almost doubled under medium pressure when compared with low. Leading on from the results discussed above, the number of ‘bad’ years for top predators was highest under the ‘max. west’ strategy and lowest under ‘max. south’ as a result of those strategies leading to increased time in the less productive south frame and more productive west frame respectively (discussed further in section 6.4).

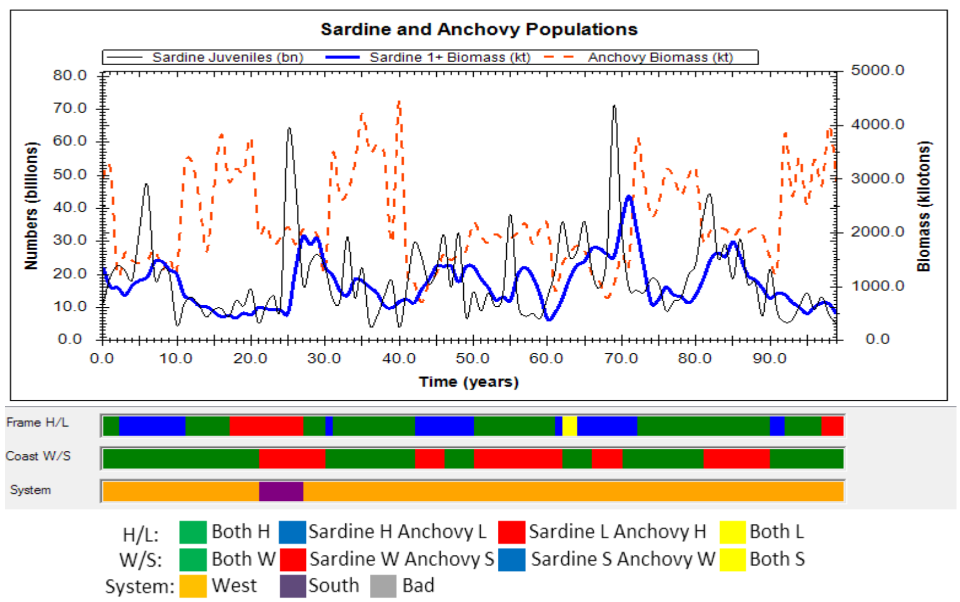


Figure 6.1: Example of a run in which ‘max. south’ and anchovy fishing were applied with a TAC of 30%. The first bar below shows sardine are in a high frame (green or blue) for the majority of the run, and the second bar shows sardine remaing in a west frame (green or red) for the entire run. The third shows that the system was in ‘west mode’ (i.e. majority of forage fish biomass is on the west coast) for most of the run.

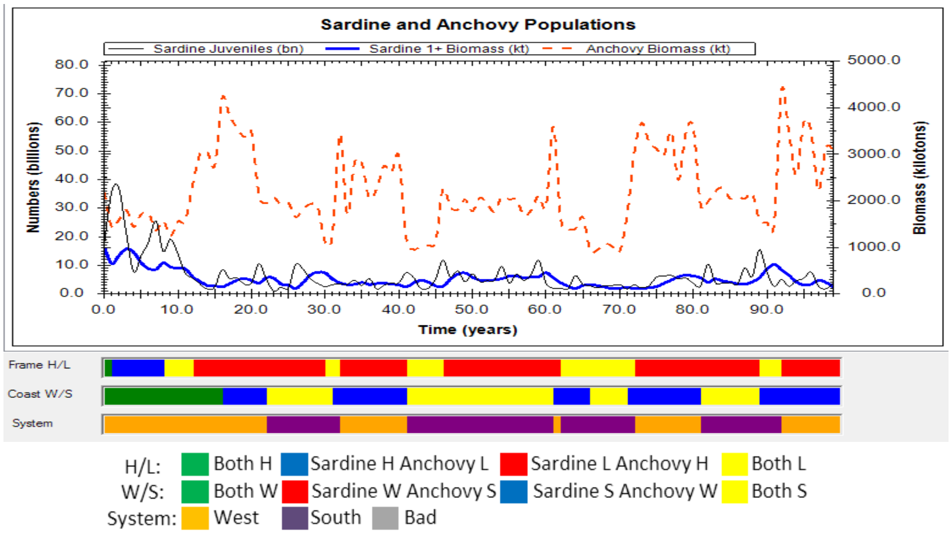
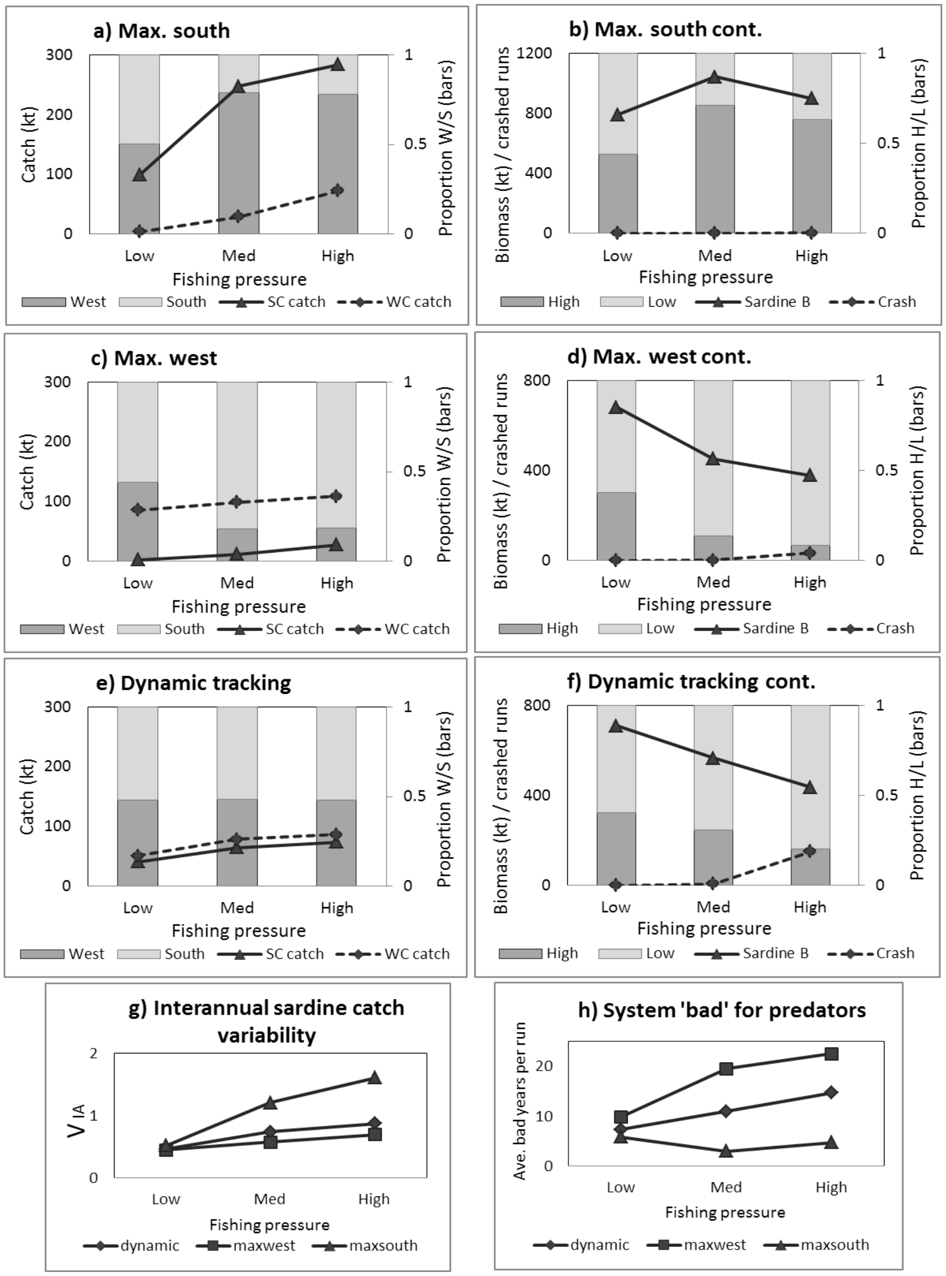


Figure 6.2: Example of a run in which ‘max. west’ and anchovy fishing were applied with a TAC of 30%. The first bar below shows sardine in a low frame (yellow or red) for the majority of the run and the second shows sardine shifting after 15 years from west (green) to south (blue or yellow) for the remainder of the run. The third shows that the system was in both west and south modes over the run.



Figures 6.3 a - h: Selected outputs for sardine in Scenario 1 over different spatial fishing strategies (dynamic tracking, maximum catch from the west coast, and maximum catch from the south coast). Low, medium and high TACs were applied. For each strategy the first plot shows the proportion of the run spent in a west or south frame with the catch from each coast, and the second shows the proportion in high or low frame with the sardine biomass and number of runs crashed. The last figures show the interannual variability of the sardine catch, and the numbers of years on which the system state is classified as 'bad' for each strategy at increasing fishing pressure respectively.

Scenario 2

When the model was run with no fishing, sardine remained on the south coast 15 to 25 years after they were allowed to shift (note sardine were forced to the south coast for the first 15 years) – i.e. sardine first moved to a west frame no earlier than 30 years and no later than 40 years into the run over 50 runs of 100 years each (see Table 6.2). When 'max. west' fishing was applied, although the earliest shift remained at 30 years, but at 10% TAC the latest shift moved to 60 years into the run, and at 20 and 30 % TACs in some runs sardine never shifted west (see example runs in Figure 6.4). When a dynamic fishing strategy was applied there was no real difference between the timing of the earliest and latest shift and the runs performed with no fishing across any levels of fishing pressure. The 'max. south' strategy at 20% and 30% fishing pressure were the only ones to change the timing of the earliest shift, which moved forward to 15 years. The latest shifts for those levels of fishing were also earlier, at approximately 32 years into the run.

