AN INDIVIDUAL-BASED MODELLING APPROACH TO EXAMINE LIFE HISTORY STRATEGIES OF SARDINE *SARDINOPS SAGAX* IN THE SOUTHERN BENGUELA ECOSYSTEM

DAVID CHARLES MOORCROFT MILLER

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Supervisors:
DR COLEEN L. MOLONEY, Marine Biology Research Institute, UCT
DR CARL D. VAN DER LINGEN, Marine and Coastal Management, DEAT
DR CHRISTOPHE LETT, Institut de Recherche pour le Développement, France

This thesis is dedicated to my family, spread all over the world, who have always supported me and had faith in my abilities

TABLE OF CONTENTS

DECLARATION

This thesis presents the results of work done at the Marine Biology Research Institute, Department of Zoology, University of Cape Town. The work was all carried out personally but much assistance and guidance was received from my supervisors and through interaction with scientists from the IDYLE project. The hydrodynamic model used was developed by Pierrick Penven, outputs provided by Bruno Blanke, and Java tools used in the programming of the IBM experiments were developed by Christian Mullon and Carolina Parada. Data presented were obtained through personal communications with scientists from Marine and Coastal Management, Department of Environmental Affairs and Tourism, and are referenced as such. Each significant contribution and citation of other people's work has been attributed and referenced. All assistance, technical or otherwise, is fully and gratefully acknowledged.

This work has not been submitted for any other degree at any other university.

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David Charles Moorcroft Miller

March 2006

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This work is a contribution to the joint South African-French program IDYLE (later ECO-UP), which involves the IRD (Institut de Recherche pour le Développement, France), Marine and Coastal Management (MCM), and the University of Cape Town (UCT), as well as the IRD research unit GEODES. I would like to acknowledge funding received through the Benguela Ecology Programme (BEP) of the Southern African Network for Coastal and Oceanic Research (SANCOR) from the National Research Foundation of South Africa (NRF), and the Branch: Marine and Coastal Management. Additional funding (Myer Levinson and KW Johnson scholarships) was obtained through UCT. The IRD funded a Java programming course (without which I would have been lost). Work from this thesis was presented at the 1st Advances in Marine Ecosystem Modelling Research (AMEMR) conference funded by a UCT student travel grant. All research was carried out at various libraries around UCT and at MCM. Many papers were found using NISC via Biblioline.

Despite the nature of my project and my initial very basic grasp of the methodologies involved, I would like to think I was not a burden on any of my supervisors. I am a very self-sufficient worker and can work efficiently when left to my own devices without constant direction or assistance. I will now set out to systematically disprove that hypothesis...

This thesis would probably be a haphazard collection of sardine anecdotes, three times as long as this, were it not for planning and editorial assistance from Coleen Moloney. The amount of red pen marks on my drafts constantly gave the impression that a small animal had been sacrificially slain over the manuscripts. Carl van der Lingen was a fount of information about sardine and has a passion for pelagic fish I only wish I had. Whenever I went to him thinking I needed some information on something, I left knowing all I possibly could about it but with the distinct feeling that now I needed to know a lot more about something else too. Christophe Lett, despite being located half way across the globe for much of my PhD, could always be relied on for rapid feedback and useful experimental design and programming assistance, often finding the bugs when my sardine eggs were flying 75m above the ocean surface or growing like Zimbabwean inflation.

I did this work as part of the loosely acronymised IDYLE (**I**nteractions and spatial **DY**namics of renewable resources in upwe**L**ling **E**cosystems) program and received a lot of technical assistance and advice from the various researchers affiliated with this program. The project was initialised through discussions with Pierre Fréon at the Southern African Marine Science Symposium (SAMSS) in Swakopmund July 2002 and he subsequently played a big role in getting the thesis rolling and I thank him for many useful discussions. Christian Mullon initially supervised this work before returning to France. He was instrumental in designing the first few experiments and training me to program the rest and I learnt a lot from

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Years from now when I look back on the time spent working on my PhD it is unlikely that I will think of sardine eggs and larvae or "6359 minutes remaining" but I will think of friends and family who were there with me through that time. Many have envied my lifestyle – unemployed friends wondering how I was getting paid to do pretty much what they were on a daily basis, without the added hassle of having to find a job; and working friends scoffing as I told them I woke up early at half past ten this morning. Thanks to everyone who has gone through this with me, in particular Stu, Simp, Age, Marc, Phill, Karl, Debs, the Hobbages, Amadoda FC and my family, Steve, Chris, Zöe and especially my parents, Jenny and Selwyn Miller.

And, FINALLY, that stringy red seaweed that drove me out of a career in Botany. I would probably be a phycologist working on an aquaculture farm if it wasn't for my brown fingers and the stubborn *Gracilaria* that refused to grow during my botany honours project.

So much for working on my own...

ABSTRACT

Hypotheses regarding the spawning strategy and recruitment of sardine (*Sardinops sagax*) in the southern Benguela ecosystem are tested using an individual-based Lagrangian particle tracking model linked with a 3-D hydrodynamic model of the region. Experiments focus on the dispersion of eggs and larvae among possible spawning and nursery areas. The two main areas of interest were the west coast upwelling region and the south coast shelf region (Agulhas Bank). A stage-based temperature-dependent development model is incorporated and vertical positioning schemes are tested. The spatial distribution and size structure of the sardine spawning stock for the period 1991-1999 are presented and a simple size-based fecundity model, combined with modelled recruitment, is used to determine the relative importance of each spawning and nursery area. The area of spawning plays a fundamental role in determining the destination of spawned eggs, and recruitment of sardine in the southern Benguela ecosystem appears to be divided into three recruitment systems by the circulation of the region: eggs spawned west of Cape Agulhas recruiting on the west coast (the WAB/WC-WC system), eggs spawned east of Cape Agulhas recruiting on the west coast (the CAB-WC system), and eggs spawned east of Cape Agulhas recruiting to the south coast (the SC-SC system). There is a slight increase in retention in the two nursery areas during winter, but the transport of eggs and larvae from the Agulhas Bank to the west coast is optimal during spring to early summer. Slow development arising from cold temperatures on the west coast could negatively impact recruitment by increasing offshore loss of individuals before they develop to a stage when they are able to actively avoid offshore currents and through its effect on mortality rate. This could explain the spatial separation of spawning and nursery areas in this system. The vertical position of individuals has an effect on the level of modelled recruitment and mortality rate, but observed vertical distributions of sardine egg and larvae do not significantly increase the level of modelled recruitment to optimal nursery areas. This suggests that efficient transport and retention are traded-off against other factors such as predator avoidance or prey abundance. Observed size structure and spatial distribution of the sardine spawning stock for 1991-1999 fluctuated greatly with most spawning centred on the western Agulhas Bank. When spawning was centred east of Cape Agulhas, recruitment was poor. No significant relationship could be established between potential reproductive output reaching the west coast and estimated recruitment, but positive recruitment anomalies required good transport to, and retention on, the west coast. A conceptual model of the early life history of sardine is proposed in light of limitations imposed by transport and retention of individuals. Lower primary production and the possibility of higher predation on the Agulhas Bank suggest that the south coast supports less recruitment than the west coast. The hypotheses tested using available data and model results could improve the understanding of recruitment of sardine in this complex ecosystem. These need to be validated by field observations. Additionally, further avenues for research that could help in developing a better understanding of the sardine life history in the southern Benguela ecosystem are suggested.

CHAPTER 1: INTRODUCTION

Members of the order Clupeoidei (anchovies, sardines, herrings and menhadens) thrive in the productive pelagic waters of upwelling ecosystems. Because of their substantial biomass in these systems, they have long supported large fisheries around the world. However, the management of these fisheries has proved to be difficult because of large variability in population size (Cushing 1971, Blaxter and Hunter 1982, Lluch-Belda et al. 1992b, Schwartzlose et al. 1999). Upwelling systems appear to be difficult reproductive habitats for fish, with most small pelagics needing to migrate to find suitable spawning habitats (Laevastu 1993). This, together with the effects of a number of other environmental and ecological factors (e.g. temperature, food availability, predation), usually results in large fluctuations in the level of recruitment, the quantity of fish that survive the early life stages to become accessible to the fishery (Bakun 1985). Recruitment variability manifests as variability in overall stock size as a result of the short life spans of most clupeoids.

1.1. THE SOUTHERN BENGUELA ECOSYSTEM

The Benguela, along with the California, Canary and Humboldt Currents, is one of the four major eastern boundary current systems of the world. Separated from the northern Benguela by a perennial cell of intense upwelling off Lüderitz **(**Barange et al. 1992**)**, the southern Benguela ecosystem consists of two main parts: the west coast upwelling area and the Agulhas Bank off the south coast (Fig. 1.1). The west coast section, from Lüderitz (27°S) to Cape Point (34°S), is extremely productive during the summer months when southeasterly winds prevail (Jury 1987), which drives very active upwelling centres along the coastline. This upwelling area is an important nursery ground for small pelagic species in the region, including sardine (*Sardinops sagax*), anchovy (*Engraulis encrasicolus*) and round herring (*Etrumeus whiteheadi*), and sardine and round herring also spawn off the west coast on occasion. Detailed reviews of the Benguela upwelling system can be found in Shannon (1985) (physical features and processes); Chapman and Shannon (1985) (chemistry and

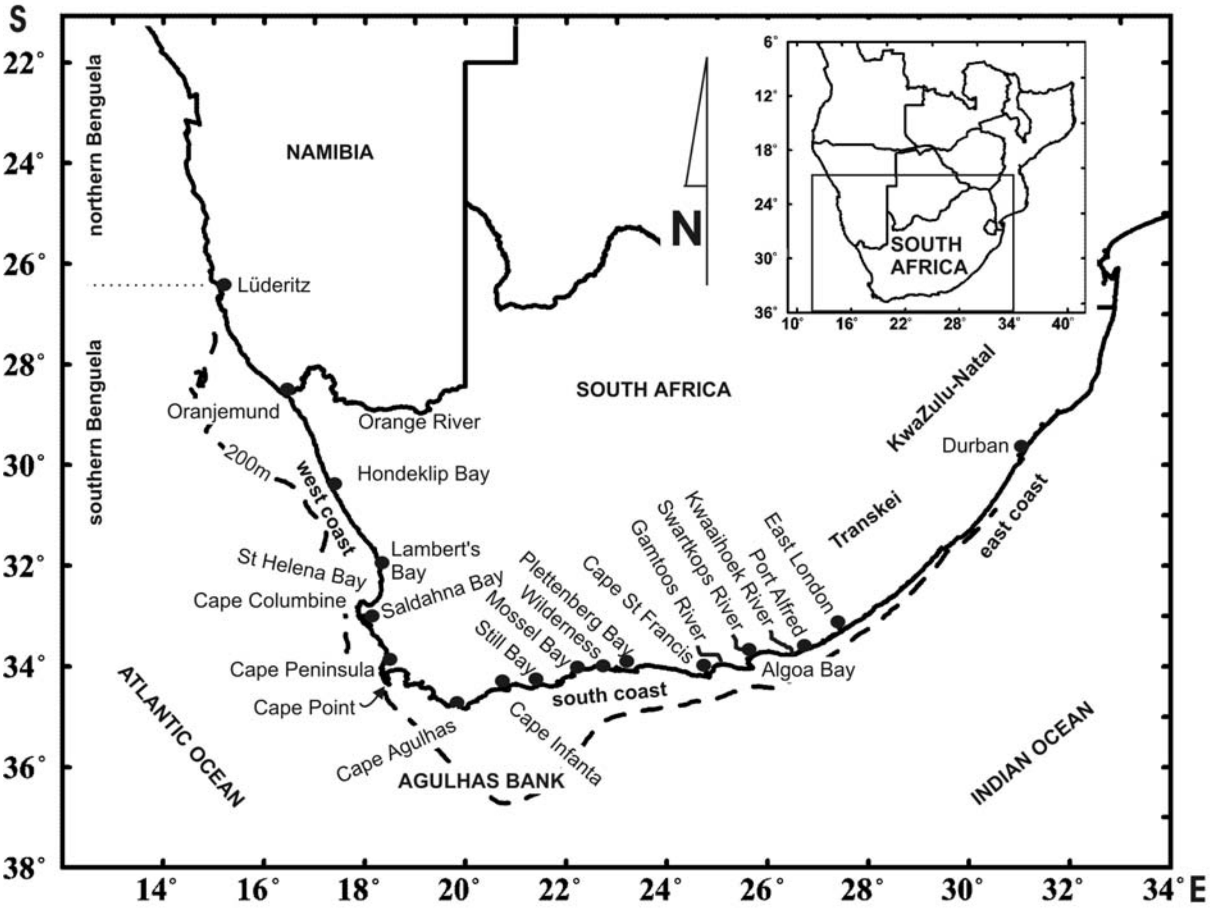

Fig. 1.1: Map of South Africa showing localities and regions mentioned in text

related processes); Shannon and Pillar (1986) (plankton) and Crawford et al. (1987) (major fish and invertebrate resources).

The Agulhas Bank is a broad, irregular extension of the South African coastal plain extending from Cape Point (18°E) to East London (28°E). It is conventionally divided into three subregions: the western (WAB), central (CAB) and eastern (EAB) Agulhas Bank. Numerous linefish species, squid (*Loligo vulgaris reynauldii*), hake (*Merluccius* spp.), and pelagic species anchovy, horse mackerel (*Trachurus trachurus capensis*) and sardine spawn to a lesser or greater degree over some portion of the Agulhas Bank at different times during the year, and the Agulhas Bank serves as a nursery area for a wide variety of species (Hutchings et al. 2002). Whereas the productive area of the Agulhas Bank is not as extensive as that of the west coast (Table 1.1), there are various sources of nutrients that maintain relatively high levels of productivity. Sharp increases in wind stress over the shelf cause a spatially anchored ridge of upwelling in the centre of the EAB (Swart and Largier 1987, Jury 1994). Lutjeharms et al. (2000) found further evidence of upwelling on the EAB in a tightly circumscribed area

Table 1.1: Percentage productive area (mean chlorophyll concentration in upper 30m > 2mg.m^{-3}) for the west and south coast (coast to 500-m isobath); (from Brown 1992)

Season	Percentage Productive Area	
	west coast	south coast
Spring	52	20
Summer	46	6
Autumn	46	29
Winter	40	4

centred at Port Alfred. They suggested that this could have a profound effect on nutrient availability and primary productivity of the EAB.

1.1.1. Circulation patterns

The southern Benguela and the Canary are the only two upwelling ecosystems that have populations of pelagic fish migrating out of the nursery grounds to spawn (Wyatt et al. 1991), hence it is crucial in these systems that an efficient means exists to transport eggs and larvae from the spawning area to productive nursery grounds during a stage when they are unable to transport themselves actively. The efficiency of this transport can affect recruitment (Shannon et al. 1996), and Parrish et al. (1981) proposed that surface drift of eggs and larvae is a dominant environmental factor influencing the recruitment of pelagic fish. Bakun (1996a) defined a 'fundamental triad' of processes that determine suitable habitats for reproduction by marine organisms: enrichment, concentration and retention. The present study focuses on the transport of eggs and larvae from spawning areas to nursery grounds, and also on the retention within nursery areas. It is therefore important to consider the basic circulation patterns in the southern Benguela (Fig. 1.2**)** and the implications of these for transport and retention.

Along the west coast, a strong northward flowing shelf edge jet current (Bang and Andrews 1974) accelerates between Cape Point and St Helena Bay as a result of strong thermal gradients induced by upwelling and Agulhas Current intrusions and eddies (Hutchings et al. 2002). The jet current can transport eggs and larvae from the WAB and CAB to the west coast. At Cape Columbine this jet current diverges into a dominant offshore arm and a weaker inshore arm (Boyd et al. 1992), and eggs and larvae from the WAB can be lost form the system if they get caught in the dominant offshore arm of the Cape Columbine

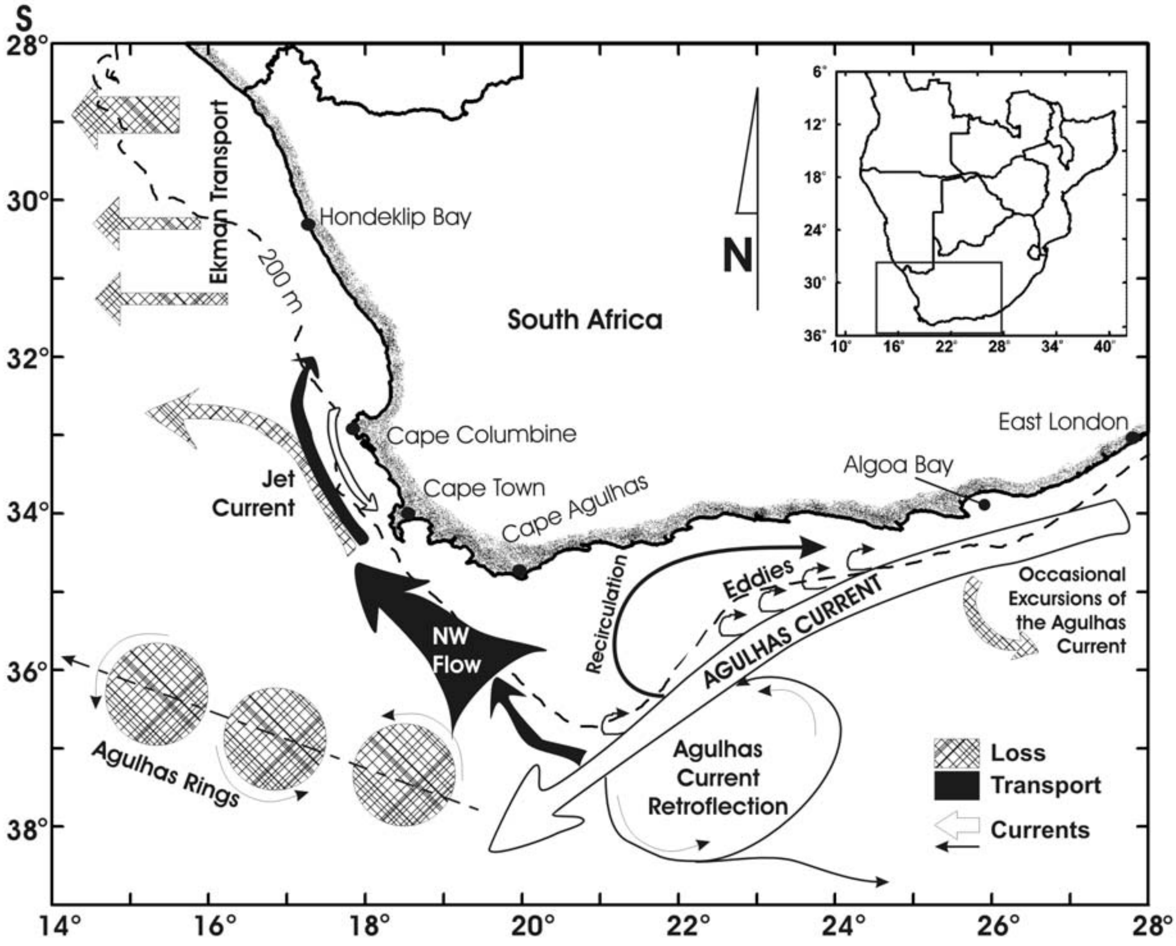

Fig. 1.2: Aspects of the circulation in the southern Benguela ecosystem affecting the transport, retention and loss of sardine eggs and larvae (amalgamated from Boyd et al. 1992, Boyd and Shillington 1994 and Hutchings et al. 2002)

jet current. Inshore of this northward flow is a southward flowing counter-current (Nelson 1983, Holden 1987, Nelson and Polito 1987).

The oceanography of the Agulhas Bank is forced by the Agulhas Current (and its inshore features), the prevailing wind field (Jury 1994), coastally trapped waves and the effect of seasonally varying insolation (Boyd and Shillington 1994). On the WAB, northerly and westerly winds dominate in winter (Shannon 1985), followed by easterly, upwelling-favouring winds in the summer (Jury 1988). The general drift of surface waters is to the northwest and this convergent water mass links up with the coastal jet current up the west coast (Hutchings et al. 2002). The effects of the Agulhas Current are mainly felt at the eastern part of the Agulhas Bank, where the current interacts intensively with the waters over the continental shelf (Swart and Largier 1987). Where the Agulhas Current moves away from the coast, near Algoa Bay, there are complex circulation patterns: cold-water eddies, intrusions of

Agulhas water onto the shelf and large offshore meanders or excursions of the Agulhas Current (Goschen and Schumann 1988, Boyd et al. 1992, Boyd and Shillington 1994). Just inshore of the current margin the flow is surprisingly predominantly eastward (Lutjeharms et al. 1989, Boyd et al. 1992), although this could be an artefact of reverse currents of westward-moving shear-edge cyclonic eddies on the inshore edge of the Agulhas Current (Mike Roberts, Marine and Coastal Management, DEAT, pers. comm.). At the apex of the Agulhas Bank, the Agulhas Current diverges from the coast and retroflects back into the Indian Ocean. The influence of the Agulhas Current does not always manifest as west or south-west flow across the Agulhas Bank as might be expected (Boyd et al. 1992), and highly variable meteorology causes an alternation between easterly and westerly flow (Jury 1994). In winter, westerly winds tend to predominate (Hutchings et al. 2002), whereas in summer easterly winds prevail, causing east to west flow along the outer portion of the Bank (Boyd and Shillington 1994).

Offshore losses of passively-drifting eggs and larvae along the west coast are primarily due to Ekman drift, but there are also losses through entrainment within eddies, upwelling filaments, or retroflection flows. Currents in St Helena Bay north of Cape Columbine permit retention of juveniles (Nelson and Hutchings 1987). Eggs from the CAB could get entrained in Agulhas Rings and get lost in the southern Atlantic (Duncombe-Rae et al. 1992). On the EAB, south-southwesterly flow appears responsible for offshore losses of eggs (Boyd et al. 1992) and the counter flow inshore of the Agulhas Current could hamper movement of eggs and larvae from the EAB across to the jet current, and instead act as a retention mechanism in the shallow parts of the EAB (Hutchings et al. 2002).

1.1.2. Migration patterns of pelagic fish in the southern Benguela ecosystem

Crawford (1980) defined two fundamental migration patterns of pelagic fish in the southern Benguela: that conducted by spring/summer spawners and that by winter spawners. The spring/summer strategy, in which he grouped species such as anchovy and sardine, is more widespread and has become the better understood of the two. Spawning occurs mainly east of Cape Point, from where eggs and larvae are passively transported northwards to the west coast nursery grounds (Shelton and Hutchings 1982, Nelson and Hutchings 1987). The juveniles then migrate back again to the spawning grounds. In contrast, the winter spawning strategy, which was found only to apply to chub mackerel (*Scomber japonicus*), relies more on the retention of reproductive products than their passive transport. In this strategy, eggs are spawned along the west coast during the winter months when, as a result of seasonal north-westerly winds, near-surface onshore flow retains them within St. Helena Bay (Boyd et al. 1992).

1.1.3. Sardine in the southern Benguela ecosystem

Since anchovy has been the main commercial target species in the southern Benguela ecosystem since 1965, far more research has been done and data collected on anchovy than sardine (Roel et al. 1994). The anchovy life cycle in the southern Benguela is therefore reasonably well understood. Anchovy spawning is restricted to the Agulhas Bank region and eggs are transported from here to nursery grounds on the west coast. Spawners then migrate back to the Agulhas Bank in order to spawn. It is often assumed that sardine follows a similar life cycle, particularly in terms of migratory patterns (e.g. Crawford 1980). However, even though their spawning behaviour in the southern Benguela is relatively poorly understood, enough evidence exists to show that sardine differ notably from anchovy.

Sardine (known locally as pilchard) are cool-water epipelagic clupeoids with an anti-tropical distribution (Beckley and van der Lingen 1999). Generally found in upwelling ecosystems, their opportunistic feeding enables them to be very successful in unstable environments such as these (James 1988). Sardine oocytes do not mature simultaneously and therefore female sardine spawn individual batches on several occasions within a single spawning season (Quintanilla and Pérez 2000). Spawners of this sort are termed batch (multiple, serial or heterochrone) spawners. Sardine have historic importance in the pelagic fishery of South Africa where, until the collapse of the sardine stock in the mid 1960s, they dominated pelagic landings. In recent times the southern Benguela stock has begun to recover and catches are on the rise **(**van der Lingen and Huggett 2003**)**.

The southern Benguela sardine stock has a wide-ranging distribution stretching along the entire South African coastline from the Orange River, along the nutrient-rich west coast, round Cape Point and up to KwaZulu-Natal (27°S) (Beckley and van der Lingen 1999).

Sardine do not appear to have a fixed spawning area and spawning has been reported along almost the entire range of the stock (Anders 1975, Armstrong et al. 1991, Barange et al. 1999). Likewise the sardine spawning season is extensive, occurring year round but mainly from August to late March (Anders 1975). The main spawning season has two peaks: September-October and February-March (van der Lingen et al. 2001).

Sardine spawn along both the south coast and the west coast (Fig. 1.3 A). Surveys conducted from 1950 to 1958 (prior to the collapse of the sardine fishery) between Lambert's Bay and Saldanha Bay found sardine eggs to be abundant up to 75 km offshore (Shannon 1998). Examination of a time series of sardine egg distribution and abundance collected on routine research cruises (Barange et al. 1999, Beckley and van der Lingen 1999, van der Lingen et al. 2001) has shown that eggs are commonly found west of the Cape Peninsula but rarely extend further north than Hondeklip Bay. For eggs spawned along the west coast successful recruitment does not require efficient transport, but rather avoidance of offshore advection and for the eggs to be retained within the nursery area. Eggs on the south coast tend to be found either west or east of the Agulhas Bank, with few in the central region, though the relative contribution of each stratum varies greatly over the length of the time

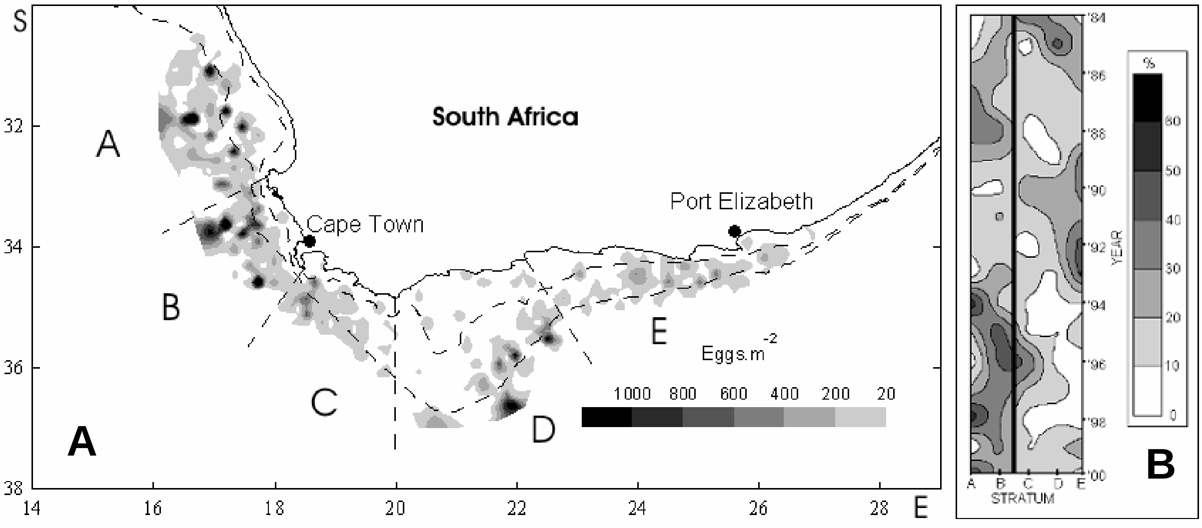

Fig. 1.3: (A) Composite distribution map for eggs of sardine derived from CalVET net samples collected during spawner biomass surveys over the period 1984-2000 (van der Lingen and Huggett 2003) and (B) changes in distribution patterns of sardine eggs through time showing the percentage of total egg numbers by stratum. Contouring is used to interpolate between years and strata. The vertical line indicates the approximate position of Cape Point (updated from van der Lingen et al. 2001). Strata: A = west coast, B = southwest coast, C = western Agulhas Bank, D = central Agulhas Bank, E = eastern Agulhas Bank

series (Fig. 1.3 B). Fowler (1998) concluded that the apparent patchiness of sardine spawning indicated great flexibility in terms of spawning habitat. Twatwa et al. (2005) confirmed sardine to be fairly unspecific with regard to spawning habitat selection and reported that spawning occurs over a broad range of environmental conditions, generally in unstable environments influenced by strong winds and currents. This flexibility frees sardine from being restricted to the Agulhas Bank as their only spawning ground (as is the case for anchovy), allowing spawning to extend up the west coast as well.

1.2. AIMS AND HYPOTHESES

In general, spawning of small pelagic fish species usually occurs in very restricted and distinct areas relative to the distribution of the species as a whole (Mullon et al. 2002), with fish spawning once or several times a year, but generally over a limited period of time. It is thought that this has evolved as a mechanism to synchronise the occurrence of larval stages with the environmental conditions that are optimal for their survival (Roy et al. 1992). However, sardine in the southern Benguela spawn along their entire distribution range and almost all year round (Beckley and van der Lingen 1999). The primary aim of this thesis is to examine the consequences of the spatially and temporally expansive sardine spawning pattern and to examine the main patterns that emerge within this all-encompassing spawning strategy. This aim is pursued by testing a few key hypotheses with a series of computer simulation experiments.

Considering the wide distribution of sardine spawning, and particularly its eastern extent, it is reasonable to assume that not all of the eggs spawned in the east ultimately reach the west coast nursery ground. It was decided to test whether it is possible for eggs and larvae to reach and be retained in a south coast nursery area on the CAB and EAB in sufficient numbers to make recruitment a possibility. The first experiment assesses whether it is possible for sardine recruitment to occur on both the west coast and the south coast? Hypothesis 1 (*H1*): *Null hypothesis (H_O): The spatial and temporal spawning pattern of sardine is such that the majority of larvae reach the west coast nursery area.*

Alternative hypothesis (H_A): Not all of the sardine recruitment occurs on the west coast. Conditions on the central and eastern side of the Agulhas Bank on the south coast are such that significant retention should occur there and that this area can act as a nursery area.

Circulation patterns in the southern Benguela, while complex, show predictable seasonal patterns. Nelson and Hutchings (1987) even proposed the southern Benguela as a closed system for the passive transport of anchovy and sardine reproductive products. Are there closed systems in which sardine spawning occurs? Hypothesis 2 (*H2*):

H_O *: There are no boundaries to the movement of eggs and larvae in the southern Benguela ecosystem. They are transported randomly and no clear spatio-temporal patterns of transport and retention of eggs and larvae exist from year to year.*

H_A *: Circulation patterns impose limitations on movement of sardine eggs and larvae across the southern Benguela. Sardine spawning occurs in closed system(s) determined by the circulation of the region.*

It is important that larvae are able to swim and feed when they arrive in any nursery ground if they are to successfully recruit. Temperature is one of the dominant environmental factors impacting on the development of eggs and larvae. Temperature on the west coast differs notably from that of the Agulhas Bank both spatially and temporally (Mitchell-Innes et al. 1999, Richardson et al. 2000). Therefore, the second experiment examines the effect of temperature on recruitment of individuals spawned on the west and south coasts. Does spawning occur on the south coast, out of the west coast nursery area, because conditions there are more suitable for good development of eggs and larvae? Hypothesis 3 (*H3*):

H_O *: There are no spatial variations in development rate across the southern Benguela ecosystem.*

H_A *: Because of the cold waters on the west coast development is slow, leading to increased offshore loss before individuals develop to the stage when they are able to recruit. Therefore, along with transport/retention efficiency, temperature plays a role in determining the level of recruitment.*

Mortality rate in the early life stages of most fish species is determined to a large degree by external physical conditions. One such factor is the temperature of ambient water and the effect this has on physiological processes. Do cold temperatures on the west coast lead to greater levels of mortality of the first stages of larvae? Hypothesis 4 (*H4*):

H_O *: Temperature-induced mortality does not significantly affect the levels of modelled recruitment to either nursery area.*

H_A *: Mortality due to lethal minimum temperatures impacts on the relative importance of transport to and retention on the west coast more than for the south coast nursery grounds.*

The vertical position of individuals affects their horizontal movement because the velocity field of the water column is often vertically tiered. This is especially true in upwelling ecosystems where a change of 10m in depth can place an individual in a current moving in the opposite direction. The third experiment assesses the effect of vertical distribution of eggs and larvae and by comparing observed vertical distributions with model outputs, examines the ability of eggs and larvae to change their vertical position through physical characteristics or active behaviour. Do eggs and larvae move vertically in the water column due to factors other than the vertical movement of the water? Hypothesis 5 (*H5*):

H_O *: The vertical position of eggs and larvae is determined by the depth at which they were spawned and the vertical movement in the water column.*

H_A *: Physical characteristics and behavioural adaptations have a significant effect on the vertical position of eggs and larvae.*

Numerous reasons, such as predator avoidance, prey abundance and energetic considerations, can be used to explain the pattern of vertical distributions of eggs and larvae. It also has been proposed that vertical movement of larvae is used as a mechanism to increase transport to, or retention in, optimal nursery areas (areas where Bakun's triad of retention, concentration and enrichment are favourable). Do observed vertical distributions of eggs and larvae increase the transport of individuals to optimal nursery areas? Hypothesis 6 (*H6*):

H_O *: The vertical position of eggs and larvae significantly increases the level of modelled recruitment to optimal nursery areas.*

H_A *: The vertical position of eggs and larvae does not significantly increase the level of modelled recruitment to optimal nursery areas. Observed vertical distributions of individuals are not principally for the purpose of enhanced transport and retention and other factors such as predation, energetics or prey abundance might be more important.*

The size structure and spatial distribution of sardine spawners differs from year to year, and specific fecundity increases with age in sardine females (Le Clus 1989). Therefore, the differences in distribution of the various size classes of sardine and quantitative differences in egg production (fecundity) determine the relative importance of each spawning area to the sardine stock. The fourth experiment assesses the implications of spawner location and age structure to the recruitment strength of sardine from year to year. Hypothesis 7 (*H7*):

H_O : *The location of sardine spawners and their age do not significantly influence the level of recruitment from year to year.*

H_A : *Spawner location and age can impact the level of recruitment from year to year.*

The west coast is considered to be a favourable nursery area because of high levels of production in this region. Does the relative amount of reproductive output reaching the west coast nursery area determine the level of recruitment success? Hypothesis 8 (*H8*):

H_O : *Both the west and south coast nursery areas support high levels of recruitment.*

H_A : *The west coast nursery area is more important in determining the level of recruitment from year to year than the south coast is.*

1.3. STRUCTURE OF THE THESIS

This thesis is made up of seven chapters. Following this introductory chapter is a chapter detailing the methodology used in the implementation of the individual-based model (IBM) experiments and the descriptive age structure experiment. The broad philosophical modelling approach is presented along with a detailed description of individual-based modelling. The coupling of IBMs to hydrodynamic models is explained and the simulation procedures are outlined, as well as the sensitivity analyses of the results. Chapters 3 to 5 describe in detail each of three IBM experiments carried out. Chapter 3 addresses the hypothesis of recruitment occurring on the south coast (*H1*) and examines the effect of spatio-temporal spawning patterns on the transport and retention of particles (*H2*). Chapter 4 incorporates a temperature-dependent development rate model to explore the possible effects this could have on levels of recruitment to the two proposed nursery grounds (*H3*). Temperature-induced mortality and the possible effects of this are also addressed (*H4*). Chapter 5 looks at the vertical movement of individuals in the model caused by physical and biological factors (*H5*) and compares different methods of vertically positioning individuals. The effect of vertical movement of individuals on transport and retention is also examined (*H6*). Chapter 6 considers differences in fecundity of each age class of the sardine stock and uses a size-based fecundity model to examine how this manifests in regional differences of reproductive output by sardine in the southern Benguela. It also looks at how spawner location (*H7*) and final nursery ground (*H8*) influence estimated levels of recruitment. The final chapter synthesises the results of the thesis in terms of the hypotheses tested and addresses the implications of the results for understanding the life history of sardine in the southern Benguela. Current patterns in sardine spawning behaviour are examined in light of the present findings and future directions for research are suggested.

CHAPTER 2: MODELLING APPROACH AND METHODS

2.1. PHILOSOPHICAL MODELLING APPROACH

In his review of the use of individual-based models (IBMs) in ecology, Grimm (1999) outlined the general philosophical approach that should be taken when developing IBMs. The same basic principles were used for this project and are detailed below (adapted from Grimm et al. 1999 and Mullon et al. 2003):

Principle 1: Clearly state the aims of the modelling.

There is a tendency for models to be thought of as predictive even though this is not always the case. Heuristic models, designed to either provide answers to very specific questions or to generate hypotheses regarding understudied areas, do not produce results that are predictive. Such models are exploratory and are designed to understand the processes underlying the system dynamics and not to try predict outcomes in the ecosystem (e.g. recruitment).

Principle 2: Keep It Straight and Simple (KISS).

Interpreting what the results of a model mean in a real context can be very difficult if the model is too complex. Therefore, models need to be kept simple so that patterns within them can be accurately attributed to particular variables and in this way simple hypotheses can be tested. Layers of complexity need to be added one step at a time and the results analysed at each step to identify what changes (if any) additional variables or constraints have effected within the model environment and how these relate back to observations of reality.

Principle 3: Use an experimental approach.

Model experiments need to be built in a logical manner, similar to all ecological studies. But as modellers are creating their own ecosystem in which to work, it is important to lay down a logical approach and not to deviate from it. Building an experiment follows four basic steps (Mullon et al. 2003):

1. Define your hypotheses in terms of processes.
2. Define the method by which you aim to test these hypotheses.

3. Test the hypotheses.
4. Accept the results, even if they are unanticipated.

The last step applies to all scientific research, but in modelling it prevents endless cycles of fine-tuning. Once the experiment has been run, it is important to apply a sensitivity analysis to the results in order to assess the sensitivity of the model to variations in its parameters.

Principle 4: Use a pattern-oriented analysis.

Grimm et al. (1996) noted that model-derived patterns could allow for a better understanding of the processes underlying observed patterns should they compare closely with these observations. Results obtained from model experiments need to be compared with real data from the ecosystem being studied in order for the results to be placed in context. Test patterns should be defined prior to the experiment, and insight into the ecosystem can then be gained by trying to simulate conditions under which these patterns are thought to occur and rejecting the rules that do not cause these patterns while accepting those that do.

Keeping to the philosophy outlined above, the modelling process was applied in a step-by-step manner. A series of IBMs was coupled with the output of a 3-D hydrodynamic model known as PLUME (the same outputs being used for each IBM). Each IBM experiment constituted a set of simulations. For each experiment the assumptions, the fixed parameters, the variables, and the criteria for the dependent variables were clearly defined. Sensitivity analyses were applied to the results as well as a number of other statistical tests (e.g. χ^2 tests, t-tests). Fig. 2.1 shows the methodological approach used for each experiment.

2.2. MODELLING OVERVIEW

2.2.1. Traditional stock models and the origin of IBMs

Huge stock sizes, extensive geographic distributions and the inaccessibility of pelagic fish stocks pose limits on the ability of ecologists to accurately sample such populations, making it unfeasible to study these stocks experimentally. As a result, modelling has long played a part

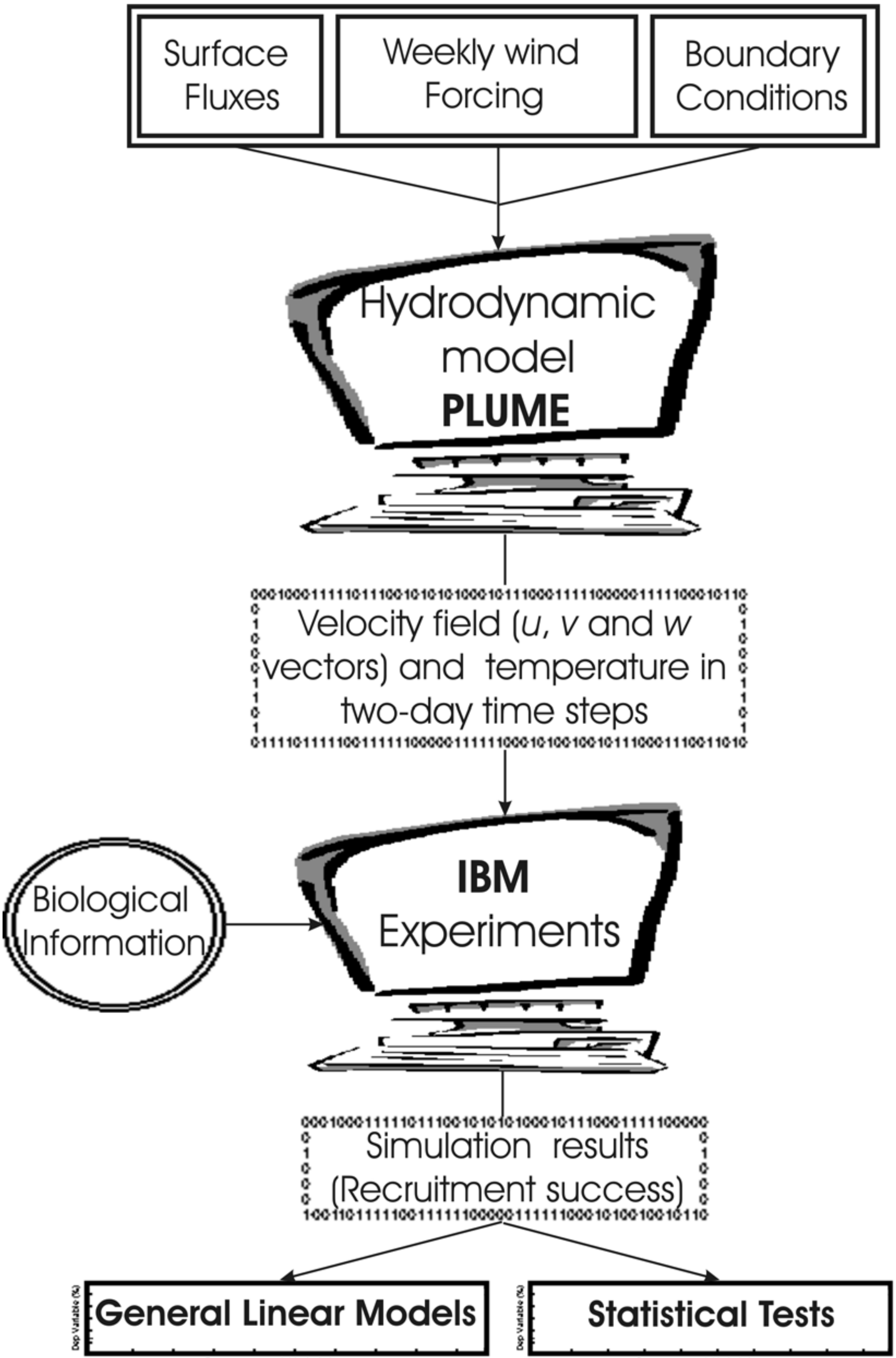

Fig. 2.1: Flowchart of the methodological approach. The PLUME model was run independently of this study (Penven 2000), which simply used its outputs to run the individual-based model (IBM) simulations

in research and management of pelagic fish stocks. Recruitment has proved to be especially difficult to model (Frank 1991). The recruitment of small pelagic fish is characterised by large interannual variability (Sissenwine 1984, Smith 1985) and this is one of the primary sources of uncertainty in many fisheries (Csirke 1980, Doubleday 1985). As fishing often begins before recruitment for the season is known, increasing the knowledge of what regulates recruitment has long been an aim of fisheries modellers (Wooster and Bailey 1989).

Traditional stock management models examine whole-stock population dynamics based on some compensatory model of the stock-recruitment relationship (Heath and Gallego 1997). But since Ricker (1954) and Beverton and Holt (1957) established the general framework for modelling recruitment dynamics, it has become clear that environmental factors cannot be ignored (Sharp 1981, Sharp and Csirke 1983). Most pelagic clupeoid fish stocks spawn massive numbers of eggs over a wide spatial and temporal range. These eggs develop into planktonic larvae that have a high mortality rate, both inherent and influenced by environmental conditions (Blaxter and Hunter 1982, Armstrong and Shelton 1990). Present recruitment models are largely based on the principle first stated by Hjort (1914) that differential larval mortality gives rise to variable recruitment. Therefore, these models focus mainly on factors, both environmental and biological, that influence larval mortality.

Since each individual has a unique spawning origin and trajectory in time and space, certain fractions of the population might have enhanced probabilities of survival compared to others (Heath and Gallego 1997). In particular, circulation features could be important in determining relative survival probabilities among different individuals (Hinckley et al. 1996). These can act directly, as in the case when early life stages need to be transported to, or retained within, a productive nursery area, or indirectly by causing individual histories of exposure to environmental conditions such as temperature and salinity to differ. Traditional population models, which aggregate individuals within a population into state variables representing population size, are not capable of effectively dealing with these spatial and temporal differences in survival. This led to the development of individual-based models (IBMs), which can be applied to problems that traditional state variable models cannot easily address (Grimm 1999).

The first IBM for fish was presented by DeAngelis et al. (1979), who developed a simulation with individuals as the basic units and explicitly considered processes relevant to individuals. Individual-based modelling became an explicitly delineated approach of ecological modelling following a review by Huston et al. (1988). Whereas the model of DeAngelis et al. (1979) and the review by Huston et al. (1988) laid the groundwork, the rise of IBMs was largely facilitated by significant increases in computer power during the 1980s and 1990s. Both hardware and software development increased processing ability and speed. New computing languages (object oriented programming in particular) and packages also made programming and development of IBMs simple and efficient. Heath and Gallego (1997) provide a comprehensive review of IBM models of early life history stages of fish.

An IBM relies on a bottom-up approach (Fig. 2.2) that attempts to understand how the properties of a system develop from interactions at the level of the individual (Grimm 1999). Emergence is the term given to the progression by which processes operating at the level of the individual manifest as properties at the population level (Lepage and Cury 1997). An effective IBM can identify which processes at the individual level give rise to observable patterns at the population level, such as spawning behaviour in fish. IBMs allow for integration of environmental, ecological and biological data, and can explicitly deal with ecosystems in which spatial distribution is important. By creating a population of distinct individuals, rather than standardising each individual with averaged population attributes, IBMs are able to describe differences and interactions among individuals and between individuals and their environment.

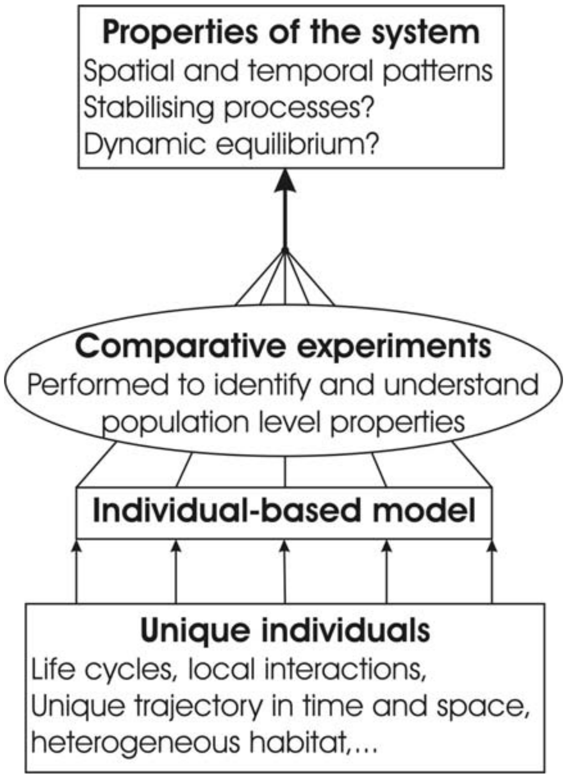

Fig. 2.2: Conceptual diagram of the 'bottom-up' approach of individual-based modelling (adapted from Grimm 1999)

Early life history stages are commonly represented in models as passive particles confronting virtual environments created by 3-D hydrodynamic models. This Lagrangian approach was used by Huggett et al. (2003) and Parada et al. (2003) for anchovy in the southern Benguela ecosystem and has also been used in the past for other fish (e.g. Heath and Gallego 1997) and zooplankton (e.g. Miller et al. 1998). When biological properties (such as egg buoyancy, density, shape, etc.) are added to these particles, they become unique individuals.

2.2.2. The PLUME hydrodynamic model

A numerical hydrodynamic model, the Regional Ocean Modelling System (ROMS), developed at Rutgers University and the University of California **(**Haidvogel et al. 2000b**)**, has been adapted to the southern Benguela (Penven 2000, Penven et al. 2001b) by a multi-disciplinary team under the umbrella of the South African-French bilateral IDYLE programme (**I**nteractions and Spatial **DY**namics of renewable resources in upwe**L**ling **E**cosystems, Fréon et al. 2002), the follow-up of the VIBES project (**VI**ability of exploited pelagic fish resources in the **B**enguela **E**cosystems in relation to the environment and **S**patial aspects, Fréon et al. 1998). The model uses basic equations of fluid motion in a rotating framework to calculate current, temperature, salinity and density fields (Penven et al. 2001b).

The southern Benguela application of the ROMS model, PLUME, consists of a curvilinear, pie-shaped grid located at the south-western portion of South Africa from 28°S to 40°S and from 9°E to 24°E (Fig. 2.3); (Penven et al. 2001b). On the northern edge the grid stops just beyond the Orange River mouth, and extends on the south coast as far east as Cape St Francis. The horizontal model resolution ranges from 9 km along the coast, where more accurate solutions are required, and increases linearly to 16 km offshore. There are twenty vertical levels, with high resolution near the surface (9m) and a gradually decreasing resolution towards the bottom layers (1000m for the deepest level along the oceanic plain). The topography of the area is realistic but is slightly smoothed in order to allow for stable and accurate simulations (Song and Haidvogel 1994, Haidvogel et al. 2000a). With 20 vertical levels, 65 alongshore lines and 144 cross shelf lines, the grid has a total of 187 200 points (some of those lie over the land section and are masked). At each point, for every time step

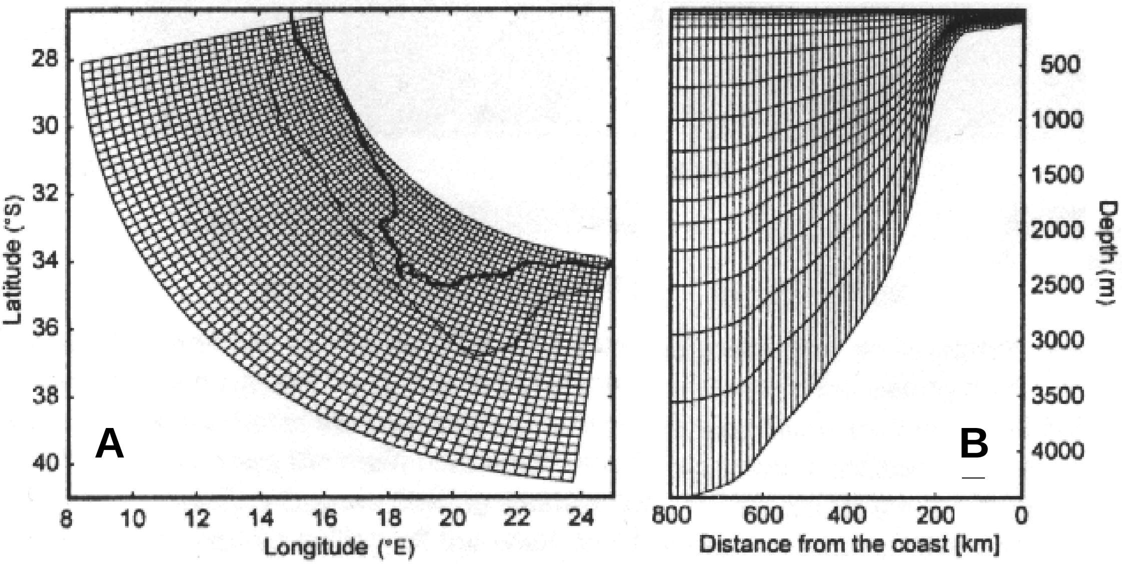

Fig. 2.3: The (A) horizontal and (B) vertical grids used in the regional configuration of ROMS in the southern Benguela ecosystem (PLUME); (from Penven et al. 2001b)

(two days), temperature, salinity, density and velocity strength and direction are calculated (Fig. 2.4).