Table 6.2: Timing of shifts to a west frame in a model where sardine were forced into a south frame the first 15 years of a 100 year run. Earliest and latest occurrences of a shift were recorded over 50 runs.

		west shift	
Fishing	**% TAC**	**earliest**	**latest**
None	0	30	40
MaxWest	10	30	60
	20	30	never
	30	31	never
Dynamic	10	30	40
	20	30	40
	30	30	40
MaxSouth	10	30	40
	20	15	32
	30	15	32

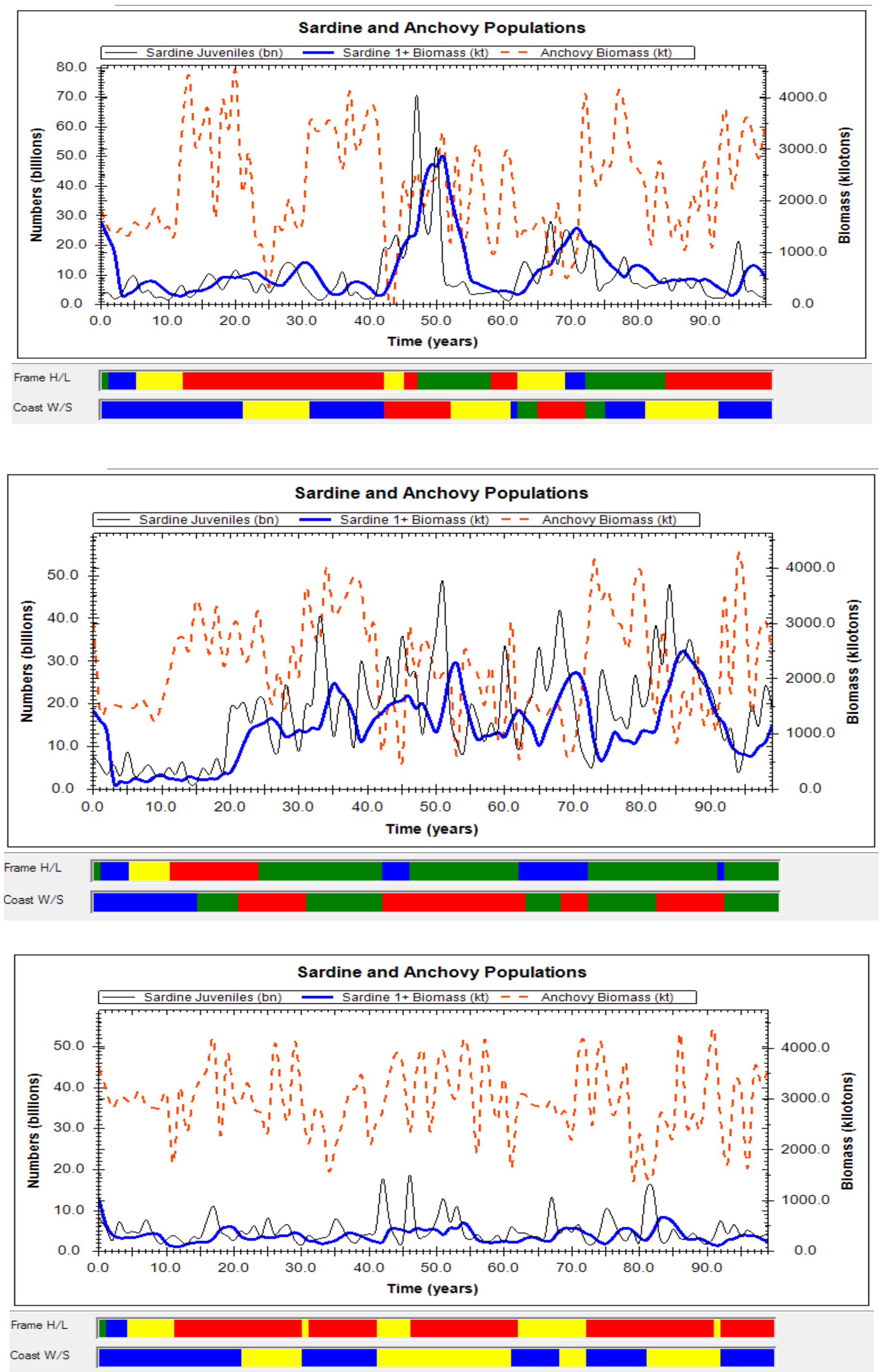


Figure 6.4: Model runs in which sardine have been forced to a south frame for the first 15 years. The top panel shows an example of a run in which zero fishing was applied, and the second and third show runs in which 'max. south' and 'max. west' fishing with TACs of 20% were applied respectively. In the first, sardine shift between south (second bar, yellow or blue) and west (green or red), while in the middle panel sardine shift west and remain there after 15 years. Sardine remain in a south frame the entire run in the lower panel.

Scenario 3

While model outputs were only slightly sensitive to alternate proportions of biomass on the ‘other’ coast under the dynamic tracking fishing strategy, as expected, multiple outputs were sensitive to extremely sensitive under the max. west and max. south strategies, notably sardine catch, frame duration , the indicator bad years for predators, and crash rate. Effects were particularly strong where the ‘other’ coast population was set to 0, At 0 % of biomass, the ‘other’ coast population is likely to experience ‘high’ fishing pressure if any fishing is directed at it under low max. west and south fishing strategies (where F is not proportional to biomass), making the coast frame unlikely to shift to this ‘other’ coast. For example under max. west fishing, as shown in scenario 1, the model is most likely to be in a south frame, making the west coast the ‘other’ coast. The added effect of forcing this population to be zero is that fishing pressure on the west coast almost always registers as ‘high’, thus the model is even more unlikely to shift back into a west frame than in the baseline model, residence in a south frame is increased, and thus so does catch on the south coast. Likewise, under max. south fishing with 0% biomass on the ‘other’ coast, the model spends more time in a west frame, and west coast catch is increased (Figure 6.5). This effect on catch is less pronounced under higher fishing pressures (20% and 30%) due to the baseline model already experiencing this effect (the other coast often evaluates as experiencing ‘high’ pressure, which it doesn’t at low/10% fishing pressure unless the ‘other’ coast population is very low). This increased time spent in a less productive south frame under max. west fishing at 0% ‘other’ coast biomass also resulted in the increased in crashed runs under higher fishing pressures.

At higher proportions of biomass on the ‘other coast (30% or 40%), catches were also affected, but due to the population available to be caught rather than to a change in frame residence time. Under max. west fishing for example, as discussed under scenario 1 the majority of the run is spent in a south frame, making the west coast more likely to be the ‘other’ coast. Because the max. west fishing strategy dictates that the TAC is directed first at the west coast and the remainder taken from the south regardless of current frame, when the west coast is the ‘other’ coast, and the ‘other’ coast population is relatively high, west coast catches increase, and likewise under a max. south strategy south coast catches increase (Figure 6.5). Crash rates were likewise sensitive to higher ‘other’ coast populations under max. west, because the TAC is calculated as a percentage of total biomass, including the ‘other’ coast population, thus a higher overall TAC is set but fishing is still targeted at the now proportionally smaller (than if the ‘other’ coast pop made up only 10% of the total) modelled population on the west coast. Under max. west fishing, juvenile sardine are also being caught, which is not the case on the south coast (see Chapter Five section 5.2.2.3.), adding to the pressure and resulting in a higher crash rate. This effect is not evident under a max. south strategy because overall population levels are higher due to the majority of the run being spent in the more productive west frame.

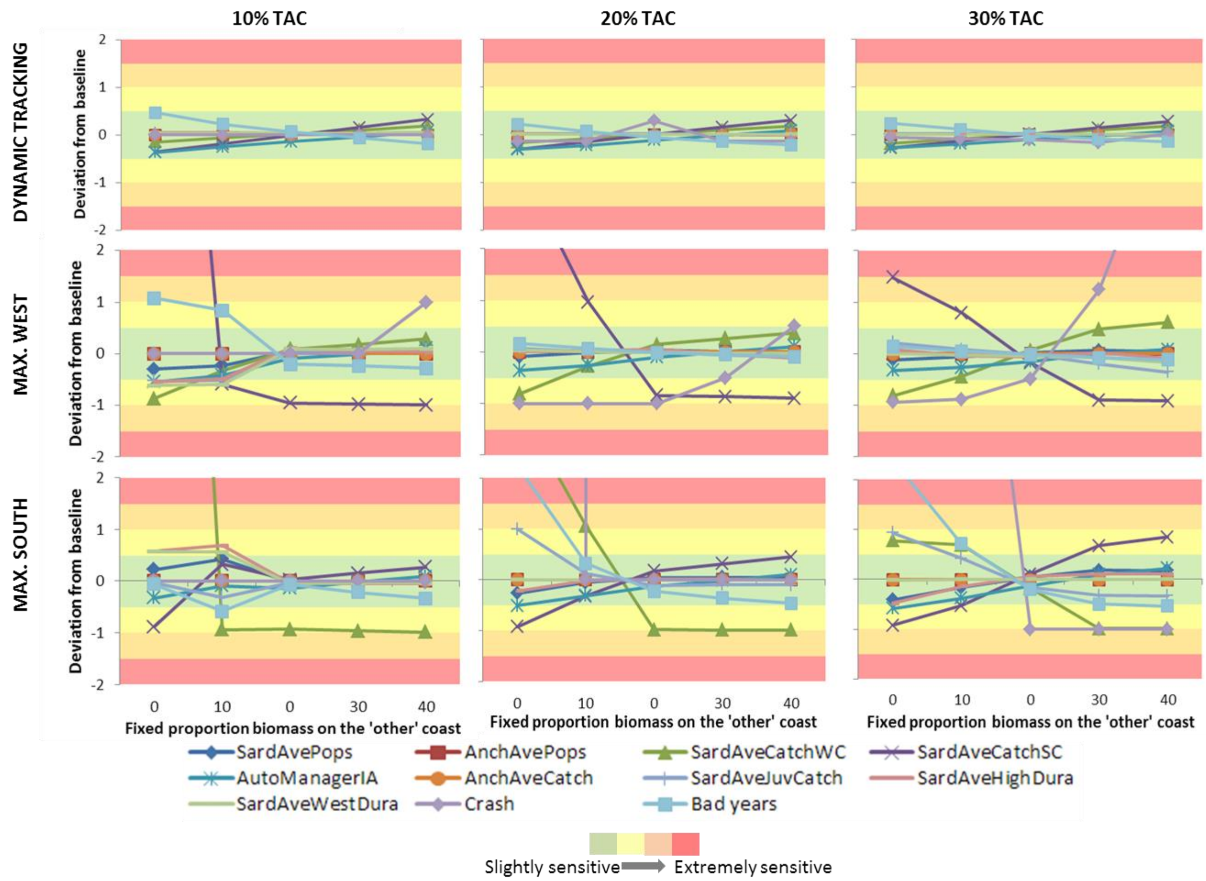


Figure 6.6: Change in outputs from baseline values for alternate fixed proportions of biomass on the 'other' coast under spatial fishing scenarios ('dynamic tracking' allows effort to track fish location, 'max. west' and 'max. south' focus effort on the west and south coast respectively) and at TAC's of 10%. 20% and 30% of biomass.