The PLUME grid has three open (seaward) boundaries. It is important that the inner solution is allowed to radiate through the open boundaries without reflection, and vital information from the surrounding ocean needs to enter the model (Lutjeharms et al. 2003). ROMS employs an active open boundary scheme (Marchesiello et al. 2001) that estimates the horizontal velocities in the vicinity of the boundaries. Features produced within the model are allowed out to the open ocean following a radiation condition. Inputs from the surrounding ocean are forced by seasonal time-averaged outputs of the Agulhas As Primitive Equations (AGAPE) basin-scale ocean model (Biastoch and Krauβ 1999). The model itself is forced by heat and salinity fluxes and a wind stress scheme. The heat and salinity fluxes are obtained from the COADS ocean surface monthly climatology (Da Silva et al. 1994) and the ERS1/2 wind stress scheme (a weekly wind field that has a 1°×1° resolution) comes from the Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER) (Bentamy et al. 1996). Blanke et al. (2002) found that sea surface temperature (SST) variability across the Agulhas Bank was mostly driven by wind and therefore had a high level of predictability (90%). The west coast was found to have a lower level of predictability of SST (30-70%) because SST in this region appears to be driven by both wind and mesoscale activity. Despite the fact that the

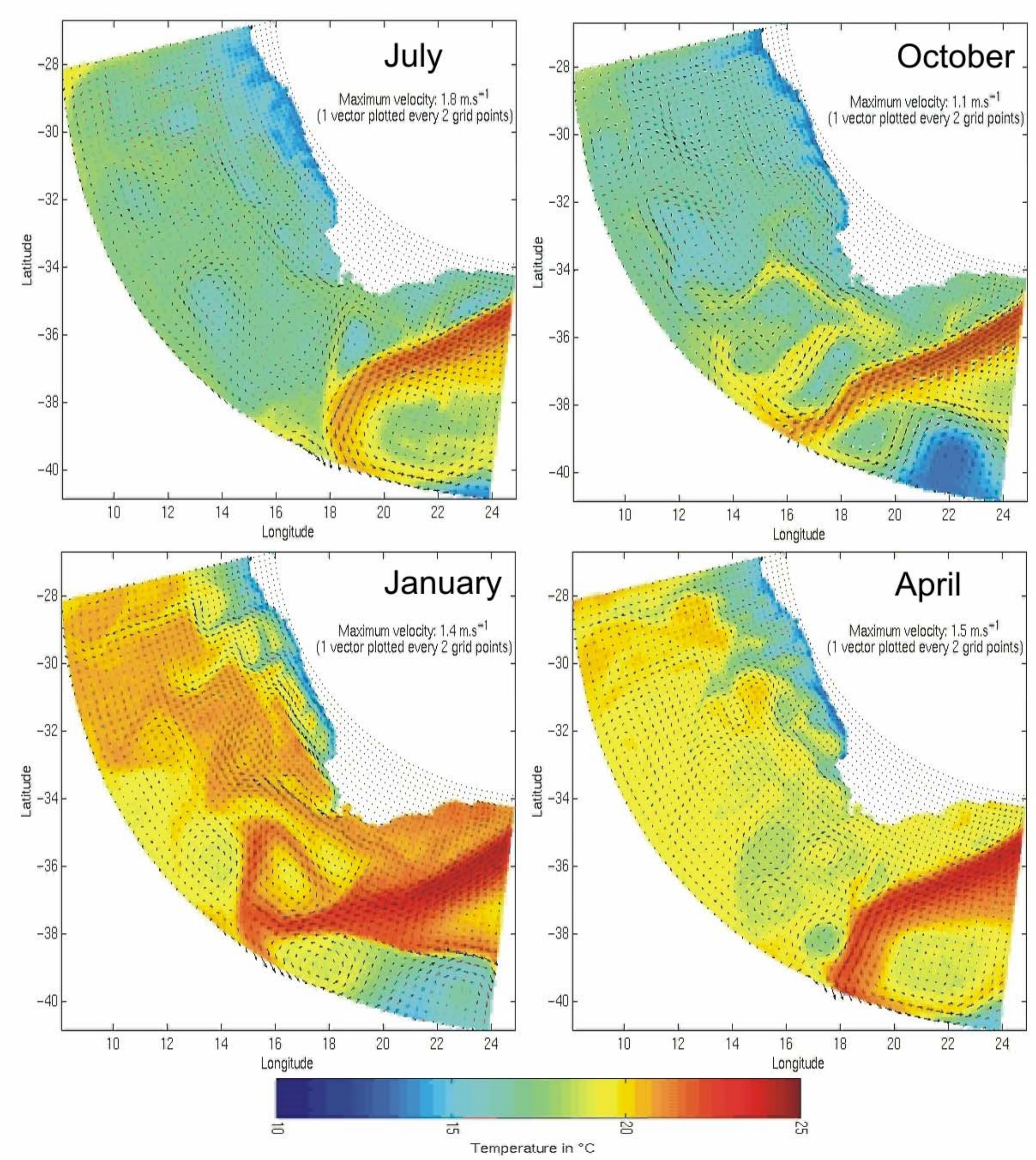

Fig. 2.4: Sea surface temperatures and flow vectors from the PLUME model for four months: July (mid-winter), October (first spawning peak), January (note intrusions of warm Agulhas Bank water up the west coast), and April (autumn)

model produces some of its own variability, Blanke et al. (2002) concluded that, in general, the model shows a high level of correlation with the real SST of the region.

2.2.3. Coupling IBMs with the outputs of the hydrodynamic model

Numerous IBMs have previously been coupled with PLUME outputs, all of them dealing with the early stages of anchovy (Mullon et al. 2003). One such IBM for the southern Benguela ecosystem was developed by Huggett et al. (2003), who applied a particle tracking model to simulate the Lagrangian transport of particles. They investigated the success of different spatio-temporal spawning strategies of anchovy in terms of the number of particles reaching the west coast nursery grounds within a certain time window. The model quantified the effect of the timing, location, frequency and patchiness of spawning on transport success and the interannual variability of this. It was found that there was good agreement between observed spawning patterns and the optimal temporal and spatial strata for successful transport, suggesting that anchovy spawning patterns are an adaptation to the circulation patterns in the region. Parada et al. (2003) found particle buoyancy and the area of particle release to be the major single determinants of transport success for anchovy in this system. Mullon et al. (2002) took a different approach by developing an evolutionary IBM for the recruitment of anchovy in the southern Benguela. They found the most important constraints determining the observed spawning pattern of anchovy was a preference for water temperatures above 14°C and the avoidance of offshore currents leading to the loss of particles. Most recently Lett et al. (in press) have used IBM techniques to examine the enrichment and retention aspects of Bakun’s fundamental triad of processes (Bakun 1996a) impacting on the survival and recruitment of the early stages of pelagic fish in the southern Benguela ecosystem. The models of Huggett et al. (2003), Mullon et al. (2002) and Parada et al. (2003) utilised repeated climatology that created inter-annual variability not corresponding to actual years. The IBMs presented here use more recent runs of the PLUME model incorporating more realistic climatological forcing (weekly wind fields: ERS time series from 1991 to 1999), corresponding to actual years in the 1990s.

2.3. PROGRAMMING

The IBM was programmed in Java using JBuilder (Borland Software Corporation 2001). Java is an object-oriented programming language, which allows for a population of individuals to be created, all of which share the same attributes but each with its own value or state for each attribute. Each individual is exposed to its own environmental conditions and follows its own path within the 3-D advective environment of the PLUME model. In addition, each individual has its own memory in which its spawning strategy (i.e. location, date and depth of release), age and stage of development is encoded.

2.4. EXPERIMENTAL PROTOCOL

2.4.1. Model assumptions

Models are not exact replicas of reality, and certain assumptions need to be made to simplify the model. It is important that these assumptions are explicitly defined, because the results of the model need to be interpreted within the limits of these assumptions. Interpreting model results in relation to reality depends to a large degree on the validity of these assumptions. For these experiments, various assumptions were made regarding both the hydrodynamic model and the IBMs. A list of some of the major assumptions made is presented in Table 2.1.

2.4.2. Parameters of the models

The majority of the parameters used in the experiments (Table 2.2), including all the fixed parameters, were the same throughout. This allowed for direct comparison between models as extra levels of complexity were added.

Nine spawning areas (*Spawning Area*, Fig. 2.5) were chosen to cover as much of the widespread spawning extent of sardine (*Sardinops sagax*) as the PLUME model would allow and particles were released randomly across these areas. Five of the areas (western Agulhas Bank (WAB), central Agulhas Bank inshore (CABin), central Agulhas Bank offshore (CABoff), eastern Agulhas Bank inshore (EABin) and eastern Agulhas Bank offshore (EABoff)) were set according to zones used in previous IBM experiments utilising PLUME (Huggett et al. 2003, Parada et al. 2003). These five areas effectively divide the Agulhas

Table 2.1: Some of the major assumptions made by the PLUME hydrodynamic model, the particle tracking model, the development model and vertical positioning schemes. Precedent = studies in which the same assumption has been made, or in which this assumption has been shown to hold true

Assumption	Precedent
Hydrodynamic model	
The temperature and velocity field outputs realistically represent the dynamics of the ecosystem	Lutjeharms et al. 2003, Penven et al. 2001a
The weekly wind scheme and monthly heat fluxes produce sufficiently realistic circulation patterns, comparable to that of the actual years being simulated	Penven 2000, Blanke et al. 2002
The simplistic bathymetry does not significantly affect the accuracy of the circulation patterns	Penven 2000, Haidvogel et al. 2000a, Lutjeharms et al. 2003
Boundary effects do not significantly hamper the performance of the model	Lutjeharms et al. 2003
Particle Tracking Model	
Particles are transported in a Lagrangian fashion - the effects of diffusion are considered to be negligible	Huggett et al. 2003, Parada et al. 2003, Mullon et al. 2003
The number of particles used (10 000) ensures stability of the IBM outputs and is adequate for statistical testing	Huggett et al. 2003, Parada et al. 2003, Mullon et al. 2003, Section 2.5.1.
The extensive spatial scale for release of particles is adequate to explore spatial variability in recruitment success	van der Lingen and Huggett 2003
Frequency and patchiness of spawning is not considered to have a significant effect on the level of recruitment success	Huggett et al. 2003
Eggs and larvae are analogous to passive drifters; other abilities and biological properties have a negligible effect on the way they are transported	Huggett et al. 2003
Development Model	
The Bělehrádek function of temperature vs. egg and larval development time is realistic	King 1977
Laboratory temperature vs. development time data does not differ significantly from that in the field	Moloney et al. 1994
Minimum temperatures exist for yolk-sac larvae, below which mortality occurs after a predetermined period	Lasker 1964, King 1977
Larvae are able to survive and retain themselves within a nursery area following the point of postflexion (late larva), as they can now feed and swim	-
Vertical Positioning	
Observations of egg and larva vertical distributions apply for all times of the year	-
There are no significant diel differences in current flow that affect the transport and retention of sardine eggs and larvae in the offshore pelagic environment	-
Sardine and anchovy larvae have similar diel vertical distribution patterns in the southern Benguela ecosystem	-

Table 2.2: The fixed parameters and variables used in the IBM experiments

	IBM Experiment		
	Lagrangian	Temperature-dependent Development	Vertical Distribution
Fixed Parameters			
Number of particles	✓	✓	✓
Duration of release of particles	✓	✓	✓
Tracking period	✓	✓	✓
Lethal minimum temperature§	✗	✓	✓
Egg density†	✗	✗	(✓)
Egg diameter†	✗	✗	(✓)
Variables			
Spawning Area	✓	✓	✓
Year	✓	✓	✓
Month	✓	✓	✓
Depth	✓	✓	✗
Trial	✓	✓	✓

✓ = present, (✓) = present in certain simulations, ✗ = absent
§ = yolk-sac larva stage only, † = drawn from a normal distribution of observed data

Bank and follow convention in the region. Armstrong et al. (1991) found that sardine spawn as far east as Durban, hence it would be preferable for the EABin and EABoff areas to extend further east than Cape St Francis but unfortunately this is beyond the eastern extent of the PLUME grid. The 125m depth contour in the model domain, which more closely represents the actual 100m isobath due to topographical smoothing, is used on the central and eastern Agulhas Bank to separate the low spawning intensity coastal zones from the high spawning intensity offshore zones. The anchovy IBMs of Huggett et al. (2003), Parada (2003) and Parada et al. (2003) included spawning across the whole Agulhas Bank, but the possibility of spawning on the west coast was not incorporated, as is required for any model of sardine spawning. Hence, the remaining four spawning areas, upper west coast inshore (UWCin), upper west coast offshore (UWCoff), lower west coast inshore (LWCin) and lower west coast offshore (LWCoff), are all on the west coast (Fig. 2.5). The west coast has a much narrower continental shelf than the Agulhas Bank, and Barange et al. (1999) found that isolated patches of sardine spawners that were often found along the west coast tended to be concentrated further offshore than sardine on the WAB. Also, previous studies (e.g. Fowler and Boyd 1998) have found that the frontal jet plays an important role in the transport of eggs between the Agulhas Bank and the west coast nursery ground and that the position of this jet varies between the 200m and 500m isobaths. Therefore, it is believed that an offshore area between

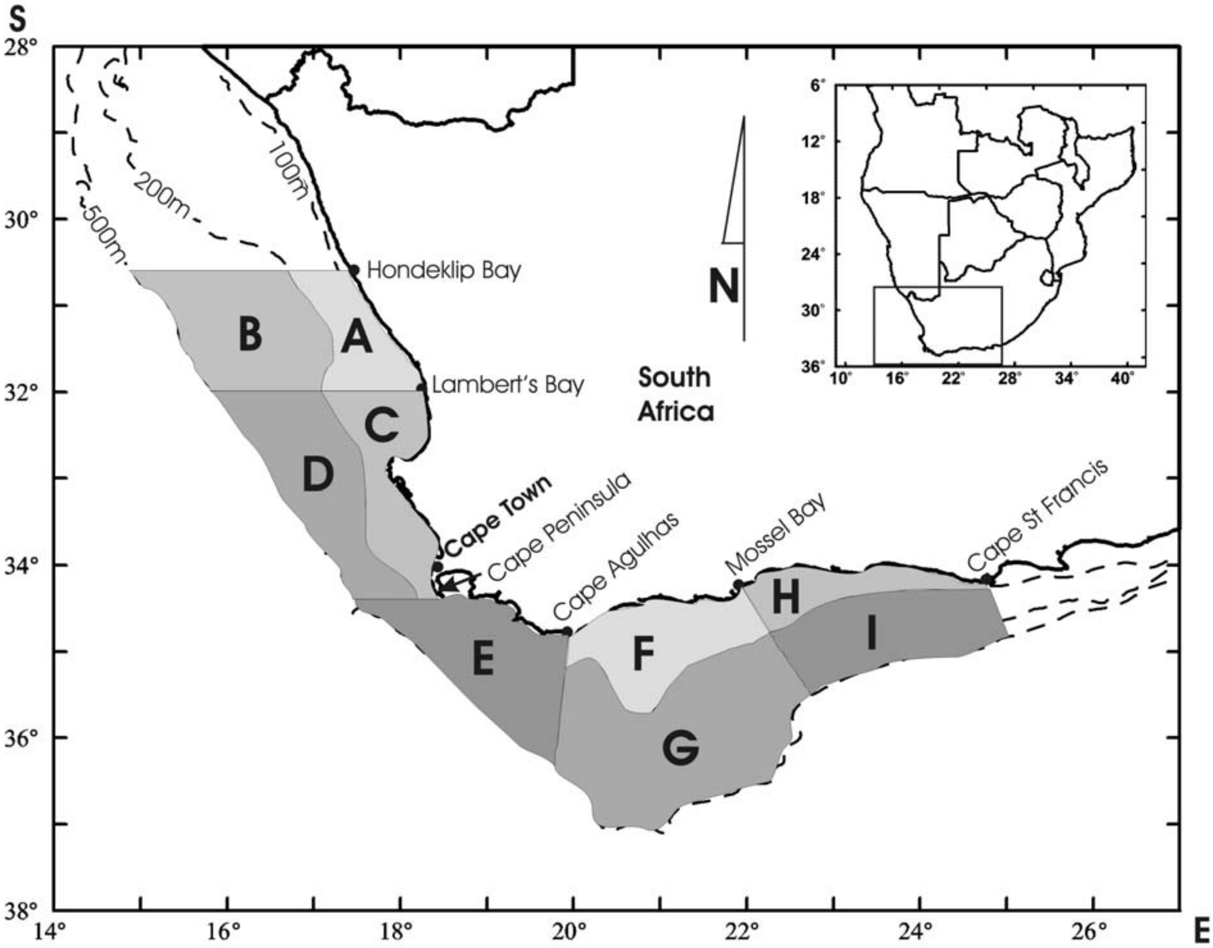

Fig. 2.5: The nine spawning areas used in the IBM experiments. A = upper west coast inshore (UWCin), B = upper west coast offshore (UWCoff), C = lower west coast inshore (LWCin), D = lower west coast offshore (LWCoff), E = western Agulhas Bank (WAB), F = central Agulhas Bank inshore (CABin), G = central Agulhas Bank offshore (CABoff), H = eastern Agulhas Bank inshore (EABin), I = eastern Agulhas Bank offshore (EABoff)

200 and 500m depth should be different in terms of current features to an area inshore of the 200m isobath. Bearing this in mind, and because the west coast has a steep coastal shelf, the west coast spawning area was divided using the 200m isobath. The majority of spawning on the west coast appears to occur west and north of the Cape Peninsula (Fig. 1.3). Hence the west coast spawning areas were divided into low intensity northern areas (upper west coast) and high intensity southern areas (lower west coast), north and south of Lambert's Bay, respectively.

Particles were released every month of the PLUME output (*Month*) from July 1991 until June 1999, effectively covering eight complete spawning seasons (*Year*). The depth ranges for release of the particles (*Depth*), 0-25, 25-50 and 50-75m, were identical to those used in anchovy IBM simulations reported by both Huggett et al. (2003) and Parada et al. (2003). These ranges are now considered standard for IBM experiments utilising PLUME. Particles were released randomly over these ranges, but since a large number of particles was released, they tend towards a uniform distribution over the whole range. After particles had been released they were allowed to move freely in the vertical domain and were not confined to their initial depth range. In a study off Southern Australia, Fletcher (1999) found that recently-spawned sardine eggs were most abundant at depths of 40-60 m (corresponding to 60% of total bottom depth). Matsuoka et al. (2002) similarly found that the spawning depth of Japanese sardine (*Sardinops melanostictus*) was approximately 40-60m. In a similar study in the southern Benguela ecosystem, Dopolo et al. (2005) found that sardine spawn mainly within the top 60m of the water column (Fig. 2.6). Hence the depth ranges used in these IBMs are assumed to adequately capture the vertical extent of sardine spawning.

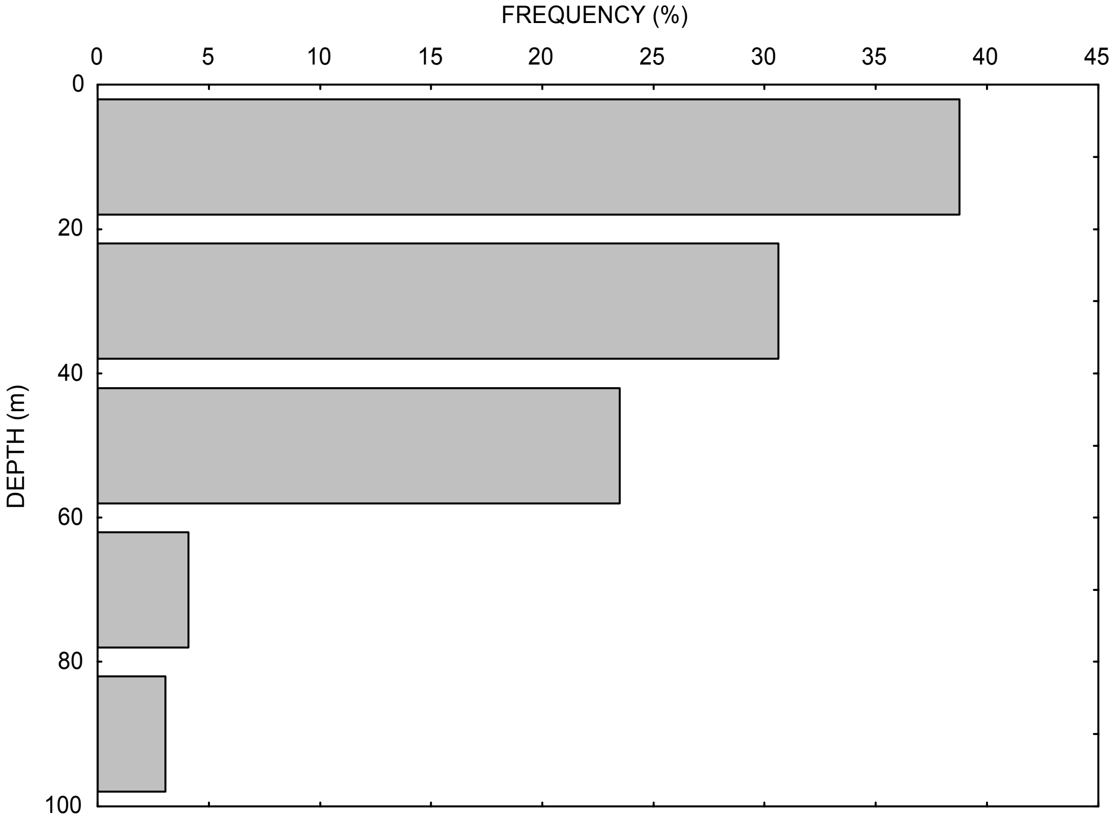

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Fig. 2.6: Percentage depth profile of sardine eggs (all stages) in the southern Benguela ecosystem. Eggs were sampled using a WPII net over the western Agulhas Bank (data from Dopolo et al. 2005). Proportions of egg development stages: newly spawned = 13%; middle stage = 54%; late stage = 33%

2.4.3. Dependent variables

The dependent variable for all the experiments is successful transport to, or retention in, a designated nursery area. For the remainder of this thesis this will be termed 'modelled recruitment'. Once a particle has recruited to a nursery area it cannot subsequently recruit to another nursery area. Modelled recruitment was expressed as the percentage of particles from each spawning area that recruit to each nursery area. Though there are no accurate data on the swimming speed of sardine larvae, Nelson and Hutchings (1987) estimated that they are not able at any stage to maintain their position by horizontal movement due to overwhelming current speeds in the southern Benguela ecosystem. However, once active swimming is possible they could be able to avoid being advected offshore by vertically migrating and/or swimming. In the absence of good data about sardine larvae in the southern Benguela ecosystem, for the first experiment the minimum age at which larvae are able to adequately move vertically was fixed at 14 days (7 time steps), based on the age at which anchovy larvae show active swimming and are able to avoid bongo nets (Badenhorst and Boyd 1980). This criterion was used in both the Huggett et al. (2003) and Parada et al. (2003) models, and since sardine and anchovy larvae are very similar at this young age, this criterion was applied to sardine as well. For later experiments (Chapters 4 and 5) incorporating growth of the individuals, the minimum age for recruitment criterion was refined to a minimum developmental stage for recruitment criterion. To successfully recruit to a nursery area, individuals needed to have reached the stage where they have developed a functional jaw and pigmented eye (so they are able to feed) and are able to swim enough to retain themselves within the nursery area. In addition temperature induced mortality (mortality rate expressed as a percentage of the total number of individuals released from each spawning area) was also used as a dependent variable in Chapters 4 and 5.

2.5. COMPARABILITY OF SIMULATION RESULTS

It is important for the results of simulations to be repeatable if they are to be compared with other simulations. IBM outputs need to be stable and not confused by factors other than the parameters of the experiment (e.g. not sensitive to the random initial distribution of particles).

To ensure the stability of outputs each simulation was run three times (*Trial*) to see whether or not random initial distributions of particles had any effect on the model results. In order for the effects of the different variables to be analysed with confidence, the effect of *Trial* needs to be almost non-existent.

2.5.1. Number of individuals/particles

Test runs were performed to see how the number of particles/individuals released affected the variation in the level of modelled recruitment and mortality rate between trials. Three trials were run for each number of individuals released (Fig. 2.7). Modelled recruitment results were shown to be quite robust to the number of individuals released. On the south coast stable outputs of mean modelled recruitment (similar means and standard deviations) were achieved if more than 100 individuals were used, while on the west cost 7 500 individuals

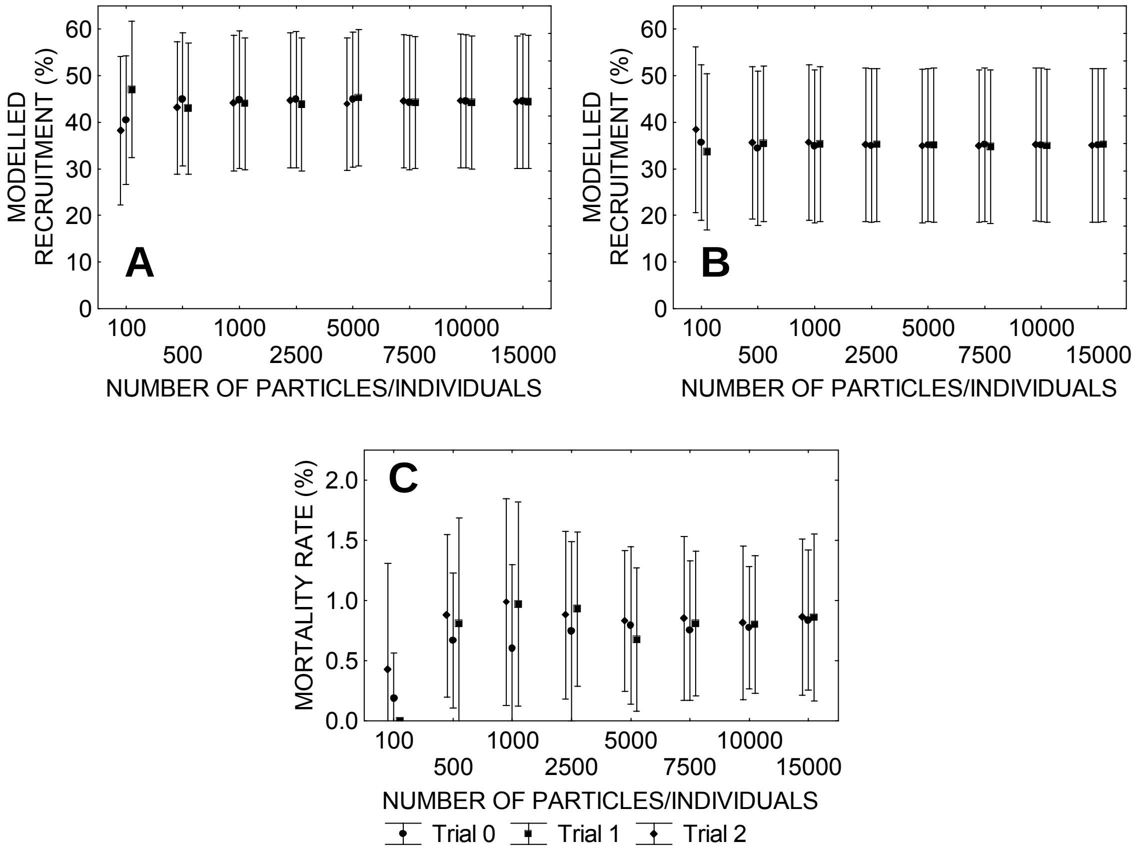

Fig. 2.7: The effect of the number of particles/individuals used in the simulations on mean modelled recruitment (± one standard deviation) to (A) the west coast and (B) the south coast; and (C) mortality rate (± one standard deviation)

were required. In order to have more stable outputs in mean mortality rate at least 10 000 individuals were required.

2.5.2. Temporal interpolation

Temporal interpolation (increasing temporal resolution by sub-dividing each time step) does not provide more realistic movement but rather allows for more frequent adjustment of an individual's position in the 3D velocity field. Increasing the number of iterations (divisions) per time step greatly increases computational time so only 5 iterations per time step were used in the first two IBMs. However, the vertical distribution experiment required a finer temporal resolution of hydrodynamic output for the movement of particles. Two-hour time steps (24 iterations) were thought to be suitable to allow variation in vertical position within each day and night period.

To ensure comparability of results a set of simulations were run with all parameters constant except the number of individuals. Simulations were carried out for the Lagrangian transport of individuals using 1, 5, 12, 18, 24, 36 and 48 iterations per time step (*Number of iterations*). The results of these simulations were analysed using general linear models to see what effect the number of iterations had on modelled recruitment and mortality and whether there was any change in the patterns of the other variables (i.e. whether any of the other variables had a significant interaction with the number of iterations). There was very little difference (<1% at any depth range at any stage of development) in the vertical distributions of individuals at each stage of development when either 5 or 24 iterations were used per time step. Likewise, little difference in the levels of modelled recruitment and mortality resulted when 5 or 24 iterations were used. Modelled recruitment was lowest when no temporal interpolation (one iteration) was used (Fig. 2.8 A). There was an increase in modelled recruitment when 5 iterations were used but thereafter modelled recruitment remained fairly constant with increasing number of iterations per time step. GLMs showed that none of the variables used in the simulations interacted significantly with *Number of iterations* and spatial, seasonal and depth patterns of success remained the same. Mortality showed the reverse pattern to that of modelled recruitment with overall rates decreasing with increasing number of iterations (Fig. 2.8 B). The rate of mortality remained reasonably constant between

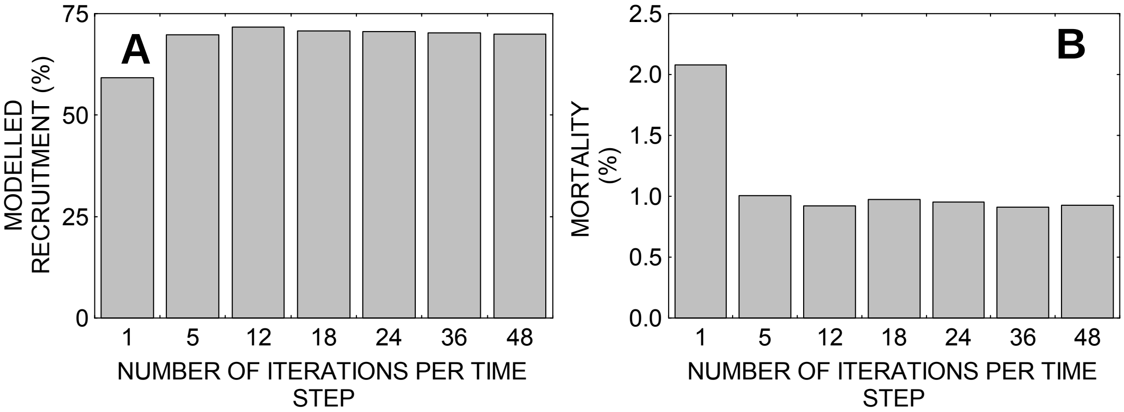

Fig. 2.8: (A) Modelled recruitment and (B) mortality when different levels of temporal interpolation (*Number of iterations* variable) are used in the IBM

5 and 48 iterations. There were no interactions between *Number of iterations* and any of the other variables in determining mortality rate.

Increasing the temporal interpolation from 5 to 48 iterations per time step does not substantially affect the modelled recruitment of Lagrangian particles, and temporal and depth patterns remained very similar. Mortality only showed a big difference between 1 and 5 iterations being used. The consistency of modelled recruitment and mortality between 5 (Chapters 3 and 4) and 24 (Chapter 5) iterations being used allows more confidence in the interpretation of results because any changes in the value of these can be attributed to processes at the individual scale and not model related artefacts.

2.6. STATISTICAL AND SENSITIVITY ANALYSES

Sensitivity analysis is an essential aspect of the modelling process (Beres and Hawkins 2001). In models with numerous parameters it is important to know the relative importance of each parameter in order to gain a good understanding of the system being modelled. Certain parameters can be surprisingly influential in determining the outcomes of a model, and these need to be identified. Likewise, parameters that exert no significant effect can be recognised.

Sensitivity analyses not only allow for the examination of "main" effects, but can also be used to explore the likelihood of interaction between pairs or larger groups of parameters (Swartzman and Kaluzny 1987). By completing a sensitivity analysis with a complete factorial design, interactions of interest can be identified. In models with many parameters the number of distinct scenarios required for a complete factorial design can be large (Beres and Hawkins 2001). In the past, various methods such as the Plackett-Burman design (Plackett and Burman 1946) had been used to reduce the number of scenarios and, consequently, computation time. However, with the increase in computing power over the last few decades, a full factorial design is now feasible.

The results of the simulations were analysed using general linear models (GLMs) using the STATISTICA 6 package (Statsoft, 2002). GLMs are often used to perform analysis of variance (ANOVA) designs with categorical predictors. All GLMs were constructed using Type III (orthogonal) sums of squares to suit the factorial ANOVA design with unequal *n*. No random factors were included and, as the design was neither nested nor included any random effects, sigma-restricted parameterisation was used. To satisfy the assumptions of the GLM, the residuals need to be normally distributed. Also, any trend in the mean and variance of the residuals in relation to the observed values may imply that the results are misleading. These assumptions were tested for each GLM by conducting a visual residual analysis.

For each GLM, modelled recruitment was used as the dependent variable and the variables of the model as categorical predictors. The *scarcity of effects* principle (Montgomery 1997) states that three-way or higher interactions are much less common than two-way interactions, so no third degree or higher interactions were considered. The adjusted R^2 and p values for each model were noted, along with all main and interaction effects and compliance with the GLM assumptions. The R^2 value indicates the proportion of the total variance in the response/dependent variable that is explained by the regression model. The relative importance of each predictor variable was calculated as the proportion of the total sum of squared deviations (SS) explained by the regression model attributed to each variable i.e.:

$$\%\,\mathrm{var\,exp} = \frac{100 \times SS_{\mathrm{var}}}{SS_{tot}} \tag{2.1}$$

A chi-squared (χ^2) test was used to test whether apparent seasonal peaks and troughs in recruitment success were significant ($p < 0.05$). The simulated seasonal distribution of recruitment success was compared to a uniform distribution (equal to the mean of the simulated recruitment success rates). In the case of a significant departure from a uniform distribution, an *a posteriori* test (Zar 1999) was done to identify which months caused the differences. Data for different months were removed and the test was repeated; if the result of the test was then found to be not significant, it is assumed that the removed months are responsible for the departure from a level distribution.

2.7. FIELD DATA

No specific fieldwork was conducted for this project. Data were obtained from various sources but primarily from the branch: Marine and Coastal Management (MCM, formally Sea Fisheries Research Institute (SFRI)) of the South African Department of Environmental Affairs and Tourism (DEAT). The South African pelagic resources have been monitored acoustically since 1983 by MCM (Barange et al. 1999, van der Lingen et al. 2001), with two pelagic surveys conducted each year. The first survey in May (winter) aims primarily to estimate the number of recruits of anchovy and sardine, and information on the spawning activity of the fish and the number and distribution of eggs is obtained in the summer (November) survey (Cochrane et al. 1991, van der Lingen et al. 2001, van der Lingen and Huggett 2003). Composite egg distribution maps were used in setting parameters (e.g. location of spawning) of the models and length frequency distributions observed during surveys were used for the fecundity model. Estimates of sardine recruitment are back-calculated from survey data and catches in a population assessment model (de Oliveira et al. 1998), assuming constant mortality. These were used for comparisons with model results. Back-calculated recruitment estimates are used for validation of model results. Other data, such as egg and larva vertical distributions, were obtained from one-off cruises.

CHAPTER 3: SPATIAL AND TEMPORAL PATTERNS IN THE TRANSPORT AND RETENTION OF PARTICLES IN THE SOUTHERN BENGUELA ECOSYSTEM

ABSTRACT

A Lagrangian particle-tracking IBM linked with a 3-D hydrodynamic model of the southern Benguela ecosystem is used to examine transport of sardine (*Sardinops sagax*) eggs and larvae. Five variables (*Spawning Area*, *Year*, *Month*, *Depth* and *Trial*) are used in the experiment and modelled recruitment to both the west and south coast is considered. High proportions of particles released on the south coast are retained there, supporting the hypothesis of the existence of a south coast recruitment area. Three recruitment systems for sardine are identified: the WAB/WC-WC (spawning west of Cape Agulhas, recruitment on the west coast) and SC-SC (spawning east of Cape Agulhas, recruitment on the south coast) retention systems, which appear to be closed systems with very high levels of retention (50-95 and 40-95%, respectively); and the CAB-WC transport system (spawning on the central Agulhas Bank (CAB), recruitment on the west coast). Transport from the CAB contributes to recruitment in both nursery areas (west coast 14.29%, south coast 36.21%). In general, the further east eggs are spawned the more likely they are to be retained on the south coast. Eggs spawned in the upper 25m are less likely to recruit to the west coast than eggs spawned deeper than this. Comparisons of modelled recruitment anomalies and back-calculated recruitment anomalies considering egg distributions for each year indicate that circulation factors could be influential in determining levels of recruitment and that all three systems potentially play an important role. By looking at the limitations to recruitment imposed by circulation factors this experiment serves as a basis with which future experiments will be compared and a platform upon which further levels of complexity will be added.

3.1. INTRODUCTION

The life histories of all marine populations must include some means for at least a portion of their reproductive products to link up with the adult population. Depending on the species and the ecosystem it inhabits, this could involve either the retention of reproductive products in the area inhabited by the adult population or some means by which they can return to this area from wherever they were spawned (Boyd et al. 1992). Upwelling systems appear to be difficult reproductive habitats for fish with most small pelagics needing to migrate to find suitable spawning habitats (Laevastu 1993). This is the case in the southern Benguela upwelling system where clupeoids such as sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) are believed to have spatially distinct spawning and nursery grounds (Crawford 1980). Because the eggs and larvae of sardine are planktonic in their early stages the circulation of the area is a primary determinant of where these eggs and larvae will end up.

Considering the widespread distribution of sardine spawning, particularly the far-reaching eastern extent, it is reasonable to assume that not all of the sardine recruitment occurs on the west coast, and that a south coast recruitment area can be hypothesised. A quasi-permanent cool ridge is found extending midshelf from Still Bay to near the coast at Mossel Bay on the south coast (Fig. 3.1), and this cool ridge is a dominant feature over the Agulhas Bank (Swart and Largier 1987, Boyd and Shillington 1994). The offshore edge of this ridge is fairly productive due to persistent shelf edge upwelling observed along the eastern Agulhas Bank (EAB; Lutjeharms et al. 2000). Probyn et al. (1994b) found phytoplankton concentrations around the ridge to be higher than in surrounding areas and this is accompanied in turn by a large biomass of copepods (Verheye et al. 1994). Hutchings et al. (2002) also suggested that this ridge might play an important role in the life-history strategies of fish on the Agulhas Bank as currents tend to circulate clockwise around it. In other words, Bakun's triad of enrichment, concentration and retention (Bakun 1996a) seems to be in action over this area, making it a potential nursery ground.

But do sardine use this area as a nursery ground? Only a few surveys have been done in the waters off the east coast, but it has been widely reported that sardine spawn along this

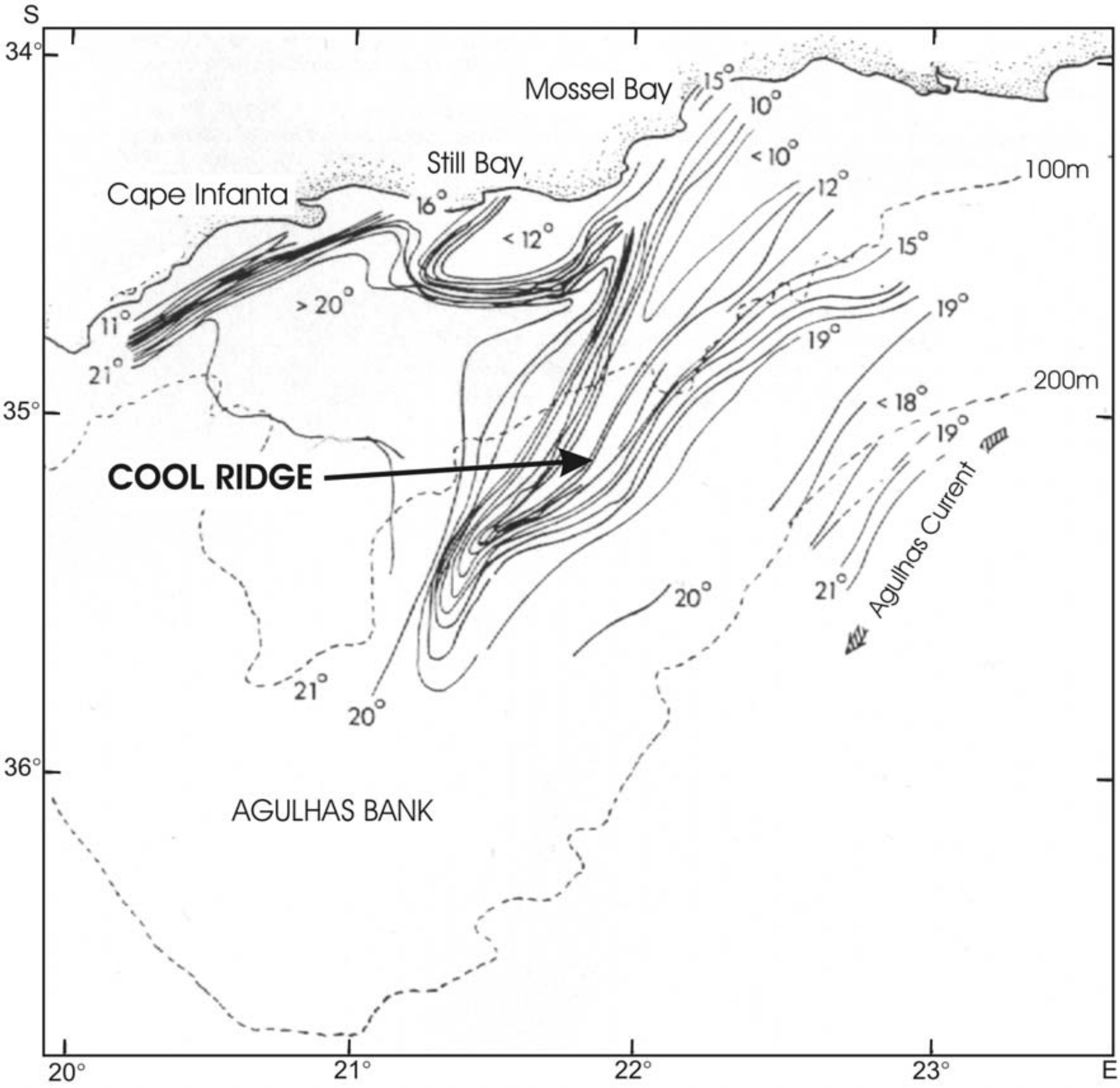

Fig. 3.1: The location of the quasi-permanent cool ridge over the Agulhas Bank (from Swart and Largier 1987). Lines represent isotherms at 20m (°C)

section of the coastline (Anders 1975, Armstrong et al. 1991, Beckley and Hewitson 1994). Due to the geographical distance involved and the complex system of currents, it is unlikely that sardine spawned on or east of the EAB recruit in the west coast nursery grounds. These sardine must therefore either recruit to the east coast, which has a very narrow coastal shelf and is considered unable to support a large population of recruited sardine (Armstrong et al. 1991), or be transported to the south coast. Beckley (1993) found that eggs spawned on the east coast could be transported south, not by the Agulhas Current itself, but rather by the peripheral inshore waters associated with this current. Griffiths and Hecht (1995) also subscribed to this view and toted this as a possible mechanism for the southward transport of geelbek fish (*Atractoscion aequidens*) larvae.

There is more direct evidence for sardine recruiting to the south coast. Beckley (1985) reported finding both sardine larvae and juveniles (14 to 31mm) in plankton tows and seine-net catches, respectively, at the Swartkops estuary mouth just east of Port Elizabeth (33° 52′ 00″ S, 25° 38′ 00″ E) in October 1980. Sardine, anchovy and round herring (*Etrumeus teres*) larvae and juveniles were found to be abundant in the inshore ichthyoplankton of Algoa Bay, together comprising 47% of the total numbers caught in a two-year survey (Beckley 1983). Strydom (2003) caught 40 sardine larvae in 8 light trap samples taken in the Swartkops estuary over two days in October and November 2000. These samples were taken in the estuary mouth itself and not in the nearshore waters where sardine larvae are more likely to be found, suggesting that a much larger number of sardine larvae could be found in this region (Nadine Strydom, South African Institute for Aquatic Biodiversity, pers. comm.). Early juveniles have been found in the surf zone off Kwaaihoek (just south of Port Alfred) as well as in the lower reaches of the Gamtoos estuary (Strydom, SAIAB, pers comm.). Evidence suggests that these larvae and juveniles are not just there accidentally but that their occurrence there may be a consistent feature.

The simulation experiment presented in this chapter examines transport and retention across the whole southern Benguela ecosystem, and assesses where sardine eggs and larvae can be retained in a nursery area on the south coast in the region of the quasi-permanent cool ridge. The null hypothesis is that all recruitment of sardine occurs in the west coast nursery ground. The simulations involve modelling particles in a purely Lagrangian fashion and therefore the results presented are the product of the modelled circulation. These circulation patterns are considered to impose limitations on movement of sardine eggs and larvae across the southern Benguela. The implications of a hypothetical south coast nursery area for the spatio-temporal spawning pattern of sardine in the southern Benguela ecosystem are explored. This experiment acts as a baseline for sardine spawning models. It defines the way in which future experiments will be analysed and serves as a platform upon which further levels of complexity will be added.

3.2. METHODS

3.2.1. Experimental design

3.2.1.1. OVERVIEW OF THE MODELLING PROCESS

The three stages of the modelling process (experimental design, IBM simulations and statistical analysis) and details of the procedure for each simulation are shown in Fig. 3.2. For each simulation a population of 10 000 particles was released randomly (tending to a uniform distribution due to the large number of particles) over all nine spawning areas, the number of particles released in each area being proportional to the size of each area. These particles were released in batches every time step (two days) for 15 time steps (30 days, roughly one month). Five times during each time step of the model (i.e. every 9.6 hours) the IBM used the 3-D hydrodynamic output from the PLUME model (*u*, *w* and *v* velocities) to estimate the horizontal and vertical trajectory of each particle and then moved the particle accordingly. Each particle increases in age with each time step until it either satisfies the criteria for recruitment (reached a nursery area and the minimum age of 14 days) or has reached the maximum age (60 days) without successfully recruiting. In both cases the particle is then removed from the population for the rest of the simulation.

3.2.1.2. MODEL PARAMETERS

Table 3.1 details the parameters used in the experiment and the ranges or values used.

Table 3.1: The fixed parameters and variables used in the Lagrangian experiment, their ranges or values and *n*

Parameter	Range/Value	*n*
Fixed parameters		
Number of particles	10 000	-
Duration of release of particles	30 days	-
Tracking period	60 days	-
Variables		
Spawning Area	(see Fig. 2.5)	9
Year	1991/92 – 1998/99	8
Month	Jul – Jun	12
Depth	0-25, 25-50 and 50-75m	3
Trial	-	3
Number of simulations		**8*12*3*3 = 864**

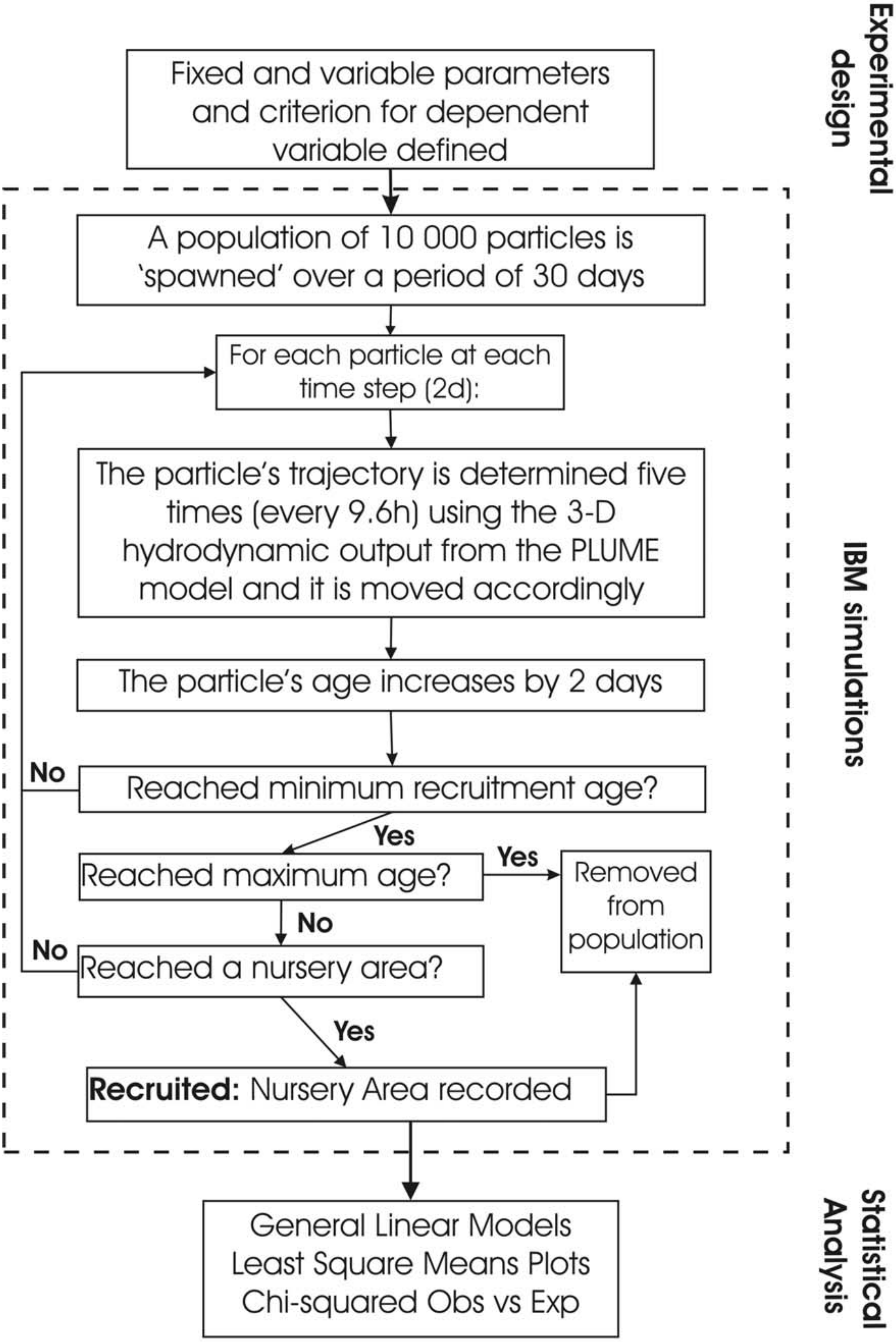

Fig. 3.2: Flow chart depicting the three stages of the modelling process for the Lagrangian transport experiment

3.2.1.3. DEPENDENT VARIABLES

Two nursery areas (Fig. 3.3) were used in this experiment - one on the west coast and the other on the south coast. The west coast nursery area, like the Agulhas Bank spawning areas, follows convention for the region. The south coast nursery area was chosen to correspond with the quasi-permanent cool ridge from the coast inshore of it, extending to slightly offshore of its usual position. Particles were considered to have recruited to one of these areas if they were located in one of these areas and were older than 14 days and less than 60 days. The dependent variable used in analyses of the IBM results was the percentage of particles released from each spawning area recruiting to each of the two nursery areas.

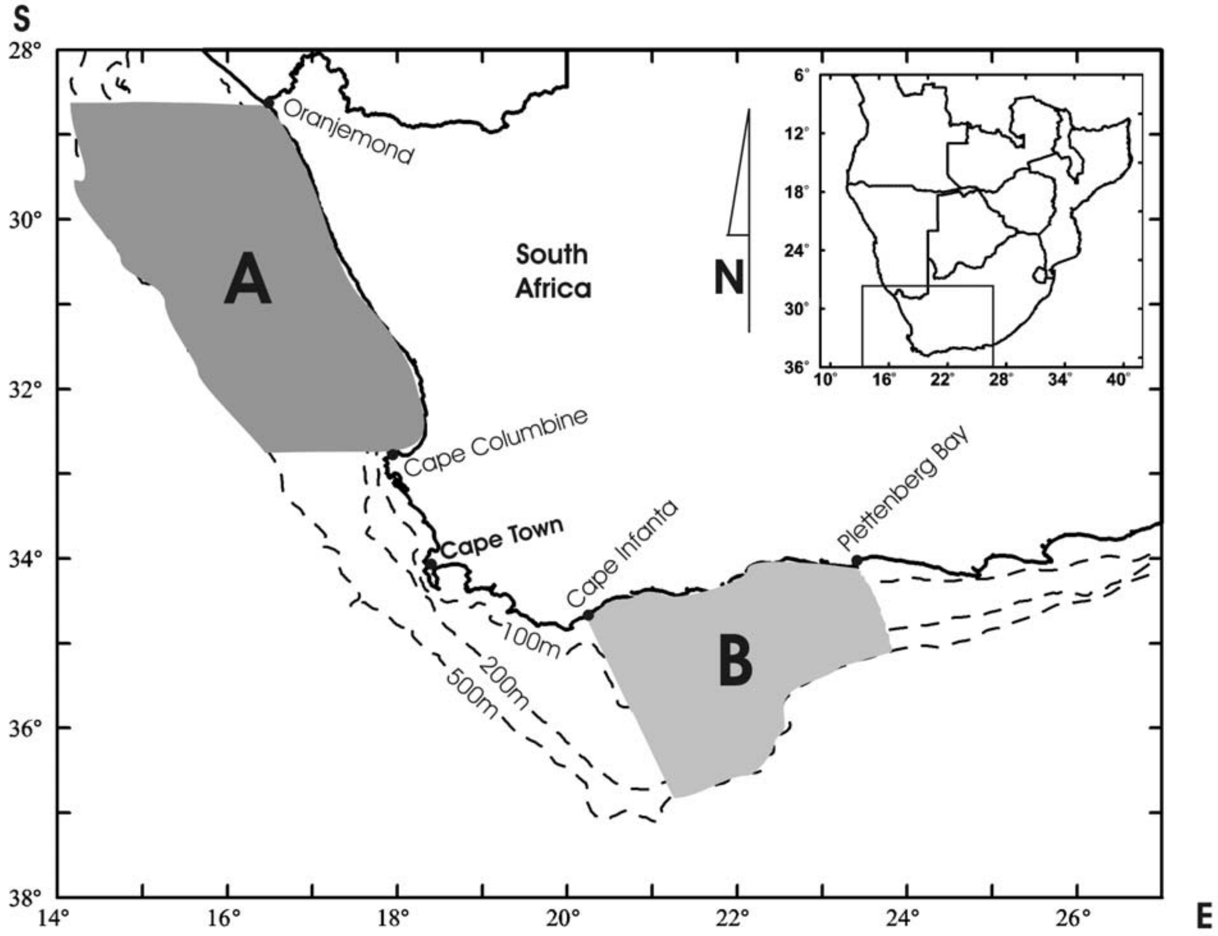

Fig. 3.3: The two nursery areas used in the IBM experiments. A = west coast, B = south coast

3.2.2. Statistical analyses

Multiple factor variance analysis using general linear models (GLMs) was performed on the modelled recruitment results. The five variables of the model (*Spawning Area*, *Year*, *Month*, *Depth* and *Trial*) were used as categorical predictors.

To examine the effect each of the variables had on determining which nursery ground recruitment occurred in a ‘recruitment location ratio’ was constructed. This was calculated according to the equation:

$$RLR = 100 \times \frac{(\%WC - \%SC)}{(\%WC + \%SC)} \tag{3.1}$$

Where: RLR = Recruitment Location Ratio (%)
%WC = modelled recruitment to the west coast nursery area
%SC = modelled recruitment to the south coast nursery area

A value of 100% indicates all modelled recruitment is occurring on the west coast, -100% indicates all modelled recruitment is on the south coast and 0 indicates that modelled recruitment is evenly spread between the two nursery areas. A GLM using the complete simulation results was constructed with the recruitment location ratio as the dependent variable. The results of this GLM were used to subdivide the simulation results among three distinct recruitment systems identified (see below).

In further GLMs the dependent variable for each recruitment system was modelled recruitment to the nursery area concerned. For all GLMs a full factorial design to the 2nd degree was used with all the predictors except *Trial*, which was not used in any of the interaction terms. The adjusted R^2 and p values for each model were noted, along with all main and interaction effects and compliance with the GLM assumptions (Chapter 2, section 2.5). The percentage variance explained by each variable or interaction term was also calculated.

Plots of least square means (LSMs) were done to visually examine the results and to identify the relationships between each variable and modelled recruitment values. The *a posteriori* Chi-squared test (Chapter 2) was used to identify significant peak or trough months to examine seasonal patterns.

Standardised anomalies of modelled recruitment and back-calculated recruitment estimates were calculated. Anomalies were calculated as the difference between the value for a given year and the mean over the eight years, divided by the standard deviation over the eight years. Correlations between modelled recruitment anomalies for each recruitment system and back-calculated recruitment estimate anomalies were calculated and the strength of these correlations were noted (R^2 and p values). A plot was made of the back-calculated recruitment and modelled recruitment anomalies for each recruitment system for each year.

3.3. RESULTS

Images of Lagrangian particle movement obtained from the IBM are shown in Fig. 3.4. The main sources of advective loss of particles can be clearly seen in these images. Patterns of movement for all four months shown are similar for all depth ranges but particles released shallower tend to be transported further offshore and are dispersed over a greater area than those released at depth. Offshore Ekman drift off the west coast is greatest during January and October when the south-easterly winds prevail. This causes greater advective losses of particles released in the 0-25m depth range and is more noticeable along the UWC. During July there is very little movement of particles released on the LWC and in October particles released here shift northwards with few offshore losses. The offshore arm of the Cape Columbine jet current can also be identified during all four months and particles released on the WAB and CAB can be transported far offshore in this current. During July and October the flow is more northwards than January and April. The inshore arm of this current is stronger during January and April, moving particles from the WAB and CAB northwards towards the west coast. There is less offshore loss of particles along the south coast. The effect of the Agulhas Current can be seen most clearly in July when many of the particles released on the EAB are transported in a south-westerly direction while in October particles

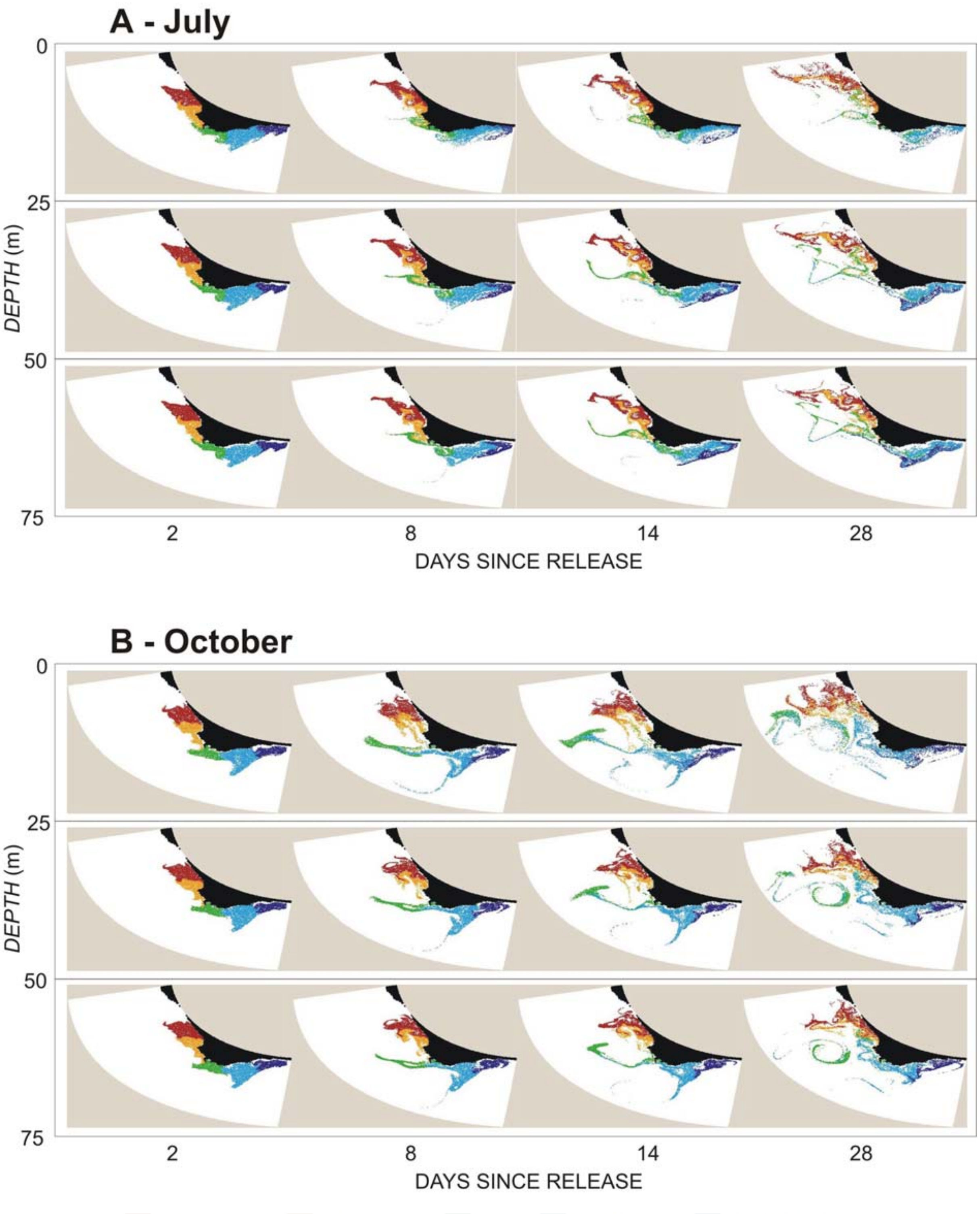

Fig. 3.4: Two-dimensional display of Lagrangian particles being transported in the domain of the PLUME model. Particles were released over the extent of the sardine spawning area at the beginning of: (A) July, (B) October, (C), January and (D) April. Inshore and offshore *Spawning Areas* have been combined, *Depth* ranges indicate the initial range of depth of release and 10 000 particles were released per simulation

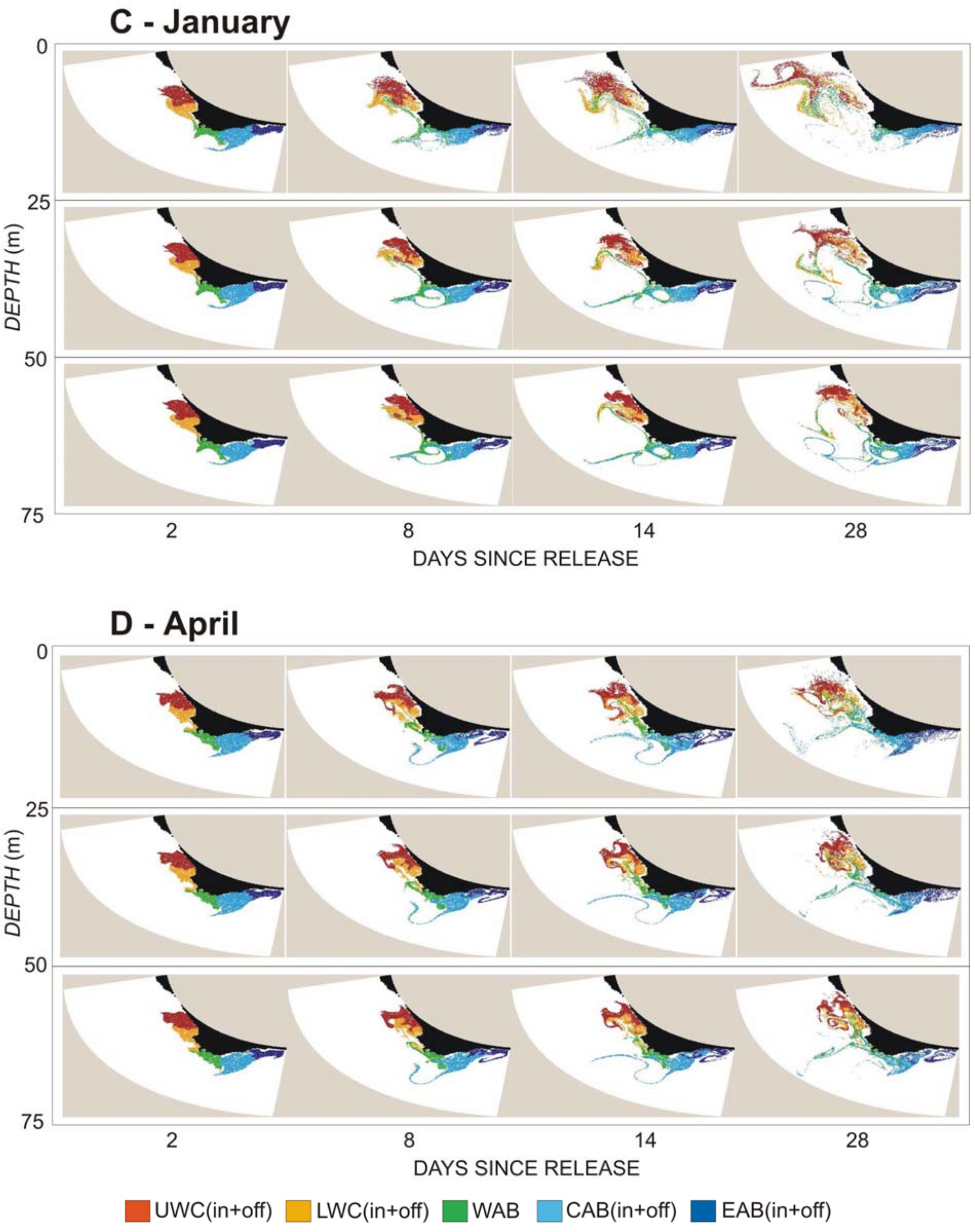
C - January
0
25
50
75
DEPTH (m)
2
8
14
28
DAYS SINCE RELEASE
D - April
0
25
50
75
DEPTH (m)
2
8
14
28
DAYS SINCE RELEASE
UWC(in+off)
LWC(in+off)
WAB
CAB(in+off)
EAB(in+off)

Fig. 3.4: *Cont.*

from the offshore edge of the CAB are caught in the flow and lost offshore. In January an Agulhas ring can be seen budding off from the apex of the Agulhas Bank and entraining a number of particles from the WAB and CAB. This is clearer at depth. Movement across the Agulhas Bank is predominantly east to west during January and April and west to east during July and October.

3.3.1. Modelled recruitment

Analysis of the GLM for the recruitment location ratio (adjusted $R^2 = 0.98$) found that *Spawning Area* explained 96.38% of the variance in recruitment between nursery areas. None of the particles released from any of the four west coast spawning areas reached the south coast nursery area. Similarly, very few of the particles released on the EAB were successfully transported to the west coast nursery area (Fig. 3.5). Only from the CAB, and to a lesser degree the western Agulhas Bank (WAB), do particles have reasonable probabilities of recruiting to either of the two nursery areas. This is clear in the plot of recruitment location

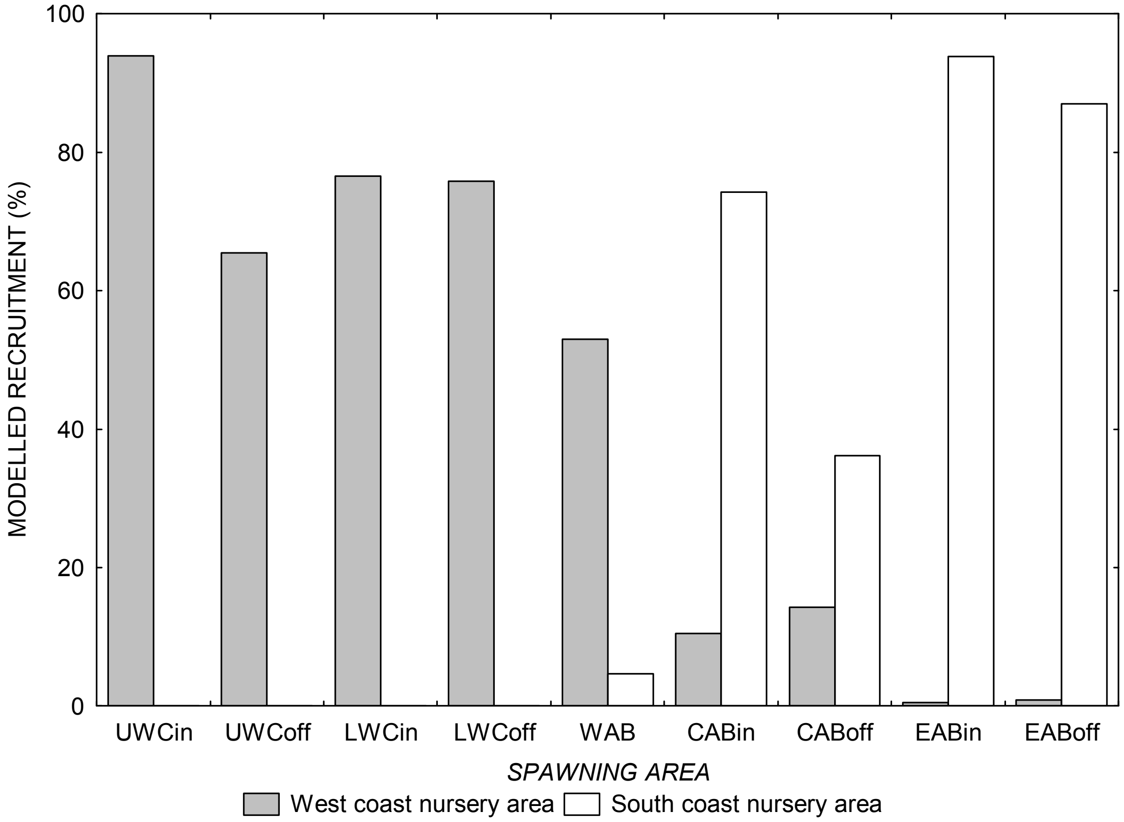

Fig. 3.5: Modelled recruitment to the west and south coast nursery areas for the *Spawning Area* variable in the Lagrangian transport simulations

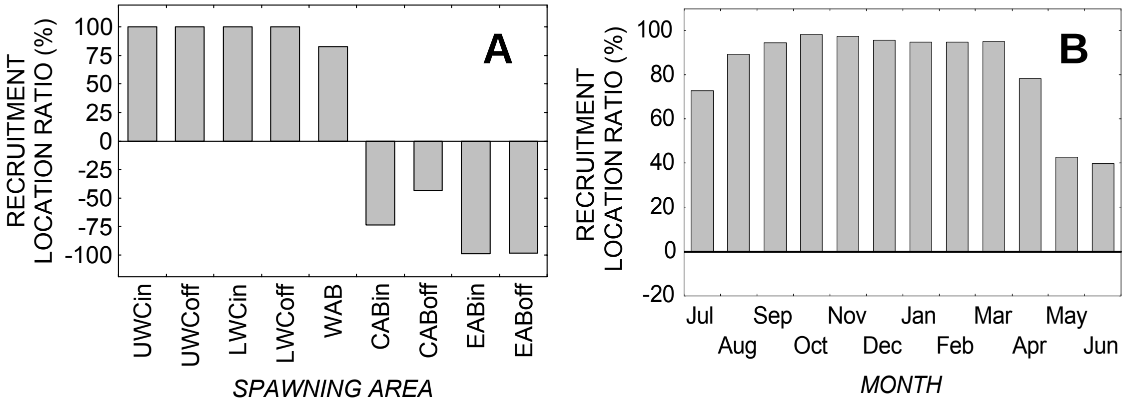

Fig. 3.6: Recruitment location ratio in the WAB/WC-WC system for (A) the *Spawning Area* variable and (B) the *Month* variable for the western Agulhas Bank only in the Lagrangian transport experiment

ratios for each *Spawning Area* (Fig. 3.6A) that clearly indicates that negligible recruitment occurs from the west coast spawning areas to the south coast nursery area or from the EAB spawning areas to the west coast nursery area. The WAB does contribute slightly to modelled recruitment on the south coast but this is mainly between April and July (Fig. 3.6B) when spawning activity is at its lowest (Beckley and van der Lingen 1999). Over the peak spawning periods of September-October and February-March a very small percentage of the particles released on the WAB reach the south coast nursery area. Particles released on the CAB, and particularly the offshore CAB, head in both directions although predominantly to the south coast (Fig 3.5). However, 14.29% of the particles released here recruit to the west coast nursery area and this is not a negligible amount.

Considering these results three recruitment systems were defined for sardine in the southern Benguela, two different retention systems and a system of transport between them:

1. The west coast/western Agulhas Bank to west coast (WAB/WC-WC) retention system.

   Modelled recruitment in this system is the proportion of particles released from the west coast spawning areas (UWCin, UWCoff, LWCin and LWCoff) areas that are retained on the west coast as well as the proportion of particles that are transported northwards from the WAB to the west coast nursery area.

2. The central Agulhas Bank to west coast (CAB-WC) transport system.

   As very little spawning occurs on the inshore section of the CAB in reality (see Fig. 1.3), and given that the recruitment location ratio indicated a tendency towards the south coast nursery grounds from this spawning area, modelled recruitment in this system is only considered to be the proportion of particles transported from the offshore CAB spawning area (CABoff) to the west coast nursery area. This is the only system where the spawning area and nursery grounds are completely spatially distinct.

3. The south coast to south coast (SC-SC) retention system.

This is a hypothesised system based on the proposition that a south coast nursery ground could exist. Despite existing inshore counter-currents, very few particles released from the west coast spawning areas are transported southward to the Agulhas Bank. Also, despite its close proximity to the south coast nursery area, very few particles are transported from the WAB to this area, especially during the summer months. Therefore only the proportion of particles released on the central and eastern Agulhas Bank (CABin, CABoff, EABin and EABoff) recruiting to the south coast nursery area contribute to modelled recruitment in this system.

3.3.1.1. THE WAB/WC-WC SYSTEM

The single variables and first order interactions together explained 79.03% of the variance in the GLM for the WAB/WC-WC system (Table 3.2). The assumptions for the GLM analysis

Table 3.2: General linear model results for the WAB/WC-WC system in the Lagrangian transport experiment showing the contributions of the different variables to determining modelled recruitment. The main effects and interaction effects explaining more than 5% of the variance are shown, together with univariate statistics of the parameter values. Test of SS Whole Model vs. SS Residual: Adjusted $R^2 = 0.79$; $p < 0.01$. * = Significant ($p < 0.01$). % variance explained = $100 \times SS_{effect}/SS_{tot}$

	Sum of Squares	**Degrees of freedom**	**Mean Squares**	**F**	**p**	**% variance explained**
Intercept	22964717	1	22964717	220511	0.00*	
Single variable						
Spawning Area	791942	4	197986	1901	0.00*	38.90
Year	6303	7	900	9	0.00*	0.31
Month	55628	11	5057	49	0.00*	2.73
Depth	309106	2	154553	1484	0.00*	15.18
Trial	5	2	3	0	0.97	0.00
Interaction terms						
*Month*Depth*	105748	22	4807	46	0.00*	5.19
Error	426986	4100	104			20.97
TOTAL	2035900	4320	376093			

were met - the residuals of transport success were normally distributed and no trend was found in the mean and variance of the residuals in relation to the observed values. The primary determinant of retention on the west coast was *Spawning Area*, which explained almost half of the variance explained by the GLM. Modelled recruitment was highest from the UWCin area and lowest from the WAB (Fig. 3.5). The UWCoff area had modelled recruitment 28% lower than the UWCin area while modelled recruitment was very similar from both the inshore and offshore LWC areas. *Depth* was the next most important explanatory variable and a *Month*Depth* interaction also accounted for over 5% of the total variance. Particles released in the upper 25m were less likely to be retained on the west coast than those released at depth (Fig. 3.7A). Also, the *Month*Depth* interaction is most noticeable for this depth range with modelled recruitment being highest during the winter months (May-August) and lowest during the summer months (November-March) (Fig. 3.7B).

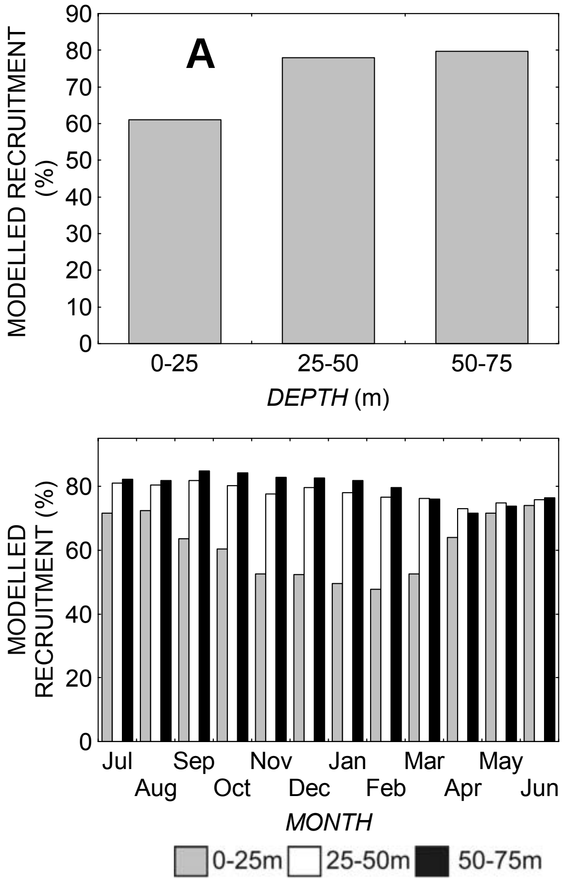

Fig. 3.7: Modelled recruitment in the WAB/WC-WC system for (A) the *Depth* variable and (B) the *Depth*Month* interaction in the Lagrangian transport experiment

3.3.1.2. THE CAB-WC SYSTEM

The single variables and first order interactions together explained 89.62% of the variance in modelled recruitment in the CAB-WC system (Table 3.3). The interaction terms were almost as important as the single variables in this system, explaining almost the same amount of the total variance. The assumptions for the GLM analysis were met - the residuals of transport success were normally distributed and no trend was found in the mean and variance of the residuals in relation to the observed values.

Table 3.3: General linear model results for the CAB-WC system in the Lagrangian transport experiment showing the contributions of the different variables to determining modelled recruitment. The main effects and interaction effects explaining more than 5% of the variance are shown, together with univariate statistics of the parameter values. Test of SS Whole Model vs. SS Residual: Adjusted $R^2 = 0.90$; $p < 0.01$. * = Significant ($p < 0.01$). % variance explained = $100 \times SS_{effect}/SS_{tot}$

	Sum of Squares	**Degrees of freedom**	**Mean Square**	**F**	**p**	**% variance explained**
Intercept	176842	1	176842	16635		
Single variable						
Year	4094	7	585	55	0.00*	5.49
Month	24039	11	2185	206	0.00*	32.23
Depth	6611	2	3306	311	0.00*	8.86
Trial	2	2	1	0	0.89	0.00
Interaction terms						
*Year*Month*	26867	77	349	33	0.00*	36.02
Error	7739	728	11			10.38
TOTAL	74596	864	6697			

The *Month* variable was the most important explanatory variable but it had a strong interaction with *Year* as well. The period from September to November had the highest modelled recruitment (Fig. 3.8A) while the winter months May-July had the lowest levels. The distribution was found to differ significantly from a level distribution of the mean modelled recruitment ($\chi^2 = 22.95$, df = 11, p = 0.018). However if October ($\chi^2 = 16.33$, df = 10, p = 0.091) or May ($\chi^2 = 17.41$, df = 10, p = 0.066) were removed the difference was no longer significant. In general there is a large degree of interannual variation in modelled recruitment levels for each month (Fig. 3.8B) though modelled recruitment is rarely lower than 15% during September-November and rarely higher than 15% during May-July. The peak in October is most noticeable during 1991/92 when more than 50% of the particles released from CABoff reached the west coast. *Depth* was the next most important single variable, particles released deeper than 25m being more likely to recruit (Fig. 3.8C).

A GLM (R^2=0.90) of the recruitment location ratio for the CABoff area showed *Month* to explain most (42.20%) of the difference in recruitment location with summer months having higher west coast recruitment than the winter months, and *Depth* also explained 9.01% of the variance. The graphs of recruitment location ratio by *Month* and *Depth* (Fig 3.9A and B, respectively) show similar patterns to the *Month* and *Depth* modelled recruitment relationships in the CAB-WC system.

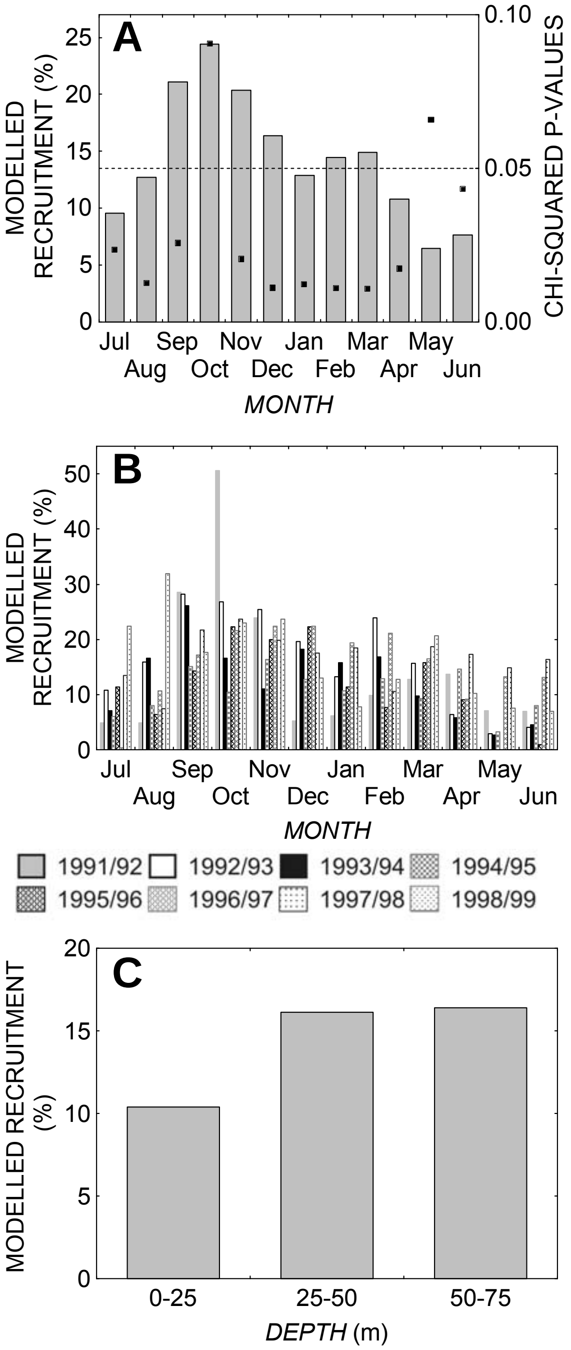

Fig. 3.8: Modelled recruitment in the CAB-WC system for (A) the *Month* variable (chi-squared values shown as points), (B) the *Month*Year* interaction and (C) the *Depth* variable in the Lagrangian transport experiment

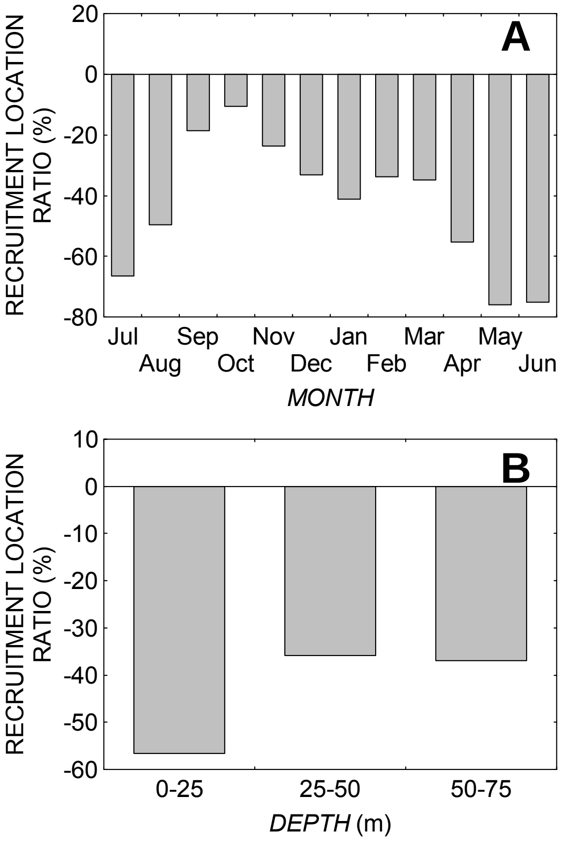

Fig. 3.9: Recruitment location ratio in the CAB-WC system for the (A) *Month* and (B) *Depth* variables in the Lagrangian transport experiment

3.3.1.3. THE SC-SC SYSTEM

The single variables in the SC-SC system explained 76.61% of the total variance in modelled recruitment (Table 3.4). When first order interactions were included this increased to 90.63%. The assumptions for the GLM analysis were met - the residuals of transport success were normally distributed and no trend was found in the mean and variance of the residuals in relation to the observed values.

Spawning Area was by far the most important variable in the SC-SC system explaining nearly three quarters of the total variance. The two EAB areas had noticeably higher modelled recruitment than the CAB areas (Fig. 3.5), and the CABin area was twice as successful as the CABoff area, which had the lowest success in this system. A *Spawning Area*Month* interaction was the only other notable term in the GLM. The CAB and EAB areas appear to have opposite seasonal patterns in modelled recruitment (Fig. 3.10). Modelled recruitment from the EAB areas is consistently very high from August to April and only decreases slightly over May-July. In contrast, modelled recruitment from the CAB areas is highest from May to July and lowest from October to March. There is a noticeable trough in modelled recruitment from the CABin area during February-March.

Table 3.4: General linear model results for the SC-SC system in the Lagrangian transport experiment showing the contributions of the different variables to determining modelled recruitment. The main effects and interaction effects explaining more than 5% of the variance, are shown together with univariate statistics of the parameter values. Test of SS Whole Model vs. SS Residual: Adjusted R^2 = 0.91; $p < 0.01$. * = Significant ($p < 0.01$). % variance explained = $100 \times SS_{effect}/SS_{tot}$

	Sum of Squares	**Degrees of freedom**	**Mean Square**	**F**	**p**	**% variance explained**
Intercept	18348204	1	18348204	276347		
Single variable						
Spawning Area	1714506	3	571502	8608	0.00*	74.28
Year	2806	7	401	6	0.00*	0.12
Month	30846	11	2804	42	0.00*	1.34
Depth	20032	2	10016	151	0.00*	0.87
Trial	3	2	2	0	0.98	0.00
Interaction terms						
*Spawning Area*Month*	217433	33	6589	99	0.00*	9.42
Error	216251	3257	66			9.37
TOTAL	2308127	3456	599728			

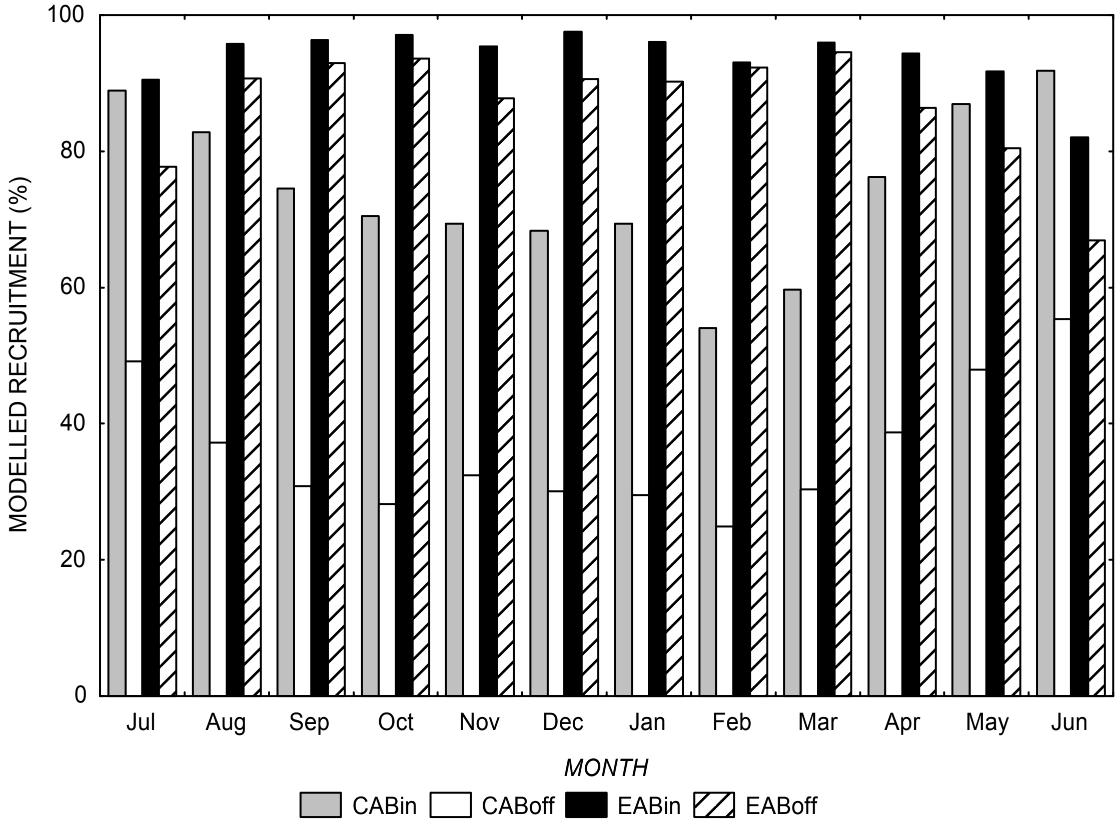

Fig. 3.10: Modelled recruitment in the SC-SC system for the *Spawning Area*Month* interaction in the Lagrangian transport experiment

3.3.2. Comparison with field estimated recruitment

None of the modelled recruitment anomalies from any of the three recruitment systems correlated significantly with back-calculated recruitment estimates, and all had very low r values (WAB/WC-WC system: r = 0.35; CAB-WC system: r = 0.17; SC-SC system: r = 0.14). With the exception of 1993/94, positive modelled recruitment anomalies in the CAB-WC system were always accompanied with positive anomalies in the SC-SC system and likewise for negative anomalies (Fig. 3.11). A significant positive correlation between these two systems was found (r = 0.77). In only three years were the anomalies of all four indices the same sign (all negative in 1995/96 and all positive 1997/98 and 1998/99). For the last two years of the series, none of the systems had modelled recruitment anomalies corresponding with the back-calculated recruitment anomaly.

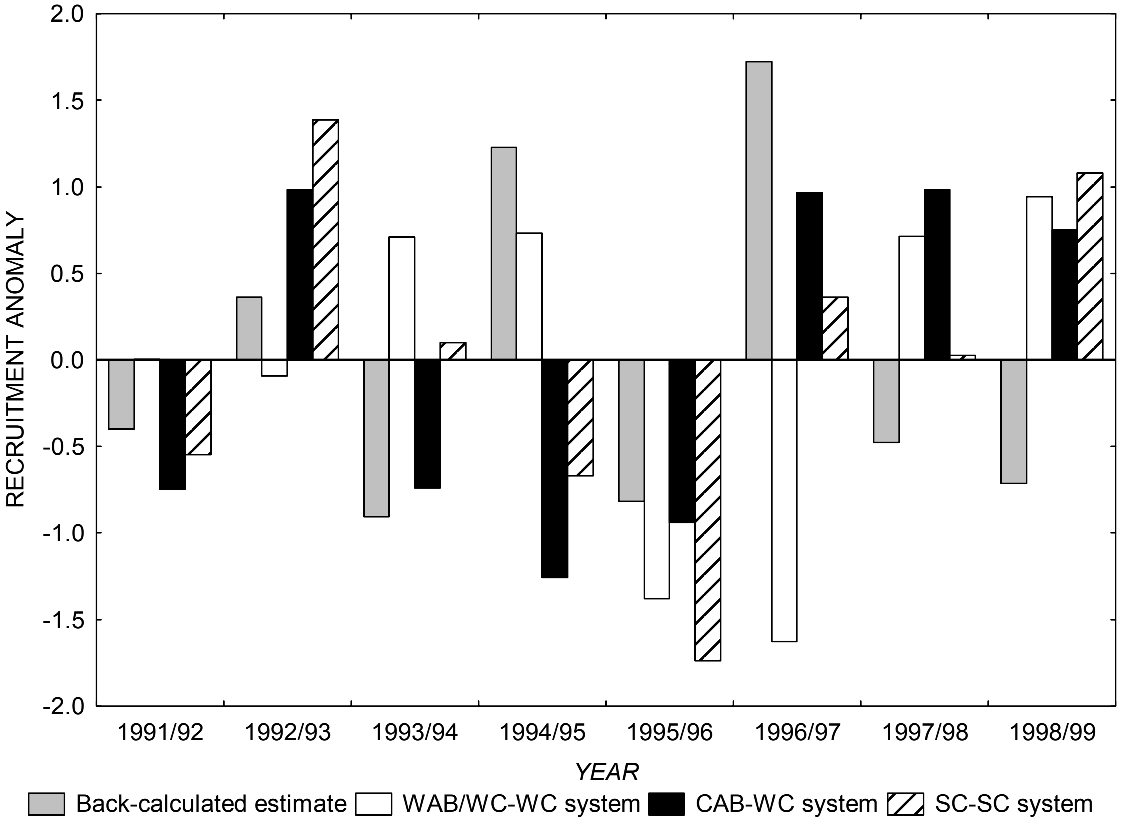

Fig. 3.11: Standardised anomalies of estimated sardine recruitment and the modelled recruitment in each system for the eight years of the Lagrangian transport experiment. Anomalies are calculated as the difference between the value for a given year and the mean over the eight years, divided by the standard deviation over the eight years

3.4. DISCUSSION

The modelled recruitment levels presented here are hypothetical and in no way relate to actual levels of recruitment. They do however give insight into how the currents of the region are likely to favour or hinder the chances of successful recruitment of eggs spawned at different areas and times. It is quite clear that the location of spawning has a massive impact on where recruitment is likely to occur and this resulted in the identification of three possible recruitment systems, two retention-based systems and a transport system between them, based on location of spawning and recruitment. Nelson and Hutchings (1987) proposed a closed system for anchovy in the southern Benguela ecosystem with spawning occurring predominantly on the WAB and all recruitment occurring on the west coast. Oppositely moving offshore (northwards) and nearshore (southwards) currents, with speeds for the most part exceeding swimming speeds of anchovy (and sardine) larvae, suggest that the species depends on passive transport of reproductive products for their survival in this system. The results generated by this model confirm this idea of a closed system on the west coast, the WAB/WC-WC system. However, the eastward spawning extent of sardine suggests that the WAB/WC-WC system alone does not incorporate all of the spawning activity of sardine. Eggs and larvae may not be transported in significant numbers out of this system but older sardine fish are able to swim beyond it to the CAB and EAB to spawn. Therefore two other recruitment systems were defined: the CAB-WC system has eggs spawned outside of this 'closed' system that are able to enter it and recruit to the west coast (i.e. it is only closed to particles leaving but not to particles entering the system) and the SC-SC system how many eggs spawned on the south coast are retained to possibly recruit there.

A fundamental difference between the three systems is one of retention vs. transport. The spawning and nursery areas in the CAB-WC system are completely spatially distinct. In this system particles will successfully recruit if they manage to find the right currents to transport them across the Agulhas Bank to the Cape Columbine jet current, which could take them up the west coast. In contrast, the SC-SC system has largely overlapping spawning and nursery areas and successful recruitment relies on particles not being transported out of the area they are spawned. Retention of particles is important, and therefore particles will successfully recruit if they don't get transported westward across the Agulhas Bank and avoid being caught in the fast-flowing Agulhas Current. The WAB/WC-WC system incorporates both transport and retention, with the WAB and sections of the LWC spawning areas being separate from the nursery grounds. Here particles will successfully recruit if they can be successfully transported to or are retained on the west coast, and then avoid offshore advection before they reach the stage where they are able to retain themselves in the nursery grounds. The WAB/WC-WC system is in part similar to the northern Benguela ecosystem where sardine spawning occurs in the upwelling areas and successful recruitment is dependent on avoiding offshore loss (Stenevik et al. 2001, 2003). However the inclusion of the WAB in this system incorporates an aspect of the generally accepted idea of sardine in the southern Benguela ecosystem having distinct spawning and nursery areas with transport between the two being essential for recruitment (Crawford 1980). This area of the WAB/WC-WC system, and the CAB-WC system, is similar to previous IBM studies carried out in the southern

Benguela (Mullon et al. 2002, 2003; Huggett et al. 2003; Parada et al. 2003), which were based on anchovy and reflect current knowledge of the life cycle of that species, which spawns off the south coast and recruits off the west coast. Parada (2003) briefly discussed a purported SC-SC system in her anchovy IBMs, but extensive modelling of this scenario was not undertaken.

Model results clearly support the hypothesis of the existence of a south coast recruitment ground. Particles can be retained in the area of the quasi-permanent cool ridge in quite large numbers, especially when released from the EAB. However, it must be noted that retention does not necessarily imply successful recruitment. A number of factors could result in recruitment levels on the south coast being low despite successful retention. High predation-linked mortality of eggs and larvae is likely because of the large biomass of pelagic and mesopelagic planktivorous fish found in this area during the summer (Japp et al. 1994, Hutchings et al. 2002), and numerous large predatory fish could cause great losses of older recruits. In addition, Carter et al. (1987) found that the relatively low primary production on the Agulhas Bank may be a limiting factor for various species, and the productive area of the Agulhas Bank is not as extensive or as uniformly productive as the west coast (Brown 1992). One would assume that due to less intense upwelling the Agulhas Bank would not be able to support as large a sardine population as the west coast nursery grounds. But the persistent shelf edge upwelling along the offshore edge of the cool ridge (Lutjeharms et al. 2000) and the associated high phytoplankton (Probyn et al. 1994b) and copepod (Verheye et al. 1994) concentrations mean this area is fairly productive. Also, Butler (1987), working on Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*), found that during an El Niño event sardine grew faster than anchovy. Based on this, he concluded that sardine might be superior competitors when food is limiting due to their highly opportunistic nature. Hence, the Agulhas Bank could support a significant spawner biomass of sardine. Roberts et al. (submitted) recently suggested the existence of a permanent cyclonic eddy between 22°E and 25°E that could account for the persistence of shelf edge upwelling along the EAB and that may retain eggs and larvae on the Agulhas Bank. Hutchings et al. (2002) also suggested that this ridge might play an important role in fish life-history strategies on the Agulhas Bank because currents tend to circulate clockwise around it. Most recently, Lett et al. (in press) used an IBM linked to the same PLUME output as in this study, and showed that two of Bakun's triad, namely enrichment and retention appear to be favourable on the south coast in the region of the cool ridge, making it a potential nursery ground. The large number of eggs that potentially could be retained on the south coast implies that even at very high levels of larval starvation and predation at least some recruitment should occur here every year.

With regards to the CAB-WC system, it is reasonable to assume that having spatially-distinct spawning and nursery areas offers the sardine either increased recruitment success or more reliable or predictable recruitment from year to year. In other words for the CAB-WC system to be more biologically efficient than the WAB/WC-WC system, losses as a result of unsuccessful transport between the Agulhas Bank and the west coast should be less than the loss due to offshore advection of eggs/larvae spawned on the west coast. However, the results of this experiment show that the spatially-distinct spawning area on the Agulhas Bank results in lower recruitment than when eggs are spawned in the nursery area itself. In addition to this, there is more interannual variation in the level of transport success from the Agulhas Bank to the west coast than in the level of retention of eggs spawned on the west coast (*Year* explaining more of the variance in modelled recruitment in the CAB-WC system than any of the other systems). Therefore, it can be concluded that either other factors on the west coast (e.g. mortality due to predation, food environment, temperatures etc.) have led to this separation of spawning and nursery areas, or eggs that are spawned further east are not intended to recruit to the west coast. Sardine are an opportunistic species and are fairly unspecific when it comes to choosing a suitable spawning habitat (Twatwa et al. 2005). It seems unreasonable to assume that potentially lower egg mortalities in the CAB-WC system would make up for the substantially lower transport/retention rate in this system compared to the WAB/WC-WC system. Predation also seems an unlikely reason for the loss of reproductive products in the WAB/WC-WC system. The Agulhas Bank is used by many species as a spawning ground (Hutchings et al. 2002) and hence demand for food in this area is high. Anchovy spawners have been shown to eat eggs of their own and other species' (Valdés et al. 1987, Valdés Szeinfeld and Cochrane 1992), although van der Lingen (2002) found few sardine eggs in stomachs of sardine on the Agulhas Bank. Nonetheless, predation on eggs and larvae by anchovy and other planktivorous fish found in abundance on the Agulhas Bank, is likely to be higher than on the west coast. All these arguments indicate that to recruit to the west coast, it is favourable to spawn there or on the western edge of the Agulhas Bank. That sardine choose on occasion to spawn much further east than this suggests the existence of an alternative recruitment ground, possibly near the quasi-permanent cool ridges. It can also be seen that the more eastward along the Agulhas Bank a particle is spawned, the more likely it is to recruit to the south coast nursery ground. In contrast, the more westward along the bank it is spawned, the more likely it is to recruit to the west coast nursery ground.