Scenario 4

At low levels of fishing pressure, outputs across all fishing strategies were only slightly sensitive to changes in switching rules (Figure 6.6). More effects are visible at 20% and 30% TACs, however overall only crash rate and years bad for predators are strongly affected. As in Test 2b, the moderate sensitivity of crash rate under 'max. west' fishing with 20% TAC as well as extreme sensitivity under 'max. south' 30% TAC, reflect relatively small changes in real rather than relative terms – in the first instance a change from a baseline rate of 2/1000 to 0/1000 in the 'ESI' and '80/20' tests, and in the second from a baseline rate of 1/1000 to 4/1000 in the 'Fishing' and 0/1000 in the 'ESI' and '80/20' tests. In this case the use of a relative measure as a sensitivity index produces an overstated result, when in reality the outputs were not particularly sensitive. The system state indicator of bad years for predators was however sensitive under the 'fishing' rule scenario for 'max. south' 20% and30% TAC, and crash rate was moderately sensitive under the same scenario ('fishing') for 'max. west' 30% TAC.

Overall, as one would expect, the model under spatial fishing was most sensitive to the switching rule scenario where only fishing pressure influences shifts. Outputs were also somewhat sensitive to the rules which resulted in increased probability of a shift (80/20), as visible in the deviation from zero for this test under 'max. west ' and 'max. south ' fishing – although outputs were still only classified as 'slightly sensitive'. These changes in output reflect the slight increase in the amount of time spent by sardine in a high frame under these rules, as one would expect if a move away from unfavourable conditions is more likely.

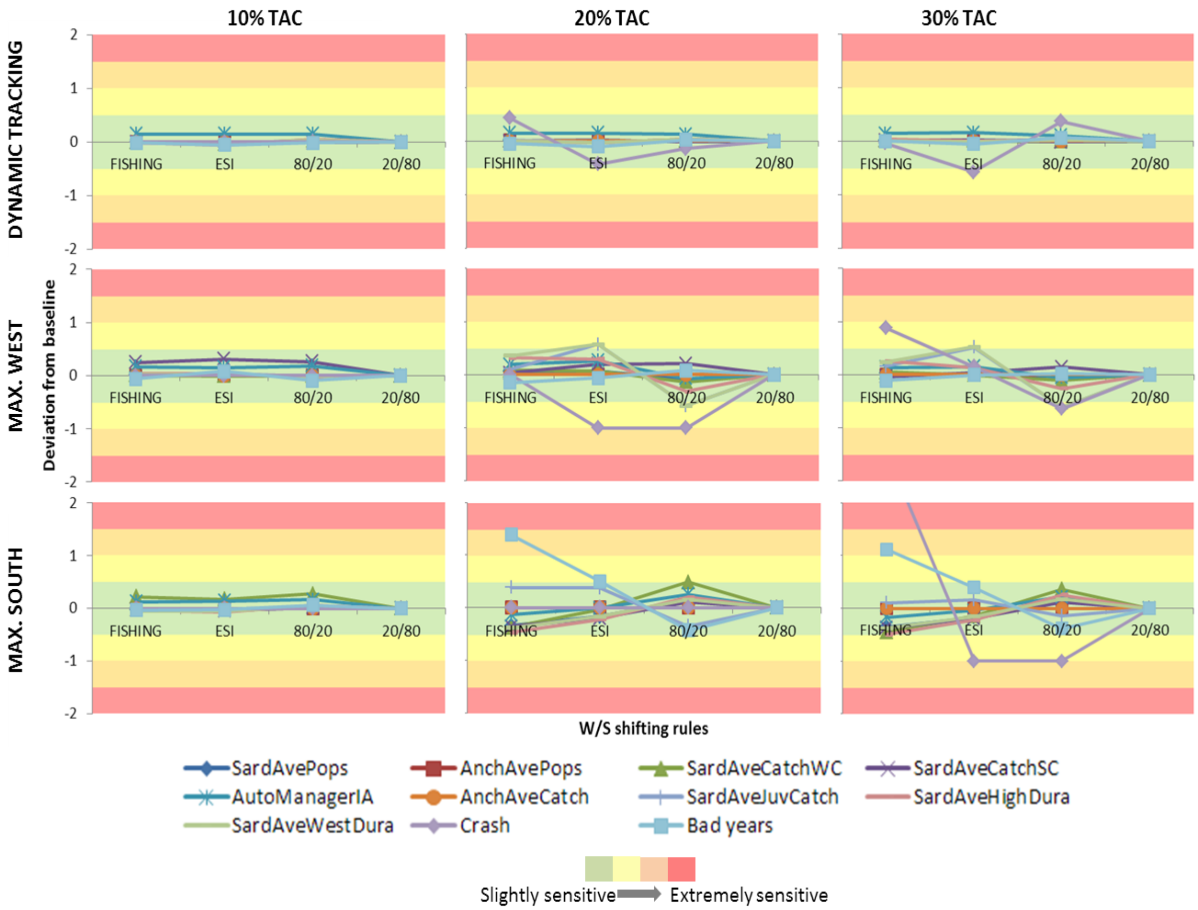


Figure 6.6: Change in outputs from baseline values for alternate west/ south frame shifting rules (only fishing pressure influences shifts; only environmental signal (ESI) influences shifts; where a probability of a shift occurs, a shift is likely; and where a probability of a shift occurs, a shift is unlikely), under spatial fishing scenarios ('dynamic tracking' allows effort to track fish location, 'max. west' and 'max. south' focus effort on the west and south coast respectively) and at TAC's of 10%. 20% and 30% of biomass.

Scenario 5

Under spatial fishing pressure the effects on outputs using alternate minimum years between shifts were similar to those shown in the previous test using automanage fishing (section 5.2.4, test 2 and Figure 6.7 here), with an increase in the number of years flagged as bad for predators, particularly at the lowest TAC (10%). This output was not as sensitive at higher TAC levels, with the added effect of fishing pressure at 20% and 30% TAC outweighing that of the increased years between shifts (i.e. 'bad' years were already relatively higher in the baseline model under these TACs), At these levels of fishing pressure however the number of crashed runs became extremely sensitive to the min. years between shifts, and was the only output variable that registered as anything more than 'slightly sensitive'. Again, this was a response to the increasingly negative effects of being forced to remain in an unfavourable frame at high fishing pressures. It should be noted that while the model crashes register as extremely sensitive under the 'Max. south' strategy at 30% TAC, showing a relative change from baseline of up to 200%, the actual crash rate only varied between 1 and 3/1000.

Sardine were most vulnerable to crashing under the 'Max. west' scenario. This fits with earlier findings showing that this strategy results in increased time spent by sardine in the less productive south frame (as shown in these results as well, with west frame duration decreasing at higher TACs), where high fishing pressure is more likely to lead to crashes. As in the previous test, outputs were on average not more than slightly sensitive to changes in the min. years between shifts, with the exception of crash rate and the indicator 'bad years' for predators to a lesser degree. Effects were minimal when there was no restriction on shifting (0 years), supporting the use of the baseline restriction of three years between shifts as means of increasing realism without greatly impacting outputs.

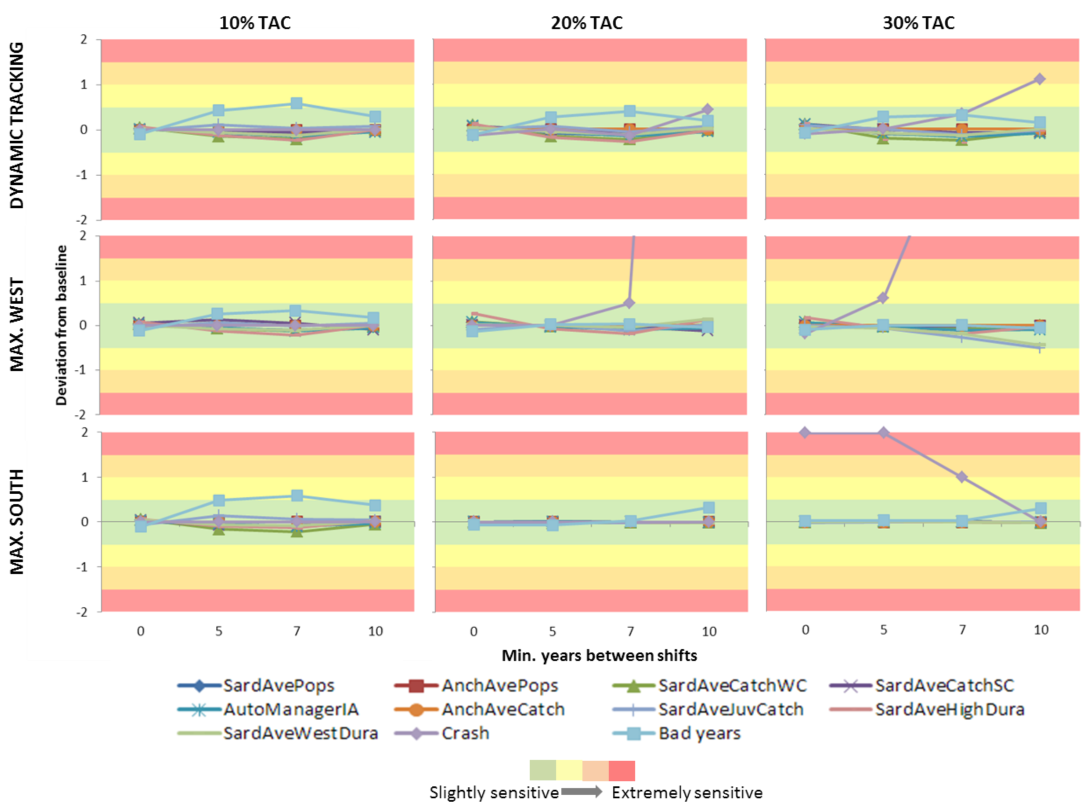


Figure 6.7: Change in outputs from baseline values for alternate minimum years between shifts under spatial fishing scenarios ('dynamic tracking' allows effort to track fish location, 'max. west' and 'max. south' focus effort on the west and south coast respectively) at TAC's of 10%. 20% and 30% of biomass.