The spatio-temporal patterns of modelled recruitment differ from system to system. In the WAB/WC-WC system *Spawning Area* was the most important variable, mainly because of exceptionally high levels of modelled recruitment from the UWCin area and a much lower level of modelled recruitment from the WAB. What was perhaps more noteworthy was the *Depth* relationship. Because modelled recruitment depends for the most part on particles being retained nearshore on the west coast, the intensity of upwelling controls success to a large degree. Parrish et al. (1981) found that a reasonable depth for the Ekman offshore transport layer is usually from the surface down to approximately 20m. In the northern Benguela ecosystem, Stenevik et al. (2001) found that the inshore moving currents were usually found just below this layer. Modelled recruitment was significantly less for particles released in the top 25m and an examination of the *Depth*Month* interaction (Fig. 3.7B) shows that this lower success can be attributed to upwelling induced Ekman transport, which is highest in the summer when south-easterly upwelling-favourable winds prevail and lowest during the winter months (May-August). A similar pattern of success by *Depth* was found for the CAB-WC system, most likely because both these system ultimately rely on the particles being retained on the west coast. However, *Month* was the most important variable in the CAB-WC system. The timing of spawning is critical in this system with September to November (peaking in October) clearly being the most likely time for particles to successfully reach the west coast, and May to July being the least likely (Fig. 3.8A). Modelled recruitment was highest during the spring and summer, even though more offshore loss from the west coast is likely during this time. Hence, in this system spawning at a time when there is good transport over the Agulhas Bank to the Cape Columbine jet current is more critical in determining transport success than is retention in the nursery area. This along shore transport is most often present over September-November and is weakest over the winter months. However, a strong *Year*Month* interaction (Fig. 3.8B) indicates that this is not a fixed seasonal pattern with the level of modelled recruitment each month varying from year to year. For spawning to be successful in this system an extended spawning season would be necessary to ensure a match between the release of eggs and favourable transport conditions to the west coast. However, the fact that patterns of success by month closely match patterns of recruitment location ratio by month in the CAB-WC system (Fig. 3.9A) indicates that the CABoff area is a safe place to spawn if south coast recruitment does occur. Essentially this eliminates the temporal match-mismatch problem because times when transport to the west coast is poor (May-July) are times of high retention on the south coast. Modelled recruitment in the SC-SC system is almost completely dependent on *Spawning Area*. Successful retention is much greater in the EAB spawning areas than the CAB spawning areas and the inshore spawning areas are also favoured. In fact, the levels of retention are so high on the EAB that it seems transport out of this area is very difficult, indicating that this may form another closed system of spawning. A *Spawning Area*Month* interaction shows that retention in the CAB is highest in the winter. In winter, westerly atmospheric troughs cause onshore Ekman transport on the EAB (Jury 1994). This, in conjunction with lower levels of transport to the west coast during this time, could explain this pattern.

The aim of this experiment was not to predict actual levels of recruitment but rather the likely impact circulation patterns, and their effect on the transport and retention of eggs and larvae, would have on this process. So it was not unexpected that none of the three recruitment systems had modelled recruitment anomalies that correlated significantly with back-calculated recruitment estimate anomalies. However, when one examines Fig. 3.11 in conjunction with the composite egg distributions for each year (Fig. 1.3) it becomes apparent that circulation factors could be very influential in determining levels of recruitment and that all three systems play an important role. In 1995/96 all three systems had a negative recruitment anomaly, and the back-calculated recruitment anomaly concurred. In 1991/92 and 1992/93 the back-calculated recruitment anomaly contradicted the WAB/WC-WC system modelled recruitment anomaly. However, in these years eggs were found mainly over the CAB and EAB and the anomalies for the CAB-WC and SC-SC systems both corresponded with the back-calculated recruitment anomaly (negative in 1991/92 and positive in 1992/93). Similarly, in 1994/95, when eggs were found mainly on the west coast, the high back-calculated recruitment anomalies corresponded with good modelled recruitment anomalies in the WAB/WC-WC system even though negative modelled recruitment anomalies were found in both the CAB-WC and SC-SC systems in this year. But there were also disagreements in the data. In 1997/98 and 1998/99 all three systems had positive modelled recruitment anomalies but back-calculated recruitment was low over these years. In 1993/94 despite eggs being found predominantly along the west coast, with some on the EAB, and the positive modelled recruitment anomalies for the WAB/WC-WC and SC-SC systems, back-calculated recruitment was low. Hence, neither transport nor retention success is the sole determinant of successful recruitment, and other factors such as food availability, suitable spawning conditions and the age structure of the stock could be more important during certain years.

In this experiment eggs and larvae were analogous to passive drifters. Biological properties and behavioural traits or abilities were assumed to have a negligible effect on the way they were transported. The results of this experiment are therefore not biologically meaningful but they do illustrate the effects of the circulation environment to which eggs and larvae are subjected once spawned. This serves as an excellent basis with which to compare the results of further experiments that incorporate biological properties and behavioural activities in the particles. The most important finding of this experiment is the apparent division of the southern Benguela ecosystem into three recruitment systems for sardine. The WAB/WC-WC and SC-SC systems appear to be closed to the loss of particles though some transport out of the SC-SC system occurs. The CAB, despite being largely separate from both nursery areas, contributes to recruitment in both and as such appears to be a transition zone between the WAB/WC-WC and SC-SC systems.

CHAPTER 4: THE EFFECT OF TEMPERATURE-DEPENDENT DEVELOPMENT RATE AND MORTALITY ON TRANSPORT AND RETENTION OF SARDINE SARDINOPS SAGAX *EGGS AND LARVAE IN THE SOUTHERN BENGUELA ECOSYSTEM*

ABSTRACT

A stage-based temperature-dependent development model is incorporated into the particle tracking IBM for sardine (*Sardinops sagax*) in the southern Benguela ecosystem. Individuals are transported in a Lagrangian manner using the 3-D velocity fields of the PLUME model and temperature output is used to drive the development of each individual. Four stages of development are used: egg, yolk-sac larva, early larva and late larva, and a Bělehrádek function was fit to development-temperature data for each stage. Individuals are considered to have successfully rectuited to a nursery area upon reaching the late larva stage, rather than a fixed age. Temperature-induced mortality is also incorporated during the yolk-sac larva stage. Temperature has a substantial effect on stage duration for all stages. The average time taken to develop to the late larva stage varies spatially, seasonally and with depth. Development times are quicker on the warm Agulhas Bank (between 300 and 310h) than on the cool west coast (between 330 and 400h). In the WAB/WC-WC recruitment system slow development (resulting in increased offshore loss) decreases the overall modelled recruitment rates, and the 25-50m depth range has the highest level of recruitment success due to good retention in the nursery area and quicker development than at depth. Mean modelled recruitment in the CAB-WC and SC-SC systems shows little change from the results of the simulations with a fixed age for recruitment. Temperature-induced larval mortality is highest for individuals released in the inshore west coast spawning areas, and less than 2% in the remaining areas. The stage-based development model is considered to be a useful method of incorporating growth into individual-based models (IBMs).

4.1. INTRODUCTION

The Lagrangian transport experiment (Chapter 3) used a fixed age recruitment criterion to determine when individuals would be able to retain themselves within a given nursery area and therefore be considered to have been successfully transported or retained there. This implies constant rates of development across the entire spatial and temporal domain of the model. However, it is too simplistic to assume all individuals develop at a constant rate. This experiment deals with this problem by incorporating a development model within the IBM that can be applied to each individual to determine its unique rate of development until a stage when it is able to maintain its position. It also includes temperature-dependent mortality in the form of lethal lower limits below which individuals cannot survive.

Before metamorphosis from larva to juvenile fish, four basic stages can be identified in the sardine life cycle (Fig. 4.1). The first stage is the egg phase, extending from fertilisation until hatching. This is followed by a yolk-sac larva stage (Louw and O'Toole 1977) during which the newly hatched larva is unable to feed and still survives on food reserves from the egg. In order to survive beyond the stage when all food reserves have been utilised, the larva requires a functional jaw (to feed) and pigmented eye (to find food). The development of these marks the start of the early larva or protopterygiolarval phase. This stage marks the transition to exogenous feeding, and the ability to swim through fin development (Jobling 1995). Swimming is possible during the late larva

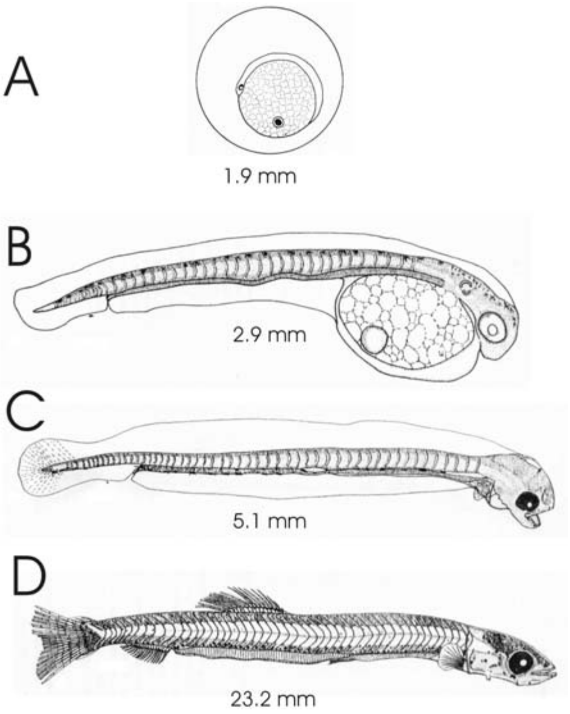

Fig. 4.1: The four basic stages of development during the early development of the sardine (*Sardinops sagax*). A = Egg (Gastrulation stage) (King 1977), B = Yolk-sac larva, C = Early larva, D = Late larva (Louw and O'Toole 1977). Measurements give mean total length

or pterygiolarval phase as fins have developed and it is during this phase that the fins fully differentiate. Once this has occurred, the larval stage is complete (Jobling 1995). The rate of development through the phases can be important, as mortality rates during these early stages are often high.

It is clearly important to incorporate temperature-dependent development rates when modelling the early life stages of fish (Fox et al. 2003). This can be incorporated easily and effectively within IBMs utilising output from hydrodynamic models, which can generate realistic, highly variable temperature fields (Blanke et al. 2002). There is a great spatial temperature range in the Benguela ecosystem, not only on a regional scale but also on a much smaller kilometre scale. In addition to this, temporal differences also occur from seasonal differences to much shorter time scales such as upwelling events. These differences make the use of a fixed age criterion for the ability of sardine larvae to recruit (i.e. actively feed and maintain their horizontal position) unrealistic. While the vertical and temporal scales of the PLUME model allow it to adequately resolve the temperature variations mentioned, the horizontal spatial scale of the PLUME model outputs are less able to capture small scale temperature variations. However, these are less likely to be important when considering questions involving the broad geographical scale of sardine spawning, allowing temperature-based development to be applied effectively using the PLUME model temperature fields.

Measuring temperature-dependent development rates *in situ* is difficult because of temperature fluctuations and the inaccuracy of sampling methods. Therefore, these rates are best determined in the laboratory in a controlled-environment incubator (King 1977). Eggs or larvae can be accurately tracked through the various stages of development under constant temperature conditions and the rates of development at each temperature estimated. A mathematical function can then be fitted to the data to describe the relationship. Numerous such studies on development rates of sardine have been done, for example in California (Ahlstrom 1954, Lasker 1964), Japan (Ito 1958) and the northern Benguela (King 1977, Le Clus and Malan 1995), although no data exist for sardine in the southern Benguela ecosystem. Lasker (1964) noted that at temperatures lower than 13°C sardine larvae fail to develop a functional jaw and pigmented eye, ultimately resulting in mortality. This was supported by the findings of King (1977) who also reported that it was possible for development to continue as usual if larvae kept in water colder than 13°C for short periods were subsequently moved into warmer water.

This experiment focuses on the interaction between egg and larval development rates and transport and retention in the southern Benguela ecosystem. The null hypothesis is that spatial differences in development times do not significantly affect the transport and retention of individuals. Alternatively, spatial differences exist and individuals in colder areas are likely to develop slower and are therefore less likely to be retained in a nursery area before developing to a stage at which they are able to recruit. It is thought feasible that sardine spawn on the Agulhas Bank because temperature induced mortality of larvae is lower here than on the west coast. The second null hypothesis is that mortality rates do not differ significantly across the southern Benguela ecosystem. The alternative hypothesis is that there are significant differences in the rate of temperature-induced mortality between the west and couth coasts.

4.2. METHODS

4.2.1. Development model for eggs and larvae

When modelling the early life stages of fish it is most convenient to model successive exponential segments (Ricker 1979). Each segment, corresponding to a different stage of development, has different growth parameters associated with it. The most commonly used temperature relationship for such stage-by-stage modelling of development utilises units known as degree-days or degree-hours (Hayes 1949). A degree-day/hour is defined as the proportion of stage development completed in one day/hour at a given temperature. Numerous studies on the development of eggs of pelagic fish species in the southern Benguela ecosystem have found that the rate of development increases exponentially with increasing temperature (O'Toole and King 1974, King 1975, King et al. 1977, King et al. 1978). Hence the number of degree-hours to complete a given stage decreases exponentially with increasing temperature. This negative exponential pattern has also been shown to hold true for the larval stages of fish (e.g. Lasker 1964, King 1977). Using field observations and laboratory study estimates of growth at different temperatures, the relationship between temperature and degree-hours can be obtained. The growth model developed here utilised a form of this method.

The relationship between stage duration and temperature was calculated for three different stages:

1. **Egg**: From spawning to hatching.
2. **Yolk-sac larva**: From hatching to development of fully pigmented eyes and functional jaw.
3. **Early larva**: From first feeding to flexion of the notochord and first fin development (egg food reserves have been depleted and limited feeding is possible).

Once the individual has developed beyond the early larva stage it is called a **late larva** (the larva is able to swim and therefore has increased searching ability for feeding) and no further development occurs in the model.

Three different curves were fit to the laboratory data for stage duration at different temperatures (King 1977): a Bělehrádek function (three parameters), a quadratic polynomial function (three parameters) and a negative exponential curve (two parameters). The Bělehrádek function was fit to development-temperature data for each stage using a method described by Edgar and Andrew (1990). The Bělehrádek function was expressed as:

$$D = (\alpha t + \beta)^{\gamma} \tag{4.1}$$

Where:

D = stage duration (h)

t = temperature (°C)

and α, β and γ are stage-specific parameters.

To estimate the values of the stage-specific parameters, a regression of $D^{1/\gamma}$ on **t** for each stage was first calculated for a range of *a priori* chosen values of γ. The best fit was found using R^2 as a measure of goodness of fit. The γ value corresponding to the best fit was then used in equation (4.1) and α was taken as the gradient of the regression $D^{1/\gamma}$ on **t** and β as the y-intercept. All fits were done using data from King (1977) for the northern Benguela sardine

(*Sardinops sagax*). In the case of yolk-sac larvae, no development occurs at temperatures colder than 13°C. If individuals in that stage remained at temperatures less than 13°C for more than two days (one time step) in the simulations, they were considered to be dead and removed from the population. No direct temperature-stage duration data were found for the early larva stage in the Benguela ecosystem so data were taken from Butler et al. (1993) for sardine (*Sardinops sagax*) in the Californian upwelling system. Only the development time at 18°C was given so the yolk-sac larvae parameters were used, adjusted by a constant factor (2.95) to fit the single available data point.

The proportion of stage development completed by each individual during each iteration (five per time step) was calculated using the equation:

$$Dev_{ts} = \frac{D_t}{l} \tag{4.2}$$

Where:

Dev_{ts} = Proportion of stage development completed per iteration

D_t = stage duration at temperature t

l = length of iteration (9.6h)

For each iteration the proportion of each individual's development through a stage was added to its development counter. Once the counter exceeds 1, that stage is complete and the individual is moved up to the next developmental stage. Any excess growth from the previous stage is converted to development in the new stage by considering the relative difference in development rate between successive stages. The process was repeated until the individual reached the late larva stage.

4.2.2. Experimental design

4.2.2.1. OVERVIEW OF THE MODELLING PROCESS

Fig. 4.2 depicts the modelling process followed. The IBM simulations were carried out in exactly the same manner as in the previous experiment (Chapter 3). The only difference was the incorporation of a stage-based egg and larval development model based on the relationship between development rate and temperature and the incorporation of a lethal temperature threshold. This allowed for an additional physical variable (sea temperature) to be incorporated in the IBM and added a biological property to the particles, turning them into unique individuals.

4.2.2.2. MODEL PARAMETERS

The parameters for this model were all those used in the Lagrangian transport experiment along with a constant lethal temperature threshold of 13°C during the yolk-sac larva stage (Table 4.1).

Table 4.1: The fixed parameters and variables used in the temperature-dependent development experiment, their ranges or values and *n*

Parameter	**Range/Value**	***n***
Fixed parameters		
Number of particles	10 000	-
Duration of release of particles	30 days	-
Tracking period	60 days	-
Lethal minimum temperature§	13°C	-
Variables		
Spawning Area	(see Fig. 2.5)	9
Year	1991/92 – 1998/99	8
Month	Jul – Jun	12
Depth	0-25, 25-50 and 50-75m	3
Trial	-	3
Number of simulations		**8×12×3×3 = 864**

§ = yolk-sac larva stage only

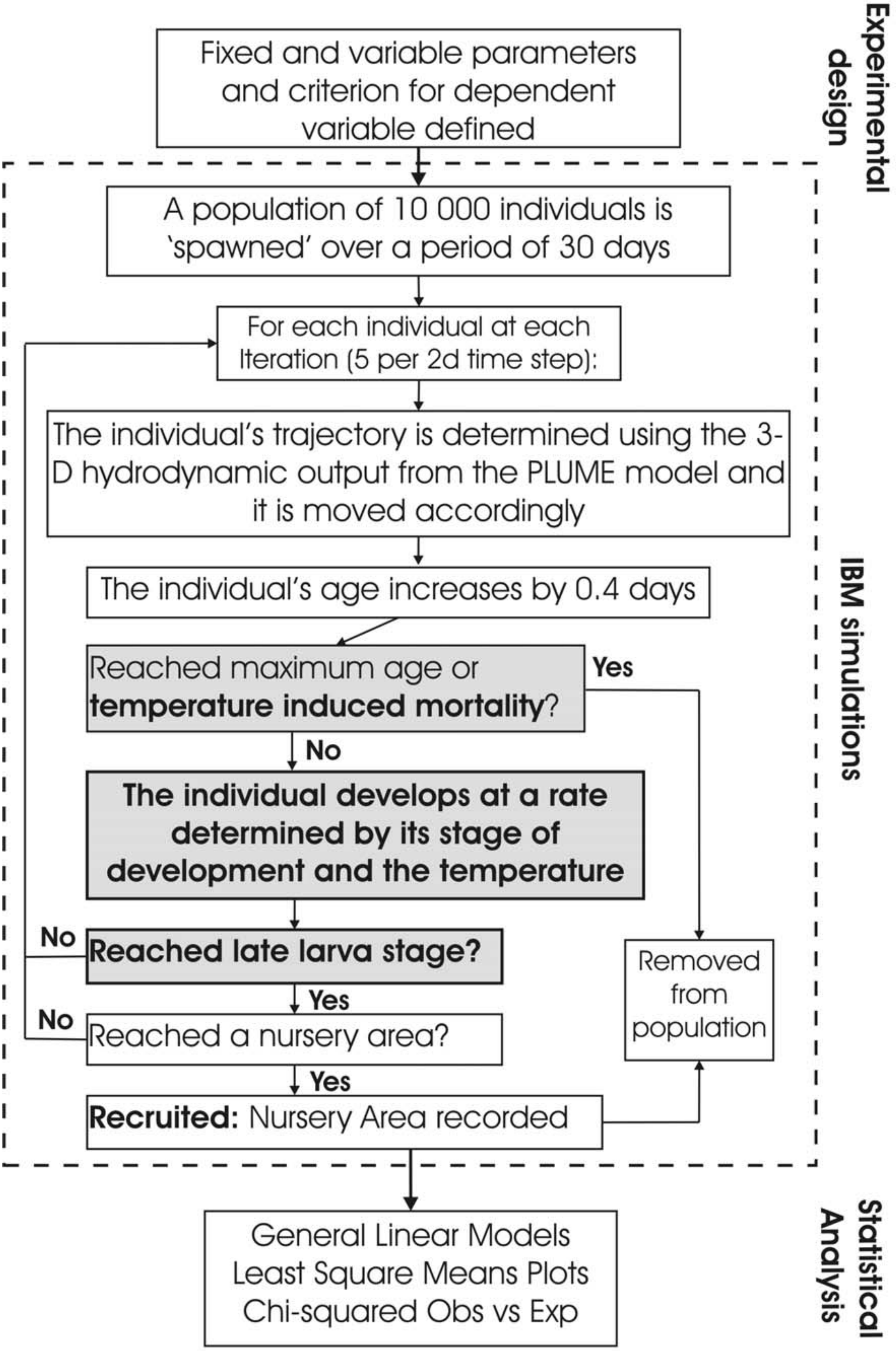

Fig. 4.2: Flow chart depicting the three stages of the modelling process for the temperature-dependent development experiment. (Shaded blocks represent added processes)

4.2.2.3. DEPENDENT VARIABLES

The same two nursery areas previously used (west coast and south coast) were used in this experiment and the same three recruitment systems (WAB/WC-WC, CAB-WC and SC-SC) were examined. However, the criterion for modelled recruitment differed. Instead of using the estimated time for development to the stage where swimming is possible (14 days), individuals needed to have reached the late larva stage before they were able to recruit to a nursery area. It is assumed that when the individual is able to feed and swim, it is able to survive and retain itself within the nursery area. Modelled recruitment was determined as the percentage of individuals released from each spawning area reaching each of the two nursery areas in the late larval stage of development. Analyses were also carried out on the rates of temperature induced mortality from each spawning area. Mortality was calculated as the percentage of individuals released from each spawning area that die as a result of lethal temperatures (not including those that reach maximum age before reaching a nursery area).

4.2.3. Statistical analyses

The main aim of this experiment was to compare the effect of the stage-based criterion for successful recruitment with the fixed age recruitment criterion used in the Lagrangian transport experiment. This was quantified by calculating a difference ratio between the results of the simulations using the stage dependent and fixed age recruitment criteria. This was calculated according to the equation :

$$DR = 100 \times \frac{(\%SB - \%FA)}{(\%SB + \%FA)} \tag{4.3}$$

Where: DR = Difference ratio (%)

SB = Modelled recruitment using the stage-dependent recruitment criterion

FA = Modelled recruitment using the fixed age recruitment criterion

Simulation results were compared directly using Wilcoxon Matched Pairs tests (Zar 1999). A GLM using the complete simulation results was constructed with the difference ratio as the dependent variable to identify which variables interacted most with the development model to alter modelled recruitment rates.

As in the previous experiment the effect each of the variables had on determining in which nursery ground recruitment occurred was examined using recruitment location ratios (Chapter 3, equation 3.1). GLMs for each system with mortality and modelled recruitment as the dependent variables were performed. The five variables of the model (*Spawning Area*, *Year*, *Month*, *Depth* and *Trial*) were used as categorical predictors. For all GLMs a full factorial design to the 2nd degree was used with all the predictors except *Trial*, which was not used in any of the interaction terms. The adjusted R^2 and p values for each model were noted, along with all main and interaction effects and compliance with the GLM assumptions (Chapter 2, section 2.5). The percentage variance explained by each variable or interaction term was also calculated.

For all GLMs, plots of least square means (LSM) were used for visual analysis of the results and to identify the relationships between each variable and modelled recruitment values. The *a posteriori* Chi-squared test (Chapter 2) was used to identify significant peak or trough months for seasonal patterns. Correlations between modelled recruitment anomalies for each system and back-calculated recruitment estimate anomalies were performed and the strengths of these correlations were noted (R^2 and p values). A plot was made of the back-calculated recruitment and modelled recruitment anomalies for each system for each year.

4.3. RESULTS

4.3.1. Development model

For all stages, the Bělehrádek function was found to provide the best fit (Table 4.2). Temperature has a substantial effect on stage duration (Fig. 4.3). Time to hatching for eggs shows a four-fold difference across the shown range (118h at 11°C to only 30h at 22°C). The difference is less sizeable for the yolk-sac larva stage but stage duration at the warm end of the spectrum is still less than half that at the cold end (116h at 13°C (no development at

Table 4.2: Equations of the functions fit to the laboratory data of stage duration (*D*) at different temperatures (*t*) and the statistics of how well each equation fits the data

Stage	Fit	Equation	R^2	p
Egg	Bělehrádek	$D = (0.0076t - 0.0014)^{-1.91}$	1.00	<0.0001
	Negative exponential	$D = 411.36e^{-0.12t}$	0.92	<0.0001
	Polynomial (quadratic)	$D = 361.48 - 29.90t + 0.68t^2$	0.92	<0.0001
Yolk-sac larva	Bělehrádek	$D = (0.0003t - 0.0025)^{-0.69}$	0.99	<0.0001
	Negative exponential	$D = 346.82e^{-0.09t}$	0.93	<0.0001
	Polynomial (quadratic)	$D = 407.11 - 32.07t + 0.72t^2$	0.93	<0.0001

temperatures colder than this) to 50h at 22°C). The early larva curve is very steep at cold temperatures. Stage duration at 11°C (560h) is twice as long as at 14°C (280h) and more than three times as long as at 22°C (160h).

The average time taken to develop to the late larva stage in the model across all spawning areas at all depths during all months is just short of 14 days (13.66d). However, this varies

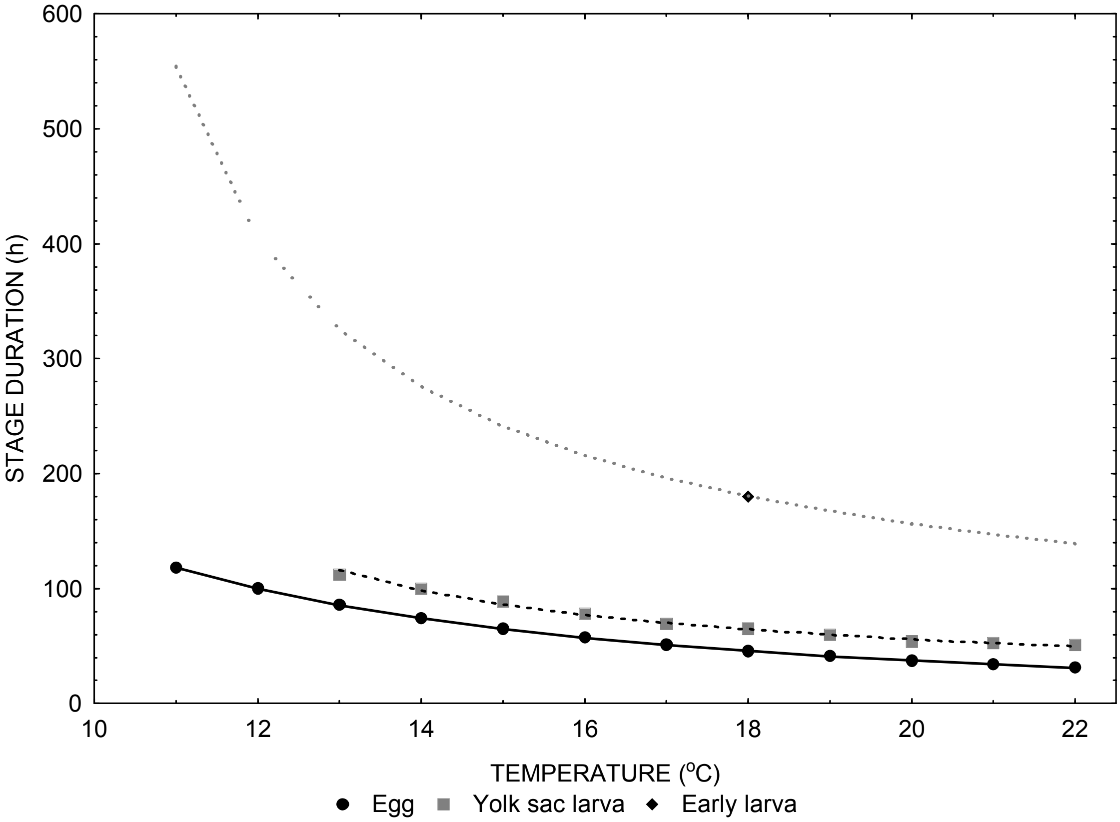

Fig. 4.3: The relationship between stage duration and temperature for the egg, yolk-sac larva and early larva stages. Points represent actual laboratory data for egg and yolk-sac larva (King 1977) and early larva (Butler et al. 1993), and lines are Bělehrádek equations fitted to the data (egg: α = 0.0076, β = -0.0014, γ = -1.9100; early and yolk-sac larva: α = 0.0003, β = -0.0025, γ = -0.6900)

with *Spawning Area*, *Month* and *Depth*. Development times are quicker on the Agulhas Bank (between 300 and 310h) than on the west coast (between 330 and 400h) (Fig. 4.4 A). The inshore west coast spawning areas had the slowest development rates while the offshore central Agulhas Bank (CAB) had the quickest developing larvae. The mean age of recruiting larvae to the west coast nursery area is generally 14 days or longer whereas, with the exception of the western Agulhas Bank (WAB), those recruiting to the south coast are all younger than 14 days. While age at recruitment to the west coast and development time to late larva is fairly similar from the west coast spawning areas, there are much greater differences for the WAB and CAB. This difference increases with distance away from the nursery area. Age at recruitment to the south coast and development time to late larva is almost identical for the CABin and EABin spawning areas and very similar for the CABoff and EABoff areas. Only larvae from the WAB take notably longer to recruit to the south coast nursery area than they do to develop. Larvae develop slowest between June and October (Fig. 4.4 B) and quickest between December and February. The development time to late larvae is more than two days shorter in January

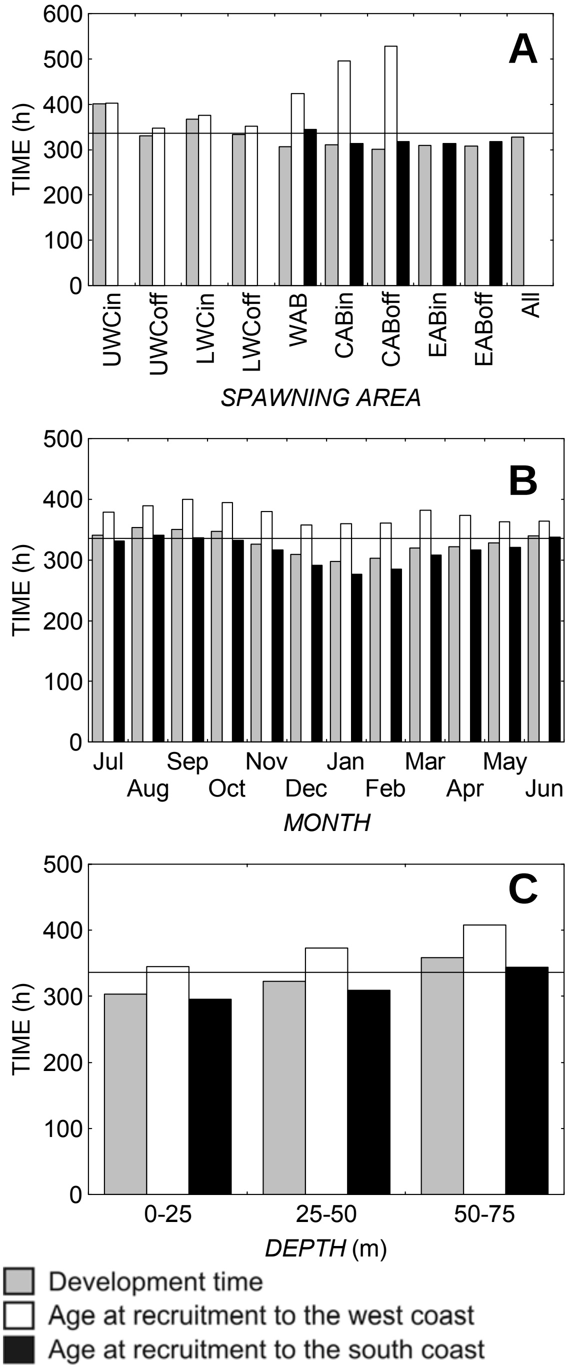

Fig. 4.4: Development times to the late larva stage and age at recruitment to the west coast and south coast nursery areas for the (A) *Spawning Area*, (B) *Month* and (C) *Depth* variables in the temperature-dependent development experiment. The solid line shows 14 days

than in August. Age at recruitment to the south coast closely follows the same pattern as development to late larvae. Despite slow development times from April to June, age at recruitment to the west coast is near its lowest over this period. Larvae develop to the late larva stage quicker in the surface waters than at depth (Fig. 4.4 C), development time increasing linearly with depth. This is reflected in the age at recruitment of larvae to both the west and south coasts.

4.3.2. Mortality

The single variable explaining most of the variance in mortality rate was *Spawning Area* (34.67%; Table 4.3). *Depth* was the only other variable to explain more than 5% of the variance (7.74%). The interaction of these two variables was also significant. There was no *Trial* effect.

Larval mortality was highest for individuals released in the inshore west coast spawning areas, the UWCin area having the highest mortality across the region (Fig. 4.5). Mortality rate increased with depth in these areas, the 50-75m depth range having substantially higher levels of mortality than the 0-25m and 25-50m ranges. The remainder of the spawning areas

Table 4.3: General linear model results across all the three systems in the temperature-dependent development experiment showing the contributions of the different variables to determining mortality rate. The main effects and interaction effects explaining more than 5% of the variance are shown, together with univariate statistics of the parameter values. Test of SS Whole Model vs. SS Residual: Adjusted $R^2 = 0.81$; $p < 0.01$. * = Significant ($p < 0.01$). % variance explained = $100 \times SS_{effect}/SS_{tot}$

	Sum of Squares	**Degrees of freedom**	**Mean Squares**	**F**	**p**	**% variance explained**
Intercept	12677	1	12677	8093		
Single variable						
Spawning Area	21522	8	2690	1717	0.00*	34.67
Year	278	7	40	25	0.00*	0.45
Month	1107	11	101	64	0.00*	1.78
Depth	4805	2	2402	1534	0.00*	7.74
Trial	0	2	0	0	0.94	0.00
Interaction terms						
*Spawning Area*Depth*	16961	16	1060	677	0.00*	22.17
Error	11705	7472	2			18.85
TOTAL	62080	7775	6434			

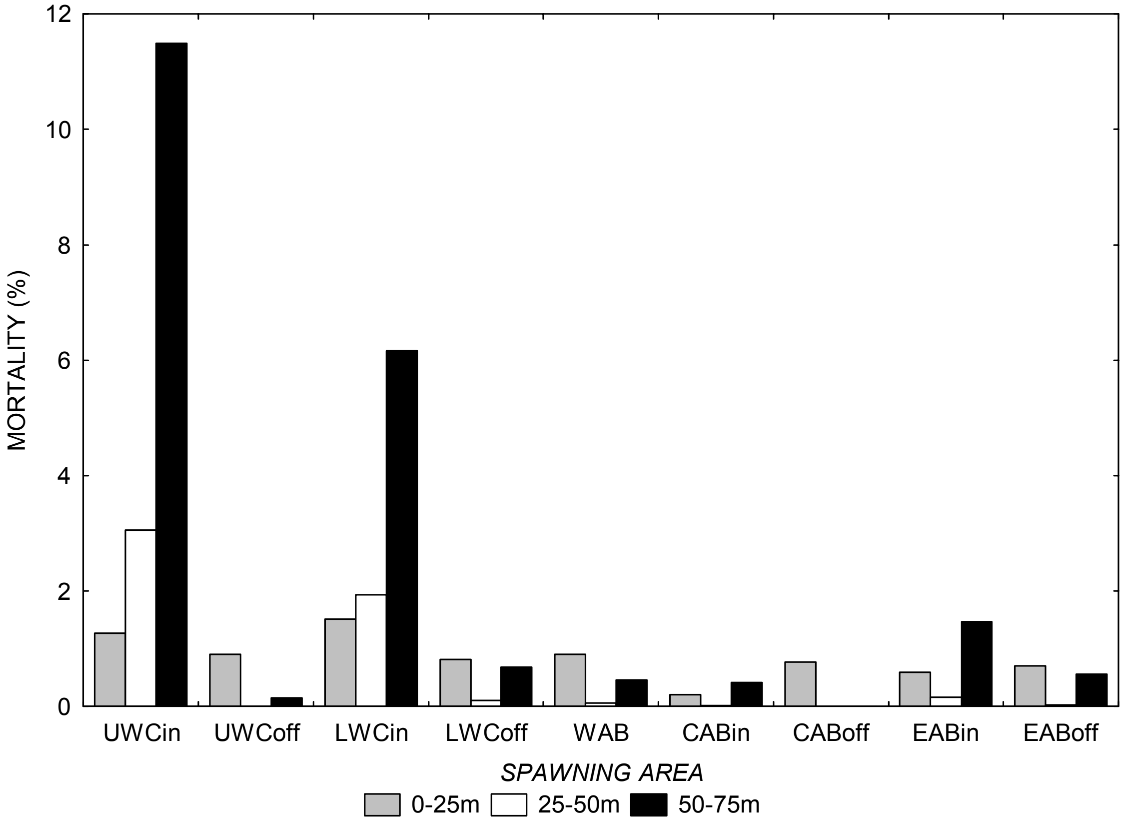

Fig. 4.5: Temperature-induced mortality rates for the *Spawning Areas*Depth* interaction

have less than 2% mortality caused by lethal temperatures. In all cases except UWCin and LWCin mortality was lowest in the 25-50m depth range.

4.3.3. Transport and retention

Mean modelled recruitment to the south coast showed little change from the results obtained using the fixed age recruitment criterion simulations (Fig. 4.6), and only the WAB had a notable decrease in modelled recruitment to the south coast (4.68%). Mean modelled recruitment to the west coast decreased using the stage-based recruitment criterion than when the fixed age criterion was used, mainly due to decreased retention success from LWCin, UWCin and EAB areas. Modelled recruitment to both the west coast and south coast nursery areas increased from the CABoff area, but by less than 2.5% in both cases.

Mean modelled recruitment to the west coast remains higher than that to the south coast (Fig. 4.7). All the west coast spawning areas have similar levels of retention (in the region of

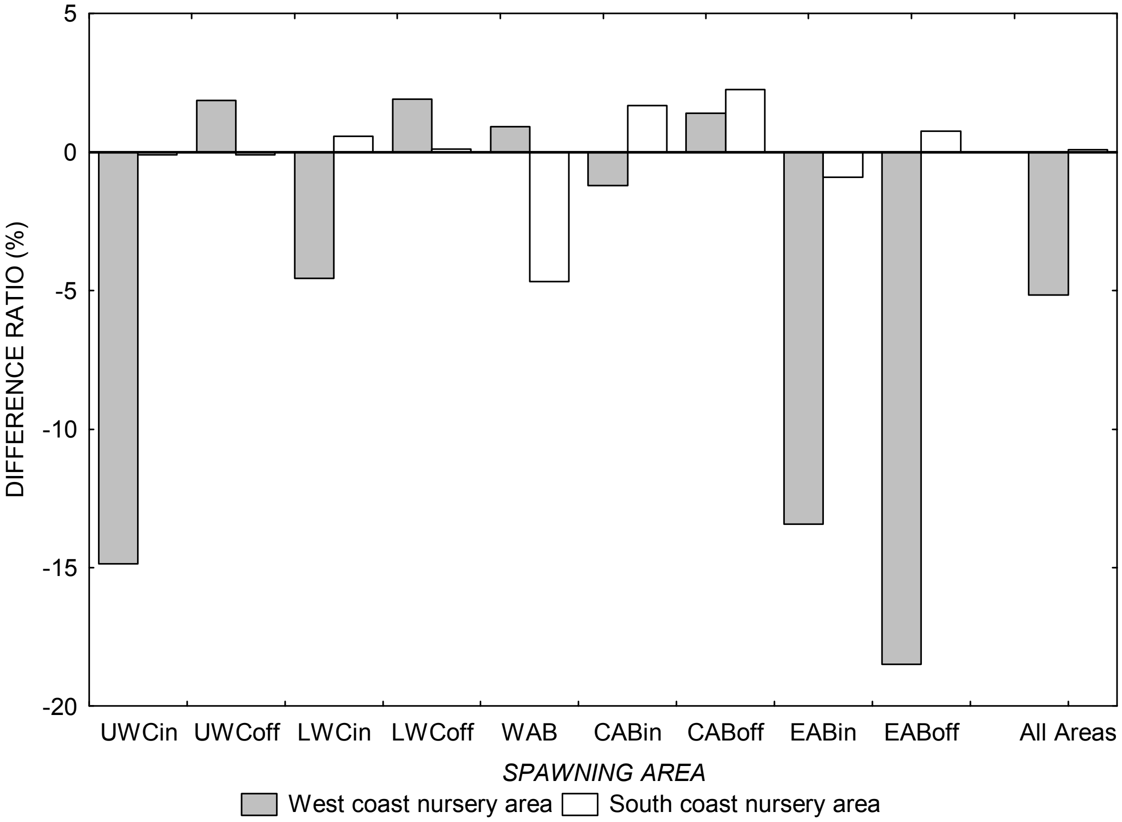

Fig. 4.6: Differences in modelled recruitment to the west and south coast nursery areas (difference ratio) between the Lagrangian transport and temperature-dependent development experiments for the *Spawning Area* variable

70%) in the west coast nursery area with no transport to the south coast occurring. More than half of the individuals released on the WAB recruit to the west coast but only 4.70% to the south coast. Retention on the south coast is higher from the CABin area than the CABoff area. Only the CABoff area has modelled recruitment rates higher than 10% to both nursery grounds. Very few of the individuals released on the EAB are transported out of the south coast nursery area before reaching the late larva stage (92.24 and 88.15% are retained from the EABin and EABoff areas, respectively).

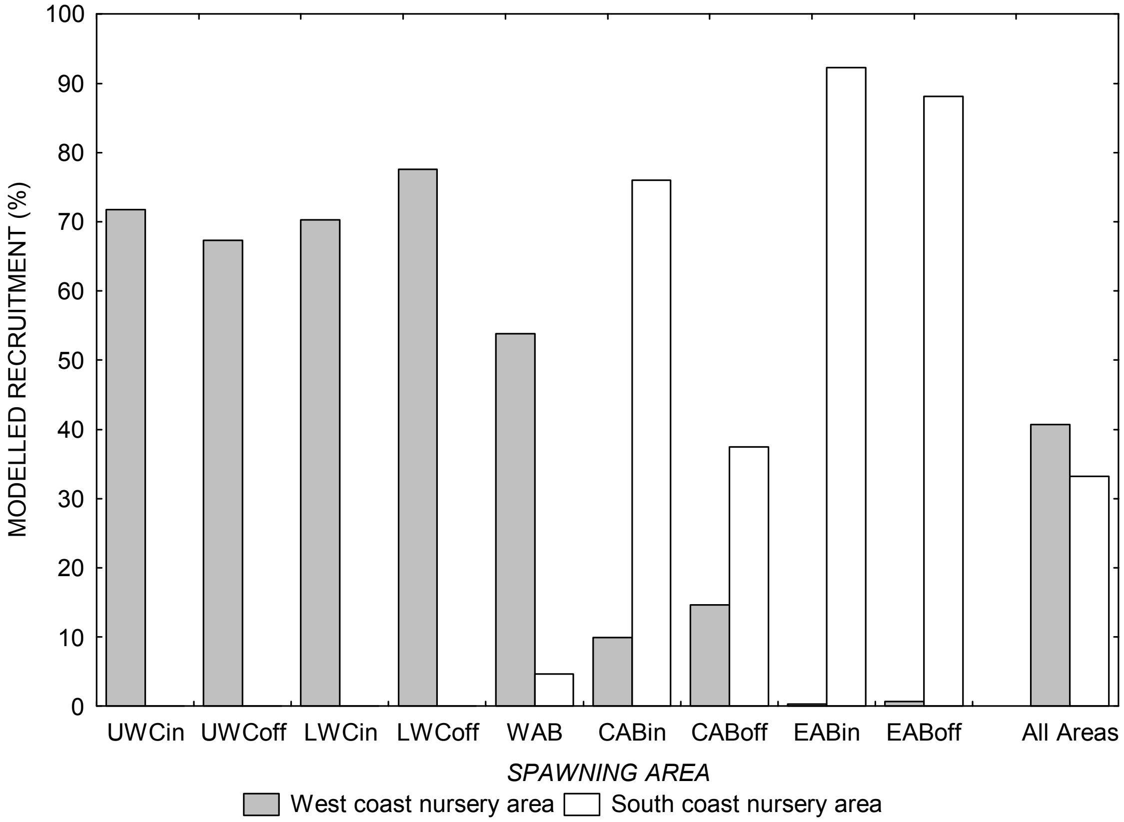

Fig. 4.7: Modelled recruitment to the west and south coast nursery areas for the *Spawning Area* variable in the temperature-dependent development rate simulations

4.3.3.1. THE WAB/WC-WC SYSTEM

Modelled recruitment results differed significantly from those of the Lagrangian transport experiment (Wilcoxon Matched Pairs test, $p < 0.001$). The GLM with the difference ratio as the dependent variable explained 83% of the total variance, with *Spawning Area* (32.41%), *Depth* (17.47%) and the interaction of these two variables (20.50%) accounting for most of this. Modelled recruitment decreased from the UWCin and LWCin areas and increased slightly from the remaining spawning areas (Fig. 4.6). The 50-75m depth range had 9.44 lower modelled recruitment and the other two ranges had negligible differences (Fig. 4.8). The single variables and first order interactions together explained 70.83% of the variance in the GLM for modelled recruitment in the WAB/WC-WC system (Table 4.4). The assumptions for the GLM analysis were met - the residuals of transport success were normally distributed and no trend was found in the mean and variance of the residuals in relation to the observed values.

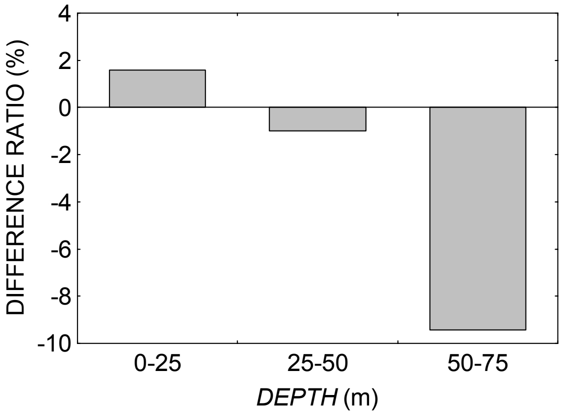

Fig. 4.8: Differences in modelled recruitment (difference ratio) between the Lagrangian transport and temperature-dependent development experiments in the WAB/WC-WC system for the *Depth* variable

Table 4.4: General linear model results for the WAB/WC-WC system in the temperature-dependent development experiment showing the contributions of the different variables to determining modelled recruitment. The main effects and interaction effects explaining more than 5% of the variance are shown, together with univariate statistics of the parameter values. Test of SS Whole Model vs. SS Residual: Adjusted $R^2 = 0.71$; $p < 0.01$. * = Significant ($p < 0.01$). % variance explained = $100 \times SS_{effect}/SS_{tot}$

	Sum of Squares	**Degrees of freedom**	**Mean Squares**	**F**	**p**	**% variance explained**
Intercept	20070323	1	20070323	161776		
Single variable						
Spawning Area	271081	4	67770	546	0.00*	15.55
Year	6242	7	892	7	0.00*	0.36
Month	70212	11	6383	51	0.00*	4.03
Depth	141469	2	70735	570	0.00*	8.11
Trial	14	2	7	0	0.94	0.00
Interaction terms						
*Spawning Area*Year*	87233	28	3115	25.1	0.00*	5.00
*Spawning Area*Month*	104161	44	2367	19	0.00*	5.97
*Spawning Area*Depth*	386599	8	48325	390	0.00*	22.17
*Year*Month*	115847	77	1505	12	0.00*	6.64
Error	508658	4100	124			29.17
TOTAL	1743776	4319	203704			

The primary determinant of modelled recruitment in this system remained the *Spawning Area* variable but this now explains less than half the amount of variance it did in the Lagrangian transport experiment (15.55%, down from 38.90%). *Depth* was again the next most important variable, explaining 8.11% of the variance. The 25-50m depth range has the highest level of modelled recruitment (Fig. 4.9 A). The inshore spawning areas had notably lower modelled recruitment from the 50-75m depth range, while the other three areas had similar levels of modelled recruitment in the 25-50m and 50-75m depth ranges leading to a strong *Spawning Area*Depth* interaction term (Fig. 4.9 B). A slight *Spawning Area*Month* interaction was found due to the WAB displaying a different seasonal pattern to the west coast spawning areas (Fig. 4.10 A). Modelled recruitment from the WAB is highest between September and March and low over the winter months, while modelled recruitment from the west coast spawning areas has the reverse pattern. The mean seasonal pattern for the WAB/WC-WC system did not differ significantly from a uniform distribution ($\chi^2 = 2.86$, df = 11, p = 0.99). The *Spawning Area*Year* interaction (Fig. 4.10 B) explains 5.00% of the total variance. The inshore west coast spawning areas show little difference from year to year. Likewise the UWC areas have fairly constant levels of modelled recruitment except in 1998/99 when lower than usual modelled recruitment was found. The WAB fluctuates little over the first five years but then has increased modelled recruitment over the last three years, peaking in 1996/97. There was no *Trial* effect.

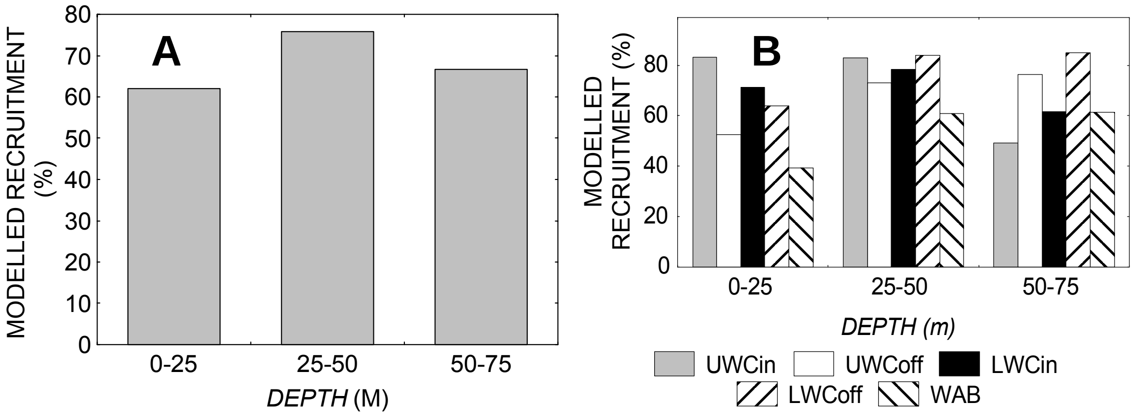

Fig. 4.9: Modelled recruitment in the WAB/WC-WC system in the temperature-dependent development experiment for (A) the *Depth* variable and (B) the *Spawning Area*Depth* interaction

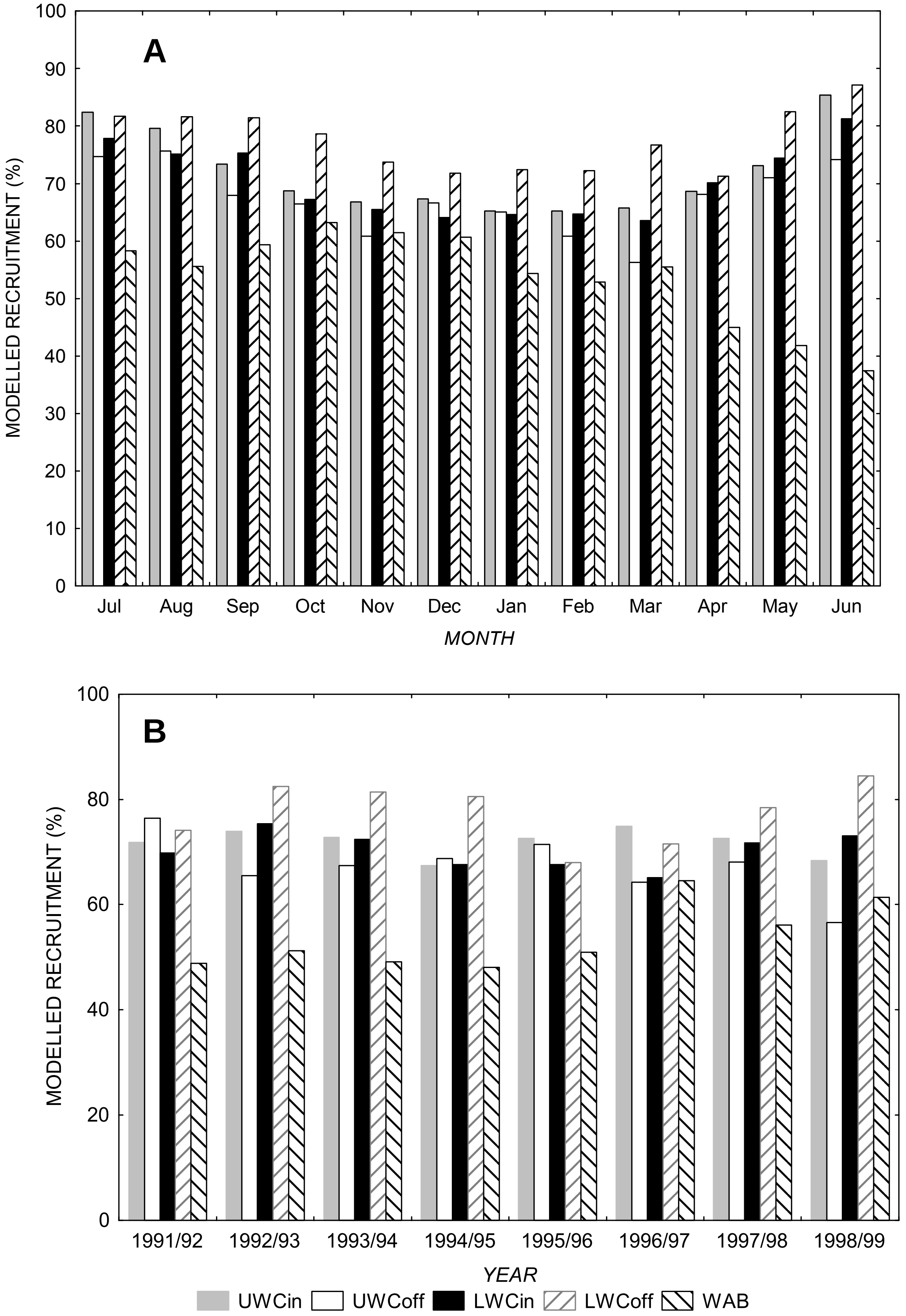

Fig. 4.10: Modelled recruitment in the WAB/WC-WC system in the temperature-dependent development experiment for (A) the *Spawning Area*Month* and (B) the *Spawning Area*Year* interactions

4.3.3.2. THE CAB-WC SYSTEM

Modelled retention results differed significantly from those of the Lagrangian transport experiment (Wilcoxon Matched Pairs test, $p < 0.001$). However, the GLM with the difference ratio as the dependent variable only explained 17.62% of the variance. None of the single variables explained more than 2% of the variance and only the *Year*Month* interaction explained a notable amount (6.06%).

In the GLM for modelled recruitment in the CAB-WC system, the single variables and first order interactions together explained 88.85% of the variance (Table 4.5). The assumptions for the GLM analysis were met - the residuals of transport success were normally distributed and no trend was found in the mean and variance of the residuals in relation to the observed values.

As before (Chapter 3), this system has a strong seasonal effect with the *Month* variable explaining 30.88% of the variance. While modelled recruitment was higher to the south coast than the west coast for all months of the year, this difference was lowest between September and November (Fig. 4.11 A). Between May and July more than twice as many individuals recruit to the south coast than to the west coast. This pattern closely matches the mean

Table 4.5: General linear model results for the CAB-WC system in the temperature-dependent development experiment showing the contributions of the different variables to determining modelled recruitment. The main effects and interaction effects explaining more than 5% of the variance are shown, together with univariate statistics of the parameter values. Test of SS Whole Model vs. SS Residual: Adjusted $R^2 = 0.89$; $p < 0.01$. * = Significant ($p < 0.01$). % variance explained = $100 \times SS_{effect}/SS_{tot}$

	Sum of Squares	Degrees of freedom	Mean Squares	F	p	% variance explained
Intercept	186319	1	186319	15761		
Single variable						
Year	3914	7	559	47	0.00*	5.07
Month	23842	11	2167	183	0.00*	30.88
Depth	8132	2	4066	344	0.00*	10.53
Trial	10	2	5	0	0.66	0.01
Interaction terms						
*Year*Month*	27226	77	354	30	0.00*	35.26
*Month*Depth*	4767	22	217	18	0.00*	6.17
Error	8606	728	12			11.15
TOTAL	77205	863	7430			

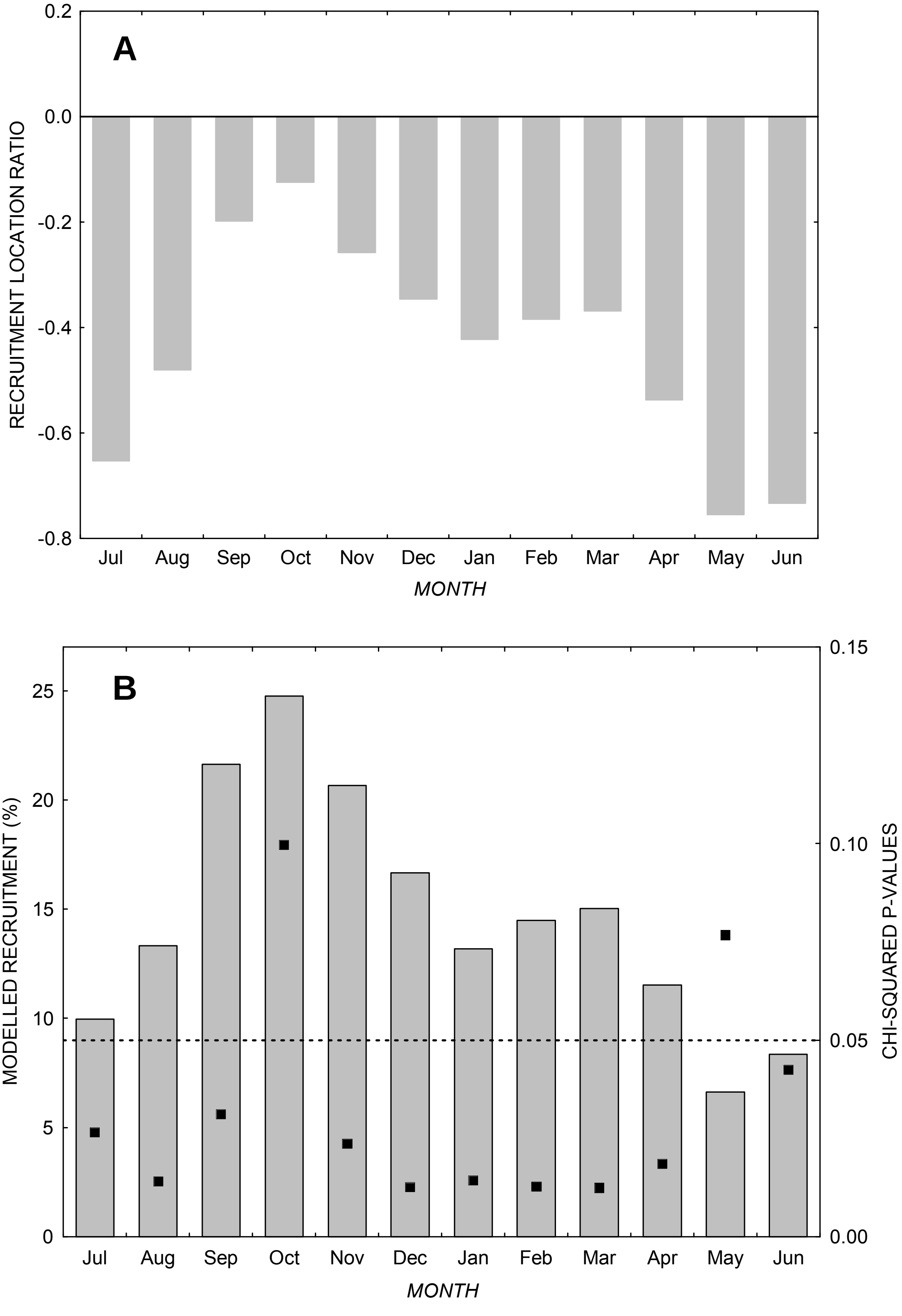

Fig. 4.11: Seasonal patterns (the *Month* variable) in the CAB-WC system in the temperature-dependent development experiment: (A) recruitment location ratio (WC:SC) and (B) mean modelled recruitment with p-values of Chi-squared tests comparing the pattern to a uniform distribution after removing each month individually (the dotted line is p = 0.05)

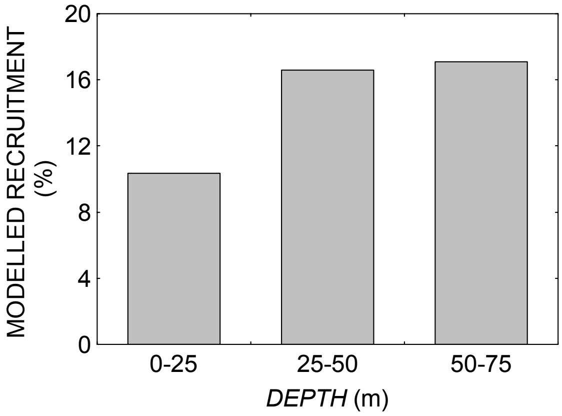

Fig. 4.12: Modelled recruitment in the CAB-WC system in the temperature-dependent development experiment for the *Depth* variable

modelled recruitment to the west coast (Fig. 4.11 B). The distribution was found to differ significantly from a level distribution of the mean modelled recruitment (χ^2 = 22.54, df = 11, p = 0.020). However if October (χ^2 = 16.00, df = 10, p = 0.010) or May (χ^2 = 16.90, df = 10, p = 0.076) were removed the difference was no longer significant. The period from September to November clearly has higher modelled recruitment with a lesser, not significant peak occurring over February and March. This pattern does vary slightly from year to year as the strong *Year*Month* interaction indicates. This is mainly due to varying levels of success in the month when modelled recruitment is at its highest (October). *Depth* is also a significant variable in this system due to the 0-25m depth range having lower modelled recruitment than the deeper ranges (Fig. 4.12). There was no *Trial* effect.

4.3.3.3. THE SC-SC SYSTEM

Modelled retention results differed significantly from those of the Lagrangian transport experiment (Wilcoxon Matched Pairs test, $p < 0.001$). The GLM with the difference ratio as the dependent variable only explained 57.55% of the variance. *Depth* was the variable accounting for most of the difference (13.37%) and there was also a strong *Month*Depth* interaction (14.44%, Fig. 4.13). The February-March period sees higher modelled recruitment from both the 0-25m and 25-50m depth ranges and much lower success from the 50-75m range. For all months modelled recruitment from individuals released shallower than 50m increased, while success decreased for individuals released deeper than this (except in June and September where negligible increases were found). A small change in the relative importance of the *Spawning Area* variable was also found (6.93%) due to increased modelled recruitment from the CAB spawning areas (Fig. 4.6).

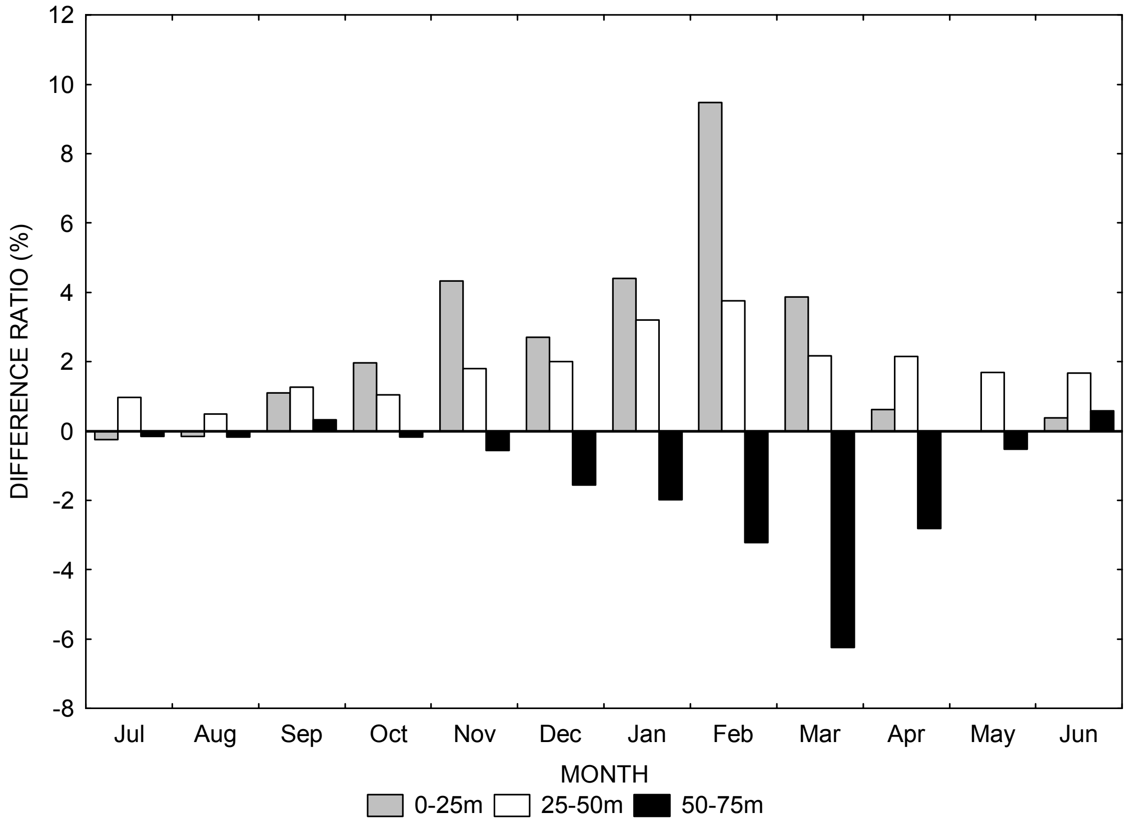

Fig. 4.13: Differences in modelled recruitment (difference ratio) between the Lagrangian transport and temperature-dependent development experiments in the SC-SC system for the *Depth*Month* interaction

The single variables and first order interactions together explained 90.18% of the variance in the GLM for modelled recruitment in the SC-SC system (Table 4.6). The assumptions for the GLM analysis were met - the residuals of transport success were normally distributed and no trend was found in the mean and variance of the residuals in relation to the observed values.

The *Spawning Area* variable is the primary determinant of modelled recruitment in the SC-SC system (76.10% of the variance is explained by this variable). Both EAB areas have extremely high success rates, while the CABoff area is by far the lowest contributor to modelled recruitment in this system (Fig. 4.6). There is also an important *Spawning Area*Month* interaction (Fig. 4.14). Seasonal patterns of modelled recruitment from the CAB areas show greater success between April and July with reduced retention for the rest of the year. Individuals released from the EAB areas are retained in large amounts almost year round

Table 4.6: General linear model results for the SC-SC system in the temperature-dependent development experiment showing the contributions of the different variables to determining modelled recruitment. The main effects and interaction effects explaining more than 5% of the variance are shown, together with univariate statistics of the parameter values. Test of SS Whole Model vs. SS Residual: Adjusted $R^2 = 0.90$; $p < 0.01$. * = Significant ($p < 0.01$). % variance explained = $100 \times SS_{effect}/SS_{tot}$

	Sum of Squares	**Degrees of freedom**	**Mean Squares**	**F**	**p**	**% variance explained**
Intercept	18659694	1	18659694	291614		
Single variable						
Spawning Area	1615003	3	538334	8413	0.00	76.10
Year	7601	7	1086	17	0.00	0.36
Month	26568	11	2415	38	0.00	1.25
Depth	5135	2	2568	40	0.00	0.24
Trial	2	2	1	0	0.98	0.00
Interaction terms						
*Spawning Area*Month*	176070	33	5335	83	0.00	8.30
Error	208408	3257	64			9.82
TOTAL	2122144	3455	556311			

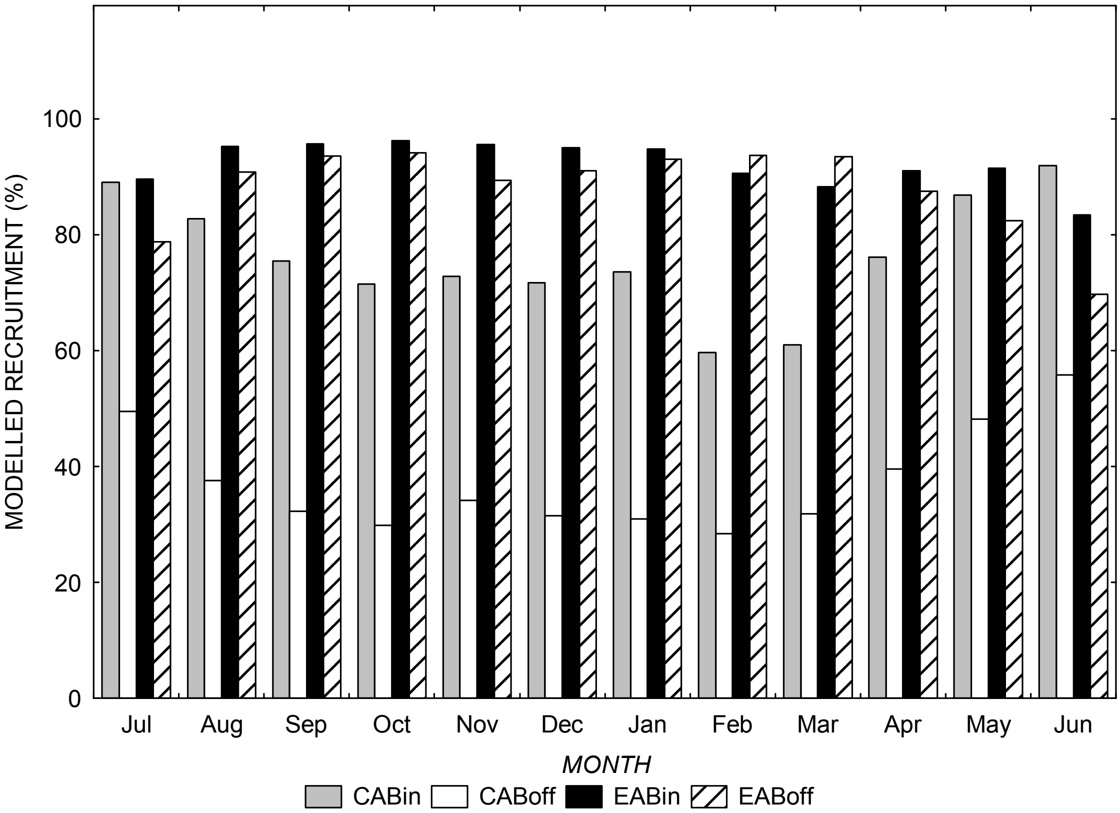

Fig. 4.14: Modelled recruitment in the SC-SC system in the temperature-dependent development experiment for the *Spawning Area* Month* interaction

with retention levels slightly lower over winter (May to July). All of the other single variables only explain minor amounts of the total variance. There was no *Trial* effect.

4.3.4. Comparison with field estimated recruitment

Interannual variation in modelled recruitment is low in all three recruitment systems (Fig. 4.15). The difference between the most successful and least successful year is only 3.60% in the WAB/WC-WC system, 6.02% in the CAB-WC system and 5.04% in the SC-SC system. The pattern of success is similar for all three systems with reduced modelled recruitment during 1993/94 to 1995/96 and increased modelled recruitment in 1992/93 and after 1996/97.

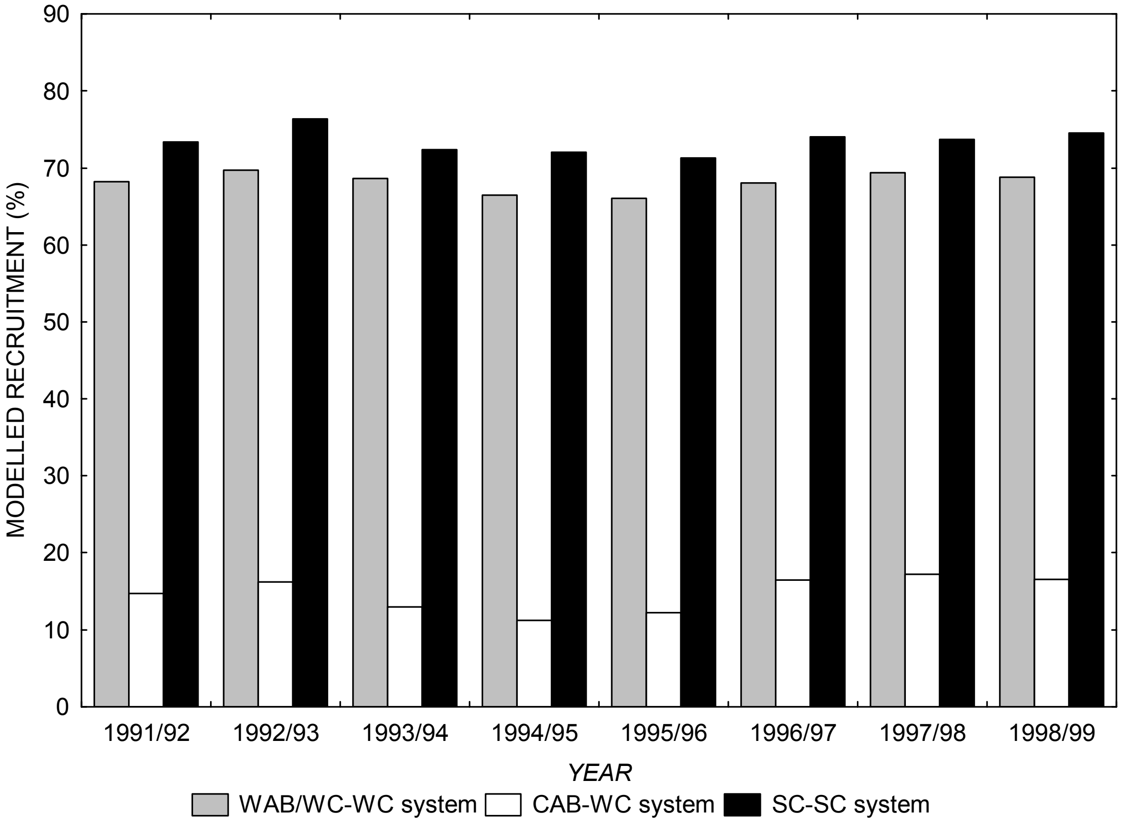

Fig. 4.15: Modelled recruitment in the three recruitment systems in the temperature-dependent development experiment for the *Year* variable

None of the modelled recruitment anomalies from any of the three systems correlated significantly with back-calculated recruitment estimates. All had very low r values (WAB/WC-WC system: r = 0.17; CAB-WC system: r = 0.00; SC-SC system: r = 0.20). Positive modelled recruitment anomalies in the CAB-WC system were accompanied by positive recruitment anomalies in the SC-SC system and likewise for negative anomalies, except in 1991/92 when the signs differed but values were negative (Fig. 4.16). Where previously (Chapter 3) the WAB/WC-WC system did not correlate with any of the other two systems, now significant positive correlations between all three systems were found (WAB/WC-WC : CAB-WC, r = 0.81; WAB/WC-WC : SC-SC, r = 0.81; CAB-WC : SC-SC, r = 0.79). In five years the anomalies of all three indices had the same sign (all negative in 1994/95 and 1995/96, all positive 1992/93, 1997/98 and 1998/99). For the last two years of the series, none of the systems had modelled recruitment anomalies corresponding with the back-calculated recruitment anomaly.

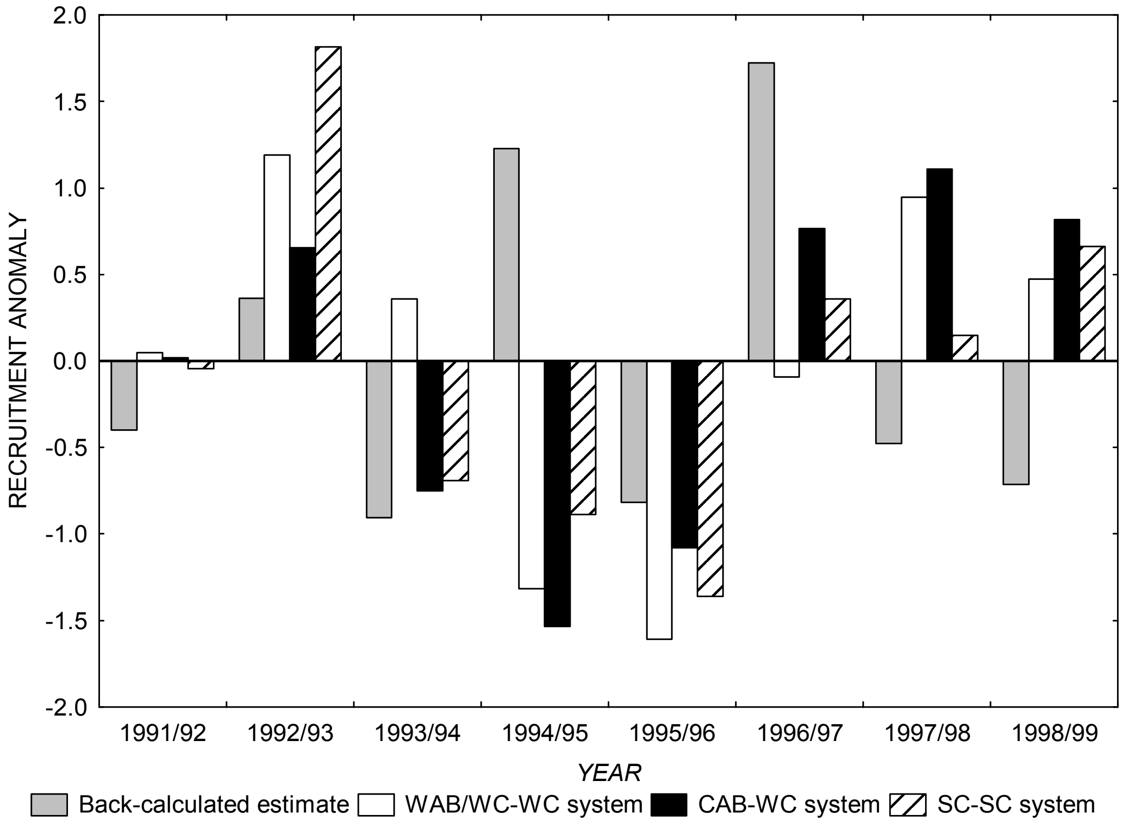

Fig. 4.16: Standardised anomalies of estimated sardine recruitment and the modelled recruitment in each system for the eight years of the temperature-dependent development experiment. Anomalies are calculated as the difference between the value for a given year and the mean over the eight years, divided by the standard deviation over the eight years

4.4. DISCUSSION

A temperature-driven development model was used in this experiment because in addition to natural variation, ambient temperature is considered by many to be the most important determining factor for the rate of development of eggs (King 1977, Smith 1981, Fox et al. 2003) and larvae (Lasker 1964, King 1977). The model divided the development process into three stages rather than implicitly modelling growth in length or size, and the duration of each stage was estimated using laboratory data. In using laboratory data such as this in a model, the assumption is made that they also apply to eggs/larvae developing in field conditions. Moloney et al. (1994) used a similar development model in an IBM of planktonic crab larvae. It was assumed that while the development times from laboratory studies might not be accurate for field conditions, the effect of temperature on the actual development rate is probably acceptable. Hence, in the absence of any *in situ* data, it is thought that this is a reasonable assumption to make.

The Bělehrádek functions produced very good fits to the data, allowing a high degree of confidence in the modelled rate at which individuals develop from one stage to another. The majority of development models linked to IBMs have modelled growth in length as a function of age and temperature, with other factors such as feeding incorporated in some cases (Heath and Gallego 1997). These models use various formulae such as logistic (Bartsch 2002), Gompertz (Parada 2003), von Bertalanffy, power (Bartsch and Coombs 2001) or exponential curves to model growth. While these methods can be very accurate, they are usually very complicated and comprise a number of parameters, many of which need to be estimated. They are often fit to limited available data points. Length is not necessarily a good proxy for developmental stage and because IBMs often assign attributes (such as ability to feed or swim) to individuals based on their stage of development rather than their size, accurate determination of the length of an individual at any given time step is not always essential. In cases where the size/length of the larvae is not required a stage-based development model, such as the one employed here, is a simpler method of modelling development.

Ambient temperature was shown to have a profound effect on the development time of eggs and larvae. Temperatures in the southern Benguela ecosystem generally range between

11 and 23ºC (Lutjeharms et al. 1996). Development times at either side of this range differ substantially. In particular, development in water colder than 14°C is very slow. Cold water such as this is often encountered at depth on both the Agulhas Bank and the west coast, and rises to the surface during upwelling events, making the inshore waters of the west coast very cold during the summer months. Often during this time, starting in December, the warmer waters from the Agulhas Bank penetrate up the west coast causing significant warm events in the offshore waters (see Chapter 2, Fig. 2.4). As offshore loss is a problem for larvae along the west coast, rapid development would be a sizeable advantage as quicker development implies an increased likelihood of retention and therefore survival. This is probably why the incorporation of the stage-based recruitment criterion had a negative effect on modelled recruitment from the inshore west coast nursery areas but enhanced modelled recruitment from the offshore zones.

As age at recruitment to the west coast of individuals from the WAB and CAB is substantially higher than the development time for larvae from these regions, larvae from these spawning areas must have reached the late larva stage before they arrive on the west coast. Therefore, age at recruitment from these two areas can be used as a proxy for transport time to the west coast. The mean age at recruitment from the WAB was 17.6d, while that from the CABoff was 21.9d. Rapid development is therefore unlikely to be of any advantage in terms of avoiding offshore advection for individuals spawned in these areas. Those individuals from these areas that do reach the west coast nursery grounds are already at an advanced stage of development and are likely to be in good condition from being able to feed during their passage up the lower west coast, and should therefore have a higher survival probability than their younger counterparts spawned off the west coast.

Temperature-dependent mortality was also considered in this experiment by using a lethal temperature threshold of 13°C for the yolk-sac larva stage. King (1977) reported that early larvae did not die at cold temperatures but rather displayed very slow growth. Hence, in the model no development occurred below 13°C in the yolk-sac larva stage only, and if an individual remained at this temperature for more than two days it was considered to have died. This is in line with a constraint used in the evolutionary IBM of Mullon et al. (2002) where in certain simulations spawning areas were favoured if anchovy (*Engraulis encrasicolus*) eggs and larvae spawned there avoided water colder than 14°C. Temperature-induced mortality was high inshore along the west coast but very low on the Agulhas Bank, particularly in the 25-50m depth range. Mortality rates for this range are likely to be lower than those in the surface waters because individuals at this depth are retained in greater numbers in the warmer Agulhas Bank water and are thus less likely to encounter cold water.

These mortality rates are by no means realistic depictions of overall mortality across the region. The egg and larval phase is generally characterised by high mortality rates, both inherent and external. Inherent factors, independent of the environment, include factors such as lethal malformations that occur during embryo developmentand have been linked to parental characteristics (Solemdal et al. 1998). External mortality arises from characteristics of the natural environment. Lethal temperatures are only one of many external mortality factors, others include predation, pollution and physical condition of the egg or larva. Predation, starvation, parasites/disease and drift (advected out of the system) are generally considered to be the leading causes of mortality for early life stages of pelagic fish (Smith and Lasker 1978, Hovenkramp 1992). This IBM deals with mortality through advective loss implicitly but predation, starvation and parasites/disease are more difficult to model accurately, both temporally and spatially. Miller et al. (1988) found that small larvae were more likely to starve than larger larvae and concluded that larval size was more instrumental in controlling starvation-induced mortality than the amount of time following the absorption of all internal food sources. On the west coast, slow development means that individuals spend a long time at the early larva stage of development (more than twice as long as the egg and yolk-sac larva stages combined). The early larva stage is often termed the ‘critical period’ (Smith 1981, Jobling 1995) because larvae can no longer rely on yolk and have to find a supply of the proper kind of food in sufficient quantities. However, as the larvae develop through the different stages, different mortality factors come into play. Whilst smaller larvae are more likely to starve, larger larvae require greater amounts of food and must search larger volumes of water to feed and therefore have a greater risk of predation (Vlymen 1977). Hence, while individuals on the south coast may develop quicker than on the west coast, their survival requires an abundant and accessible food supply likely higher than the patchy productivity of this region can supply (Brown 1992). Nevertheless, fast development is likely to have a positive effect on an individual’s chances of successfully recruiting because the rate of development controls how long larvae experience high mortality rates associated with the early stages of development (Hunter 1984, Butler 1991). Considering that development rate is closely linked with temperature, being spawned in an area with a suitable temperature range is very important for larval survival.

Mean development times in the model showed the 14 day estimate at which larvae are able to recruit (Chapter 3) to be an accurate estimate of development time to the late larva stage. Using a fixed age criterion to determine when larvae are able to retain their position, as was done in previous IBM simulations of the region (Huggett et al. 2003, Mullon et al. 2003, Parada et al. 2003), implies equal development times across the entire spawning range of the stock. However, considerable regional and seasonal differences in temperature exist across the southern Benguela, leading to considerable differences in development time.

There are no empirical data that support the assumption that the late larva stage is one where larvae are able to actively retain themselves within a nursery area. However, as larvae reach the late larval stage they become more mobile (due to fin development), which enables them to more effectively maintain themselves in favourable areas through horizontal and vertical movement. Their feeding range increases and they are more likely to be able to locate sufficient food for further development at this stage. Also, these larvae are able to avoid adverse conditions (Miller et al. 1988) and have improved predator escape ability, which is correlated to larval length and swimming speed (Bailey 1984). This stage-based recruitment criterion therefore makes theoretical and biological sense, as does the assumption that the age at reaching this stage is temperature-dependent.

The modelled recruitment results from this experiment differed from the Lagrangian transport (fixed age recruitment criterion) experiment in all three systems but the implications of this change were more prominent in the WAB/WC-WC system. Slow development (and therefore increased offshore loss) and high mortality due to low temperatures in this system decreased the overall success rates. All west coast spawning areas have similar levels of modelled recruitment. However, quicker development rates, and therefore less time spent in the more vulnerable, mortality-prone early stages, implies that individuals spawned in the offshore spawning zones on the west coast have a better chance of survival compared to those spawned inshore. The increasing importance of the *Depth* variable in the GLMs supports the argument that successful recruitment in this system is depth-based. The 0-25m range had the worst recruitment levels, probably as a result of offshore loss (poor retention). The 50-75m depth range had substantially lower levels of recruitment success than in the previous experiment (especially from the inshore spawning areas), because of the cold water found at such depths. The 25-50m range had the highest level of recruitment success, perhaps striking the right balance between retention in the nursery areas and rapid development. A similar trade-off between retention and temperature was identified by Mullon et al. (2003) and Parada et al. (submitted) for anchovy. Those simulations used a temperature-dependent Gompertz equation for growth, and showed that recruitment success was greatest when anchovy larvae remained at a depth of 40m. Similarly, in their IBM study of sardine in the northern Benguela, Stenevik et al. (2003) showed that eggs spawned below the offshore Ekman transport layer (around 40m depth) had higher levels of retention success than those within the Ekman layer.

The stage-based recruitment criterion had very little effect on the CAB-WC system because the age at recruitment to the west coast is substantially higher than the time required for individuals from the CAB to develop to the late larva stage. The CAB is clearly still a transition zone between the WAB/WC-WC and SC-SC systems. Modelled recruitment is very seasonal, with a significant, predictable monthly pattern. For individuals being transported from the WAB and CAB to the west coast, the warm period starting in December and lasting till after March promotes rapid larval development. In September and October, when the water column over the WAB is well mixed and cold water is often found near the surface (Lutjeharms et al. 1996), development is slow. However, this is a period of efficient transport to the west coast. Therefore, it may be that the two peaks in spawning activity observed for sardine might occur for different reasons: September-October because of good transport from the Agulhas Bank to the west coast and February-March because of rapid development.

The SC-SC system was also hardly affected by the new recruitment criterion when compared to the Lagrangian transport experiment (Chapter 3). There was a slight increase in the importance of the *Depth* variable as a predictor of modelled recruitment due to temperature induced mortality in deeper waters. From December to March, a more stratified water column leads to increased survival and retention of individuals spawned shallower than 50m and increased mortality below this in the colder waters. In general, quick development coupled with little offshore loss results in very high retention on the EAB. Once fully developed, a lack of an adequate food supply in this area could see late larva actively targeting a means of reaching the west coast by selecting westerly cross shore currents. Once on the CAB, transport to the west coast is more likely.

Interannual modelled recruitment anomalies changed noticeably in the WAB/WC-WC system compared to the Lagrangian experiment. Anomalies changed from negative to positive and positive to negative in 1992/93 and 1994/95, respectively. There was also a substantial decrease in the magnitude of the negative anomaly in 1996/97 (Fig. 3.11 and Fig. 4.16). This system has a very narrow range of variance around the annual mean modelled recruitment (3.60% difference in modelled recruitment between the most and least successful years). Because this system was affected most by temperature dependent development these large anomaly changes are not surprising. None of the systems are now able to explain the successful back-calculated recruitment anomaly in 1994/95, as all had negative modelled recruitment anomalies for this year. 1996/97 had the highest back-calculated recruitment anomaly of the time series. The overall WAB/WC-WC system modelled recruitment anomaly for this year was slightly negative. However, the *Spawning Area*Year* interaction for the system shows that this year had the greatest level of modelled recruitment from the WAB, where the majority of eggs were found that year and this could explain the positive back-calculated recruitment anomaly. Modelled recruitment in the last two years of the time series can still not explain the negative recruitment anomalies then, although in 1998/99, when the majority of the eggs found were on the UWC, this area had its lowest level of modelled recruitment.

By quantifying development times across the region this simple, yet effective, temperature-dependent development rate model allowed further insight into environmental influences on the spatio-temporal spawning pattern of sardine in the southern Benguela ecosystem. Having individuals that pass through distinct stages of development provides a realistic criterion for recruitment success. In addition, including a development component to the model, as was done in this study, provides a basis for introducing further levels of biological complexity, such as diel vertical migration (DVM), feeding or predation. The inclusion of a development model had a notable effect on modelled recruitment in the WAB/WC-WC system, but had a less pronounced effect in the other two systems. The west coast experiences slower development, more offshore loss and higher mortality (both directly via temperature, and possibly indirectly due to more time spent in the vulnerable early stages of development). Modelled recruitment there is more sensitive to interannual variations in temperature making it a less predictable spawning ground from year to year than on the south coast. On the Agulhas Bank quicker development occurs, but a less predictable and patchier food supply mean starvation of larvae is more likely. The WAB and CABoff areas have rapid development rates and fair levels of transport success to the better food supply on the west coast (especially from the WAB). Also, being fully developed by the time they reach this area means individuals from there are better able to take advantage of the food supply when they arrive on the west coast.

CHAPTER 5: THE EFFECT OF THE VERTICAL DISTRIBUTION OF SARDINE SARDINOPS SAGAX *EGGS AND LARVAE ON TRANSPORT AND RETENTION IN THE SOUTHERN BENGUELA ECOSYSTEM*

ABSTRACT

An IBM is developed to examine the effect of vertical distribution patterns of four early life history stages of sardine on their transport and retention and mortality rates in the southern Benguela ecosystem. The amount of vertical movement in the modelled flow fields and the effect of the initial distribution of individuals on modelled vertical distributions are examined at each stage of development. Vertical positioning schemes are tested by comparing modelled vertical distributions with observed egg and larva vertical distributions, and the optimal positioning schemes (those best matching observations) for each stage are used in the IBM. Lagrangian particles are transported downwards if released below 40m, particles released at 20-40m aggregate at that depth, and particles released above 20m remain near the surface. Highest levels of modelled recruitment are found at 30-50m in the WAB/WC-WC system and 20-40m in the CAB-WC system. In the SC-SC system individuals released near the surface (top 30m) are mainly retained inshore of the cool ridge but below 30m retention is highest over the cool ridge. Mortality increases with depth and is higher on the west coast than on the south coast. However, the use of realistic vertical positioning schemes does not notably change spatial and temporal patterns of modelled recruitment and only reduces mortality rates slightly compared the previous experiment (Chapters 4). Optimal sub-nursery areas are defined where conditions are thought to be more suitable for recruitment. Modelled recruitment to the optimal inshore west coast sub-nursery area only increases slightly from the western and central Agulhas Bank compared with the previous experiment (Chapters 4), whereas the EABoff spawning area is the only area that has high levels of modelled recruitment in the optimal south coast offshore sub-nursery area, indicating that the cool ridge may act as a barrier against cross-shelf transport. It is concluded that transport and retention are not the sole reasons behind the physical and behavioural processes affecting the vertical distribution of eggs and larvae.

5.1. INTRODUCTION

In Chapters 3 and 4, the movement of individuals was determined solely by the 3-D velocity fields of the hydrodynamic model. Particles were transported in a Lagrangian fashion, and although the particles developed through four distinct stages, no allowance was made for individual differences in particles at any stage that could affect how they are transported within the model. The egg and initial larval stages are not able to actively transport themselves because eggs have no means of propulsion and current speeds generally greatly exceed the swimming speeds attainable by larvae (Nelson and Hutchings 1987). However, in reality the physical characteristics of the eggs and larvae are likely to impact how they are transported. Sardine (*Sardinops sagax*) eggs and larvae are planktonic and thus have minimal movement ability. Given the large spatial scales involved in the transport of individuals they are not able to actively affect this process through movement on the horizontal plane. However, both physical characteristics (e.g. buoyancy) and behavioural traits (e.g. diel vertical migration) of individuals can determine their vertical position. In this chapter the interaction between the vertical distribution of individuals and their transport within the southern Benguela ecosystem is examined.

The transport of larvae usually involves the interaction between the vertical position of larvae and the vertical structure of cross-shelf currents (Hare et al. 1999). The water column is often vertically tiered and the horizontal flow may vary in magnitude or direction at different depths. This is particularly evident in coastal upwelling ecosystems where larvae inhabiting the surface layers are likely to be swept offshore by strong Ekman transport, while at depth they are likely to be kept close to the shore by opposite flowing inshore currents (Stenevik et al. 2001). There is also a temporal pattern to this because offshore Ekman transport in the upper layer fluctuates with varying intensity of upwelling linked to variations in wind force and direction (Shannon 1985). Also, transport from the western Agulhas Bank (WAB) to the west coast in the Cape Columbine jet current can be optimised if larvae are in the strongest flowing part of the current, around 30m depth (Fowler and Boyd 1998).

Pelagic fish eggs are widespread throughout the water column. Characteristics of eggs that affect their vertical position include depth spawned, density, and their shape and size.

These interact with elements of the physical environment such as water density (a function of temperature, salinity and depth), currents and vertical mixing or turbulence (Sundby 1983, 1991, 1997; Coombs et al. 2004) to produce observed vertical distributions. Their positive buoyancy acts to move sardine eggs upward in the water column (van der Lingen in prep. a), which results in older sardine eggs generally being found in the surface layers as observed off California (Ahlstrom 1959), Japan (Konishi 1980), the English Channel (Coombs et al. 1985), Australia (Fletcher 1999) and in the southern Benguela ecosystem (Dopolo et al. 2005). Sardine eggs are large relative to those of other small pelagic fish species such as anchovy (*Engraulis encrasicolus*) and round herring (*Etrumeus whiteheadi*). The eggs are spherical and transparent, with segmented yolk and a single oil globule surrounded by a large perivitelline space (Hart and Marshall 1951, Davies 1954, King 1977). The eggs have a smooth, thin, water permeable chorion (Holliday 1971, Olivar 1987) through which osmoregulation occurs. This results in sardine eggs changing in density according to the external medium in which fertilisation occurs (Coombs et al. 1985, Tanaka 1992). May (1974) found that the salinity of the medium at the time of fertilisation affects the buoyancy of eggs until hatching and the buoyancy of eggs is only altered slightly if they are transferred into a different density medium. In other words, the initial density of eggs adjusts according to the ambient water in which the egg is spawned.

Modelling the vertical distribution of fish eggs involves determining vertical mixing of the water column, the buoyancy properties of eggs and how these interact. Such models are usually one-dimensional. The buoyancy of eggs is usually calculated by applying Stoke's Law for terminal velocity as a function of the difference in density between the egg and surrounding water. Sundby (1983) designed a one-dimensional model for the vertical distribution of pelagic fish eggs considering the terminal velocity of eggs (according to Stoke's law), wind-mixing and mean vertical eddy diffusivity co-efficients. Other examples of similar one-dimensional models that have been developed include models for haddock eggs (*Melanogrammus aeglefinus*, Page et al. 1989), pelagic fish eggs (Westgård 1989), Japanese anchovy (*Engraulis japonicus*, Tanaka 1992), blue whiting (*Micromesistius poutassou*, Adlandsvik et al. 2001) and sardine (*Sardinops sagax*) in the Northern Benguela ecosystem (Stenevik et al. 2001). Boyra et al. (2003) furthered Sundby's (1983) model by incorporating wind induced turbulence, settling velocities, and changing buoyancy by developmental stage for anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) eggs.

Sardine larvae display active movement shortly after hatching. At first yolk-sac larvae are held in an inverted position due to the positively buoyant yolk-sac and oil globule, but they soon begin to swim with short bursts of rapid tail movement (Davies 1954). This swimming behaviour has also been observed for Northern anchovy (*Engraulis mordax*) yolk-sac larvae, which display short bursts of continuous energetic movement followed by long periods of rest (Hunter 1972, Weihs 1980). As larvae develop and their fins begin to differentiate more they are able to sustain these periods of active movement. One to two weeks after hatching sardine larvae have been observed to swim at speeds between 0.5 and 1cm.s^{-1} whilst feeding and are able to attain maximum cruise speeds between 1 and 3cm.s^{-1} (Nelson and Hutchings 1987). This improves the larva's ability to move around within its immediate environment and increases its ability to feed. They are able to position themselves vertically within the water column through both energetic movement and by changing their buoyancy by inflating or deflating their swim bladder, which develops when larvae are roughly 10mm in length. Studies have shown that larvae of pelagic fish can inflate or deflate their swim bladders by swallowing air at the water surface and releasing gas as bubbles through the pneumatic duct into the alimentary canal, e.g. larvae of sardine (Stenevik 2003) and the Northern anchovy (Hunter and Sanchez 1996).

Diel vertical migration (DVM) is frequently found in many planktonic taxa. The underlying mechanisms behind this behavioural trait differ between species but it is generally accepted that there is no single causative factor. Evidence suggests that DVM is controlled by both endogenous and exogenous factors (Moloney and Gibbons 1996, Richards et al. 1996). Intrinsic factors such as internal rhythms, age and size often go hand in hand with extrinsic environmental or ecological factors such as light, temperature, salinity, oxygen concentrations, food availability and predation. The relative importance of these factors varies not only between species, but within populations as well. For example, the propensity for an individual to change its vertical position to a more favourable food environment is likely to be related to its need for food (i.e. hunger). It is generally agreed that the majority of vertical migrations are cued by the diel light cycle (Forward 1988, Haney et al. 1990, Ringelberg 1995, Richards et al. 1996). Richards et al. (1996) used an IBM approach to investigate light mediated-mechanisms for diel vertical migration and found swimming responses resulting in congregation near the surface during the day and deeper distribution during the night could be explained by properties of the light field.

In upwelling ecosystems sardine nursery grounds are often nearshore where nutrient rich waters are drawn to the surface (Fowler and Boyd 1998). Pre-recruit surveys along the west coast show that the size of individuals generally increases onshore (Hampton 1987, van der Lingen and Merkle 1998), which suggests movement towards these inshore regions. Individuals that position themselves appropriately in the water column could minimise offshore loss and increase onshore transport by selecting the inshore moving subsurface layer during upwelling events or the surface layer during relaxation events (Pillar and Stuart 1988, Verheye et al. 1991, Stenevik et al. 2001, van der Lingen pers comm.). Whether they are actively targeting these regions is a matter for debate because no open-ocean behavioural study of this species has yet been undertaken (Nelson and Hutchings 1987). However, larvae can respond to a variety of environmental stimuli (Kingsford et al. 2002) or changes in endocrine physiology (Woodhead 1975) that may be used for navigation. Light gradients, sun angle, magnetism, turbulence and detection of water chemistry are just a few possible means by which larvae may select favourable flowing currents. Additionally, there could also exist a trade off between predator avoidance and selecting vertical positions for favourable transport.

This chapter focuses on the vertical distributions of individuals and how this changes through development. The aim is to assess the relative importance of vertical movement of the water column and physical and behavioural characteristics of the individuals in determining their vertical position. The first null hypothesis is that the vertical position of individuals is determined solely as a result of their initial distribution (depth of spawning) and Lagrangian movement within the water column. The alternative hypothesis is that physical and behavioural characteristics of individuals determine their vertical position at each stage. Different schemes for determining the vertical position of individuals at each stage will be presented and compared with observed vertical distributions in the southern Benguela ecosystem. It is thought that the vertical position of individuals is likely to have an impact on transport to, and retention in, favourable nursery areas. Modelled recruitment using the schemes that best match observations for determining the vertical position of individuals at each stage will be examined and compared with the temperature-dependent development experiment (Chapter 4), in which particles were transported in a Lagrangian manner determined solely by the current fields of the 3-D hydrodynamic model. The second null hypothesis is that the vertical position of individuals does not significantly increase modelled recruitment success (to both nursery areas and to optimal sub-nursery areas). Alternatively, the vertical position of individuals does enhance the level of modelled recruitment and the physical properties or behaviours that determine the observed distributions are adapted to provide this advantage.

5.2. METHODS

For all simulations in this experiment, 24 iterations per timestep were used to increase the temporal resolution for the movement of individuals.

5.2.1. Modelled recruitment and mortality by depth

Because this experiment examines the effect of vertical distribution of individuals, simulations were performed to see how modelled recruitment and mortality vary with depth (VP Exp. 1). In these experiments individuals moved randomly up or down within one of eight 10m depth intervals (from 0-10m down to 70-80m) and were kept at that depth range for the duration of the simulation. Modelled recruitment and mortality were recorded for each depth range in each recruitment system.

5.2.2. Vertical mixing in the model

An examination of how Lagrangian transported individuals move vertically in the model was done for five spawning areas (UWCoff, LWCin, WAB, CABoff, EABoff), four months (September, December, March, June) and all years of the time series (VP Exp. 2). The four months were selected to match the times when observations were made and also to cover each season (September – spring, when observed egg vertical distributions were recorded and development times are quick; December – summer, when upwelling occurs on the west coast and development there is slowest; March – autumn, when observed larva vertical distributions were recorded; and June – winter, when no upwelling occurs on the west coast). Individuals were released uniformly in the top 80m of the water column, and the vertical distribution of particles was recorded at four different stages of development: mid-way through the egg stage and at the beginning of the yolk-sac, early and late larva stages. Modelled distributions were compared with observed egg and larva distributions at these four stages. Egg vertical distributions for three stages of egg development observed on the WAB in September 2000 were reported by Dopolo et al. (2005). No data on the vertical distribution of sardine larvae are available for the southern Benguela hence observations of the vertical distribution of early and late stage anchovy larvae sampled of the west coast in March 2002 and 2003 (van der Lingen et al. in prep. b) were used as a proxy for sardine. These were used for comparison with modelled distributions from the same areas and months.