Scenario 6

Assuming that the south coast is actually beneficial for anchovy rather than making them less productive does not affect model outputs more than expected beyond anchovy biomass and catch (Table 6.3). The only other output that changed more than 3% from the standard model outputs was crash rate, although these are actually reflecting very minor changes – tests that have no or very few crashes in the standard model reflect a high percentage change when the crash rate changes by only one or two points (e.g. the 28.6% change under 20% dynamic fishing reflects a change from 7/1000 – 9/1000 crashes, and the 100% changes are from 1/1000 to 2/1000).

Table 6.3: Percentage change in model outputs when the south frame is beneficial for anchovy rather than decreasing their productivity as in the standard model (Scenario 5) when compared with the standard model.

		Biomass		Sardine catch				Anchovy catch	Sardine frame duration		Crash
Strategy	**% TAC**	**Sardine**	**Anchovy**	**WC**	**SC**	**V IA**	**Bycatch**	**WC**	**High**	**West**	**rate**
dynamic	**10**	-0.9	34.6	-1.3	-0.9	-1.8	-0.7	34.8	-1.9	-0.5	0.0
	20	0.5	35.0	0.9	0.6	0.9	2.9	35.1	0.2	0.7	28.6
	30	0.6	34.7	0.7	1.0	-0.1	1.0	34.9	2.5	0.2	-1.3
maxwest	**10**	-0.5	34.6	-0.4	-2.2	0.3	-0.1	34.9	-0.6	-0.5	0.0
	20	0.4	34.4	0.2	1.0	0.3	-0.2	34.7	0.9	0.9	-100.0
	30	-0.3	34.0	-0.5	0.3	-0.2	-1.7	34.7	0.6	-2.0	-12.1
maxsouth	**10**	0.5	34.7	-0.7	0.7	0.7	-0.1	34.8	1.1	0.7	0.0
	20	0.1	34.4	1.2	0.0	0.8	-0.5	34.7	-0.4	-0.1	0.0
	30	0.9	34.0	0.1	1.2	0.9	2.4	34.4	0.6	0.2	-100.0

6.4. Discussion

The main factor behind the differences in outputs under different fishing strategies (Scenario 1) relates to west or south frame switching and duration. Most of the changes can be traced back to the fact that increased time in a west frame/ west coast mode increases productivity, while increased time in a south frame/ south coast mode means lower productivity. For example, the 'max. south' strategy results in more time spent by sardine in a west frame: fishing pressure on the south coast will more often than not be classified as 'high' making it less likely for the sardine daemon to shift south and more likely to shift west. This in turn results in higher, west coast based sardine biomass under a 'max. south' strategy, increased high frame residency, a higher total catch and a lower chance of falling below the threshold below which the system is classified as 'bad' for predators (in terms of forage fish availability).

Counterintuitively, catches are highest on the south coast under 'max. south' fishing. This is because of the overall increase in biomass induced when sardine are in a west frame where, as discussed above, they are more likely to be under the 'max. south' strategy. As discussed in Chapter Five, the current frame is assumed to be the location of only the *majority* of biomass, and the 'other' coast population – the south population when sardine are in a west frame, for example - is modelled simply as a proportion of that explicitly modelled biomass (see Chapter Five section 2.2.1 for details). As a result, when the modelled biomass is high, so is that of the 'other' coast population given their proportional relationship. For example in this case because sardine are in a west frame and the modelled population is high, the estimated and proportional 'other' (or south coast) population from which the south coast catch is taken is also higher than normal. This results in a high south coast catch even though sardine are in a west frame.

Conversely, when a 'max. west' strategy is applied, sardine are more likely to be in a south frame. This results in lower productivity. Consequently, biomass and catches from both coasts during those runs are also relatively low, and the system is more likely to be limiting ('bad') for predators.

Interannual catch variability may be higher during 'max. south' runs due to the increased influence of the 'other' coast catches in those runs, which are in turn correlated with the fluctuating minority population on that 'other' coast.

Another unexpected result is that the 'dynamic tracking' strategy had the highest crash rates. This can be explained by the fact that the TAC is set as a percentage of the total biomass, rather than just the biomass modelled on the dominant coast. Because dynamic tracking splits the TAC according to biomass distribution, this means that both coasts are always experiencing the specified fishing pressure.If this is not strictly conservative, it will lead to increasing crashes. For example, 'max west' fishing tends to drive sardine to the south frame, but the fishing pressure remains directed at the west coast. This means the part of the population on the 'other' (in this case west) coast will generally be subjected to a substantial proportion of the TAC before any fishing pressure is placed on the sardine in the south frame, making the likelihood of crashing lower.

The system state indicator included in the model is useful in that it allows an interpretation of the implications of fishing strategies within the model for seabirds, which is based on quantitative results. Although the indicator is generalised, it does allow for a link between small pelagic fish and top predators. It also adds some depth to the discussion of the implications of spatial fishing strategies within the context of an EAF by providing a link between fishing on lower trophic level species and top predators.

Within the model, heavy fishing focusing on the west coast (and resulting in increased residence of sardine in the south frame) leads to more years in which forage fish are too low to sustain seabird populations. Again this is due to the sardine productivity being lower in the south frame. If this is the case, it lends further weight to the question of whether spatialised fishing pressure has a role to play, in the real world, in increasing the biomass of sardine on the west coast, where they are more accessible to both the fishery infrastructure and seabird predators. This is particularly relevant for birds such as penguins, which are restricted in their breeding habitat, and less able to adapt to change in prey distribution.

As expected, and as suggested by the results of Scenario 1 testing, model results imply that the fishing strategy applied has a significant impact on whether or not sardine ever move back into a west frame from a south frame. In the absence of fishing pressure, the environmental signal drives a shift to the west at some point, but given focused pressure on one coast or the other, the shift may be hastened or prevented entirely. This has implications for distributions and productivity, impacting both the fishery and dependent predators.

The sensitivity of the model to changes in the proportion of biomass found on the 'other' coast under spatial fishing places further emphasis on the need to investigate spatial management of the small pelagic fisheries. Decisions in this regard may strongly influence the shift or lack thereof of sardine from a west to a south frame or vice versa. This sensitivity reflects what is suspected to have occurred in the early 2000s on the west coast, where fishing remained directed at the west coast despite the majority of biomass shifting to the south (Coetzee et al. 2008a), and which may have prevented a complete shift back to the west since.

Although the results under alternate switching rules tested (Figure 6.5) do not suggest changes be made to the baseline model, they do highlight the need to better understand how the relative environmental suitability of each coast affects whether or not a shift occurs, similar to results from tests in Chapter Five. Given that the biggest determinant of outputs is the current frame, this factor – shift or no shift – ultimately determines the productivity of a stock. If shifts away from unfavourable condition are more or less likely either directly, due to probability settings in the model, or because of relative conditions on each coast, this can mean the difference between a crash and a stable, productive stock. Increased understanding of this interaction in the real world should be a priority.

Although whether or not the environment on the south coast is beneficial to anchovy definitely warrants further investigation, for reasons previously discussed the focus of the development of this model has been on sardine. As a result the model is not particularly sensitive to changes in anchovy productivity (see also Chapter Five section 5.4), and in its current iteration is not well suited to answering questions in that regard.

The bycatch of juvenile sardine in anchovy catches does influence the model sardine population. Sardine bycatch is related to the proportion of anchovy catch. Therefore, sardine bycatch is not affected by changes in anchovy population but only by an increase in the proportion of anchovy caught. In further development of this FBM, the anchovy population model should distinguish anchovy recruits from adults, and also refine the anchovy fishery.

The design of the ESI within the model is also currently quite simplistic, although it is functional. It assumes that completely disparate conditions are favourable for sardine and anchovy (or, in testing, that suitable conditions completely overlap), and that what is unfavourable for one is favourable for the other. This excludes conditions that are unfavourable for both and the possibility of some overlap in the range of suitable environmental states. This area also warrants further attention in view of the expected climate change.

While the current approach of using coupled single-species stock assessment models to manage sardine and anchovy fisheries in the southern Benguela is successful in terms of short-term prediction and the output of specific and quantifiable assessments of risk, it is not well suited to addressing more long-term changes in conditions, or variability in productivity over time (e.g., Fréon et al. 2005; Jarre et al. 2006). Given that no approach at this time can be assumed to take into account all relevant variables, considering multiple modelling techniques when attempting to answer management problems is the only way to achieve a more well-rounded understanding of the issues at hand. The model described here could in no way be used in the capacity of a stock assessment model for tactical management recommendations, since it is not designed in this way. It can and does provide insight unavailable from that approach in terms of the possible system-level implications of various management strategies. The assumptions made when designing the switching rules for this model should however be kept at the forefront when considering model outcomes, given that by determining frame (west or south) they heavily influence results. Nonetheless, a FBM does add to the overall understanding of in terms of overall system stability related to strategic management choices. The system state indicator is a useful addition to the toolkit of quantitative indicators.

The advantages of using a FBM approach are that the model structure is well-suited to represent regime shifts such as those observed in the system; the model assumes the same stock structure as used in the current OMP – that of a single stocks whose main distribution shifts around the coast; and it is readily modified further along with increased understanding of the processes in the real world.

Although a FBM does require the proportion of biomass on the ‘other’ coast to be estimated within the model, this estimate can be based on observed proportions on each coast. Tests showed that the corresponding model assumptions (i.e. proportion of and variability in biomass on the ‘other’ coast) did not affect outputs greatly. Outputs were only affected notably when the model system was subjected to spatial fishing pressure, as thought to be the case in reality.

Outputs of a FBM are by definition highly dependent on the rules used to drive shifts. While the current rules are based on the best available information to date, our understanding of the relative importance of fishing pressure and environmental signal remains fairly crude. When this understanding improves, it will be straightforward to change the model in line with the improved understanding.

The spatial fishing scenarios tested here allow for useful exploration of potential outcomes based on various candidate strategies. Although a spatial model may produce similar results, the clearly defined breaks that are inherent in a FBM as shifts occur are particularly useful in the context of regime shifts. These breaks or shifts also make for clearer interpretation, allowing for the simplification of a complex situation.

On the other hand a spatial model would represent the hypothesised two-stock structure previously discussed, with no need to estimate biomass on the other coast. The two stock hypothesis however has so far not been supported by genetic data (Hampton 2014). Additionally an estimate would still need to be made; this time of the degree of mixing between the two stocks, and based on what is currently very limited knowledge.