To examine the effect of the initial distribution of particles on the distribution of particles at the four developmental stages, the three initial distributions of individuals used in the previous experiments (Chapters 3 and 4, uniform distribution over the 0-25, 25-50 and 50-75m depth ranges), and the observed egg distribution for early stage eggs (initial distribution) were used (VP Exp. 3). Vertical distributions resulting from these starting positions were compared with observed distributions at each stage.

5.2.3. Vertical positioning schemes

Two egg and two larval vertical positioning schemes were modelled and the resulting vertical distributions were compared with observed distributions and distributions resulting from Lagrangian transport of individuals from the observed initial egg distribution. A chi-squared observed vs. expected test was used to compare depth frequencies to find which scheme resulted in the most accurate representation of observed distributions for each stage.

5.2.3.1. EGGS

Two approaches for determining the vertical movement of eggs as a result of buoyancy were used. The first was a theoretical approach in which the vertical velocity is calculated from egg density and diameter and the physical and chemical characteristics of the water column (Sundby 1983, Boyra et al. 2003, Parada 2003). The second was an empirical approach using egg density and observed egg settling rates (Coombs et al. 1985, Zeldis et al. 1995, Cambalik et al. 1998). Both calculate egg buoyancy based on the density difference between the egg and the surrounding water. Water density was determined using the PLUME temperature and salinity fields and the UNESCO equations of state (Fofonoff and Millard 1983).

Eggs were assigned a density value from an observed egg density distribution. This created a population of eggs with a realistic distribution of egg density values. The density of each particle was determined on the first time step and kept constant for the duration of the egg stage. Egg density data were taken from van der Lingen (in prep. a), measurements being made using a density gradient unit (Coombs 1981) during pelagic spawner biomass cruises (Barange et al. 1999) in the southern Benguela during November 2001 and November 2002. When eggs were 'spawned' in the model they were randomly assigned an initial density from a normal distribution of equidistant classes (Boyra et al. 2003) centred on the mean observed egg density using the probability function:

$$P(d) = \frac{1}{\sqrt{\pi}.\sigma} e^{-\frac{(d-d^0)^2}{2\sigma^2}} \tag{5.1}$$

Where:

d = a number of equidistant possible egg density values (10)

$P(d)$ = probability of the egg having a density of d

d^0 = mean observed egg density (1.0235g.cm^{-3}, n = 1282, range: 1.0208 – 1.0277)

σ = standard deviation of egg density (0.0011g.cm^{-3})

Egg diameters were taken from Davies (1954), King (1977) and Brownell (1979). Egg diameters were also assigned from a normal distribution using equation (5.1), where:

d = a number of equidistant possible egg diameter values (10)

$P(d)$ = probability of the egg having a diameter of d

d^0 = mean observed egg diameter (1.66mm, n = 6298, range: 1.4-1.9mm)

σ = standard deviation of egg diameter (0.1mm)

For the theoretical scheme, the vertical velocity of eggs is confined to Stoke's regime when the Reynolds number is less than 0.5 (i.e. viscosity is more important than friction). The vertical velocity of each egg at each time step was determined by (Sundby 1983):

$$w_p = \frac{\Delta pgd^2}{18v} + w_w \tag{5.2}$$

Where:

w_p = vertical velocity of the egg (m.s^{-1})

Δp = density difference between the egg and the surrounding water (g.cm^{-3})

g = gravitational constant (cm.s^{-2})

d = diameter of the egg (cm)

v = kinetic viscosity of sea water (g.m^{-1}.s^{-1})

w_w = vertical velocity of the water obtained from the PLUME model (m.s^{-1})

For the empirical scheme a power function ($R^2 = 0.81$, equation 5.3) was used that related sardine egg settling rate (w, m.h^{-1}) to the density difference between the egg and the surrounding water (g.cm^{-3}). This was obtained from van der Lingen (in prep. a), who recorded the time taken for individual eggs to descend through 1cm intervals of continuously increasing density in the density gradient column, and corrected these values for wall and end effects from the experimental apparatus.

$$w = 302216.\Delta p^{1.5834} \tag{5.3}$$

5.2.3.2. LARVAE

No data on the vertical distributions of yolk-sac larvae exist, so individuals at this stage were transported in a Lagrangian manner during that stage and the resulting vertical distribution was assumed to be realistic. Observations of early and late larval vertical distributions suggest that these larvae display Type 1 diel vertical movement (i.e. at the surface during the night and deeper during the day). Two schemes of determining an individual's position depending on the time of day were used for the early and late larval stages. The first is a theoretical scheme based on the level of light intensity at the ocean surface. The second is an empirical scheme in which an individual's position is set according to observed early or late larval distributions

For the theoretical light mediated scheme, the change of light intensity on the sea surface was calculated according to an equation derived by Richards et al. (1996). A dimensionless value ($\tau(t)$) between 0 and 1 (1 at midday, 0 at midnight) was determined at each iteration of each time step (time t) as:

$$\tau(t) = I_s + \frac{(1-I_s)}{2}\left[(1+\sin(\frac{\pi}{t_d}(t-t_r)) + \sqrt{\varepsilon + \sin^2(\frac{\pi}{t_d}(t-t_r))} - \sqrt{\varepsilon+1}\right] \tag{5.4}$$

Where:

$\tau(t)$= light intensity at time t

I_s = fraction of midday surface light present at midnight (10^{-6})

t_d = day length (time of sunset – time of sunrise)

t_r = time of sunrise

ε = transition factor for light intensity at sunrise and sunset

Sunrise and sunset times at Cape Point (33°58′S, 18°28′E) for each day of the year calculated by the South African Astronomical Applications Department were obtained from the South African Astronomical Observatory (SAAO) website (www.saao.ac.za). The position of each larva in the water column was determined as a function of the light intensity and a maximum depth:

$$z_t = \tau(t).D \tag{5.5}$$

Where:

z_t = vertical position of each larva at time t (m)

D = maximum depth (m)

Observations of anchovy (and presumably sardine) larval distributions showed that few larvae migrate deeper than 50m and rarely congregate directly below the surface but rather are found throughout the top 10m during the night. Hence, 50m was used as the maximum depth of DVM and if z_t was less then 10m, larvae were positioned randomly anywhere in the top 10m.

The empirical individual re-positioning scheme used observed larval vertical distributions to position individuals. It is not an attempt to model vertical distributions but rather a means of utilising the observed distributions to position larvae. Any differences arising are only due to the temporal resolution of the model. The frequency of observations of larvae at each depth range was used as an estimate of the amount of time each indivdual would spend at that depth during its decent-ascent cycle. Sunset and sunrise times were used to divide each model time step into two day and two night periods. During the day periods, individuals started at the surface and moved downwards, spending a number of iterations at each depth range proportional to the daytime frequency of larval observations in that depth range. During the night periods, individuals moved towards the surface starting from the maximum observed depth, spending a number of iterations at each depth range proportional to the night time frequency of larval observations in that depth range. For example, if daytime observations found 50% of the individuals between 0 and 10m and 17% between 10 and 20m, for three iterations (50% of the six daytime iterations for each day during each time step) individuals would be positioned randomly in the 0-10m depth range. After that the individuals would be positioned in the 10-20m depth range for one iteration (17% of the 6 daytime iterations).

5.2.4. Modelled recruitment and mortality using vertical positioning schemes

Simulations were run to determine modelled recruitment and mortality using the statistically best vertical positioning schemes for the egg, early larva and late larva stages that best matched observations (according to the chi-squared tests). Closer scrutiny was paid to the location of modelled recruitment within each nursery area in this experiment by dividing the west coast into two and the south coast into three sub-nursery areas. The WCin and the SCoff sub-nursery areas were considered as optimal sub-nursery areas because larvae and pre-recruits in these two areas are likely to have a greater survival rate due to better food supply than those in other areas. The inshore west coast region is nutrient rich due to strong upwelling driven by south-easterly winds over the summer months. The offshore EAB, while not as productive as the WCin area, also has some dynamic shelf edge upwelling (Boyd and Shillington 1994) caused by shear-edge eddies of the Agulhas Current (Lutjeharms et al. 1996), which increases local productivity. In addition to this, an intensive cell of upwelling on the far eastern Agulhas Bank provides cold, nutrient rich water to the EAB (Lutjeharms et al. 1996). The cool ridge separates the outer, offshore region of the central and EAB from the deep mixing region inshore (Boyd and Shillington 1994). In this study the assumption is made that to optimise recruitment success, high levels of modelled recruitment to the WCin and SCoff sub-areas would be necessary.

5.2.4.1. OVERVIEW OF THE MODELLING PROCESS

Fig. 5.1 depicts the modelling process followed. The IBM simulations were carried out in the same manner as in the previous experiments (Chapters 3 and 4), with the only difference being the incorporation of vertical positioning schemes for the egg and larva stages.

5.2.4.2. MODEL PARAMETERS

The variables for the vertical distribution experiment included all those used in the previous two experiments except *Depth* (Table 5.1).

5.2.4.3. DEPENDENT VARIABLES

The same two nursery areas previously used, west coast and south coast, were used in this experiment and the same three systems (WAB/WC-WC, CAB-WC and SC-SC) were examined. For these simulations the nursery areas were sub-divided (Fig. 5.2). The west coast was divided at the 200m isobath into inshore (WCin) and offshore (WCoff) sub-nursery areas, and the south coast was divided into inshore, over and offshore of the cool ridge (SCin, SCover, SCoff, respectively). Individuals needed to have reached the late larva stage before they were able to recruit to a nursery area. Modelled recruitment was determined as the percentage of individuals released from each spawning area reaching each nursery area (or sub-area thereof) in the late larval stage of development.

Analyses were also carried out on the rates of mortality from each spawning area. Mortality was calculated as the percentage of individuals released from each spawning area that die as a result of lethal temperatures during the yolk-sac larva stage (not including those that reach maximum age before reaching a nursery area).

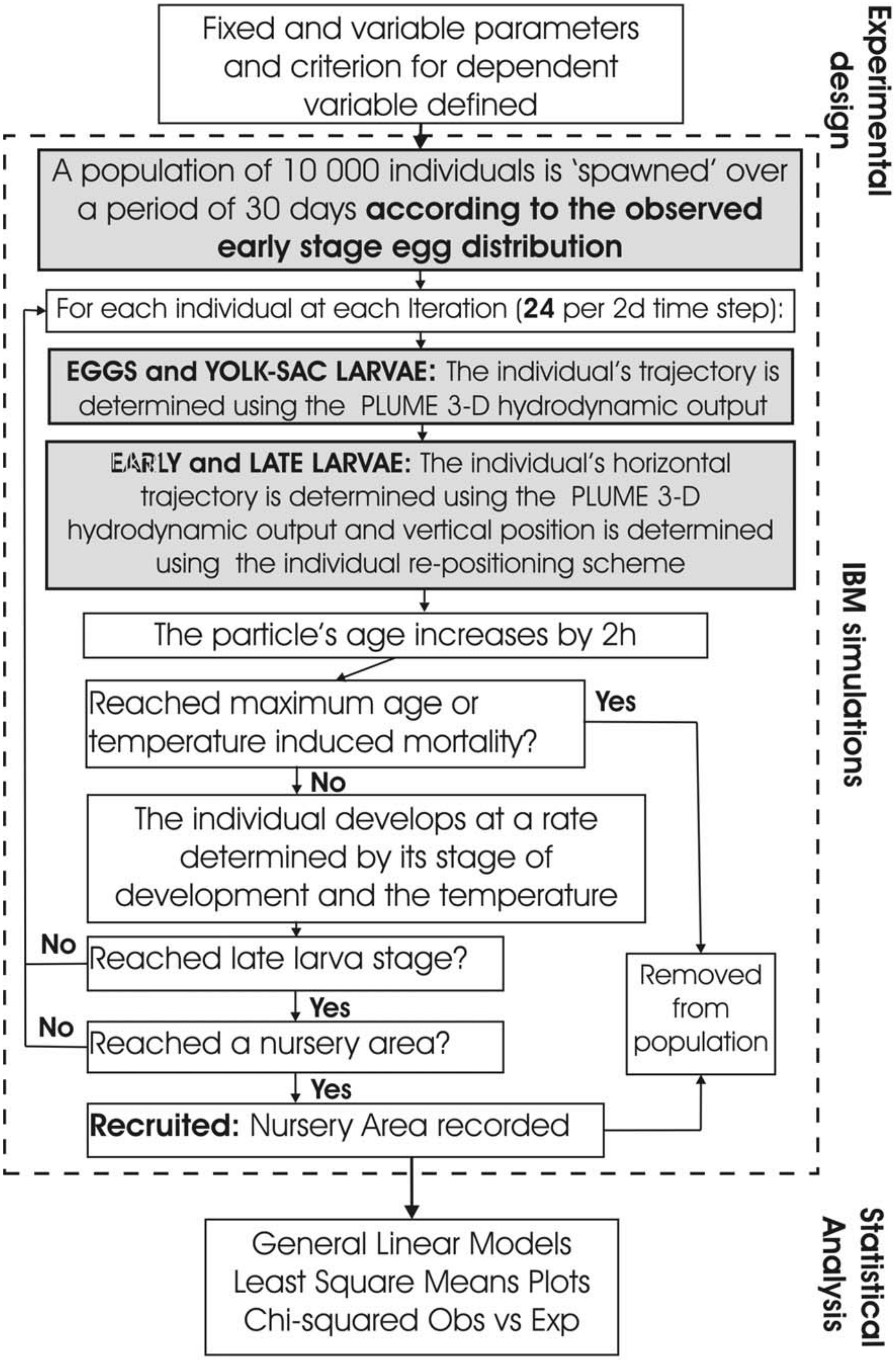

Fig. 5.1: Flow chart depicting the three stages of the modelling process for the vertical distribution experiment. (Shaded blocks represent modified processes)

Table 5.1: The fixed parameters and variables used in the vertical distribution experiment, their ranges or values and *n*

Parameter	Range/Value	*n*
Fixed parameters		
Number of particles	10 000	-
Duration of release of particles	30 days	-
Tracking period	60 days	-
Lethal minimum temperature§	13°C	-
Variables		
Spawning Area	(see Fig. 2.5)	9
Year	1991/92 - 1998/99	8
Month	Jul – Jun	12
Trial	-	3
Number of simulations		**8*12*3 = 288**

§= (yolk-sac larva stage only)

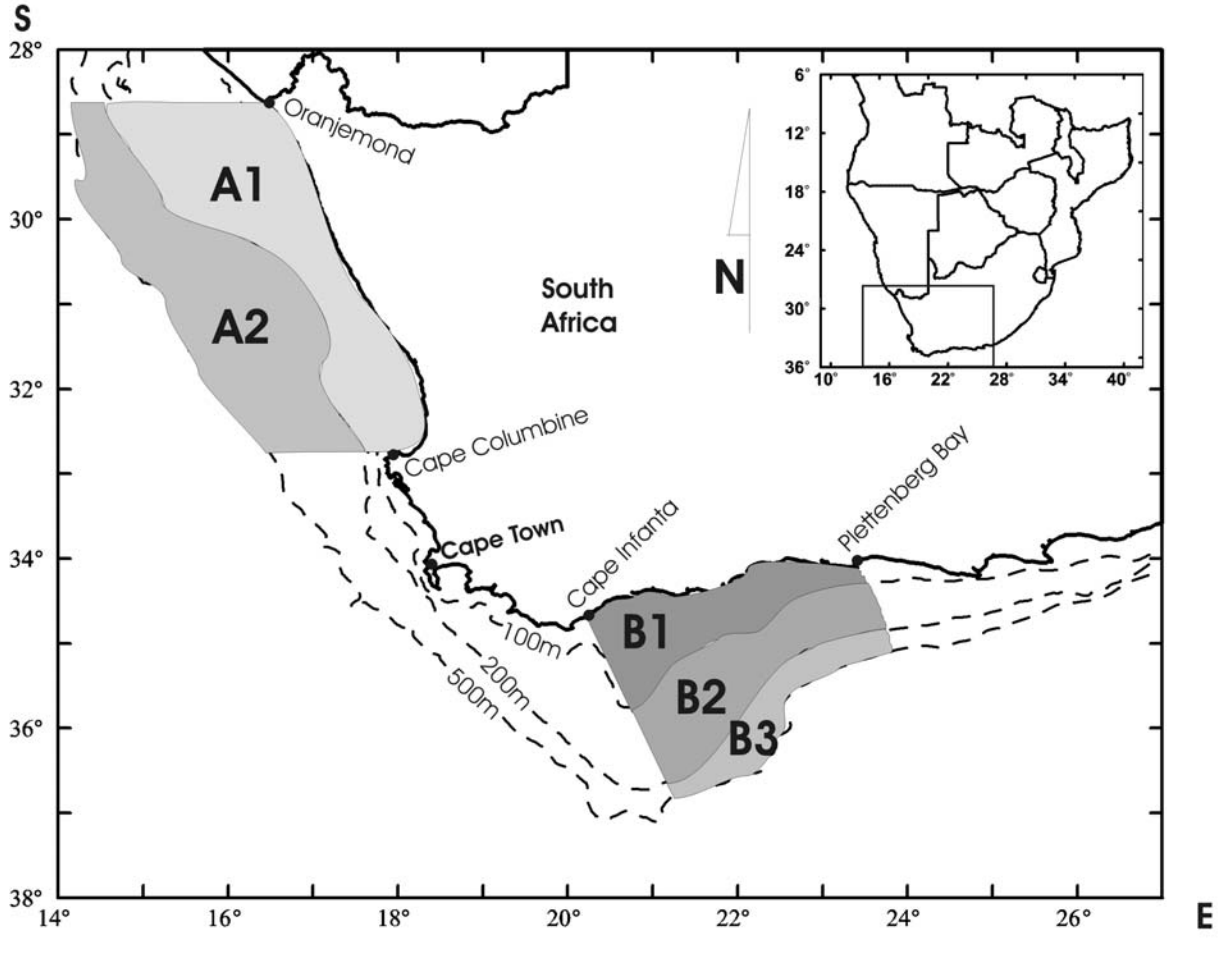

Fig. 5.2: The two subdivided nursery areas used in the vertical positioning experiment. A1 = west coast inshore (WCin), A2 = west coast offshore (WCoff), B1 = south coast: inshore (SCin), B2 = south coast: over (SCover) and B3= south coast offshore (SCoff)

5.2.5. Statistical analyses

An observed vs. expected χ^2 test was used to compare modelled depth frequencies with observed frequencies. Multiple factor variance analysis using general linear models (GLMs) was performed on the modelled recruitment and mortality results. The variables of the model (*Spawning Area*, *Year*, *Month* and *Trial*) were used as categorical predictors. The modelled recruitment patterns were analysed and compared with the results of the previous experiment (Chapter 4). Difference ratios (Chapter 4, equation 4.3) between the results of this experiment and the temperature-dependent development experiment were calculated in order to examine the effect of vertical distribution on modelled recruitment. A GLM was constructed with the difference ratio as the dependent variable to identify which variables interacted most with vertical positioning of individuals to alter modelled recruitment rates. Separate GLMs for each system with mortality and modelled recruitment (to both nursery areas, and sub-areas WCin and SCoff, which are considered to be the optimal sub-nursery areas) as the dependent variables were performed. For all GLMs a full factorial design to the 2nd degree was used with all the predictors except *Trial*, which was not used in any of the interaction terms. The adjusted R^2 and p values for each model were noted, along with all main and interaction effects and compliance with the GLM assumptions (Chapter 2, section 2.5). The percentage variance explained by each variable or interaction term was also calculated. Least square means (LSM) plots were used for visual analysis of the results and to identify the relationships between each variable and modelled recruitment values. The *a posteriori* Chi-squared test (Chapter 2) was used to identify significant peak or trough months for seasonal patterns. A plot was made of the back-calculated recruitment and modelled recruitment anomalies for each system for each year.

5.3. RESULTS

5.3.1. Modelled recruitment and mortality by depth

The modelled recruitment of individuals confined to 10m depth ranges (VP Exp. 1) showed different patterns of modelled recruitment to each of the sub-nursery areas for all three systems (Fig. 5.3 A-C). In the WAB/WC-WC system, modelled recruitment to the WCoff

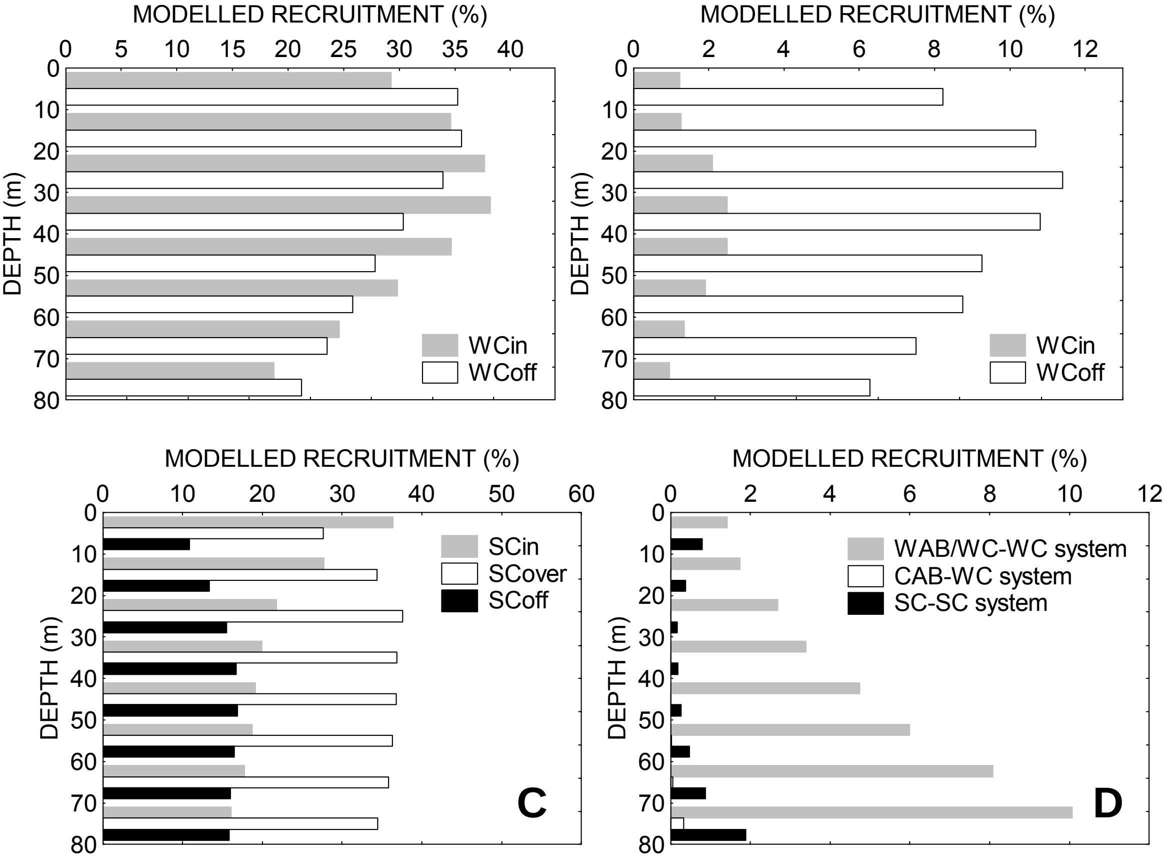

Fig. 5.3: Modelled recruitment to each of the sub-nursery areas for individuals kept in 10m depth ranges in (A) the WAB/WC-WC system, (B) the CAB-WC system and (C) the SC-SC system; and (D) lethal temperature mortality rates for individuals kept in 10m depth ranges for the three systems

area decreased with depth whereas modelled recruitment to the WCin area was highest at an intermediate depth (30-50m). Levels of modelled recruitment to both sub-nursery areas are similar. In the CAB-WC system, substantially fewer individuals recruited to the inshore than the offshore sub-nursery area, and highest levels of modelled recruitment were found between 20 and 30m to WCoff and 30 and 40m to WCin in this recruitment system. Modelled recruitment to the south coast sub-nursery areas was about the same at all depths below 30m, the majority of individuals being retained over the cool ridge and equal amounts being retained on the inshore and offshore sides. The majority of individuals released near the surface (above 30m) were retained inshore of the cool ridge, though good modelled recruitment over the cool ridge was found at all depths. The pattern of mortality rate for each 10m depth range is different for each of the recruitment systems (Fig. 5.3 D). The west coast shows a steady increase in mortality with depth whereas what little mortality does occur in the

CAB-WC and SC-SC systems is mainly below 50m, though there is a slight increase in mortality in the top 10m in the SC-SC system.

5.3.2. Vertical mixing in the model

The distribution of individuals released uniformly between 0 and 80m (12.5% in each 10m depth range) only changed slightly during development (VP Exp. 2, Fig. 5.4 A-D). The most marked change was the increase in the proportion of individuals below 70m of eggs on the LWCin area; yolk-sac larvae on the LWCin and CABoff areas and early and late larvae on all areas except the UWCoff area. There was a general decrease in the number of individuals in

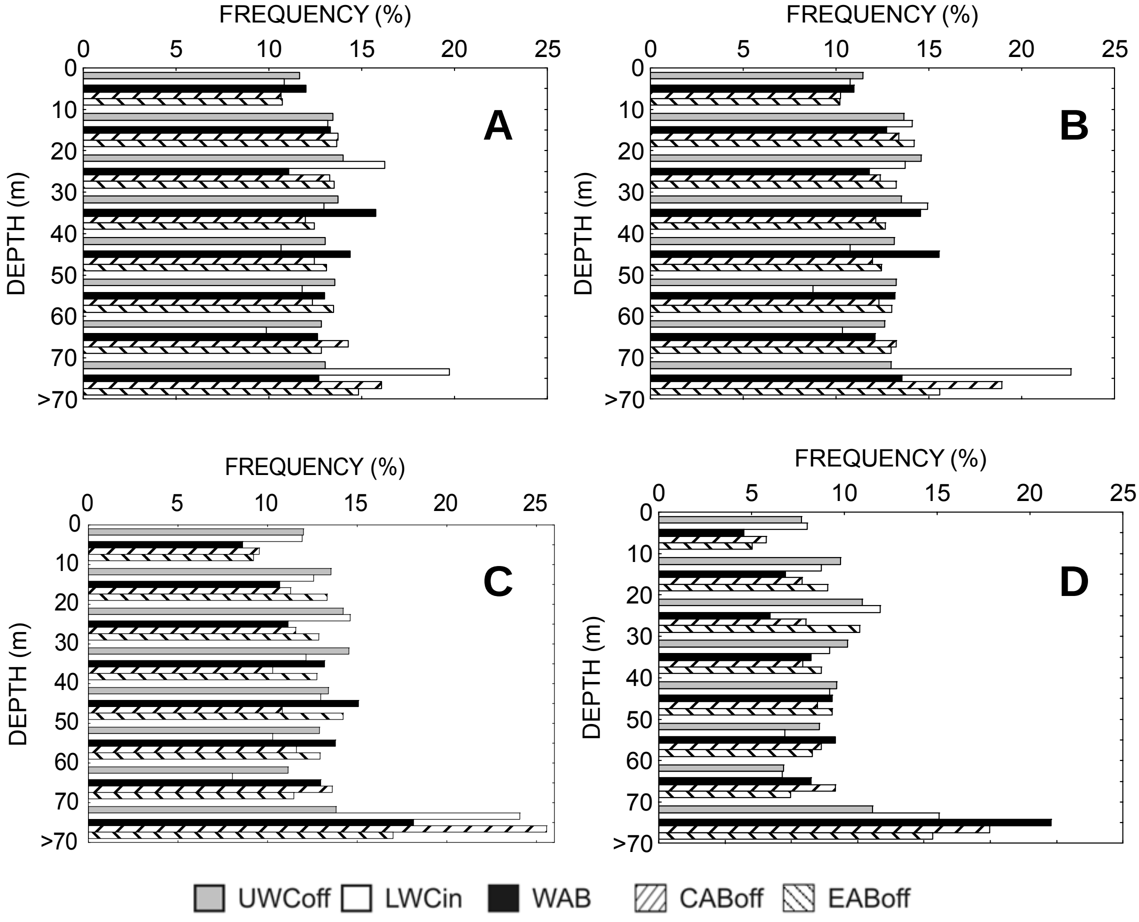

Fig. 5.4: The vertical distribution of individuals released uniformly over the top 80m of the water column in the five spawning areas and transported in a Lgrangian manner examined at (A) halfway through the egg stage (B) the beginning of the yolk-sac larva stage (C) the beginning of the early larva stage and (D) the beginning of the late larva stage

the top 20m, particularly in the Agulhas Bank spawning areas. However, during December and March, the proportion of individuals in the surface layers increased and the proportioning located below 70m decreased (Fig. 5.5 A-D), particularly during the later stages. The frequency in the 20-30m depth range changed the least through development with just over 10% of individuals being found in this range in all stages of development for most areas and all months.

None of the vertical distributions resulting from individuals being released in the same three depth ranges used in the previous simulations (Chapters 3 and 4) matched observed egg or larva (over the full diel cycle) distributions (VP Exp. 3, Fig. 5.6 A-D). There appears to be little movement of modelled particles out of the 20-30 and 30-40m depth ranges, and above 20m particles tended to move upwards. This ascent is quite rapid because most of the individuals released in the top 25m concentrate in the top 20m by the end of the egg stage.

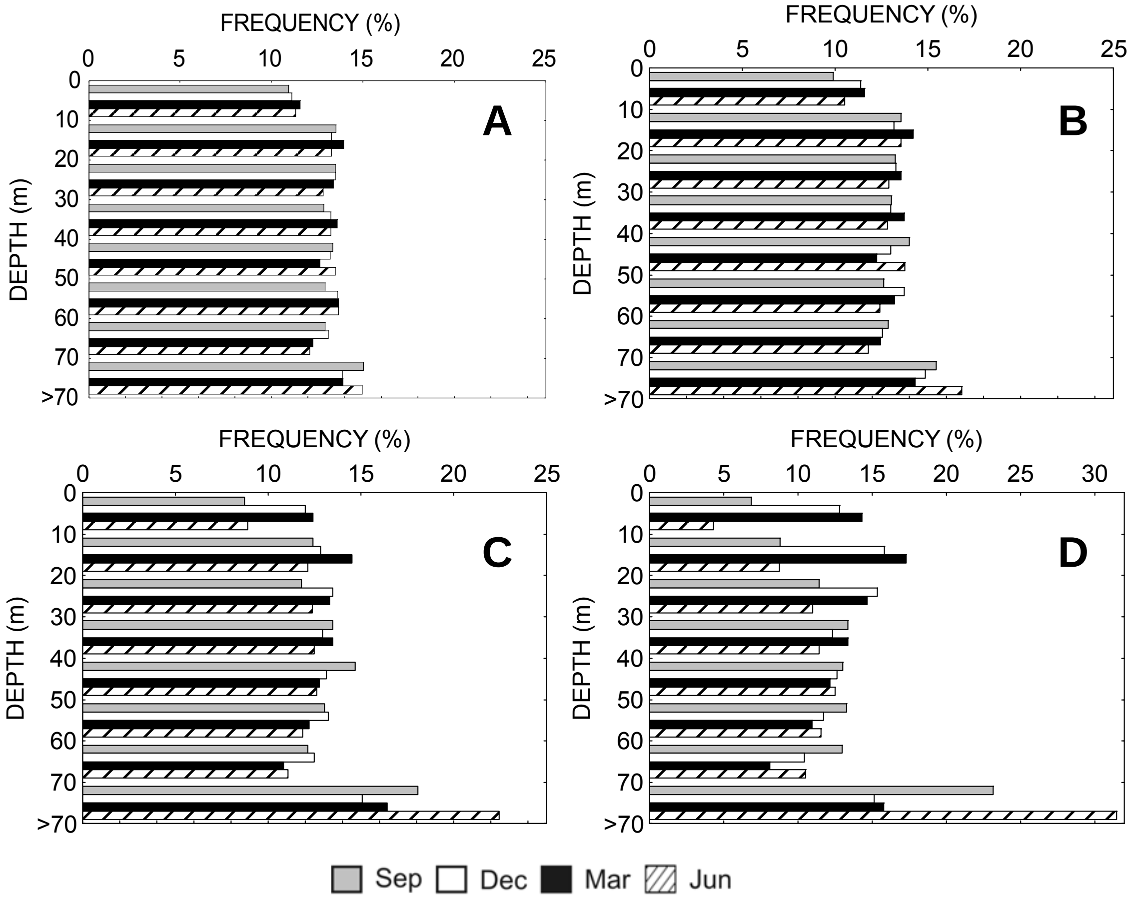

Fig. 5.5: The vertical distribution of individuals released uniformly over the top 80m of the water column during the four months examined at (A) halfway through the egg stage (B) the beginning of the yolk-sac larva stage (C) the beginning of the early larva stage and (D) the beginning of the late larva stage

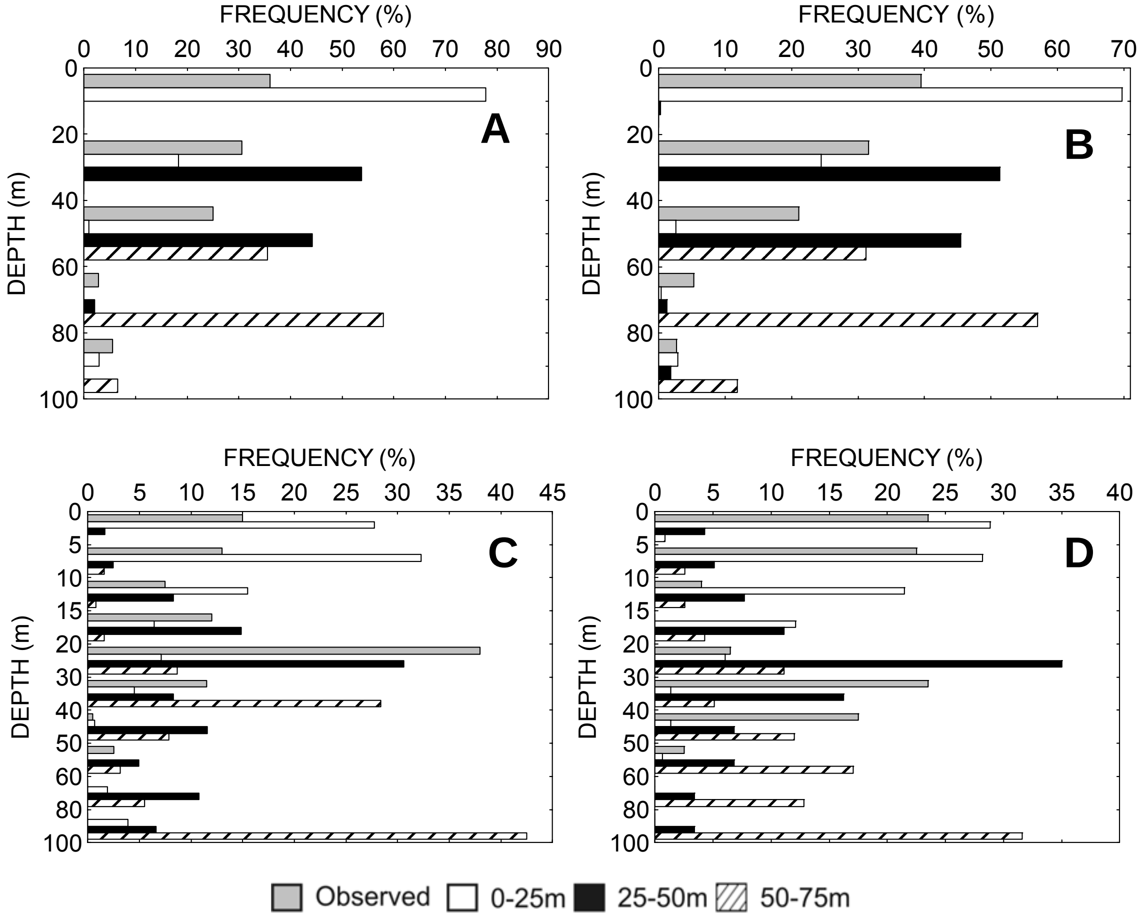

Fig. 5.6: Observed and modelled vertical distributions of individuals released in the 0-25m, 25-50m and 50-75m depth ranges in the five spawning areas examined at (A) halfway through the egg stage (mid-stage eggs) (B) the beginning of the yolk-sac larva stage (late stage eggs) (C) the beginning of the early larva stage and (D) the beginning of the late larva stage

There is also a gradual increase with development in the frequency of occurrence in the surface layers of individuals released between 25 and 50m. Below 40m individuals tend to be transported downwards; most of the individuals released between 50 and 75m remain below 50m with the greatest proportion of early and late larvae being found below 80m.

When individuals are released according to the observed early stage egg vertical distributions the modelled vertical distribution at the end of the egg stage is very similar to observed late stage egg vertical distributions (VP Exp. 3, Fig. 5.7). Observed early and late stage larva distributions cannot be achieved by Lagrangian transport irrelevant of the initial distribution of individuals used. The observed early larva distribution has a distinct peak between 20 and 30m and a lesser peak in the top 10m. The surface peak is achieved through Lagrangian transport but the concentration of individuals in the 20-30m depth range does not

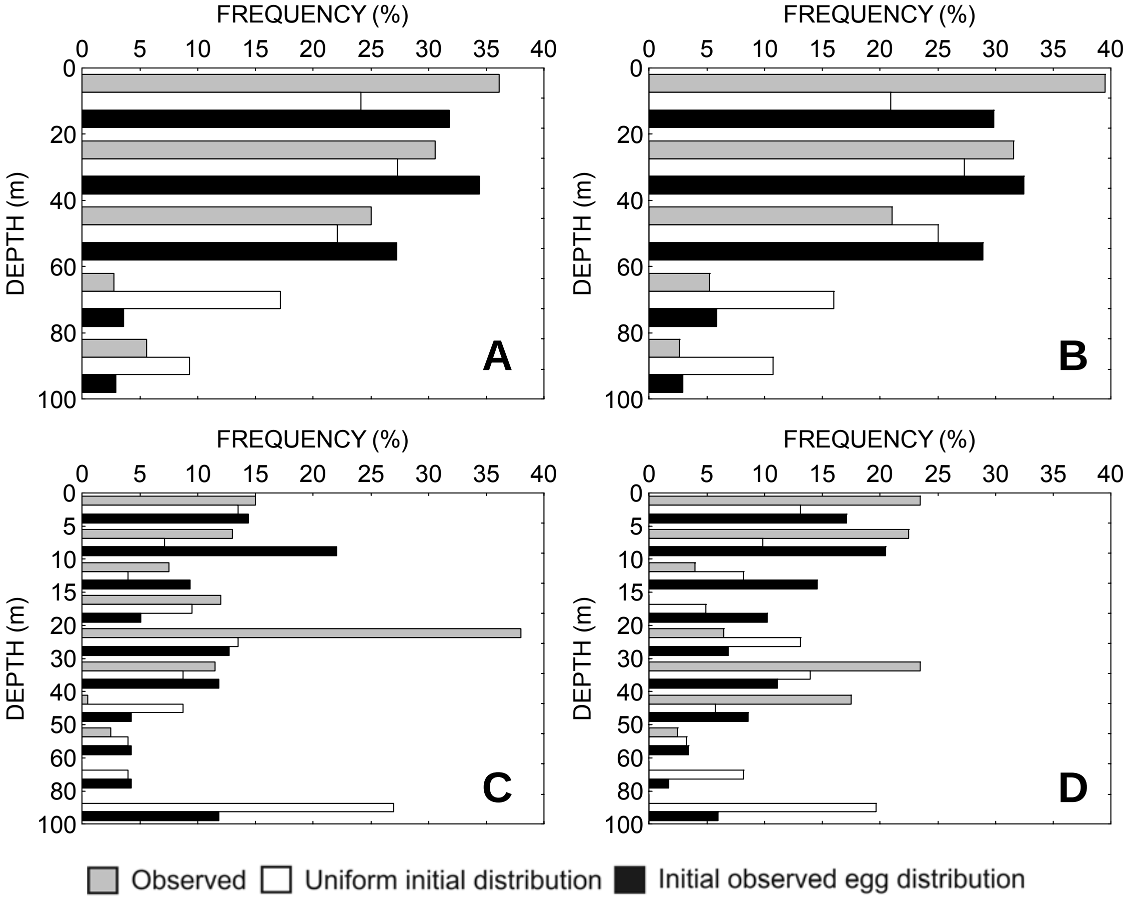

Fig. 5.7: Observed and modelled vertical distributions of individuals released uniformly between 0 and 80m and according to the observed early stage egg vertical distribution for (A) mid way through the egg stage (B) the beginning of the yolk-sac larva stage (C) the beginning of the early larva stage and (D) the beginning of the late larva stage

occur. The observed late larva distribution is also distinctly bimodal with almost half the individuals found in the top 10m and most of the rest between 30 and 50m. Again surface frequencies can be explained by Lagrangian transport but the frequency of occurrence between 30-50 is not matched through Lagrangian transport.

5.3.3. Vertical positioning schemes

5.3.3.1. EGGS

Neither the theoretical buoyancy model ($\chi^2 = 23.75178$, df = 4, $p < 0.001$), nor the empirical settling rate scheme ($\chi^2 = 52.58889$, df = 4, $p < 0.001$), led to accurate vertical distributions at the late larva stage compared to the observed late stage egg distribution (Fig. 5.8). The buoyancy model led to a slight increase in the frequency of individuals near the surface and a slight decrease in the frequency of individuals below 60m but there was not a marked change from the initial uniform distribution. The settling rate scheme resulted in eggs reaching the surface layers very quickly and concentrating in the top 10m. When eggs were released according to observed initial egg distributions, Lagrangian transport resulted in a vertical distribution similar to the observed late stage egg distribution (χ^2 = 5.791303, df = 4, p = 0.215288), and this egg vertical distribution scheme was used for the IBMs that follow.

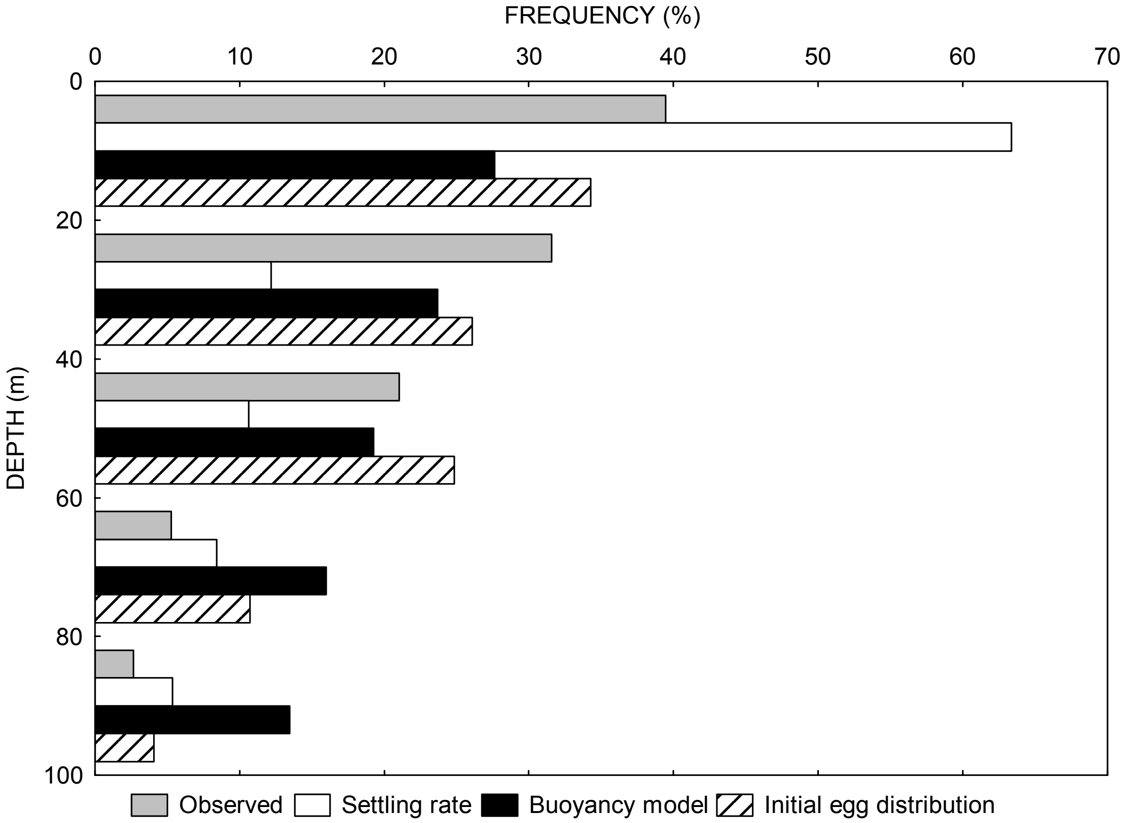

Fig. 5.8: Observed and modelled vertical distributions of individuals at the end of the egg stage, using the empirical settling rate scheme, using the theoretical buoyancy model and when particles are released according to the observed initial egg distribution

5.3.3.2. LARVAE

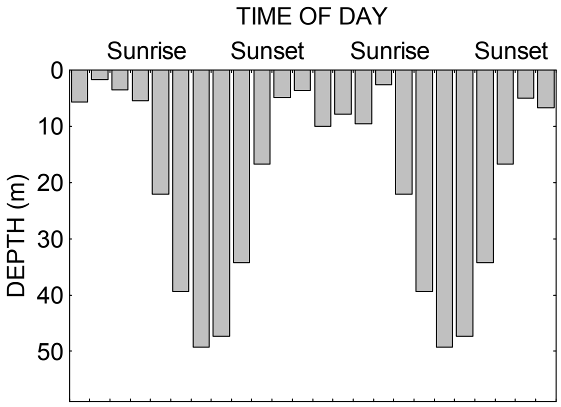

Fig. 5.9: Vertical position of early and late larvae in response to changes in surface light intensity during one time step of the 3-D hydrodynamic model

The light mediated depth of each individual during each time step in March is shown in Fig. 5.9. This movement resulted in individuals being found too frequently between 40 and 50m (near the maximum depth) compared with observed early larva distributions (Fig. 5.10). While 50m is a reasonable limit for the maximum depth of early larvae (which are found, though infrequently, below 40m) most early larvae are observed between 20 and 30m. The light mediated DVM model also over-estimated the frequency of occurrence near the surface at night and incorrectly estimated the depth of individuals during the day. Hence the vertical distribution pattern using this scheme significantly differed from the observed pattern (χ^2 = 142.5779 df = 7 p < 0.001). The light mediated vertical distribution more closely matched the observed late larva vertical distribution (Fig. 5.11), particularly during night time when distributions were almost exactly the same. The observed daytime distribution of late larvae shows them to concentrate between 20 and 50m, avoiding the surface layers entirely. However, while individuals are frequently positioned between 20 and 50m using the light mediated DVM scheme they are also positioned above 20m for a number of iterations. Hence the light mediated scheme resulted in a vertical distribution found to be significantly different from the observed distribution (χ^2 = 23.64883 df = 7 p < 0.001). The individual re-positioning scheme resulted in very similar distributions to the observed patterns for both early and late larvae (early larvae: χ^2 = 4.444673 df = 7 p = 0.727368; late larvae: χ^2 = 2.578597 df = 7 p = 0.921), indicating that the temporal resolution of the model does not significantly affect the incorporation of the observed data. Hence this scheme was used for the IBMs that follow.

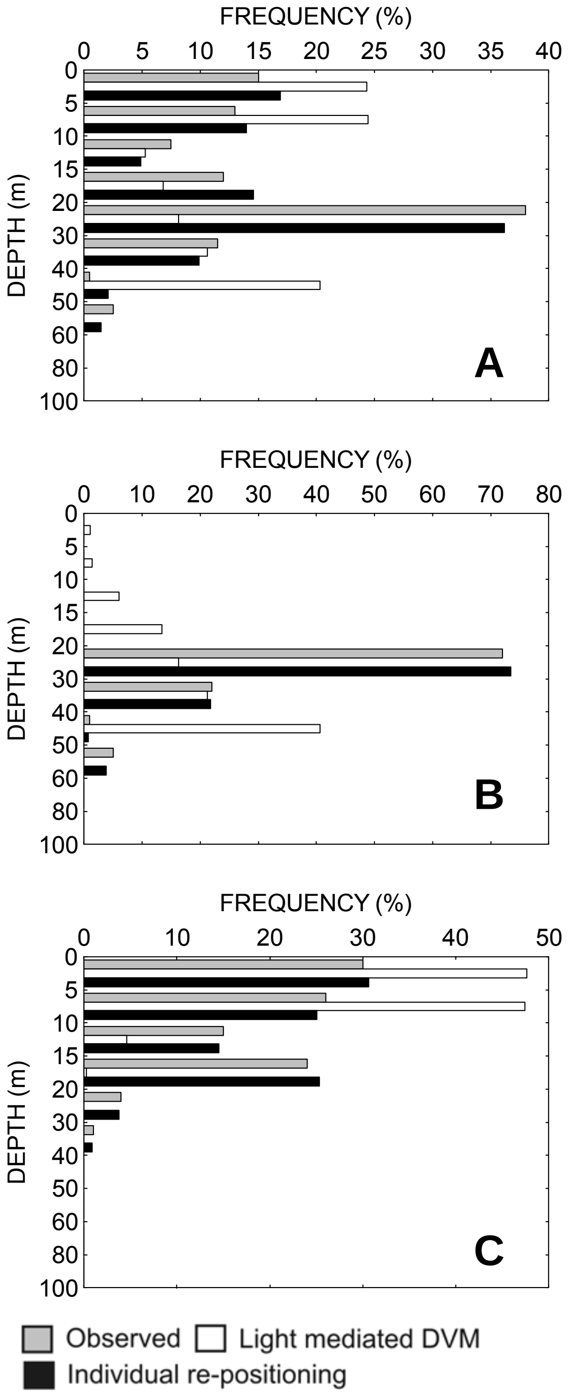

Fig. 5.10: Observed and modelled vertical distributions of individuals during the early larva stage using the theoretical light mediated diel vertical migration scheme and the empirical individual re-positioning scheme for (A) day and night combined; (B) day time and (C) night time distributions

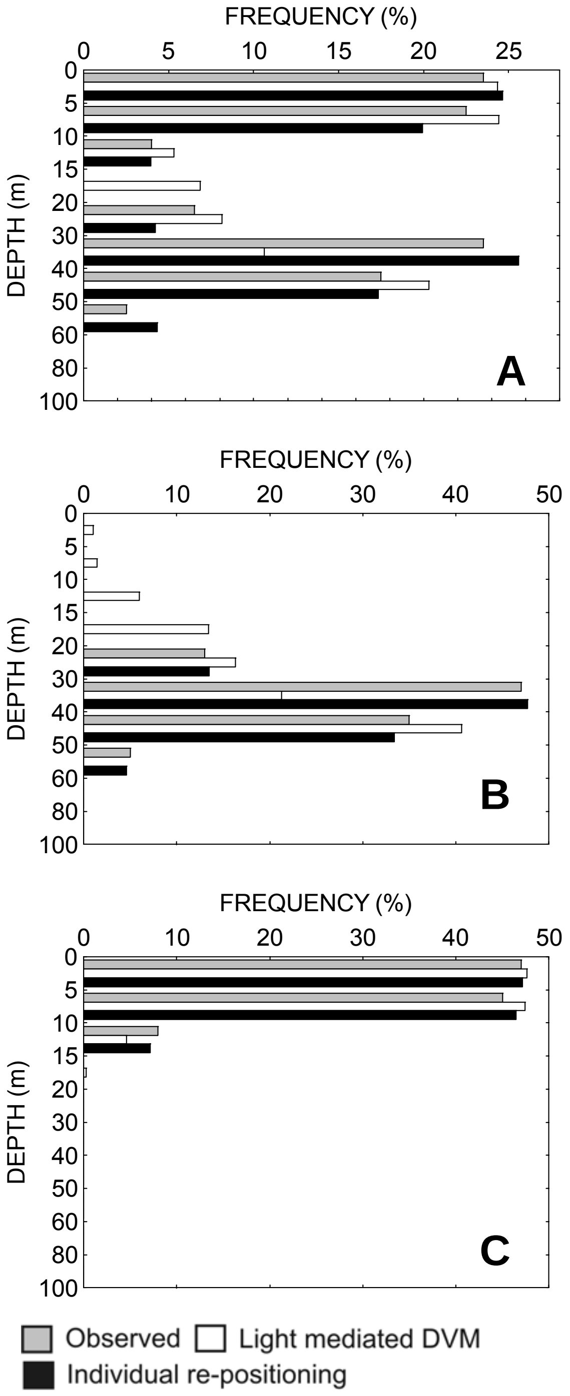

Fig. 5.11: Observed and modelled vertical distributions of individuals during the late larva stage using the theoretical light mediated diel vertical migration scheme and the empirical individual re-positioning scheme for (A) day and night combined; (B) day time and (C) night time distributions

5.3.4. Modelled recruitment and mortality using optimal vertical positioning schemes

Mean modelled recruitment to the west coast (39.73%) was slightly higher than that to the south coast (34.41%; Fig. 5.12 A). Retention on the west coast was >60% for all the west coast spawning areas, and markedly more individuals released on the WAB are transported to the west coast than the south coast nursery area (45.74 and 7.91%, respectively). In contrast, few of the individuals released on the central and eastern Agulhas Bank (EAB) are transported to the west coast nursery area before reaching the late larva stage, with only the CABoff area having >10% of individuals transported to the west coast. The CABin, EABin and EABoff all have extremely high (>75%) levels of retention on the south coast. The addition of vertical positioning schemes resulted in fewer particles being successfully retained in the west coast nursery area from all spawning areas (Fig. 5.12 B). This reduction was most noticeable in the level of transport from the Agulhas Bank spawning areas. There were negligible differences with or without vertical positioning in modelled recruitment to the south coast nursery area from all of the spawning areas except the WAB, which saw a moderate increase (25%) in modelled recruitment.

Temperature induced mortality rates were very low (<1.5%) for all Spawning areas. Mortality was highest in the UWCoff area (1.2%) and lowest in the LWCin area (0.7%). No noticeable spatial or seasonal trend in mortality was found.

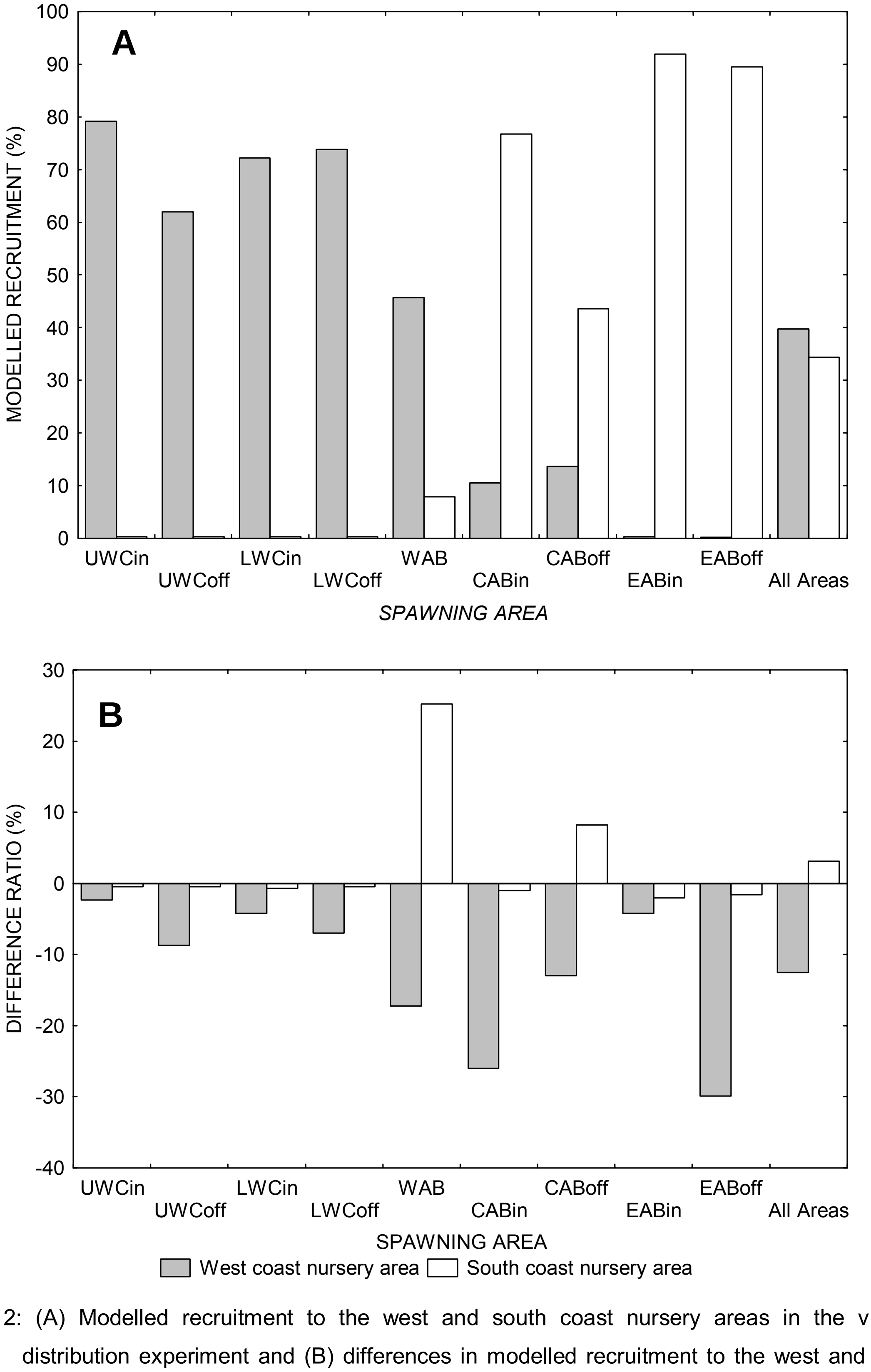

Fig. 5.12: (A) Modelled recruitment to the west and south coast nursery areas in the vertical distribution experiment and (B) differences in modelled recruitment to the west and south coast nursery areas (difference ratio) between the temperature-dependent development and vertical distribution experiments for the *Spawning Area* variable

5.3.4.1. THE WAB/WC-WC SYSTEM

The single variables and first order interactions together explained 73.38% of the variance in the GLM for modelled recruitment in the WAB/WC-WC system (Table 5.2). The assumptions for the GLM analysis were met - the residuals of transport success were normally distributed and no trend was found in the mean and variance of the residuals in relation to the observed values. There was no *Trial* effect.

The primary determinant of modelled recruitment in this system is *Spawning Area*, explaining nearly half (41.21%) of the variance in modelled recruitment, and none of the other variables explained more than 5%. There was a significant *Spawning Area*Month* interaction (Fig. 5.13) and mean modelled recruitment by *Month* shows a trough from February to April (though this pattern did not differ significantly from a uniform distribution, $\chi^2 = 1.85$, df = 11, p = 0.9990). The WAB spawning area has a more distinct seasonal pattern compared to the other areas; modelled recruitment from eggs released here is highest between October and December and low over the winter months. In contrast, modelled recruitment from the remaining areas shows little change between months (although the UWCoff area shows more variability than the rest), with a slight increase in winter.

Table 5.2: General linear model results for the WAB/WC-WC system in the vertical distribution experiment showing the contributions of the different variables to determining modelled recruitment to the west coast nursery area. The main effects and interaction effects explaining more than 5% of the variance are shown, together with univariate statistics of the parameter values. Test of SS Whole Model vs. SS Residual: Adjusted $R^2 = 0.73$; $p < 0.01$. * = Significant ($p < 0.01$). % variance explained = $100\times SS_{effect}/SS_{tot}$

	Sum of Squares	Degrees of freedom	Mean Squares	F	p	% variance explained
Intercept	6384276	1	6384276	62307		
Single variable						
Spawning Area	200805	4	50201	490	0.00*	41.21
Year	3336	7	477	5	0.00*	0.68
Month	14742	11	1340	13	0.00*	3.03
Trial	3	2	1	0	0.99	0.00
Interaction terms						
*Spawning Area*Year*	42302	28	1511	15	0.00*	8.68
*Spawning Area*Month*	49907	44	1134	11	0.00*	10.24
*Year*Month*	46436	77	603	6	0.00*	9.53
Error	129720	1266	102			26.62
TOTAL	487251	1439	55370			

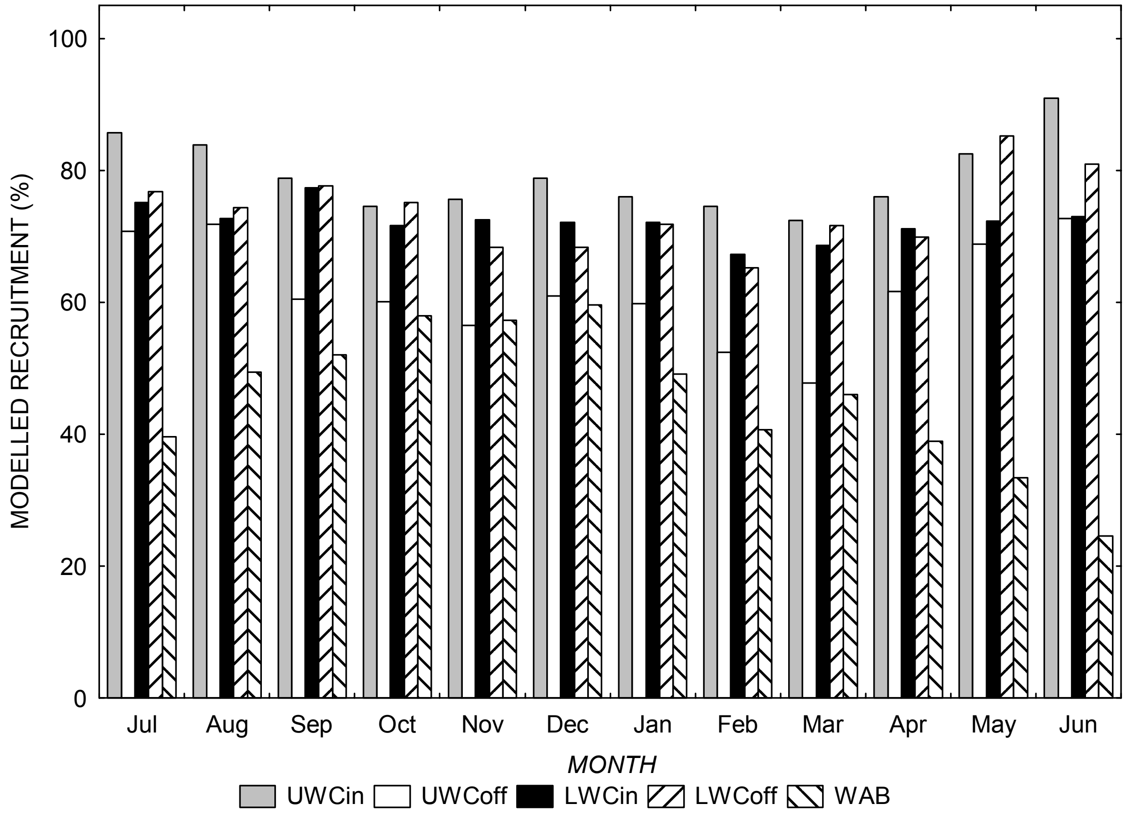

Fig. 5.13: Modelled recruitment for the *Month* variable in the WAB/WC-WC system in the vertical distribution experiment for each *Spawning Area*

Spawning Area was by far the most important variable in determining the level of modelled recruitment to the inshore sub-nursery area in the WAB/WC-WC system (Table 5.3). Modelled recruitment to this area was highest from the inshore west coast spawning areas (Fig. 5.14 A), and individuals from the WAB were least likely to be transported inshore.

Table 5.3: General linear model results for the WAB/WC-WC system in the vertical distribution experiment showing the contributions of the different variables to determining modelled recruitment to the WCin sub-nursery area. The main effects and univariate statistics of the parameter values are shown. Test of SS Whole Model vs. SS Residual: Adjusted $R^2 = 0.89$; $p < 0.02$. * = Significant ($p < 0.01$). % variance explained = $100 \times SS_{effect}/SS_{tot}$

	Sum of Squares	**Degrees of freedom**	**Mean Squares**	**F**	**p**	**% variance explained**
Intercept	515979	1	515979	51585		
Single variable						
Spawning Area	409717	4	102429	2202	0.00*	73.89
Year	6037	7	862	19	0.00*	1.09
Month	13667	11	1242	27	0.00*	2.46
Trial	26	2	13	0	0.75	0.00
Error	58881	1266	47			10.62
TOTAL	554492	1439	106049			

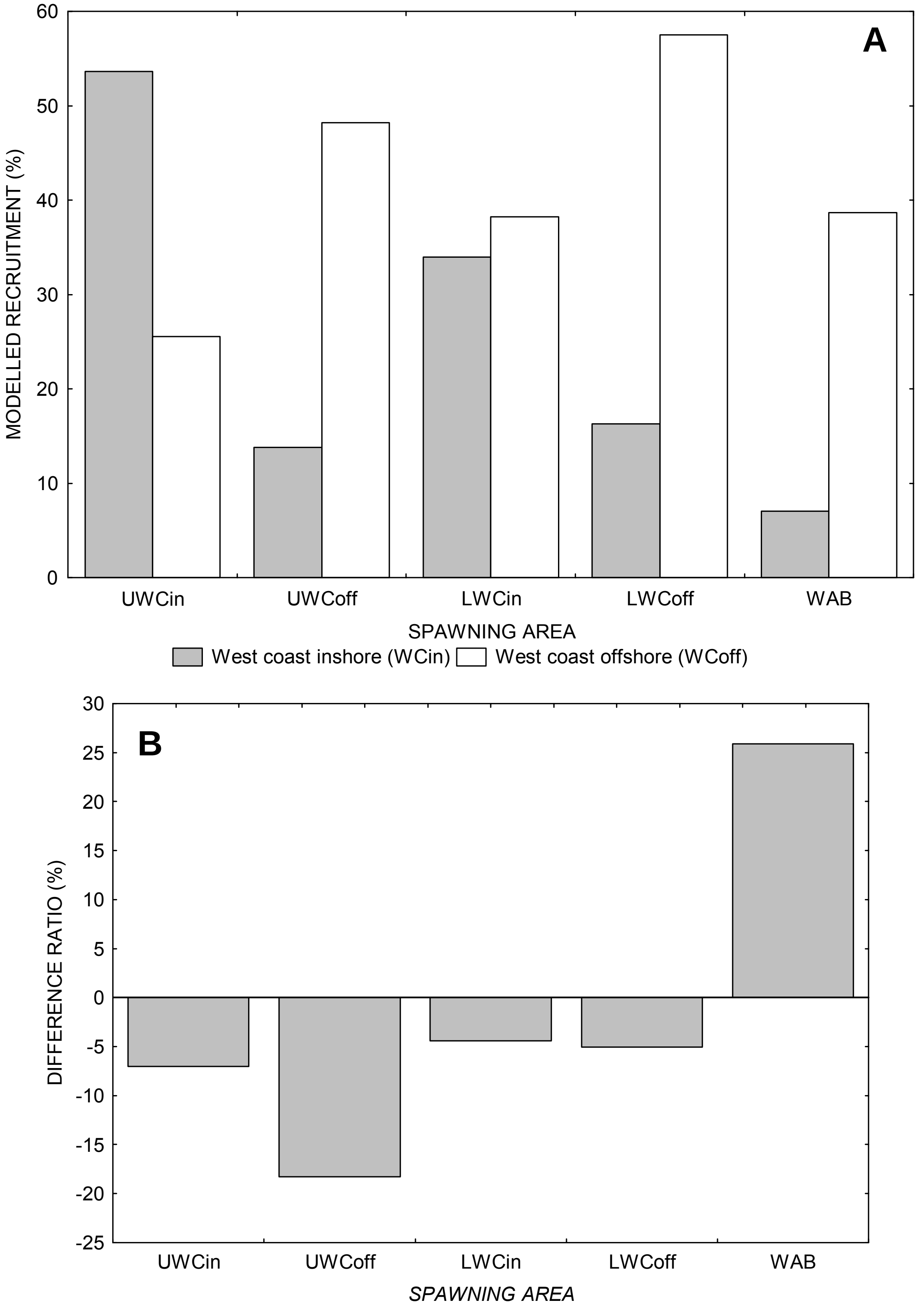

Fig. 5.14: (A) Modelled recruitment to the two west coast sub-nursery areas, west coast inshore (WCin) and west coast offshore (WCoff) in the WAB/WC-WC system in the vertical distribution experiment for each *Spawning Area* variable; and (B) differences in modelled recruitment to WCin (difference ratio) between the temperature-dependent development and vertical distribution experiments for the *Spawning Area* variable

Recruitment to the WCoff sub-nursery area was high in both offshore west coast spawning areas. The incorporation of vertical positioning schemes markedly increased recruitment to the inshore nursery area from the WAB (while decreasing transport to the WCoff sub-nursery area) but decreased inshore transport from the remaining areas (Fig. 5.14 B).

5.3.4.2. THE CAB-WC SYSTEM

The single variables and first order interactions together explained 97.87% of the variance in the GLM for modelled recruitment in the CAB-WC system (Table 5.4). The assumptions for the GLM analysis were met - the residuals of transport success were normally distributed and no trend was found in the mean and variance of the residuals in relation to the observed values. There was no *Trial* effect. The majority of the variance (45.85%) is explained by the *Month* variable; while modelled recruitment was higher to the south coast nursery area than the west coast nursery area for all months of the year, this difference was lowest between September and November (Fig. 5.15 A). This pattern closely matches the mean modelled recruitment to the west coast (Fig. 5.15 B); this latter seasonal pattern being significantly different from a uniform distribution (χ^2 = 39.72, df = 11, $p < 0.0001$) and remaining significantly different when any single month was removed (Fig 5.16 B, χ^2 p-values). Modelled recruitment is highest between September and November and if these three months are removed the pattern is no longer significantly different from a uniform distribution (χ^2 =

Table 5.4: General linear model results for the CAB-WC system in the vertical distribution experiment showing the contributions of the different variables to determining modelled recruitment to the west coast nursery area. The main effects and interaction effects explaining more than 5% of the variance are shown, together with univariate statistics of the parameter values. Test of SS Whole Model vs. SS Residual: Adjusted $R^2 = 0.98$; $p < 0.01$. * = Significant ($p < 0.01$). % variance explained = $100 \times SS_{effect}/SS_{tot}$

	Sum of Squares	**Degrees of freedom**	**Mean Squares**	**F**	**p**	**% variance explained**
Intercept	53720	1	53720	16868		
Single variable						
Year	2912	7	416	131	0.00*	10.25
Month	13021	11	1184	372	0.00*	45.85
Trial	0	2	0	0	0.93	0.00
Interaction terms						
*Year***Month*	11859	77	154	48	0.00*	41.76
Error	605	190	3			2.13
TOTAL	28397	287	1757			

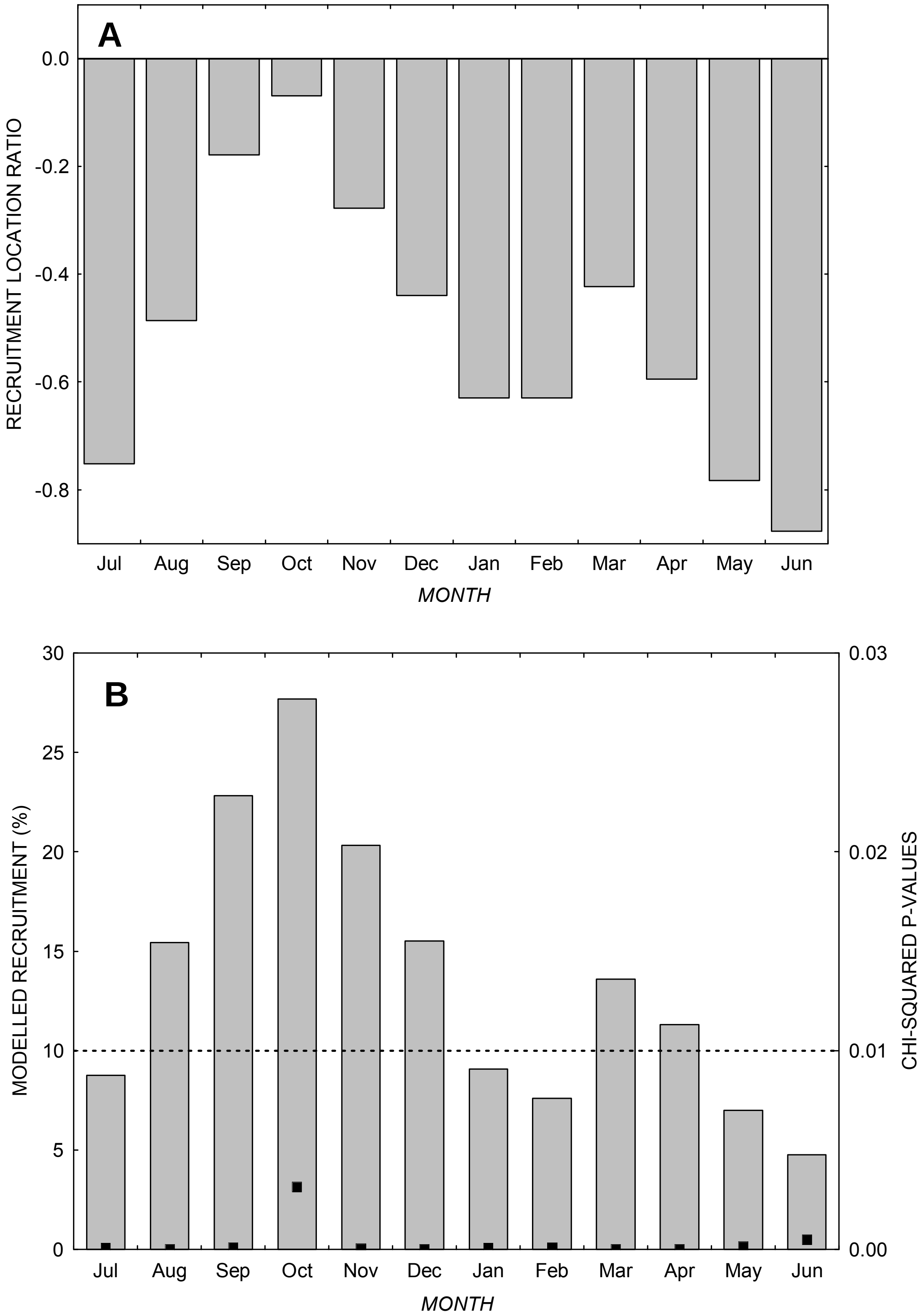

Fig. 5.15: Seasonal patterns (the *Month* variable) in the CAB-WC system in the vertical distribution experiment: (A) recruitment location ratio (west coast:south coast) and (B) mean modelled recruitment with p-values of Chi-squared tests comparing the pattern to a uniform distribution after removing each month individually (the dotted line is p = 0.01)

11.43, df = 9, p = 0.1784). The smaller peak in modelled recruitment to the west coast in March and April was not significant. The mean seasonal pattern does vary from year to year as the strong *Year*Month* interaction indicates; 1991/92 and 1992/93 had considerably higher levels of recruitment in October while the years 1991/2, 1993/4 and 1994/5 had very poor transport in December and January. April to July showed reduced modelled recruitment compared to September to February for all years of the time series (not shown).

Month also explained 13.15% of the variance in the level of modelled recruitment to the WCin sub-nursery area (Table 5.5). Individuals are most likely to reach the WCin area in the winter months from April to August but the proportion recruiting here is very low (<5%) all year round (Fig. 5.16). As a result, recruitment to the WCoff sub-nursery area closely matches the seasonal pattern of modelled recruitment on the whole west coast. However, more than half of the variance was explained by the *Year*Month* interaction, which indicates that the seasonal pattern differs greatly from year to year. The incorporation of vertical positioning increased transport to the inshore west coast nursery area (though only slightly in absolute values) for all months of the year except January and February (Fig. 5.16 B).

Table 5.5: General linear model results for the CAB-WC system in the vertical distribution experiment showing the contributions of the different variables to determining modelled recruitment to the WCin sub-nursery area. The main effects and interaction effects explaining more than 5% of the variance are shown, together with univariate statistics of the parameter values. Test of SS Whole Model vs. SS Residual: Adjusted $R^2 = 0.93$; $p < 0.01$. * = Significant ($p < 0.01$). % variance explained = $100 \times SS_{effect}/SS_{tot}$

	Sum of Squares	**Degrees of freedom**	**Mean Squares**	**F**	**p**	**% variance explained**
Intercept	501	1	501	1259		
Single variable						
Year	161	7	23	58	0.00*	15.30
Month	138	11	13	32	0.00*	13.15
Trial	1	2	0	1	0.48	0.06
Interaction terms						
*Year*Month*	675	77	9	22	0.00*	64.29
Error	76	190	0			7.21
TOTAL	1049	287	45			

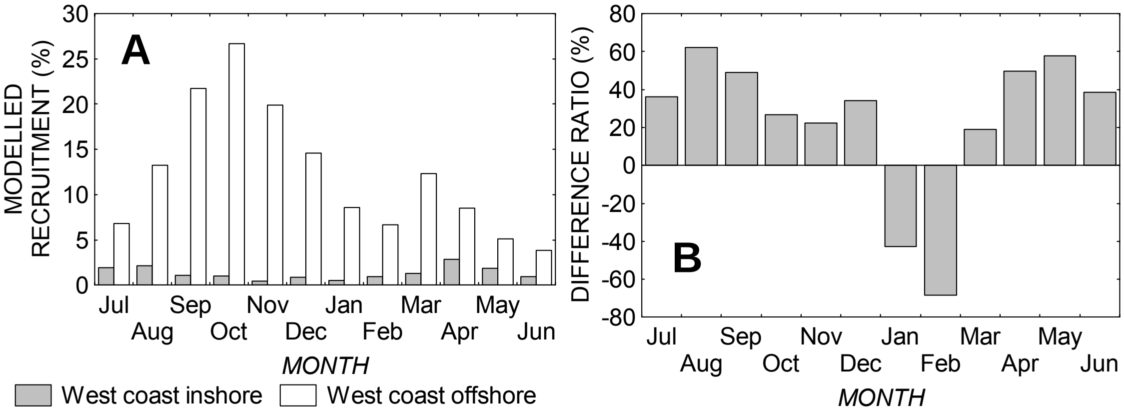

Fig. 5.16: (A) Modelled recruitment to the two west coast sub-nursery areas, west coast inshore (WCin) and west coast offshore (WCoff), in the CAB-WC system in the vertical distribution experiment for the *Month* variable and (B) differences in modelled recruitment to the inshore west coast sub-nursery area (difference ratio) between the temperature-dependent development and vertical distribution experiments for the *Month* variable

5.3.4.3. THE SC-SC SYSTEM

The single variables and first order interactions together explained 90.06% of the variance in the GLM for modelled recruitment in the SC-SC system (Table 5.6). The assumptions for the GLM analysis were met - the residuals of transport success were normally distributed and no trend was found in the mean and variance of the residuals in relation to the observed values. There was no *Trial* effect.

Table 5.6: General linear model results for the SC-SC system in the vertical distribution experiment showing the contributions of the different variables to determining modelled recruitment to the south coast nursery area. The main effects and interaction effects explaining more than 5% of the variance are shown, together with univariate statistics of the parameter values. Test of SS Whole Model vs. SS Residual: Adjusted $R^2 = 0.90$; $p < 0.01$. * = Significant ($p < 0.01$). % variance explained = $100\times SS_{effect}/SS_{tot}$

	Sum of Squares	**Degrees of freedom**	**Mean Squares**	**F**	**p**	**% variance explained**
Intercept	6455587	1	6455587	319812		
Single variable						
Spawning Area	427484	3	142495	2203	0.00*	65.90
Year	4072	7	582	9	0.00*	0.63
Month	20666	11	1879	29	0.00*	3.19
Trial	2	2	1	0	0.98	0.00
Interaction terms						
*Spawning Area*Month*	107286	33	3251	50	0.00*	16.54
Error	64496	997	65			9.94
TOTAL	648685	1151	148849			

Spawning Area is the primary determinant of modelled recruitment in the SC-SC system, with 65.90% of the variance explained by this variable. Retention from the EAB spawning areas is consistently high for all months while retention from the CAB spawning areas is reduced between September and March particularly for the CABoff area (Fig. 5.17) resulting in a *Spawning Area*Month* interaction that explains 16.54% of the variance. Mean modelled recruitment to the south coast nursery area is lowest from February to March but the seasonal patterns was not significantly different from a uniform distribution (χ^2 = 2.85, df = 11, p = 0.9925). This is could be because seasonal trends from the CAB and EAB spawning areas show opposite trends (Fig. 5.17), effectively cancelling out any notable peaks or troughs for the system as a whole.

Spawning Area was the only variable explaining a notable amount of the variance (90.65%) in recruitment to the SCoff sub-nursery area (Table 5.7). More than half of the individuals released on the CABin area are retained inshore of the cool ridge and less than 2% of them recruit to the offshore edge of the cool ridge (Fig. 5.18). Conversely, slightly less

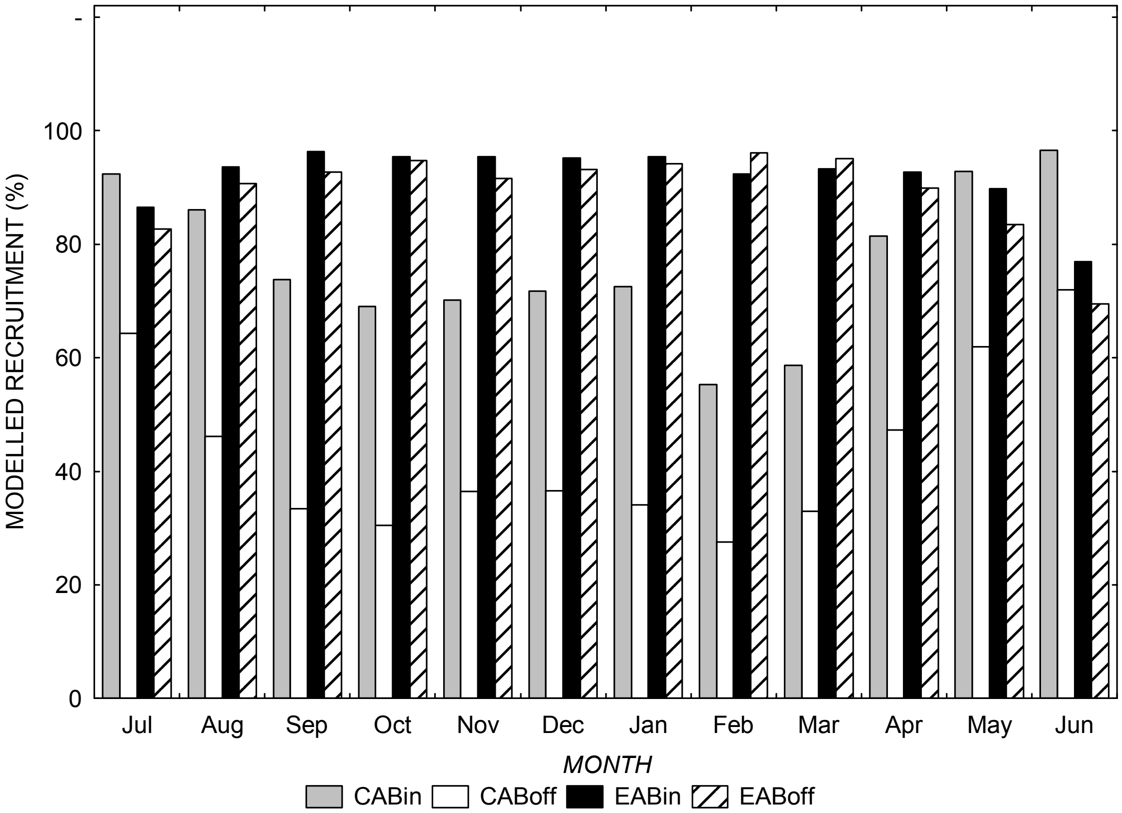

Fig. 5.17: Modelled recruitment in the SC-SC system in the vertical distribution experiment for the *Spawning Area*Month* interaction

Table 5.7: General linear model results for the SC-SC system in the vertical distribution experiment showing the contributions of the different variables to determining modelled recruitment to the SCoff sub-nursery area. The main effects and univariate statistics of the parameter values are shown. Test of SS Whole Model vs. SS Residual: Adjusted $R^2 = 0.95$; $p < 0.01$. * = Significant ($p < 0.01$). % variance explained = $100\times SS_{effect}/SS_{tot}$

	Sum of Squares	**Degrees of freedom**	**Mean Squares**	**F**	**p**	**% variance explained**
Intercept	212778	1	212778	13125		
Single variable						
Spawning Area	301629	3	100543	6202	0.00*	90.65
Year	784	7	112	7	0.00*	0.24
Month	582	11	53	3	0.00*	0.17
Trial	12	2	6	0	0.68	0.00
Error	16164	997	16			4.86
TOTAL	332752	1151	101001			

than half of the individuals from the EABoff area recruit to the SCoff area, and slightly more than 10% to the SCin area. The EABoff spawning area contributes significantly more to recruitment offshore of the cool ridge than any of the other spawning areas. Individuals from the CABoff and EABin spawning areas are most likely to recruit over the cool ridge. The incorporation of vertical positioning reduced modelled recruitment to the SCoff area for all months of the year except for February (Fig. 5.19).

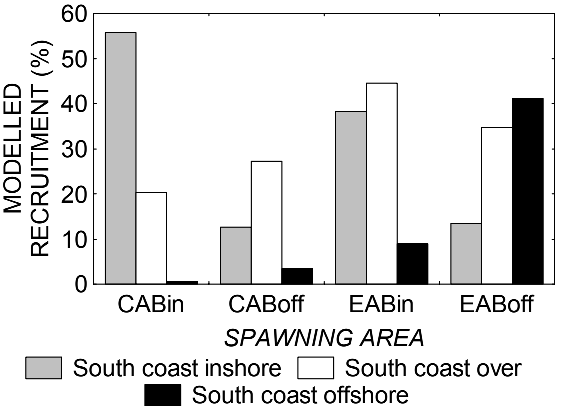

Fig. 5.18: Modelled recruitment to the three south coast sub-nursery areas, south coast inshore (SCin), south coast over (SCover) and south coast offshore (SCoff) of the cool ridge, in the SC-SC system in the vertical distribution experiment from the *Spawning Area* variable

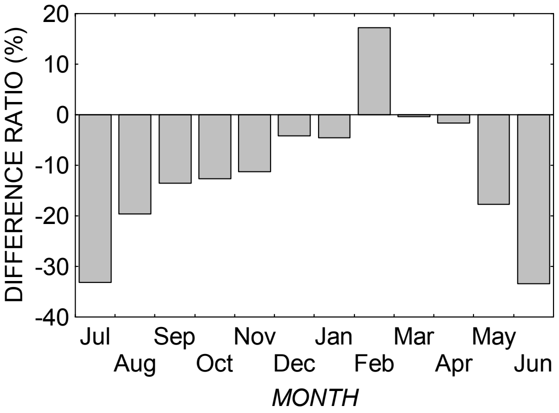

Fig. 5.19: Differences in modelled recruitment to the offshore south coast sub-nursery area (difference ratio) between the temperature-dependent development and vertical distribution experiments in the SC-SC system for the *Month* variable

5.3.4.4. COMPARISON WITH FIELD ESTIMATED RECRUITMENT

Interannual variation in modelled recruitment is low in the WAB/WC-WC system and SC-SC recruitment systems (*Year* explained 1.09 and 0.24% of the variance, respectively). Both of these systems have high levels of modelled recruitment and the difference between the most successful and least successful year is only 4.21% in the WAB/WC-WC system and 6.41% in the SC-SC system. In contrast, the interannual range of modelled recruitment values in the CAB-WC system is 9.11% and modelled recruitment values are lower in this system than the other two. There were a few changes in the value of modelled recruitment anomalies compared with the previous experiment (Chapter 4). In the WAB/WC-WC system, the modelled recruitment anomaly changed from positive to slightly negative in 1993/94. The modelled recruitment anomaly for 1991/92 decreased notably for the WAB/WC-WC system and the anomaly in 1994/95 shifted from strongly negative to very close to zero (Fig. 5.20). The only modelled recruitment anomaly that changed in the CAB-WC system was 1991/92, which shifted from slightly positive to negative. In the SC-SC system modelled recruitment anomalies for 1991/92 and 1997/98 changed from negative to positive and positive to negative, respectively. In general, the pattern of modelled recruitment success is now more similar for all three systems than was the case in the temperature-dependent development experiment (Chapter 4), with reduced modelled recruitment during 1993/94 to 1995/96 and increased modelled recruitment in 1992/93 and from 1996/97 to 1998/99. None of the modelled recruitment anomalies from any of the three systems correlated significantly with back-calculated recruitment estimates, and all had very low r values (WAB/WC-WC system: r = 0.01; CAB-WC system: r = 0.26; SC-SC system: r = 0.26). Positive modelled recruitment anomalies in the CAB-WC system were accompanied by positive recruitment anomalies in the SC-SC system and likewise for negative anomalies, except in 1991/92 and 1997/98, and these two systems are positively correlated (r = 0.71). The WAB/WC-WC system does not correlate with any of the other two systems (CAB-WC: r = 0.49 and SC-SC: r = 0.39). In four years the anomalies of all three systems anomalies were the same sign (all positive in 1992/93 and all negative from 1993/94-1995/96). For the year of the time series, none of the systems had modelled recruitment anomalies corresponding with the back-calculated recruitment anomaly.

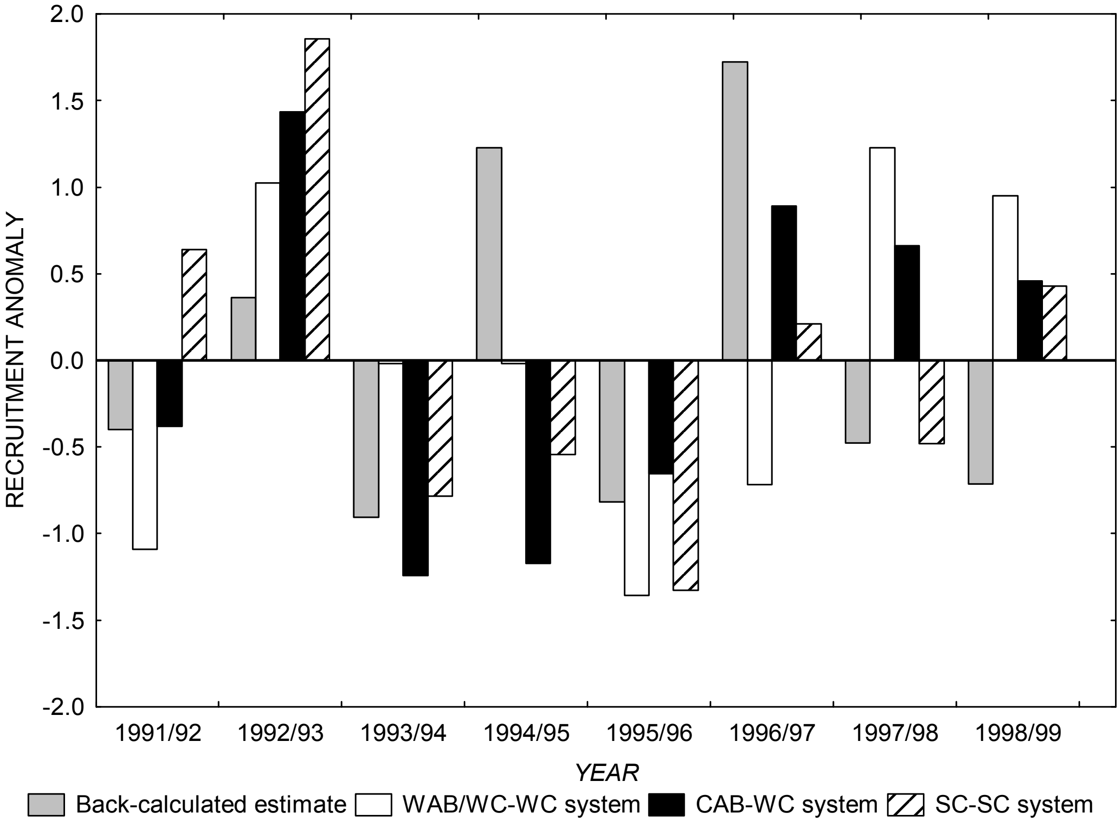

Fig. 5.20: Standardised anomalies of estimated sardine recruitment and the modelled recruitment in each system for the eight years of the vertical distribution experiment. Anomalies are calculated as the difference between the value for a given year and the mean over the eight years, divided by the standard deviation over the eight years

5.4. DISCUSSION

The simulations where individuals were confined to 10m depth ranges (VP Exp. 1) showed notable differences in the patterns of modelled recruitment to each of the sub-nursery areas at different vertical positions in the water column (Fig. 5.3). In the WAB/WC-WC system, transport to the WCin area was highest at 30-40m, just below the offshore-moving Ekman transport layer. This pattern of success matches that reported by Stenevik et al. (2003) for sardine in the northern Benguela. At this depth flow is onshore and mortality is less than that experienced in the colder, deeper waters. Offshore transport is stronger in the lower west coast spawning areas and hence individuals in the surface layers are lost from these areas in greater amounts than for the upper west coast. In the CAB-WC system, highest modelled recruitment to the WCoff area is at 20-30m depth, which corresponds with the depth that is believed to be optimal for transport of eggs and larvae in the Cape Columbine jet current (Boyd et al. 1992, Fowler and Boyd 1998). Optimal modlled recruitment to the WCin area is slightly deeper (30-50m) and shows the same pattern as seen in the WAB/WC-WC system, with inshore movement on the west coast favouring transport to this sub-area rather than transport between the Agulhas Bank and the inshore west coast. Levels of modelled recruitment to the WCin area from the Agulhas Bank are very low, but this is considered to be a model artefact resulting from the criterion used for individuals to be considered as successfully transported. Individuals from the CAB have already developed to late larvae by the time they reach the west coast, and since the position of the jet current varies between the 200m and 500m isobaths (Fowler and Boyd 1998) and the 200m isobath separates the WCin and WCoff areas, most individuals are likely to be recorded as recruiting to WCoff before they are able to reach the WCin area. However, Huggett et al. (2003) also noted that modelled recruitment to the inshore region of the west coast was substantially lower than to the offshore region. In the SC-SC system, the surface layers clearly favour retention inshore (SCin). Modelled recruitment to the SCover and SCoff areas in the surface layers is reduced, possibly because of individuals getting entrapped in the Agulhas Current and lost from this region. The SCover sub-nursery area has very high levels of modelled recruitment at most depths (although the 0-10m depth range is lower than the rest), probably due to this being the largest of the sub-nursery areas, and having individuals from both inshore and offshore are retained in this area when released at depth. The intrusion of cold upwelled water to the surface layers of the west coast leads to greater mortality in shallower waters in the WAB/WC-WC system than the other two systems. The slight increase in mortality near the surface in the SC-SC system could be due to the cold water intrusion forming the cool ridge. Water at 20m can get as cold as 10°C in places (Swart and Largier 1987) and good retention over the cool ridge at this depth is likely to keep many individuals in contact with this colder water.

The differences in both transport and mortality for individuals released at different depths in the water column indicate that the vertical position of individuals is important when modelling their transport and growth. The vertical position of an egg or larva is a balance between vertical mixing or diffusive forces in the water column and the vertical movement of the egg (buoyancy properties) or larva (buoyancy properties and swimming behaviour).

However, the vertical resolution of the PLUME model is quite coarse; the minimum resolution in the uppermost layer being 1m inshore and broadening to 5m offshore, and vertical resolution becomes even coarser at depth. It is therefore unlikely that the model will accurately represent fine-scale structures and downward mixing in the water column (Parada et al. 2003). The changes in distribution of individuals released uniformly through the top 80m (VP Exp. 2) show that there is a tendency for downward movement of Lagrangian individuals and many individuals are transported to below 70m from all areas during all months examined (Fig. 5.4). Retention in the surface layers is generally highest in the west coast spawning areas and during December and March, and particularly for the older stages. This is most likely because individuals are transported upwards as deep waters are upwelled to the surface by the strong south-easterly winds often present along this coastline during this time. The relative numbers of individuals between 20 and 40m remain fairly constant (in time and space) and this layer appears to act as a barrier to the vertical movement of individuals. This depth corresponds to observed thermocline depths on the CAB and EAB. These thermoclines are dynamically stable because they are principally advectively maintained by an intrusive cold bottom layer rather than seasonal insolation changes (Carter et al. 1987). On the WAB, thermoclines are both advectively and atmospherically controlled, and are generally deeper than on the CAB and EAB (Largier and Swart 1987). Thermoclines along the west coast are less dynamically stable, especially in the inshore areas because of seasonal changes in wind forcing and upwelling. Thermoclines separate upper mixed layer surface waters from colder, more stable water masses below. The existence of strong thermoclines as been reported as one of the aspects of the water column affecting the vertical distribution of plankton (Angel 1968, Sameoto 1984, Cornet and Gili 1993). This could explain why individuals released above 25m largely remain in the surface waters.

It is clear that Lagrangian transport of individuals from a uniform initial distribution does not produce a realistic representation of the vertical position of individuals. It was therefore necessary to incorporate vertical positioning schemes in the model to adjust the vertical position of individuals at each step. When modelling the vertical position of early life stages it is best to use a stage-structured vertical positioning scheme (e.g. Hare et al. 1999, Pedersen et al. 2001). Individuals change greatly through development and at each stage different physical or behavioural characteristics affect how they move vertically in the water column. Also, with changes in size and feeding requirements, individuals tend towards different patterns of distribution in the water column for reasons such as visual predator avoidance or to locate greater concentrations of food.

When individuals were released uniformly through the water column or across the three 25m depth ranges used in the previous experiments (Chapters 3 and 4) the resultant vertical distributions did not match observed distributions at any stage of development (VP Exp. 3). However when individuals were released according to the observed early stage egg distribution, the simulated vertical distribution at the end of the egg stage did not differ significantly from observed late stage egg distributions. In sardine eggs, the ratio of the volume of the perivitelline space (which is filled with ambient water during hydration) to the volume of the egg is 0.8, determined from egg and yolk measurements reported by Brownell (1979) and King (1977). Because the initial density of an egg adjusts according to the ambient water in which it is spawned (Tanaka 1992), almost 80% of the egg's density is determined by the ambient seawater, which results in sardine eggs having densities close to that of seawater. Also, the density of sardine (Coombs et al. 2004) and anchovy (Tanaka 1990) eggs does not change significantly during development until shortly (less than 10 hours) before hatching, when they become more dense. This means that for much of their duration sardine eggs are effectively transported as Lagrangian particles.

The apparent lack of a need to model sardine egg buoyancy contradicts the findings of Parada et al. (2003) who found that transport of anchovy eggs was sensitive to changes in density controlling their buoyancy. Sardine eggs are larger than anchovy eggs, are spherical rather than oblate spheroids, and have a much larger perivitelline space. These differences will affect the buoyancy of eggs and therefore their transport. Most IBMs of the transport of the early stages of fish include some method of vertical positioning of eggs in the water column. A common method is to apply buoyancy schemes similar to that of Sundby (1983), which relates terminal velocity to the density difference between the egg and the surrounding water (e.g. Hinckley et al. 2001, Parada et al. 2003). This was attempted for the sardine eggs in the present IBM but was found to not adequately reproduce observed egg distributions and was therefore deemed unsuitable. Another common method is to assign individuals representing eggs fixed positive buoyancy (Hare et al. 1999) as was done in the empirical settling rate scheme. Dopolo et al. (2005) noted that because sardine eggs are fairly large (in comparison with anchovy and round herring eggs) and contain an oil globule, they have a low specific gravity and hence are likely to ascend towards the surface rapidly. While the settling rate scheme reflected this observation, this was found to not adequately represent observed egg distributions because of overestimating vertical velocities. It appears that for sardine in the southern Benguela ecosystem the depth of spawning plays a greater role in determining the vertical position of eggs than the physical characteristics of the egg itself. Bartsch and Coombs (2004) used fixed vertical positions matching observations of blue whiting (*Micromesistius poutassou*) egg depth, but this does not allow for slight changes in egg depth that occur as a result of vertical water movement. Hence, releasing eggs according to observed egg vertical distributions and determining their position according to vertical water movement within the model was considered the best means of reproducing observed vertical positions of individuals during the egg stage for this study. In addition, the duration of the egg stage is short relative to that of the larval stages so using observed egg vertical distributions precludes the need to incorporate a buoyancy model to maintain expected vertical distributions of individuals during the egg stage.

Yolk-sac larvae are not very mobile, and their limited swimming ability prevents them from being able to conform to a well-defined diel pattern of movement. Dekshenieks et al. (1996) found that upwelling and downwelling velocities can overwhelm behavioural responses of smaller larvae of the Eastern oyster (*Crassotrea virginica*) in the water column and result in different distributions of these individuals. While the buoyancy and shape of the yolk-sac larvae are different from sardine eggs, their movement is still to a large degree determined by the current. Hare et al. (1999) treated the individuals in the yolk-sac larva stage as passive drifters when modelling the vertical position for Menhaden (*Brevoortia tyrannus*) and Spot (*Leiostomus xanthurus*) larvae. Because this stage is also relatively short compared to the following larval stages it was thought reasonable for individuals in the yolk-sac stage to be transported as Lagrangian particles, like the eggs.

While using observed initial egg distributions and Lagrangian transport for eggs and yolk-sac larvae produced adequate vertical distributions of individuals during these stages (VP Exp. 3), it did not enable the generation of vertical distribution patterns significantly similar to observed early or late larvae distributions. The early and late larva stages are each longer at any given temperature than both the egg and yolk-sac stages combined (Chapter 4). During these long stages Lagrangian particles are transported too deep. Vertical distributions of sardine larvae have been observed in the Northern Benguela (Stenevik et al. 2003), Southern Australia (Fletcher 1999) and in the Northwestern Mediterranean (Sabatés 2004) among others, but no data on the vertical distribution of sardine larvae exist in the southern Benguela ecosystem. The fundamental assumption made in this chapter is that individuals display vertical distribution patterns specifically adapted to the current and turbulence regimes of the ecosystem in which they live in order to obtain some adaptive advantage. Hence, observed anchovy larvae vertical distribution patterns in the southern Benguela ecosystem were used for comparison and for setting vertical positioning schemes for sardine larvae, rather than using observed sardine distributions from another ecosystem. At this young stage sardine and anchovy larvae are similar in size and presumably their swimming ability (C. D. van der Lingen, Marine and Coastal Management, pers. comm.). Hence, it was considered reasonable to assume that sardine and anchovy larvae would display similar patterns of vertical movement in the early and late larva stages.

Post yolk-sac larvae are observed to display Type 1 DVM, and there is an absence of individuals in the top 20m of the water column during the day in both the early and late larva stages. Peak frequencies of late larvae are found slightly deeper than early larvae (30-40m and 20-30m respectively) possibly because swimming ability increases as larvae develop. The late larva vertical distribution pattern is distinctly bimodal because of this clear-cut difference in day and night distributions and their great range of movement. The early larva vertical distribution has a clear peak from the daytime distribution, a lesser peak at the surface during the night and individuals are generally spread through the water column. Using the individual repositioning scheme required increased temporal interpolation in order to accurately divide up the amount of time each individual spends at each depth. Increasing the number of iterations per time step allows for more frequent vertical positioning of particles within a single day to more accurately represent the individuals' pathways through the water column. This created modelled vertical distribution patterns very similar to observed distributions and was found to be the most accurate way of vertically positioning both early and late larvae.