Although a spatial model could certainly add to the toolkit that will enhance our evaluation of likely consequences of fishing, there were no key sensitivities that came up in the FBM that would be resolved within a spatial model. Roughly the same population models would be used as a basis for both approaches, retaining sensitivities to parameters such as mortality and the thresholds used in applying fishing pressure. As long as migration in the spatial model is not linked to an environmental signal, this FBM provides a unique perspective which is in line with our understanding of long-term, ecosystem-scale processes.

Hence, the FBM is a useful approach, providing insights unavailable from current approaches. Model results reported here suggest that the productivity of the sardine resource within the model is highly dependent on the spatial characteristics of the fishing pressure it experiences, as is the ability of the system to sustain top predators. Results suggest that future research should focus on understanding the implications of the relative environmental conditions on each coast for the sardine stock, and how these affect the probability of a shift occurring. The role of anchovy within with model system has not yet been fully developed, and further effort in this area may allow for more robust results.

CHAPTER SEVEN
SYNTHESIS AND CONCLUSIONS

System-level changes on a decadal-scale have been shown to be a feature of upwelling systems around the world, primarily in the form of decadal-scale fluctuations in abundance and the alternating dominance of small pelagic fish species (Schwartzlose et al. 1999; Cury & Shannon 2004). Given the importance of these species within the trophic structure of the ecosystem, and the potential system-wide impact of anthropogenic and particularly environmental drivers of change, long-term changes have not been restricted to sardine and anchovy. Here I have assumed the definition of a regime shift as a sudden shift from one relatively stable ecosystem state to another, involving changes to the structure of that ecosystem (de Young et al. 2004; Jarre et al. 2006).

In the southern Benguela, previously identified changes in physical variables (wind, SST and upwelling indices) along with small pelagic fish abundance and demersal fish assemblages have suggested a system-level shift occurred between the mid- 1990s and early 2000s (Howard et al. 2007; Atkinson et al. 2011b; Blamey et al. 2012). Documented impacts on top predator species, such as seabirds (Crawford 2007; Crawford et al. 2008a; Crawford 2013) following the increase in the proportion of small pelagic fish biomass found east of Cape Agulhas since the late 1990s (van der Lingen et al. 2002; Coetzee et al. 2008a), also support the postulated change in the ecosystem. These changes in predator species highlight the importance of understanding the trophic linkages within a system and hence potential implications of change. By way of addressing these issues, the key questions laid out in Chapter One sought to understand differences in structure and function between the west and south coasts, identify any concurrent changes in the distributions of other key species, re-evaluate SST as a potential driver of change, and assess the suitability of a frame-based modelling approach to changes in small pelagic distribution. Progress on these points is discussed below.

There has been a concerted effort within South African fisheries research towards providing a solid scientific background for the application of an EAF in the southern Benguela (Cochrane et al. 2004; Shannon et al. 2006). Given the inherent complexity of the topic however, there are still many knowledge gaps to be filled in our understanding of ecosystem functioning and possible responses to system-level change. The work in this thesis builds on suggestions made by Shannon et al. (2006), and further examined by Shannon et al. (2010), as to future steps toward EAF in South Africa, both in terms of increasing understanding of spatial issues and species interactions and physical drivers and by broadening the current modelling approaches applied to the southern Benguela.

This thesis aimed to increase understanding of potential ecosystem-level impacts of distributional changes in small pelagic fish during the 1990s. I addressed this using a combination of data-derived indicators and modelling to answer the key thesis questions as follows:

1) Does the south coast function differently to the west coast, and if so, what are the implications for a large-scale change in the location of the majority of the biomass of small pelagic and other species affected?

Although they contribute to the same ecosystem, the west and south coasts of the southern Benguela have quite different characteristics. This can lead to complications and over-simplifications when making assumptions about the system as a whole, and about the potential outcomes of system-level change.

When discussing biological variables or the distribution of species in the southern Benguela, the break between the west and south coasts is variably used as either Cape Point or Cape Agulhas in the literature. Because the physical environment on the western Agulhas Bank is more similar to the west coast than to the remainder of the Agulhas Bank, those regions were grouped together for the purposes of further analyses, and the 'south coast' defined as the southern Benguela east of Cape Agulhas as discussed in Chapter Two. This approach is also in line with current discussion regarding possible spatial management approaches for the small pelagic fishery (van der Lingen 2011; de Moor et al. 2014).

On compiling and reviewing available literature on the physical characteristics and biological components of the southern Benguela with a focus on the variation between west and south coasts, it was previously shown that although the west coast as a classic wind-driven upwelling system has higher productivity, the south coast, with shelf system characteristics and diverse drivers of upwelling, is more diverse and supports a higher year-round biomass of consumers (see Chapter Two and references therein for this and the following statements, and Table 2.1 for a summary). Nutrient availability is lower but less variable on the south coast than on the west coast, thus the south coast system is likely to be more constrained than the west coast in terms of nutrients. A large number of resident species, particularly fish, have migratory patterns that take them to both coasts over their lifecycle: the west coast plays an important role as a nursery area for many fish species that may move south and east with age to spawn as adults on the south coast. As a result of these linkages the two regions cannot be thought of as completely discrete, however the conditions on each coast are distinct enough that the location of the majority of a species' biomass (i.e. west or south coast) is likely to have an influence on its overall productivity. Based on published literature concerning the two regions, the spatial distribution of a stock is likely to affect the structure and functioning of the ecosystem as a whole, with on average slower growth rates, but higher productivity, on the west coast.

Compiling and assimilating our current understanding of the differences between the west and south coast systems was an important step in increasing our ability to interpret the implications of change, spatial or otherwise, within the southern Benguela. The findings from this chapter (Chapter Two) were used in the interpretation of the results in Chapter Three, and informed the reasoning behind the construction of the frame-based model (Chapters Five and Six).

2) Have the distributions of any other prominent species changed over a similar timeframe, and if so, what are the likely impacts?

This question was addressed in Chapter Three. Any differences in the degree to which various species overlap as a result of changes in the small pelagic fish distribution or a concurrent reaction to its drivers may have had implications for the trophic flows within the system by impacting prey availability to selective predators and the diet composition of opportunistic predators. The construction of distribution maps of important species in the southern Benguela in this chapter allowed for the comparison of their distributions over time. The following indicators were calculated and compared before, during, and after the change in small pelagic fish distribution in the late 1990s: proportion of biomass east of Cape Agulhas; relative overlap in biomass and area; and index of diversity; and connectivity, derived from the relative overlap of species.

Some species underwent similar increases in biomass found east of Cape Agulhas to that of sardine, although less pronounced: anchovy; redeye; chub mackerel; kingklip; chokka squid; yellowtail (a predatory pelagic fish) and yellowfin tuna. In the case of anchovy the shift is primarily evident in the spawner biomass, with recruits found on the west coast through all time periods examined, while redeye recruits showed a greater increase in proportion on the south coast over time than redeye spawners. Other species, including *M. paradoxus*, chub mackerel and snoek, showed an increase on the south coast only in the intermediate period, i.e., the period which was considered representing the transition from a “west coast” to a “south coast” ecosystem state. There have been changes in the degree to which species overlap with one another over the periods examined, with the majority showing an increasing average overlap with small pelagic fish species in the most recent period. This is seemingly due to a combination of incidental increased overlap with higher small pelagic biomass on the south coast, e.g. in the case of *M. capensis*, as well as increases in the proportion of the overlapping species on the south coast, for example yellowtail, shown here, or changes in seabirds distributions in response to small pelagic prey (Crawford et al. 2008a). At least one species, namely *M. paradoxus,* overlapped less with sardine and anchovy over time. Both connectivity and diversity were lowest during the intermediate period, and while starting highest on the west coast, were higher east of Cape Agulhas during the last period than during the intermediate period. The low values in the intermediate period can be interpreted as indicative of a system in transition, and both of these indicators highlight the increasing importance of the south coast over time, notably in terms of trophic interactions within the system.

Evidence of the direct impacts of changing forage fish distributions on top predators such as seabirds is already available (Crawford et al. 2008a). The effects on the less well-monitored species discussed in Chapter Three had not previously been shown, and also contribute to the overall thesis question of the ecosystem implications of observed changes. The implied potential indirect effects of change in small pelagic fish distribution on higher trophic level species shown here should also be kept in mind when advising decisions regarding management and monitoring within the region.

3) How robust is the hypothesis that changes in anchovy distribution can be linked to changes in sea surface temperature (SST)?

Changes in anchovy spawner distribution in 1996 have been linked to a concurrent change in cross-shelf SST gradient on the central and eastern Agulhas Bank on the examination of decadal means (Roy et al. 2007). When a more rigorous analysis of the dataset was applied in Chapter Four, and the domains examined extended and refined, previous findings were confirmed - that a shift in the cross-shelf SST on the CAB and EAB occurred in the mid-1990s. Additional shifts in the late 1990s in the cross-shelf SST gradient on the WAB where none had previously been identified were also evident, as well as in the offshore SST on the CAB. These findings lend weight to the hypothesis that environmental changes were drivers of the change in anchovy distribution, and when combined with evidence for change throughout the system (e.g. seabird distribution (Crawford et al. 2008d; Crawford 2013), changes in other species shown in Chapter Three, and other previously identified shifts in physical variables (Howard et al. 2007; Blamey et al. 2012) are linked to a system-level shift. Recent investigation has shown that shifts are not apparent in available *in situ* data however (Schlegel 2014), highlighting the need for further comparative studies of any other available datasets, and improved monitoring and collection of *in situ* data in the future.

4) Can a frame-based modelling approach be useful in exploring our current understanding of the processes involved?

Both a frame-based approach and a spatial model could have been implemented in the context of exploring changes in small pelagic fish distribution, as discussed in section 5.1.2. A frame-based model (FBM) in this context requires the assumption that the majority of the population, which is explicitly modelled, is at any time on one particular coast, while some unknown proportion that must be estimated remains on the other coast. A spatial model on the other hand, modelling a separate population on each coast, requires an assumption as to the degree of mixing between the two populations – a variable known to exist but of which there is currently no estimate. A FBM was chosen as the approach to be pursued given i) the advantages of a FBM in the context of a system undergoing possible regime shifts, represented as switching between defined, stable, frames, and ii) the suitability of a FBM in terms of a minimum realistic approach to objective-driven modelling, or a model of intermediate complexity (Plagányi et al. 2014), discussed in Chapters One and Five, as well as iii) the connections between the west coast and the south coast in terms of early life history of many species.

A frame-based model of sardine and anchovy abundance and distribution was constructed, as described in Chapter Five, using findings in previous chapters to inform model design and parameterisation. When model sensitivity to inputs was tested and the model exercised under various climate and fishing scenarios, results highlighted the importance of understanding environmental drivers and the relative conditions on each coast. Productivity of sardine within the model, and hence the availability of this species as prey to top predators such as seabirds, was also highly dependent on the spatial characteristics of fishing pressure it experienced, regardless of whether the system was in a west coast frame or south coast frame. Counter to expectations, a fishing strategy aiming to take maximum catch on the south coast actually resulted in higher catches at higher pressure, unlike the converse strategy (with catches taken largely on the west coast). This was a result of the rules governing frame switching, in that high fishing pressure (along with environmental conditions on south versus west coast) is a driver of shifts to the opposite coast. As a result, high pressure on the south coast make sardine in the model more likely to be operating under a more productive west coast frame, increasing the biomass and thus the modelled landings.

A FBM approach is useful in the context of a system undergoing regime shifts. The addition of a spatial element implemented here, which required major restructuring of the initial abundance-focused frame-based model previously developed for the southern Benguela in "west coast" mode or frame alone (Smith & Jarre 2011; Botha 2012), allows for the exploration of current thinking regarding the possible drivers of distributional changes and the potential role of fishing, as well as the implications for top predators. The FBM approach also allowed for the development of the system state indicator used here as a measure of the ability of the system to support top predators in terms of prey availability, something not currently implemented in the management of the South African small pelagic fishery.

As discussed however, it is not the only means of addressing the problem. In using a FBM, an assumption is made that the system functions sufficiently differently in "west coast mode" and "south coast mode" to warrant separate frames, i.e., different parameterisation of the anchovy and sardine population models. Given the degree of connectedness of both the biological systems (via migratory lifecycles of component species), and the physical systems (to a degree influenced by the same large-scale weather systems) of the two, describing them as two components of the same system, following Hutchings et al. (2009), seems the most accurate. This does not reduce the value of the model constructed here however. One of the tenets of the approach taken here is the idea that the model should address the objective using the minimum complexity required. This, along with the findings that what has been observed within the southern Benguela is an ecosystem regime shift from one state to another (Howard et al. 2007, Blamey et al. 2012, Chapter Three of this thesis), was the basis of the decision to design the two separate frames within the model. If we have seen the real world system switch from operating in one mode, where biological components are based largely on one coast under its specific set of conditions, to the other, then the FBM approach is particularly suited to model the situation, provided that the reality of an interconnected system of two parts is kept in mind. It is also of particular relevance given the difficulties encountered during the current investigations into the feasibility of modelling the dynamics of the system based on spatial characteristics alone (de Moor et al. 2013; Smith et al. 2013). Both these approaches are relevant for the considerations of spatial management of the small pelagic fishery currently underway (de Moor et al. 2013).

Findings from all chapters show that the distributional change of small pelagic fish cannot be considered outside of the context of the ecosystem as a whole. Other species have responded to either the same drivers as sardine and anchovy, or to the resultant change in prey availability (See Chapter Two Table 2.1; Chapter Three), resulting in the south coast becoming more important than previously in terms of trophic functioning interactions within the system. Frame-based model results highlighted the significance of applying spatialised fishing pressure to the region, given the capacity of this strategy to influence the location of the majority of small pelagic biomass. This in turn was shown to potentially impact prey availability to top predators such as seabirds in the model, using an indicator of prey availability to top predators ('system state' in the model). Given the findings in Chapter Three and the documented effects on seabirds (Crawford et al. 2008a; Sherley et al. 2013), there is reason to believe that this model world effect parallels observation made in the real world.

Limitations and future research

Re-examining changes in SST on the Agulhas Bank as a driver of distributional change in small pelagic fish

The reanalysis of the SST data for the Agulhas Bank in Chapter Four was performed using the dataset assumed acceptable at the time, however a warm bias has since been identified in the Pathfinder SST data used to derive the dataset used (Dufois et al. 2012). Although this bias has since been improved and the data could be reanalysed to confirm previous findings, the dataset remains at a fairly coarse resolution of 1^{o} x 1^{o}. Given the scale of the region and processes under discussion, ideally this analysis should be performed using data of a greater resolution, for example the Pathfinder SST (as opposed to the Optimally Interpreted SST used here) at a resolution of 4km. Note that although MODIS data at an even greater resolution of 1 km also exists, it is only available from 2000, hence is unsuitable here. Although unfortunately not possible within the timeframe of this project, it is recommended that further analyses using these greater resolution data are conducted to increase our understanding of SST as a driver of change in the southern Benguela.

The frame-based modelling approach

If the frame-based model described here in Chapter Five and Six is to be further developed, the focus should be on refining both anchovy and the Environmental Suitability Index (ESI) within the model. Although anchovy is included in the current version, the population model used is simple and the population dynamics are unaffected by fishing. If this approach is to be taken any further in its ability to explore the movements of small pelagic fish in relation to environment and fishing pressure, the anchovy model used needs to be refined. Currently the frame-based model can only be used to explore anchovy movement and abundance given large proviso's regarding the simplicity of the underlying model.

Similarly, although the use of a simplified index representing environmental variability (ESI) in this and previous versions of the model was justified (given that the approach focuses on developing the simplest useful version first and adding detail as necessary), further development of the ESI and its interpretation within the model would add value to model outputs. As discussed in Chapter Six, while different environmental conditions do favour sardine and anchovy, in reality there is some overlap between both favourable and unfavourable conditions for the two species, and a more nuanced approach taking this into account could be a sensible next step.

Another aspect of ESI worth considering for future models is the inclusion of a correlation between west and south coast conditions. Rouault et al. (2010) demonstrated positive, significant correlations between monthly SST anomalies for the west and south coasts, due at least in part to the large scale of the weather systems affecting the southern Benguela influencing both regions. Exploring the effect of the inclusion of a relationship between the ESI on the two coasts would be an interesting addition to the model, although would require some restructuring of the ESI and how it is interpreted given that in the current model the ESI's for the two coasts do not represent the same characteristics. On the west coast, for example, a favourable ESI for sardine is assumed to represent weak upwelling, which would lead to a smaller-sized zooplankton community preferentially consumed by sardine, while strong upwelling leads to a food environment more favourable for anchovy (van der Lingen et al. 2006c). Thus opposite ESI conditions favour each species in the model. On the south coast however we are assuming a more nutrient-limited environment, and thus that any upwelling or increase in nutrients is beneficial to both species (hence not distinguishing between 'weak' or 'strong' upwelling). The ESI for the south coast therefore represents slightly different conditions to that for the west coast. This could be addressed by increasing the complexity of the ESI as previously suggested, as would be necessary if the effect of a relationship between the environments on the two coasts within the model is to be explored.

Although the correlation in physical conditions described by Rouault et al. (2010) can be linked to weather systems crossing both regions, perhaps a more important relationship between the west and south coasts in terms of ecosystem function and biological systems is the link between the Agulhas Bank spawning grounds and feeding grounds on the west coast. The recruitment success of sardine and anchovy is dependent on the retention and transport of eggs and larvae from spawning grounds on the

Agulhas Bank to feeding grounds on the western Agulhas Bank and west coast as detailed in Chapter Two). This may also be important for understanding the implications of west coast- or south coast-based sardine and anchovy populations. Here the south coast was assumed to have a negative effect on productivity of both stocks, based on the more limited nutrient availability and higher biomass of predators established in Chapter Two. It appears however that while sardine populations have declined since their increased easterly abundance, anchovy may not have felt the same negative effects and biomass has remained relatively high, at least up until 2010 (Coetzee et al. 2008b; Shabangu et al. 2012). This difference may result from the timing of peak spawning for each species (sardine spawning peaks in early spring and autumn, on either side of anchovy peak spawning in summer (van der Lingen et al. 2001), with anchovy possibly benefiting from better timing in terms of transport current strength. Given what we know about the factors affecting recruitment success of small pelagic fish, and the potential influence of the environment on the necessary processes of enrichment, concentration and retention (Bakun 1996; Hutchings et al. 1998; Miller & Field 2002; Huggett et al. 2003; Miller et al. 2006), a greater understanding of how distribution and the timing of spawning affect these factors would allow for better interpretation of environmental signals, whether in a model world (e.g. ESI) or the real world.

The possible changes to the model structure described above may be worth pursuing in the interests of exploring the situation further, but one of the ideals behind, and advantages of, the approach taken here is that complexity should be added only where necessary to address the objective. When considering in retrospect whether any of the current complexity is perhaps extraneous, given the lack of sensitivity of the model to quite substantial changes to model parameters, one could be tempted to point to anchovy as an inconsequential component. Although this may be appealing, because the issue to be addressed is the implications for the ecosystem, anchovy remain integral. In addition to bycatch issues, it would be difficult to interpret either the potential bottom-up or top-down implications of changes in sardine distribution without some idea of anchovy abundance or distribution, due to their shared role as prey and predator with respect to early life history stages. Likewise, other model components were all included to address a particular function or problem, and seem indispensable at this point, barring a substantial reworking of rules governing frame switching.

Conclusions

This thesis has shown that changes in small pelagic fish distribution do affect other species in the system by way of changes in prey availability, and in some cases have resulted in distributional changes for other more selective predator species (fish, e.g. Chapter Three, and birds). Changes at the system level are represented by spatial, system-scale indicators presented in Chapter Three. Changes in these species may also be a result of response to the same physical drivers, given the concurrent shifts in physical variables that have been identified (Howard et al. 2007; Blamey et al. 2012; Chapter Four), particularly in the case of low trophic level species. Results shown here support the hypothesis that the location of pelagic fish within the system influences the productivity of the specific stock, given the physically and biologically distinct nature of the sub-systems off the west and south coasts, and should be taken into account when management options are being considered. Results from the frame-based model suggest implications for future distributional changes in small pelagic fish under spatial management of the pelagic fishery. Results support the hypothesis (Coetzee et al. 2008a) that maintaining relatively high levels of fishing pressure on the remaining west coast population may make a shift back from the system in south coast mode to a system in west coast mode less likely. Additionally, although it may appear more feasible (at least from a biological viewpoint, since economic considerations are not included in this thesis) to heavily fish a less productive south coast stock that is not contributing significantly to overall production, the importance of that biomass in terms of prey for the high biomass of predators in that region (Chapter Two) should be kept strongly in mind. Investigations into possible spatial management options for the small pelagic fishery are currently underway based on the hypothesis of multiple stocks of sardine in the southern Benguela (van der Lingen 2011; van der Lingen & van der Westhuizen 2013). Even under the current single-stock, non-spatial management approach, however, insights into the respective functioning of the west and south coast systems or of the system as a whole while in “west coast” or “south coast” mode, are of particular value. The results presented here add to the base of knowledge from which defensible and strategic management decisions can be made, and add insight to the interpretation of results produced by the models currently used in the management of the small pelagic fishery in South Africa. Irrespective of whether or not the modelling approach presented here is further pursued, the results of this thesis should be considered during the development of a revised management plan for the small pelagic fishery.

APPENDIX: All overlaps by species and coast

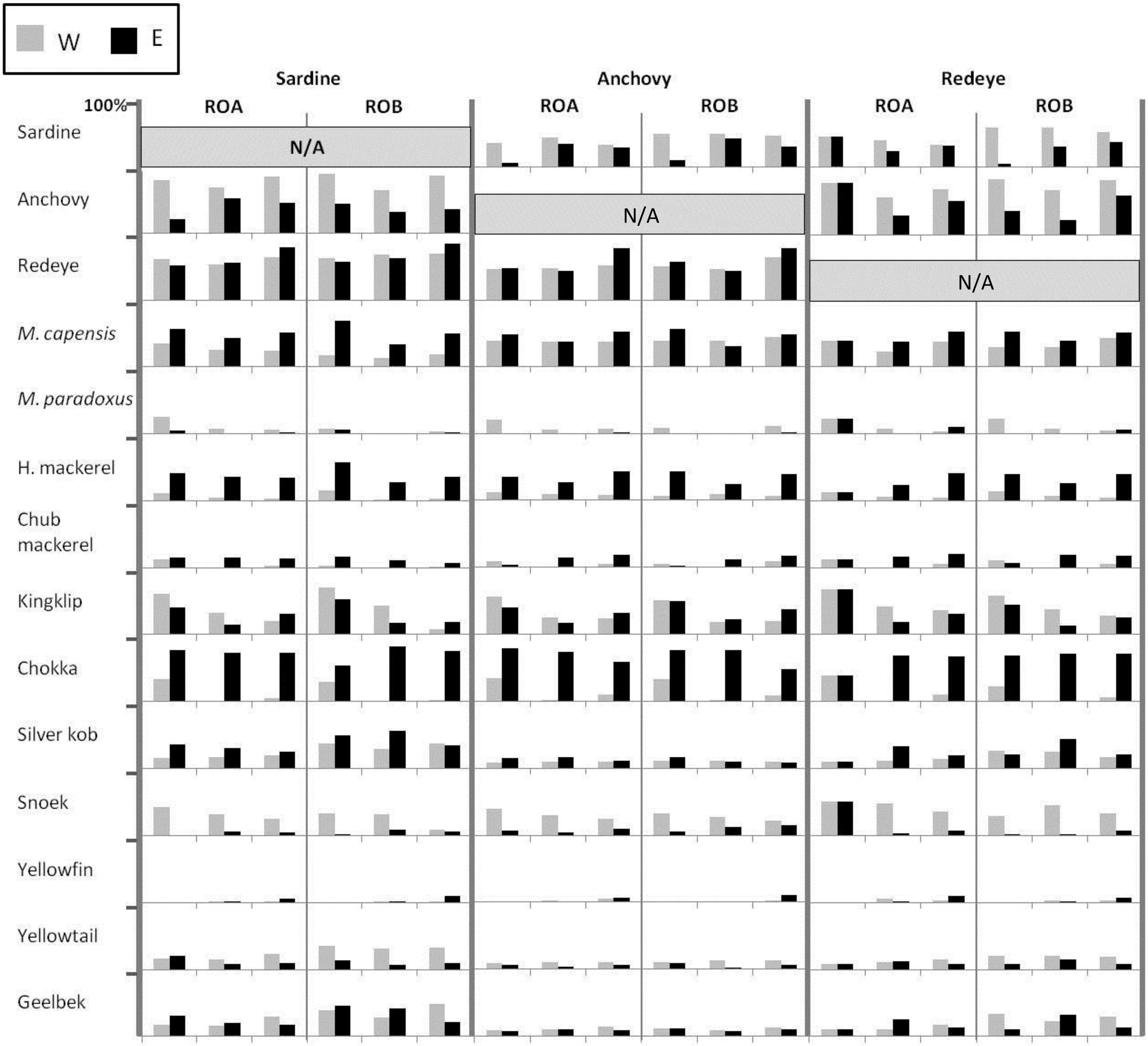


Figure A1: Overlap in area (ROA) and biomass (ROB) between sardine, anchovy and redeye and all other species, east and west of Cape Agulhas.

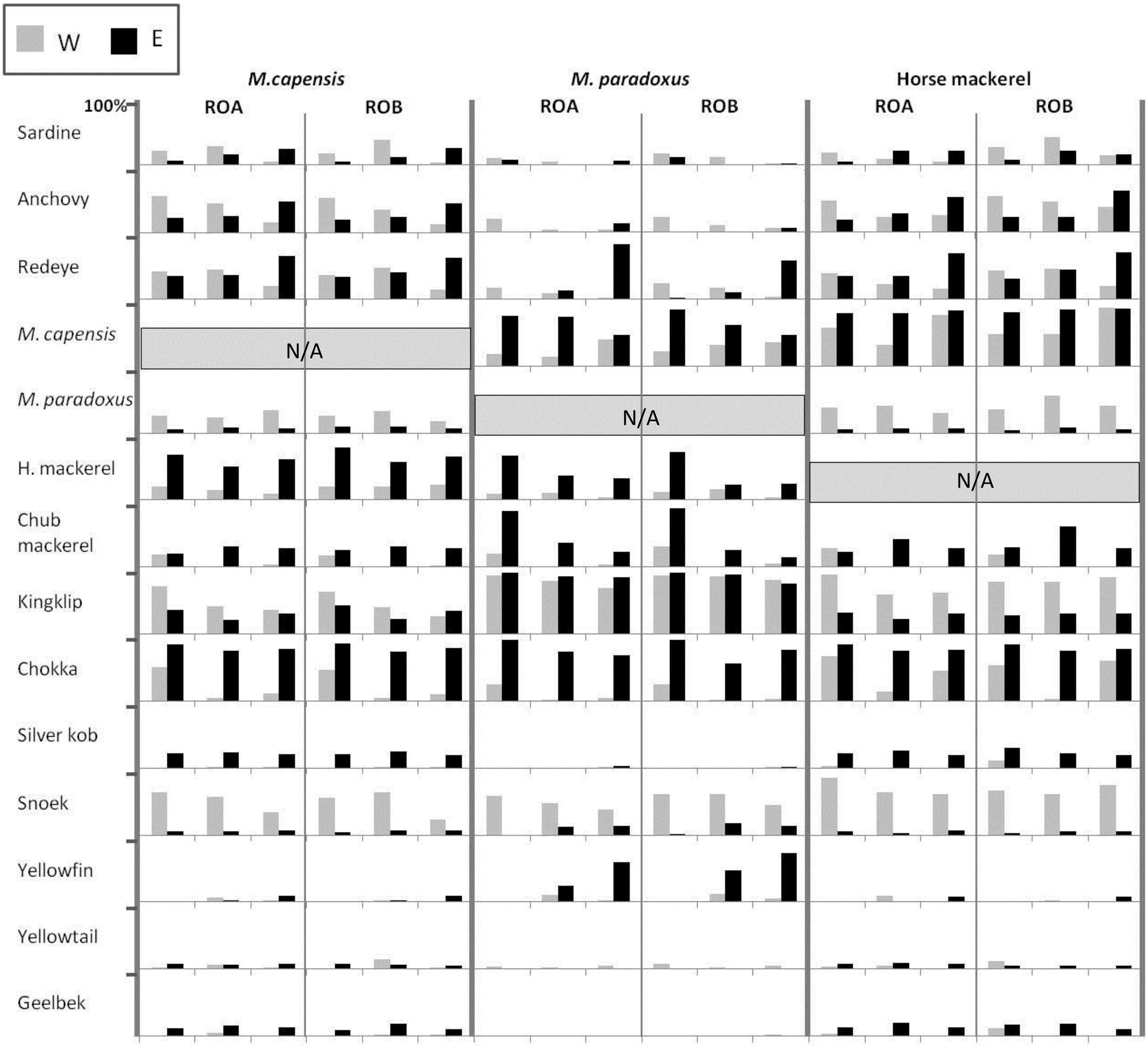


Figure A2: Overlap in area (ROA) and biomass (ROB) between *M. capensis*, *M. paradoxus* and horse mackerel, and all other species, east and west of Cape Agulhas.

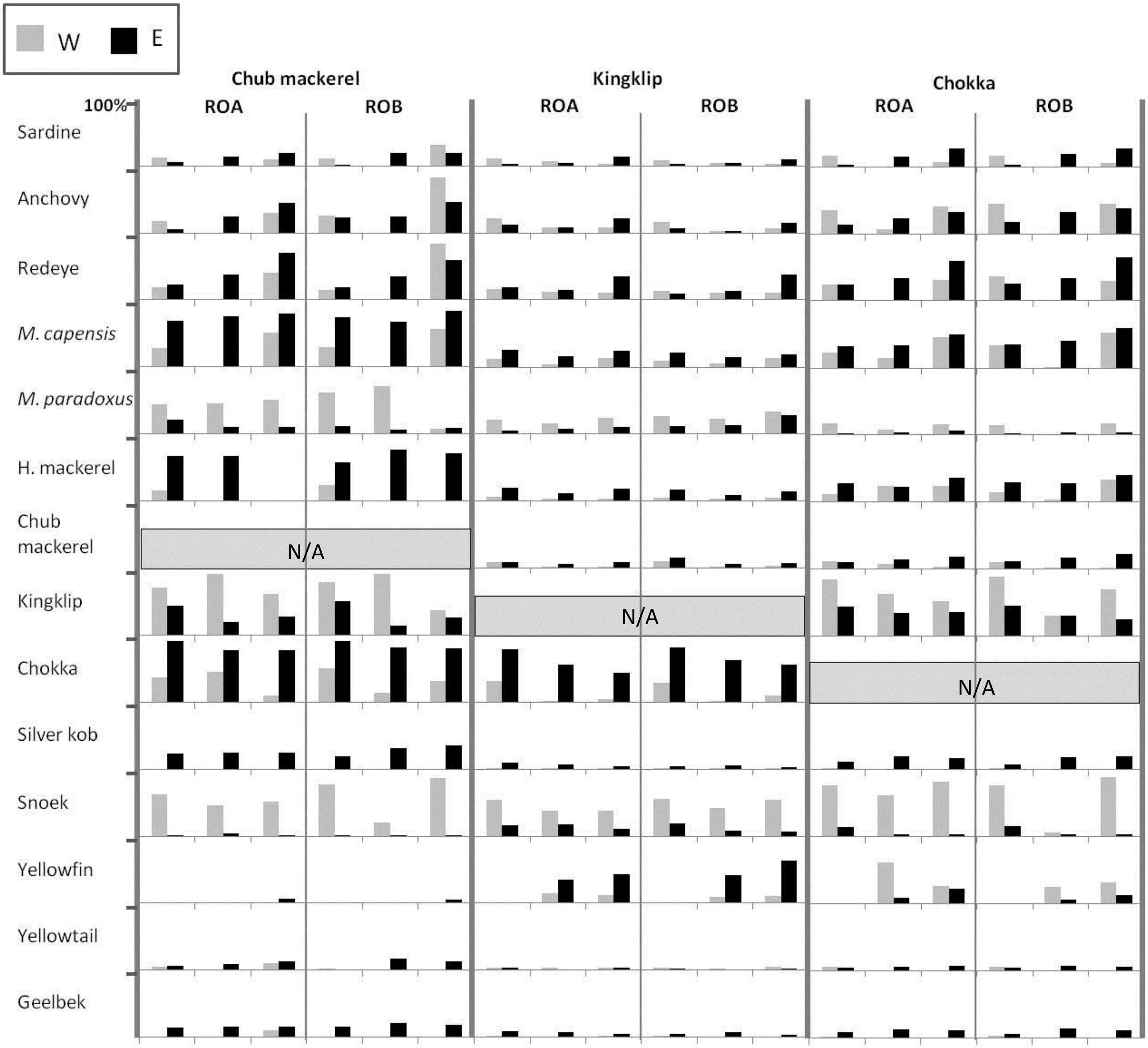


Figure A3: Overlap in area (ROA) and biomass (ROB) between chub mackerel, kingklip and chokka squid, and all other species, east and west of Cape Agulhas.

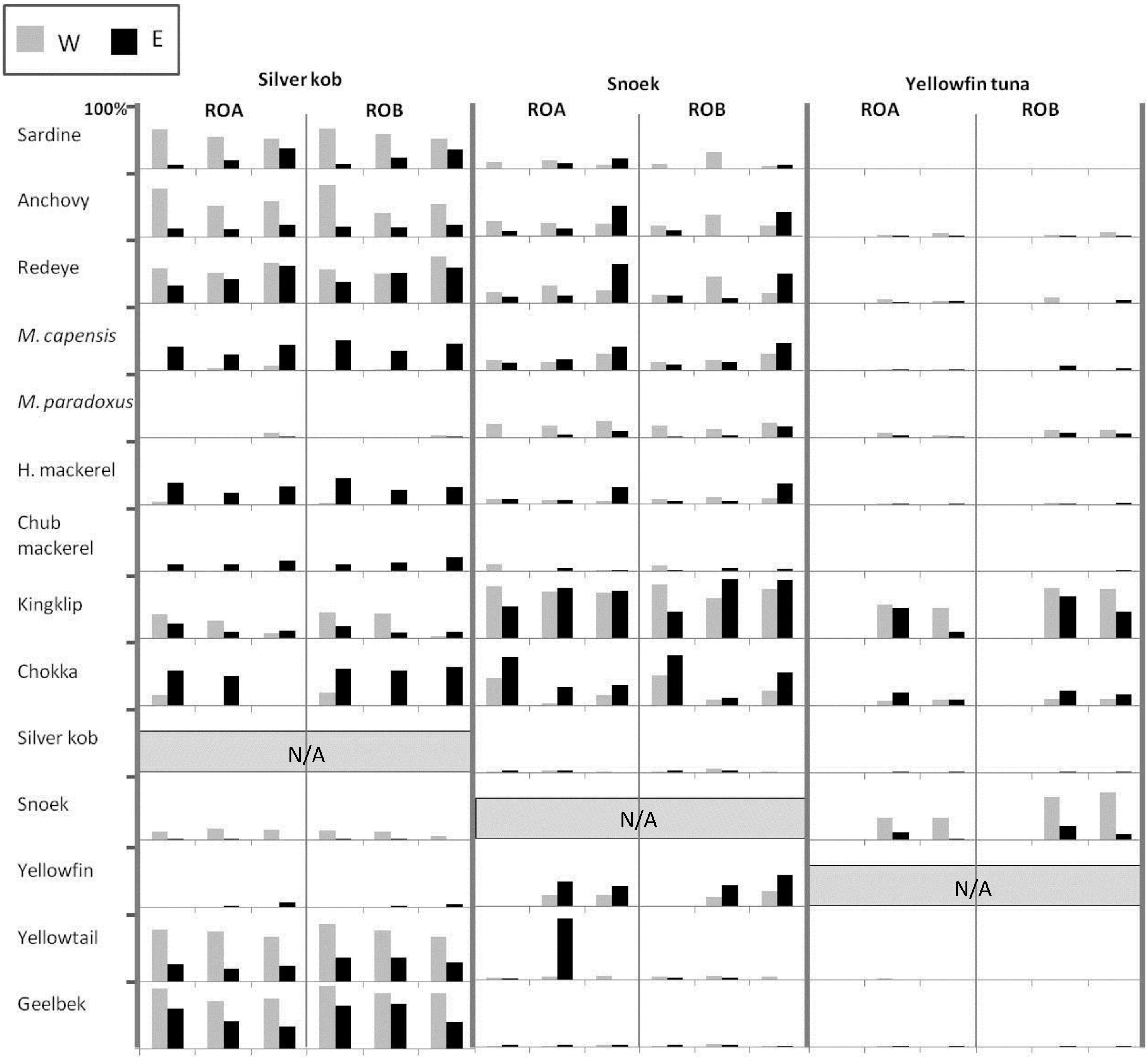


Figure A4: Overlap in area (ROA) and biomass (ROB) between Silver kob, snoek and yellowfin tuna, and all other species, east and west of Cape Agulhas.

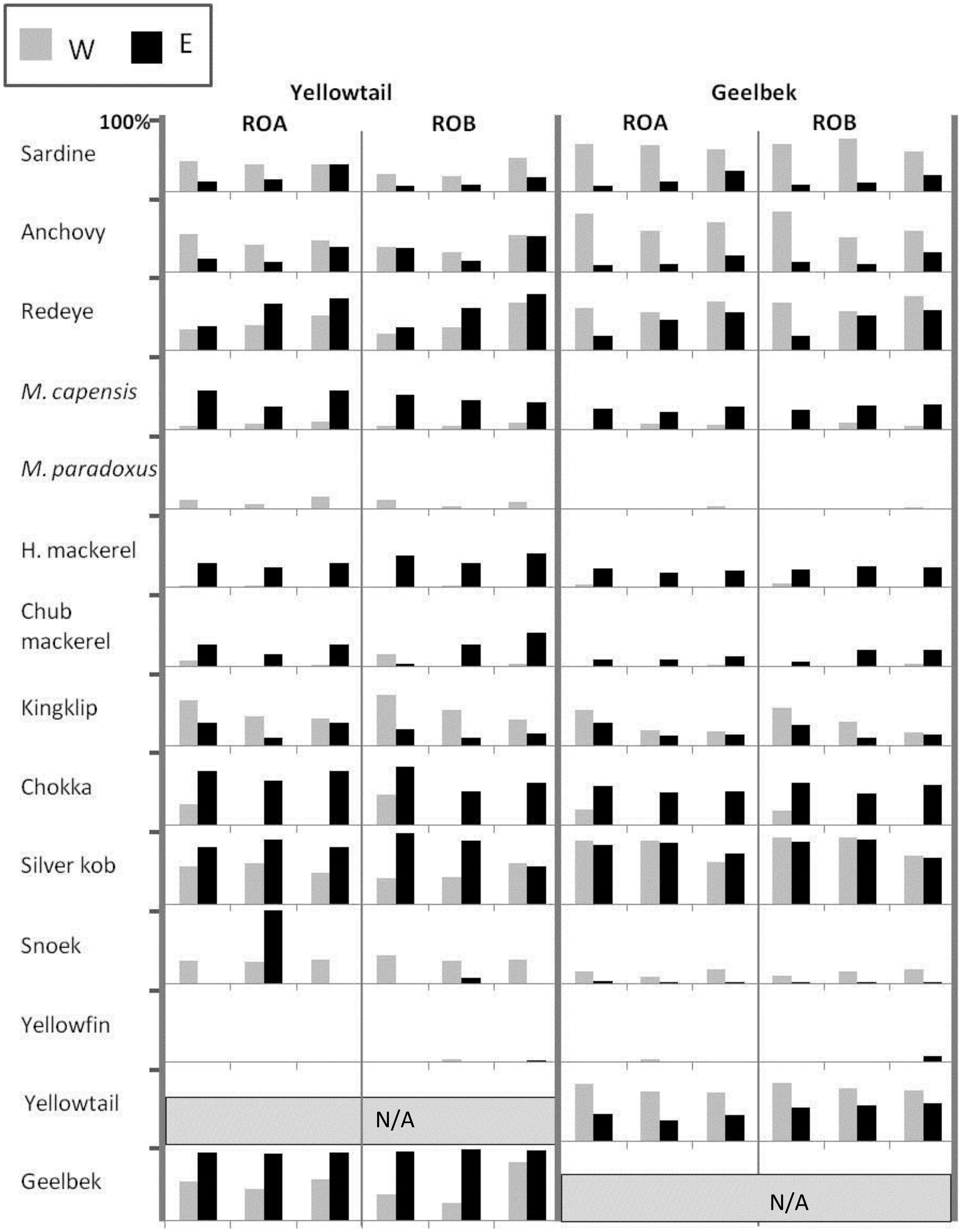


Figure A5: Overlap in area (ROA) and biomass (ROB) between yellowtail and geelbek, and all other species, east and west of Cape Agulhas.

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