The light mediated vertical positioning scheme, while producing fairly similar vertical distribution patterns (especially for the late larva stage), was not found to significantly reproduce observed larva distributions. This may be because of the number of assumptions that were made in order to simplify this model. Firstly, it was assumed that DVM is controlled solely by changes in light intensity. While this is commonly reported as a cue for vertical movement of the larvae of planktonic taxa, numerous other factors are likely to moderate this process. It also assumes that individuals are always physically able to move to the expected depths. Observed late larva vertical distributions were similar to those predicted using the light mediated scheme. However, it appears that the limited swimming ability of early larvae means that they are not able to follow a light mediated pattern, as can be seen in the vertical spread of individuals. It is also possible that, because early larvae are small, they are less at risk from visual predators and therefore are less compelled to position themselves deeper, and consequently at lower light levels, so as to reduce the risk of predation. One aspect in which the light mediated vertical positioning scheme is superior to the individual re-positioning scheme is that vertical positions are determined according to a process rather than observations that were spatio-temporally limited. This allows for a more realistic representation of the actual movement of each individual down or up the water column, whereas the individual re-positioning scheme assumes that larva distributions observed at one haul are representative of larva positions throughout the day or night.

The spatial and temporal patterns of modelled recruitment did not change notably with the inclusion of vertical positioning of individuals compared to previous experiments (Chapters 3 and 4). In the WAB/WC-WC system modelled recruitment was high from both inshore and offshore spawning areas. The seasonal pattern of spawning became more important in determining modelled recruitment in the CAB-WC system in the absence of the *Depth* variable. Modelled recruitment was significantly highest between September and November and this corresponded with the time when individuals from the CABoff were least likely to recruit to the south coast. This indicates that success depends largely on westward movement across the Agulhas Bank rather than temporal changes in transport to the west coast or avoiding offshore loss there. There is very little onshore movement from CABoff. Because most westerly movement across the Agulhas Bank occurs at the offshore edge (Boyd and Shillington 1994) this explains why retention on the south coast is lowest from this spawning area. Modelled recruitment in the SC-SC system was virtually unaffected by vertical positioning; this was expected because *Depth* was shown previously (Chapter 4, Table 4.6) to have little effect on retention success here.

Interannual modelled recruitment anomalies were affected more by vertical positioning in the WAB/WC-WC and SC-SC systems than in the CAB-WC system. Mean annual recruitment values in the former two systems have very small ranges making anomalies more sensitive to small changes in the level of modelled recruitment. These changes have not significantly increased the correlation between modelled recruitment and observed back-calculated recruitment. The increase in modelled recruitment in the SC-SC system in 1991/92 and the location of eggs on the EAB during this year contradicts the negative back-calculated recruitment anomaly. The decrease in modelled recruitment in the WAB/WC-WC system for 1993/94 and the increase in 1994/95 when most eggs were located on the west coast could now explain the negative and positive back-calculated recruitment anomaly experienced in those years, respectively. However, modelled recruitment in the last two years of the time series can still not explain the negative recruitment anomalies, despite a negative SC-SC system modelled recruitment anomaly in 1997/98. In that year the majority of eggs found were on the UWC and that region showed the highest modelled recruitment in the WAB/WC-WC system that year, which should have enhanced recruitment success.

The reduced levels of Lagrangian transport to the assumed optimal sub-nursery areas compared to other sub-nursery areas (results not shown here) indicate that passive transport alone is not likely to allow larvae to reach the areas considered optimal for successful recruitment. Active behaviour by larvae (e.g. current selection through diel migration) was thought to be a possible mechanism for increasing access to the WCin and SCoff sub-nursery areas. However, results showed that there was no great improvement in modelled recruitment to the WCin sub-nursery area except from the WAB spawning area in the WAB/WC-WC system, and in the CAB-WC system. Modelled recruitment was slightly higher using vertical positioning schemes compared to Lagrangian transport possibly because individuals from these two areas spend more time in the late larva stage before recruiting (age at recruitment exceeds development time to the late larva stage, Chapter 4). Late larvae are found frequently between 20 and 40m, which is thought to be the best depth for transport to the west coast nursery area in the Cape Columbine jet current. Results indicate that the vertical positioning of individuals on the CAB only decreases the westward transport of individuals during January and February, corresponding to the period of reduced observed spawning activity between the September-October and February-March peaks. This suggests that the observed temporal spawning pattern of sardine on the CAB is adapted to increase transport to the west coast nursery area. On the south coast there was found to be very little offshore movement. A lack of eastward transport of individuals released on the CABin area resulted in very high levels of retention in the SCin area but very low modelled recruitment to the SCoff area. There is high retention over the cool ridge (SCover) from the EABin spawning area, a result of a large overlap between these two areas and little offshore loss from the inshore section of the EAB. The EABoff spawning area was the only area that had high levels of modelled recruitment in the SCoff sub-nursery area. This indicates that the cool ridge may act as a barrier against cross-shelf transport in this area and may explain why the majority of spawners observed on the EAB are found along the edges of the continental shelf (Hutchings et al. 2002).

DVM has been identified as a possible mechanism for regulating transport to favourable areas (Bakun 1996b, Hare et al. 1999). The results presented here indicate that the observed pattern of DVM in the southern Benguela is not adapted exclusively to increase levels of retention and transport of larvae. Stenevik et al. (2001, 2003) found that in the Northern Benguela ecosystem the vertical behaviour of sardine larvae was one of the factors preventing loss from the nursery grounds and it was expected that this too would be the case in the WAB/WC-WC system. However, the only improvement in transport of individuals was from the WAB and CAB to the west coast. Jenkins et al. (1999) also found that observed vertical behaviour did not influence transport of post larvae of demersal fish in Port Phillip Bay, Australia, which were found closer inshore than expected, possibly due to behaviours other than vertical migration. Model results suggest transport to optimal sub-nursery areas is not the reason for DVM and other factors must be more important determinants.

The adaptive advantages of DVM can also not be attributed to any one factor or benefit, and DVM is often seen as a trade off between predator avoidance and net energy gain (Lambert 1993). Surface waters often have high food concentrations and warm temperatures that together promote energetic activity but they also have an increased risk of predation by visual predators during high light intensities in the daytime. De Robertis (2002) tested this hypothesis by using a trade-off model to minimise the ratio of predation risk to energy gain and found that it results in size-dependent timing of DVM based on the diel vulnerability of individuals to size-selective predators and the potential for net energy gain in the food-rich surface waters. Anchovy (and presumably sardine) larvae in the southern Benguela ecosystem show DVM, but despite some incidental increase in transport of individuals to optimal nursery areas, it is apparent that this is not an effective means of targeting preferred nursery areas. Hence, observed vertical movement of larvae in the southern Benguela ecosystem appears most likely to be a trade-off between predation risk and food requirements or energetics.

The spatial and temporal resolution of model flow fields and difficulty in applying both theoretical and empirical buoyancy and DVM schemes makes the implementation of accurate vertical positioning models problematic. Cross-shelf transport in upwelling areas changes greatly, in magnitude and direction, over short periods. Upwelling is the main driver behind this, not only in terms of offshore Ekman transport during upwelling events but also in terms of strong onshore flow during relaxation events, and larvae may use this strong onshore flow to reach the inshore nursery area (C. D. van der Lingen, Marine and Coastal Management, pers comm.). The weekly forcing used in the PLUME hydrodynamic model does not allow for these small-scale temporal changes in current velocity, and the temporal interpolation of 3-D hydrodynamic output data makes the implicit assumption that there is no diel effect on the current field. However, it is likely that diurnal differences in the thermal flux could affect vertical turbulent mixing and this could significantly impact simulated vertical distributions, though it is not likely that this would affect inshore/offshore transport (P. Fréon, Institut de Recherche pour le Développement, pers comm.). Other possible diurnal effects could be changes in the wind field (e.g. land and sea breezes). However, off the South African coast the overwhelming wind force is generated by large high and low pressure cells (which change location seasonally) that override smaller scale winds in this system. DVM patterns according to tidal flow are commonly incorporated in models of transport for nearshore plankton such as the pelagic phase of sessile rocky shore species (e.g. Eastern oyster, Dekshenieks et al. 1996) or larvae utilising estuarine habitats (e.g. Menhaden, Forward et al. 1999). However, tidal forces are unlikely to play a significant role in cross shore transport off the upwelling west coast region or over the broad Agulhas Bank and therefore the lack of tidal flux in the hydrodynamic output is unlikely to affect transport of particles representing sardine eggs and larvae in this system.

Comprehensive data on the vertical distribution of eggs during different stages of egg development were available. This allowed for the implementation of an empirical egg vertical positioning scheme that could be shown to confidently reproduce observed egg distributions making theoretical schemes to model this stage redundant. In the case of larvae there are a large number of different factors that are likely to shape DVM patterns and the relative importance of these factors are likely to differ spatially and temporally. This makes the modelling of this process particularly difficult. The empirical approach used here was effective because the experiment aimed to examine the effect of DVM on the transport and retention of individuals rather than attempting to explain the reasons behind it. However, more comprehensive data on vertical distributions of sardine larva at different times and across the large spatial domain of their distribution would allow for a more accurate implementation of this scheme and increase the confidence in the model results.

CHAPTER 6: IMPLICATIONS OF SIZE STRUCTURE AND SPATIAL DISTRIBUTION OF THE SOUTHERN BENGUELA SARDINE SARDINOPS SAGAX *STOCK ON MODELLED RECRUITMENT, 1991-1999*

ABSTRACT

The spatial distribution and size structure of the sardine (*Sardinops sagax*) spawning stock in the southern Benguela ecosystem is presented for the period July 1991- June 1999. Small spawners (14-18cm) predominated (>50%) and large spawners (≥21cm) were rare (<10%), and whilst few fish longer than 18cm were found on the central Agulhas Bank, the eastern Agulhas Bank had the greatest proportion of large spawners. Few spawners were found on the west coast and spawning appeared to be centred on the western Agulhas Bank during the period examined. A simple size-based fecundity model is used to quantify reproductive output from each spawning area. Potential reproductive output increases substantially with fish length. The effect of spatial variation in sardine reproductive output on observed recruitment and interactions of this spatial variation with modelled recruitment in the two nursery areas (west and south coast) are examined by correlation analysis. Simulations suggest that nearly two thirds (62.5%) of the potential reproductive output produced by the sardine spawning stock reaches the west coast nursery area, but estimated recruitment does not correlate with the proportion of reproductive output reaching the west coast nursery area. However, recruitment was low in years when spawning is centred east of Cape Agulhas. In order to have better recruitment estimates, survey cruises need to extend further east than the current design allows.

6.1. INTRODUCTION

It has long been recognized that fish species that display high variability in recruitment often have great longevity (Murphy 1967). It is believed that longevity confers a selective advantage in areas with a high degree of oceanographic variability where reproductive success often depends on matching reproductive effort with short periods of suitable conditions (e.g. matching the time of first feeding of larvae with the availability of a suitable food supply such as plankton pulses in upwelling ecosystems). The importance of this evolutionary adaptation in fish life histories is increasingly being recognised, and numerous researchers (e.g. Longhurst 2002, Berkeley et al. 2004b, Birkeland and Dayton 2005) are beginning to conclude that longevity may be a crucial factor in sustaining recruitment of fish populations.

A direct implication of longevity is an increased number of age-classes within a fish stock. The age structure of a fish stock is essentially the number of age classes and the relative abundance of each age class, the latter being a function of mortality and the strength of recruitment for each year. In many fish stocks there are age-related differences in the timing and location of spawning (Berkely and Houde 1978, Lambert 1987, Hutchings and Myers 1993). Also, not all fish produce eggs with an equal chance of survival (Palumbi 2004), and in many cases old fish produce larvae that are more viable than those produced by their younger counterparts (Hislop 1988, Marteinsdottir and Steinarsson 1998). Houde (1987) noted that small changes in the survival probabilities of larvae could have substantial effects on the probability of successful recruitment, hence it appears likely that stock age structure will have implications for recruitment and therefore fisheries management (Aubone 2004).

Numerous studies have been done examining the effect of fish size/age on the quantity and quality of eggs and larvae produced. It is well known that fecundity increases with both fish length and weight (Weatherley 1972, Wootton 1990), both of which generally increase with fish age. In the case of batch spawners, overall fecundity is a function of the number of eggs per batch, the length of the spawning season and the frequency of spawning during this season. All three of these have been shown to increase with age for a number of different species e.g. herring *Clupea harengus* (Lambert 1987), haddock *Melanogrammus aeglefinus*

(Hislop 1988), sardine *Sardinops ocellatus* (now *Sardinops sagax*) (Le Clus 1988, 1989), Atlantic cod *Gadhus morhua* (see Kjesbu et al. 1996, Bleil and Oeberst 1998, Solemdal et al. 1998, Trippel 1998 and references therein), and black rockfish *Sebastes melanops* (Bobko and Berkeley 2004). Wright et al. (1999) suggested that an additional benefit of the long spawning season of old age-classes is a likely reduction in the risk of poor recruitment, due to the increased likelihood of matching reproductive output with suitable environmental conditions.

In addition to these quantitative increases in reproductive output, old/large fish have been shown to produce better quality eggs than young/small fish and larvae that have a higher probability of survival and therefore recruitment. Atlantic cod have been well studied in this regard. It has been found that egg size increases with spawner age (Kjesbu et al. 1996, Trippel 1998) and that large larvae (generally from large eggs) at the onset of feeding are more likely to survive than smaller larvae (Kjesbu et al. 1996). Valin and Nissling (2000) confirmed that larval viability was positively related to female size/age but found no significant relationship between larval viability and egg size. Solemdal et al. (1998) showed that the incidence of malformations of developing cod embryos is substantially higher for recruit (first time) spawners than for repeat spawners. Trippel (1998) further concluded that recruit spawners' eggs exhibited lower fertilization and hatching rates (13%, compared to 62% of repeat spawners' eggs) and their larvae were less likely to hatch in environmental conditions favourable for survival. Considering all these size/age effects, Cardinale and Arrhenius (2000) used a general additive model (GAM) approach to assess important influences on cod recruitment. They found that young spawners' eggs only had a positive impact on recruitment at very high quantities whereas older spawners' eggs had high positive effects at low levels of reproductive volume leading Cardinale and Arrhenius (2000) to conclude that the number of cod recruits is strictly dependent on the age structure of the population. Similar increases in larval quality with fish size/age have been shown for haddock (Hislop 1988), winter flounder *Pseudopleuronectes americanus* (Buckley et al. 1991) and black rockfish (Berkeley et al. 2004a).

Sardine can live as long as ten years (C.D. van der Lingen, MCM, pers. comm.) and therefore the sardine population in the southern Benguela ecosystem contains a number of age classes. This makes sardine stock size less dependent on recruitment than the shorter lived anchovy, where 0-year fish make up as much as 70% of the catch for each year (Cochrane et al. 1991, Cochrane and Hutchings 1995). Studies that have been done on sardine in the northern Benguela have shown that both batch fecundity and relative fecundity increased linearly with fish size and age (Le Clus 1988). She also found that old sardine not only have greater batch fecundity than young sardine but also spawn for a longer period over the spawning season and more frequently as well. The total number of spawnings over the spawning season increases by 50 to 70% for each 1cm increase in sardine length (Le Clus 1989), hence older sardine contribute disproportionately more to the total reproductive output spawned over the season than do younger sardine, and this could be important in affecting recruitment.

In the southern Benguela the different age classes of sardine vary not only in terms of their reproductive ability but in their distribution patterns as well. New sardine recruits tend to remain on the west coast or western Agulhas bank (WAB), and gradually move eastwards towards the central Agulhas Bank (CAB) as they age. They then either spread eastward along the eastern Agulhas Bank (EAB) or west and northward along the WAB and up the west coast as they near maximum age (Barange et al. 1999, Fig. 6.1). Those authors noted that this results in a separation of spawners (fish longer than 14cm) at Mossel Bay on the CAB, which becomes particularly clear among the oldest sardine (>21cm; Fig. 6.1).

Clearly, it is highly likely that the age structure of the sardine stock has implications for recruitment success and also the importance of different spawning areas. Numerous studies have been done on quantitative and qualitative effects of age structure on recruitment (see above) and temporal changes in stock reproductive potential (e.g. Scott et al. in press). In this chapter, the spatial effects of the quantitative differences in stock reproductive potential due to the age structure and distribution of sardine, and how these interact with modelled recruitment, are examined. The age structure and distributions of different size classes in the sardine population for each year of the model time series are presented. Barange et al. (1999) presented average distributions of size classes over 12 years (1984-1996) but did not examine interannual variation in distributions. The relative importance of each spawning area will be determined by considering quantitative differences in potential reproductive output inferred from age-structure and levels of modelled recruitment to each nursery area, and by comparing the potential reproductive output reaching each nursery ground and how this relates to

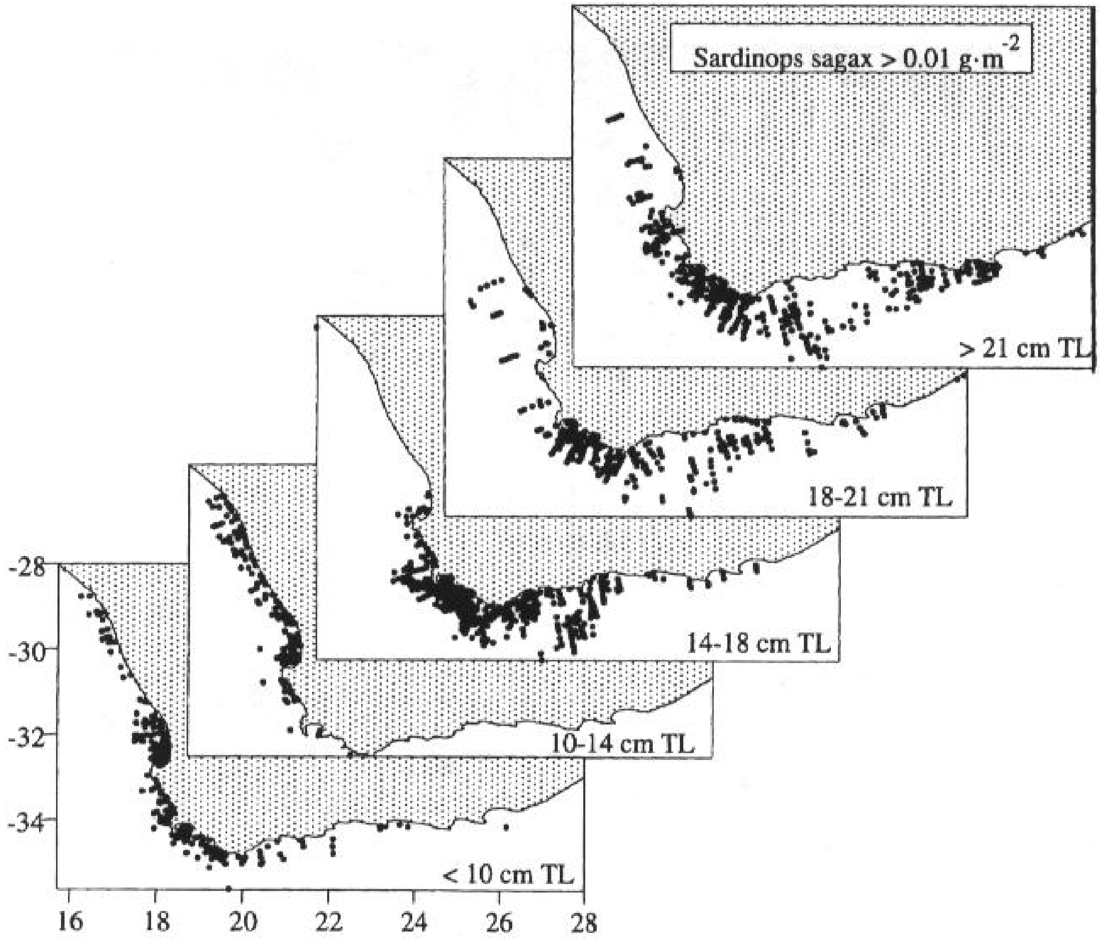

Fig. 6.1: Distribution patterns of five length classes of sardine derived from all hydroacoustic and midwater trawl surveys in South Africa over the period 1984-1996. Dots represent localities where sardines are present at densities above a threshold value of 0.01 g.m^{-2} (from Barange et al. 1999)

estimated (back-calculated) recruitment levels. Spawner location will also be related to estimated recruitment. It is hypothesised that when most reproductive output is transported to the west coast nursery area recruitment is likely to be higher.

6.2. METHODS

Spawner biomass surveys have been conducted annually since 1984 during the early summer (November) by Marine and Coastal Management of the Department of Environmental Affairs and Tourism, since 1984 (Barange et al. 1999). Cruises extend from Hondeklip Bay on the west coast to Port Alfred on the south coast (although in 1992 and 1994 surveys only extended as far as Algoa Bay) (Fig. 1.1). Data on the abundance and distribution of adult sardine are collected from hydroacoustics, details of which can be found in Hampton (1987) and Barange et al. (1999). Trawl samples are used to identify acoustic targets and determine length frequency distributions. Acoustic and trawl data from these surveys were obtained from Janet Coetzee (Marine and Coastal Management, Department of Environmental Affairs and Tourism).

The distribution of the sardine spawners was divided into five strata corresponding to the spawning areas used in the IBM experiments (combining inshore and offshore areas when such a separation was previously made):

1. Upper west coast (UWC) – Hondeklip Bay to Cape Columbine.
2. Lower west coast (LWC) – Cape Columbine to Cape Point.
3. Western Agulhas Bank (WAB) – Cape Point to Cape Agulhas.
4. Central Agulhas Bank (CAB) – Cape Agulhas to Mossel Bay.
5. Eastern Agulhas Bank (EAB) – Mossel Bay to Port Alfred.

Size structure was used as a proxy for age structure due to data constraints. For plots of size structure, three different size classes, the same as those used by Barange et al. (1999), were used: small (14-18cm), medium (>18-21cm) and large (≥21cm). These correspond to age classes of roughly one to two years old, two to three years old and more than four years old, respectively.

The relative reproductive output for sardine spawners was calculated based on the results of Le Clus (1988, 1989). An assumption of deterministic spawning is made for this experiment. Total fecundity was considered as a product of the average number of batches per season and the average number of eggs per batch, both of which increased with fish length (exponentially and linearly, respectively). It was estimated that spawner fecundity would increase exponentially by 64% for each 1cm increase in length up to 25cm, the longest fish reported. Relative reproductive output was calculated as the number of eggs produced relative to that of a 14cm (first time) spawner:

$$RRO_l = 1.64^{l-14} \tag{6.1}$$

Where:

RRO_l = Relative reproductive output of a fish of length l
l = fish length (cm)

Relative reproductive output was used to determine the proportion of reproductive output coming from each stratum for each year, using equations 6.2 and 6.3.

$$RO_{S,y} = \sum_{l=14}^{25} n_{S,l,y} RRO_l \times PS_{S,y} \tag{6.2}$$

Where:

$RO_{S,y}$ = Reproductive output of stratum S in year y
$n_{S,l,y}$ = Proportion of the fish in stratum S that are length l in year y
$PS_{S,y}$ = Proportion of the total number of spawners that are found in stratum S in year y

Then:

$$PR_{S,y} = \frac{RO_{S,y}}{\sum_{S=0}^{4} RO_{S,y}} \times 100 \tag{6.3}$$

Where:

$PR_{S,y}$ = Percentage of reproductive output in year y from stratum S
Strata 0 to 4 = UWC, LWC, WAB, CAB and EAB

The relative contribution of each spawning area (stratum) to potential reproductive output that successfully recruited (i.e. were transported to, or retained in, the west coast nursery area or the south coast nursery area) was determined by combining these $PR_{S,y}$ values with mean transport/retention success from each spawning area to each nursery area (equations 6.4, 6.5 and 6.6). No new simulations were performed; instead this experiment modifies the results from the optimal transport model from the vertical distribution experiment (Chapter 5). Mean modelled recruitment values from each spawning area to each nursery area between August and March (main spawning season) were used.

For each year (*y*):

$$RC_{S,N,y} = PR_{S,y} \times T_{S,N,y} \tag{6.4}$$

Where:

$RC_{S,N,y}$ = Reproductive contribution of stratum *S* to nursery area *N* in year *y*

$T_{S,N,y}$ = Transport/retention success between stratum *S* and nursery area *N* in year *y*

N = west coast or south coast nursery ground

Then:

$$CTR_{S,y} = \frac{RC_{S,WC,y} + RC_{S,SC,y}}{\sum_{S=0}^{4} RC_{S,WC,y} + \sum_{S=0}^{4} RC_{S,SC,y}} \tag{6.5}$$

Where:

$CTR_{S,y}$ = Contribution to total potential recruitment from stratum *S* in year *y*

Or:

$$CR_{S,N,y} = \frac{RC_{S,N,y}}{\sum_{S=0}^{4} RC_{S,N,y}} \tag{6.6}$$

Where:

$CR_{S,N,y}$ = Contribution to the potential recruitment in nursery area *N* from stratum *S* in year *y*

An index of spawner location was derived from the spawner distribution data to test if the location of spawners had an effect on the level of sardine recruitment. This location index represented the centre point either side of which 50% of the spawners were located. It ranged from 0 (northern edge of UWC) to 1 (eastern edge of EAB). This was correlated with relative recruitment, calculated as the recruitment for year *x* divided by the spawner biomass for year *x-1* (van der Lingen et al. 2002).

The back-calculated recruitment anomaly was correlated with the contribution of the west coast nursery area to total recruitment for each year.

6.3. RESULTS

The size structure of the sardine spawning stock fluctuated greatly over the eight years of the time series (Fig. 6.2), but small (14-18cm) spawners accounted for more than 50% of the spawning stock for all years except 1995/96. In 1992/93 and 1996/97 small spawners accounted for more than two thirds of the entire spawning stock. Conversely, large (≥21cm) spawners never exceeded 10% of the total number of spawners. Hence, the major fluctuations in size structure are due to shifts in the relative amounts of small and medium (>18-21cm) spawners.

The WAB was the favoured spawning ground for sardine over the period 1991-1999 (Fig. 6.3), with more than a third of the spawning stock over the eight years was found in this stratum (more than the two west coast strata combined). Few spawners, although not a negligible amount, are found on the west coast and the majority of these are in the medium to large size classes. The small spawners are spread evenly over the three Agulhas Bank strata. Most of the medium spawners are found on the WAB, but the greatest proportion of large spawners is found on the EAB. For only two of the years (1993/94 and 1998/99) were more spawners located east than west of Cape Agulhas (Fig. 6.4). The proportion of spawners either side of Cape Agulhas fluctuates a lot as the location of spawners seems to shift every year. The location of spawners each year seems unrelated to the location of spawners the previous year.

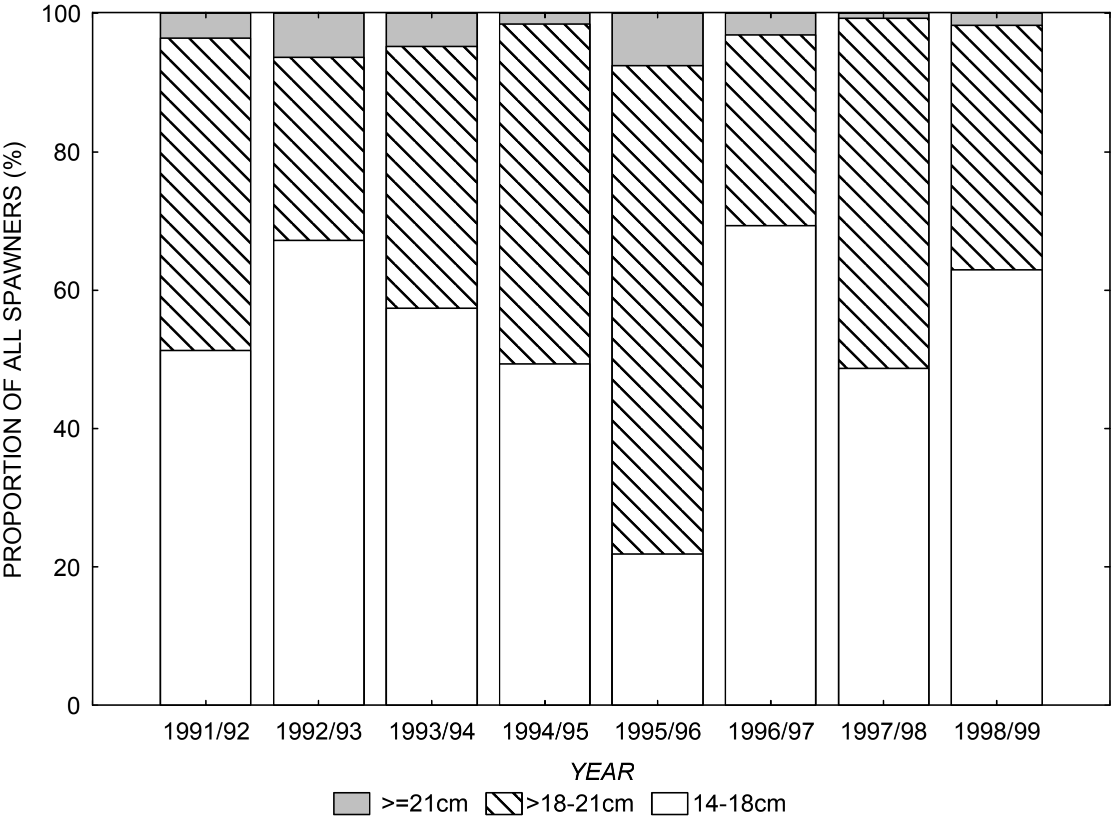

Fig. 6.2: Size structure of the southern Benguela sardine spawning stock, 1991-1999

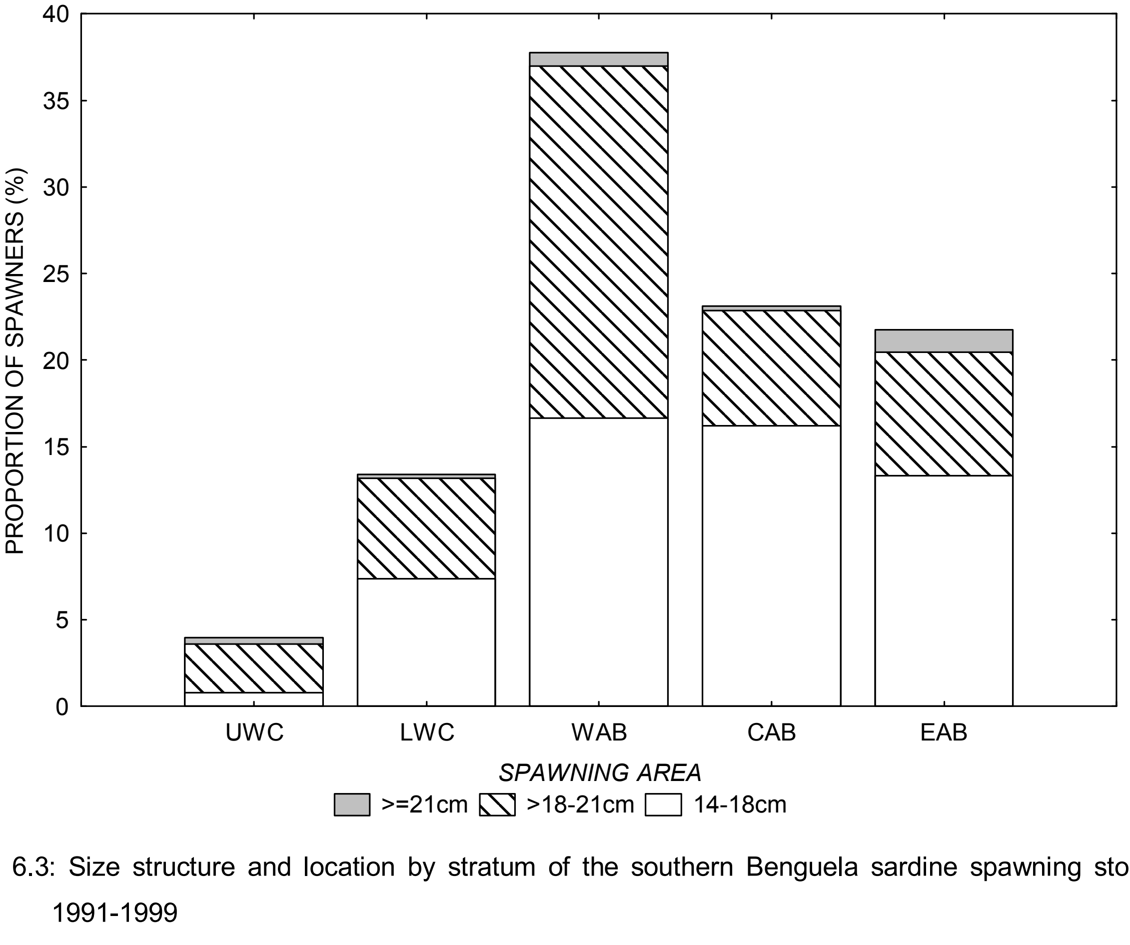

Fig. 6.3: Size structure and location by stratum of the southern Benguela sardine spawning stock, 1991-1999

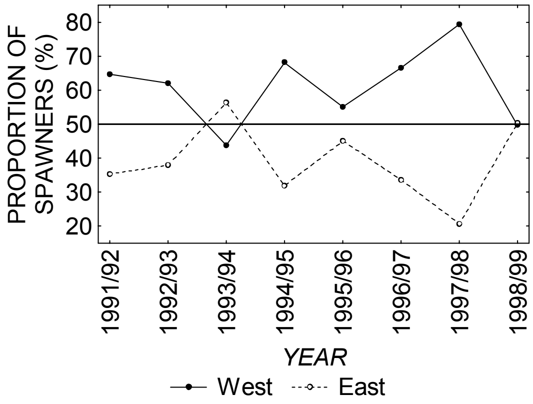

Fig. 6.4: Location of the sardine spawning stock in relation to Cape Agulhas

Fig. 6.5 shows the size structure and location of spawners by stratum for each year of the time series. No fixed patterns in either the distribution of spawners or the size structure for each stratum are apparent in the data, although the WAB has consistently more than 25% of the spawning stock each year. Over the period 1995-98 more than half of all spawners were located in this stratum. The UWC has the fewest spawners for all years except 1996/97, and very few small spawners are found here. The LWC shows a general decline in the proportion of spawners from 1991-97 and then shows a slight increase over the last two years. Both the amount of spawners and the size structure on the CAB fluctuate greatly but there are always very few large spawners. Similarly, the proportion of spawners and their size structure on EAB fluctuates notably but all three size classes are found in this stratum in most years when spawners are present.

When these data are combined with modelled recruitment results for the eight years of the time series, nearly two thirds (62.5%), on average, of the potential reproductive output produced by the sardine spawning stock reaches the west coast nursery area ($CTR_{S,y}$, equation 6.5, Fig. 6.6). More than half of this west coast recruitment is from the WAB (54.4%) with the LWC contributing the next largest amount (28.6%). The majority of the reproductive output reaching the south coast nursery ground originates from the EAB (66.9%), and the CAB contributes almost four times as much to potential south coast recruitment than it does to the west coast. The EAB contribution to potential west coast recruitment is negligible.

Fig. 6.7 shows the contribution of each spawning area to the potential recruitment in each nursery area ($CR_{S,N,y}$, equation 6.6) for each year of the time series. There is a very sporadic occurrence of spawners on the UWC, and the contribution of this spawning area to potential recruitment on the west coast appears to be strongly linked with the proportion of spawners

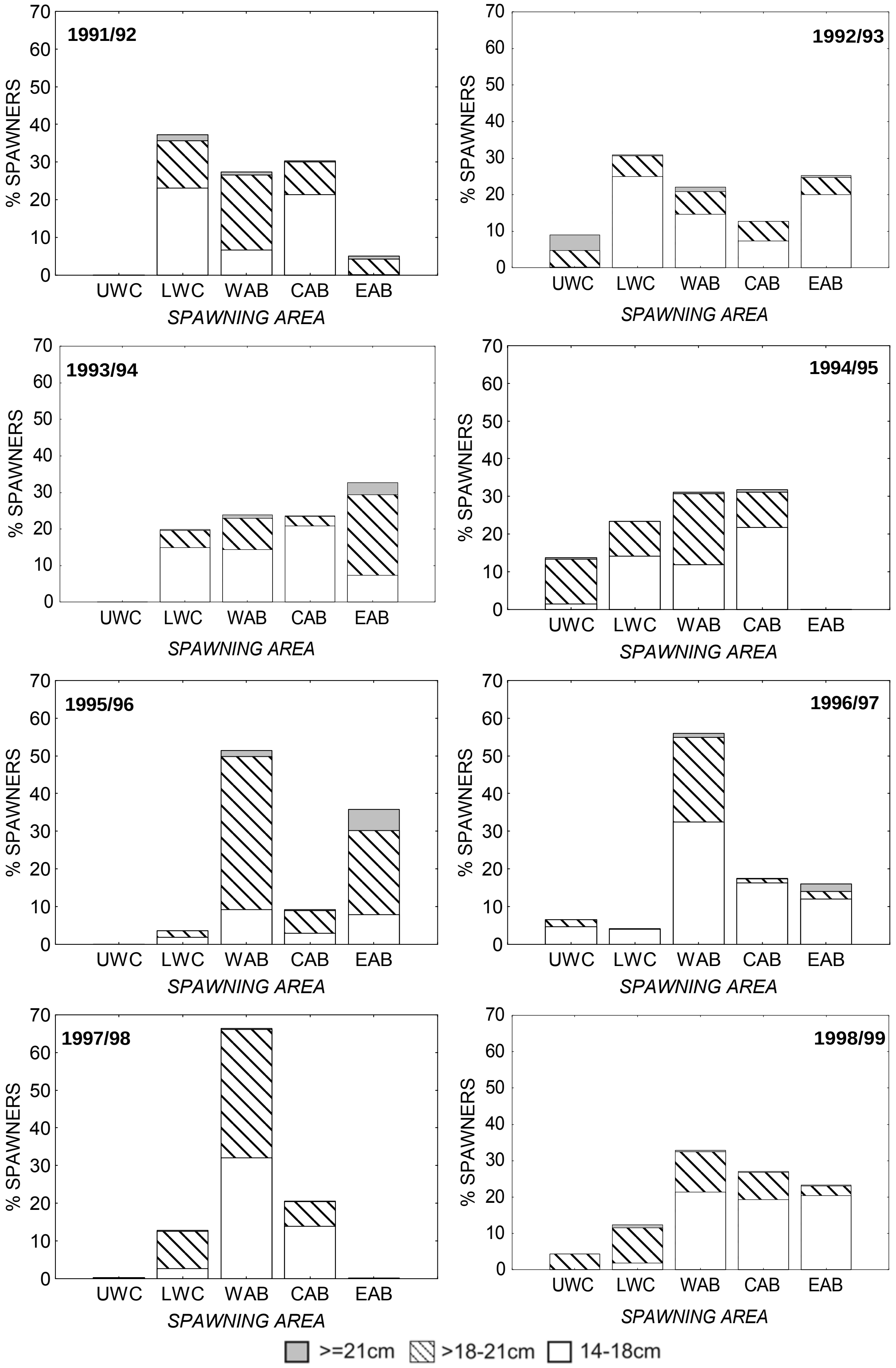

Fig. 6.5: Size structure and location by stratum of the southern Benguela sardine stock for each year of the time series, 1991-1999

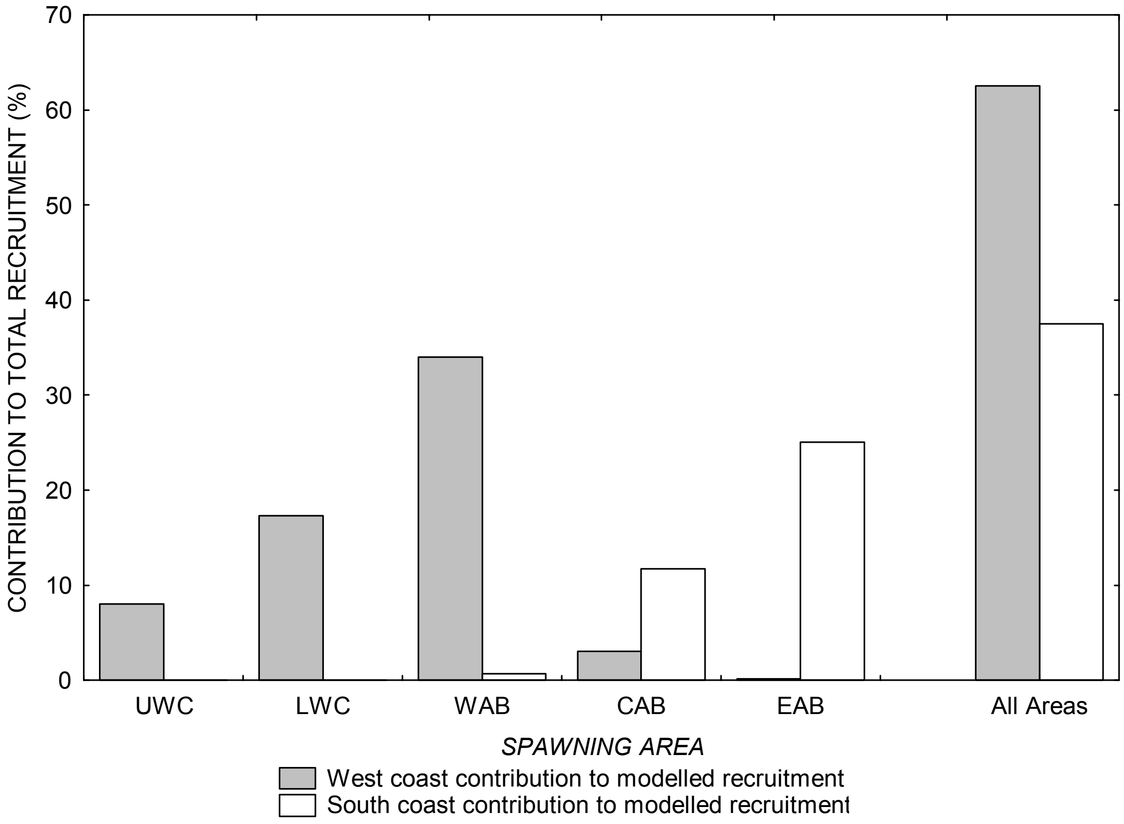

Fig. 6.6: Contribution to the total potential reproductive output (modelled recruitment) to each nursery area from each spawning area ($CTR_{S,y}$, equation 6.5)

found there, except in 1992/93 when a higher than expected contribution is observed. Spawners are more frequently found on the LWC, but were only present in very small amounts in 1995/96 and 1996/97. The contribution to potential recruitment from the LWC is less closely linked to the proportion of spawners found there. The WAB contributes fairly consistently 40 and 50% on average of the potential recruitment on the west coast, although that area showed a period of substantial contribution (>70%) between 1995 and 1998 and a season of low contribution (1992/93). This appears to be closely related to the proportion of spawners located there. Contribution from the WAB to potential recruitment on the south coast is very low. The contribution to the potential recruitment on the west coast from the CAB area is consistently low (never exceeding 10%), despite large fluctuations in the proportion of spawners found here. The contribution to potential south coast recruitment from the CAB area fluctuates to a much higher degree. Almost all of the potential south coast recruitment in 1994/95 and 1997/98 being derived from the CAB. The contribution to potential west coast recruitment from the EAB is negligible in all years, but the contribution to potential south coast recruitment varies considerably. In 1994/95 and 1997/98 practically

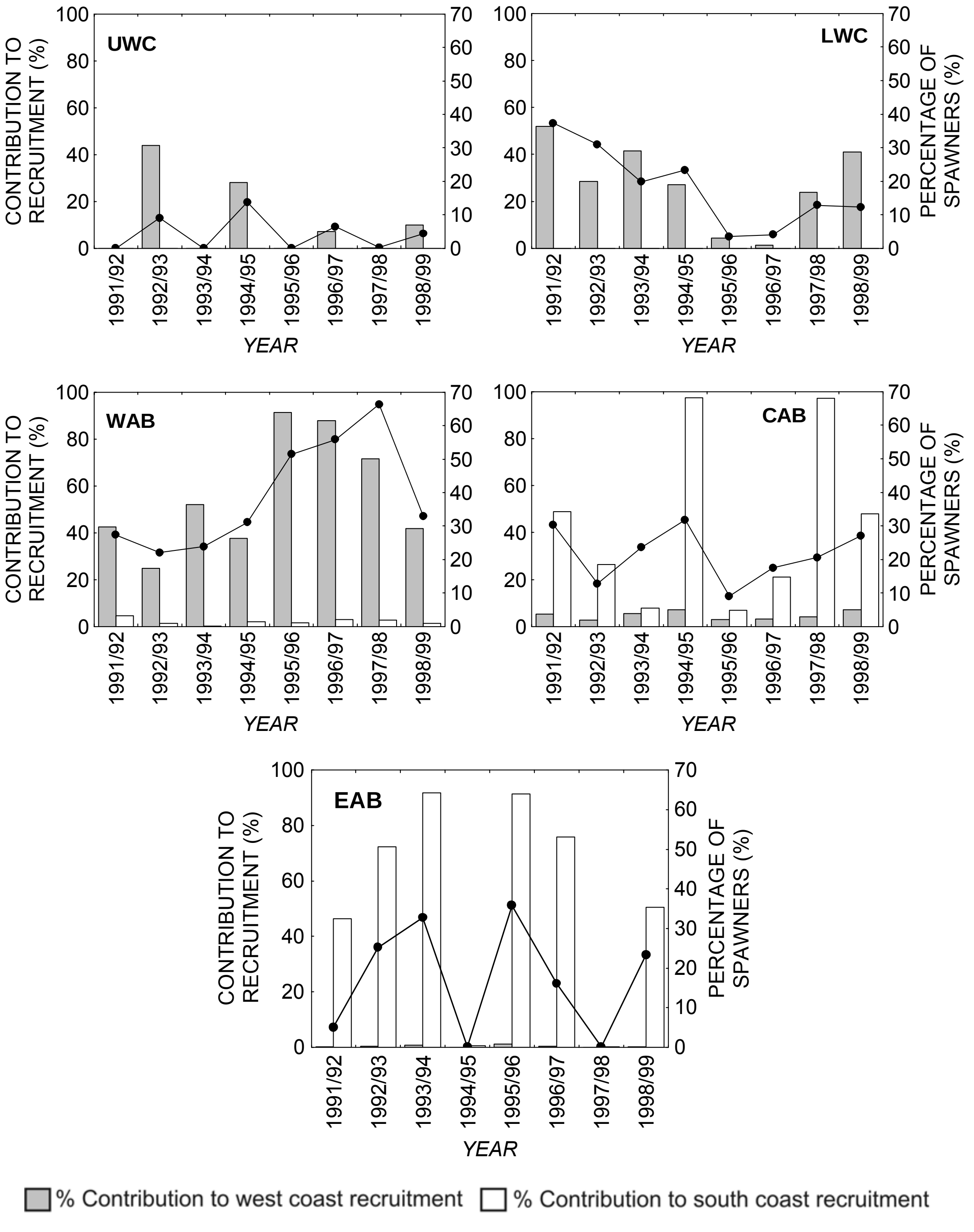

Fig. 6.7: Contribution to the total potential reproductive output (modelled recruitment) to each nursery area over the eight years of the time series for each spawning area. Solid lines show the percentage of the total number of spawners found in each spawning area (CT$_{S,N,y}$, equation 6.6)

no spawners were found on the EAB, and these are the only two years showing less than 40% of the potential south coast recruitment was from the EAB. In most of the other years more than two thirds of the potential south coast recruitment is from this stratum.

A slight negative linear relationship was observed between relative recruitment and spawner location index (Fig. 6.8) though this was not significant (p = 0.14). However, it is clear that relative recruitment is low in years where spawning is centered east of Cape Agulhas, although this was only observed for two years. Relative recruitment is much more variable from spawning centered west of Cape Agulhas, being very high in some years but as low as that east of Cape Agulhas in others. It can also be seen that there is not a great deal of variation in the centre of spawning for the sardine spawning stock with the location index ranging from roughly 0.48 (centre of WAB) to just over 0.65 (just east of Cape Agulhas, the western boundary of the CAB).

The back-calculated recruitment anomaly appears to correspond to the proportion of potential recruitment reaching the west coast nursery area fairly well, particularly for the period 1992/93 to 1996/97 (Fig. 6.9). However, the two are not significantly related (p = 0.2639) when the entire time series is considered.

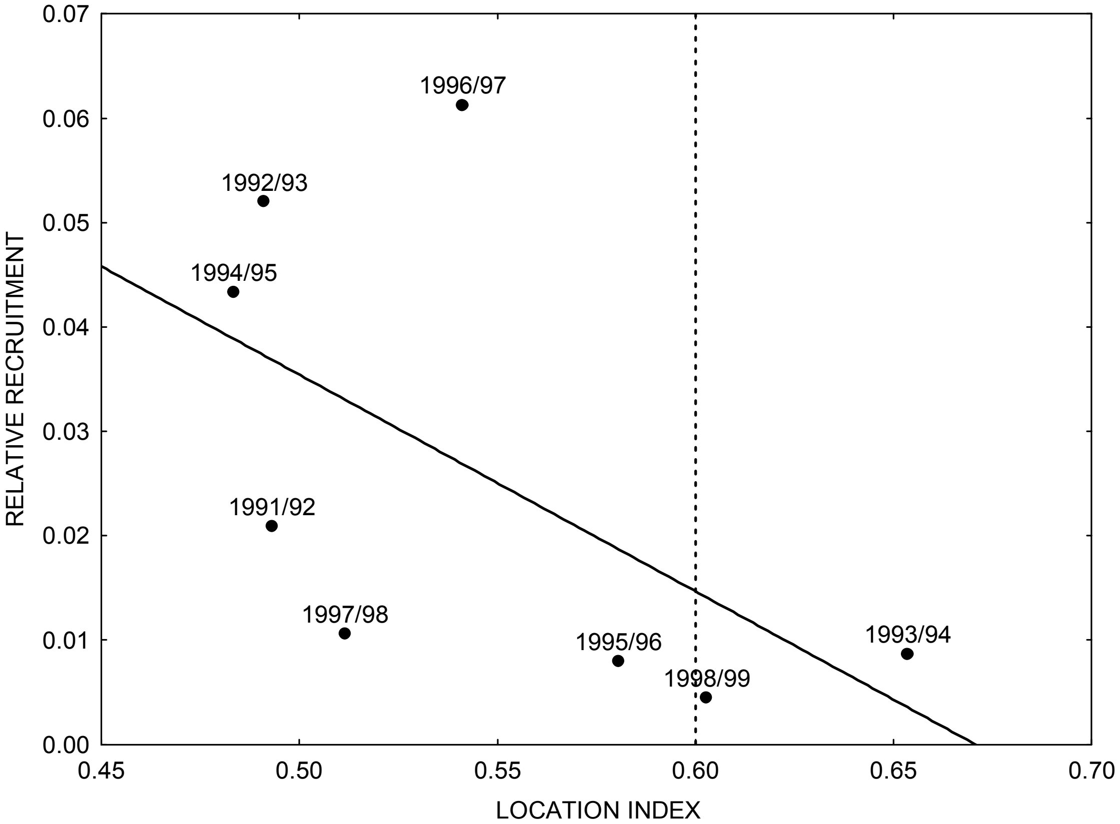

Fig. 6.8: The relationship between relative recruitment and spawner location index. The dotted line represents Cape Agulhas

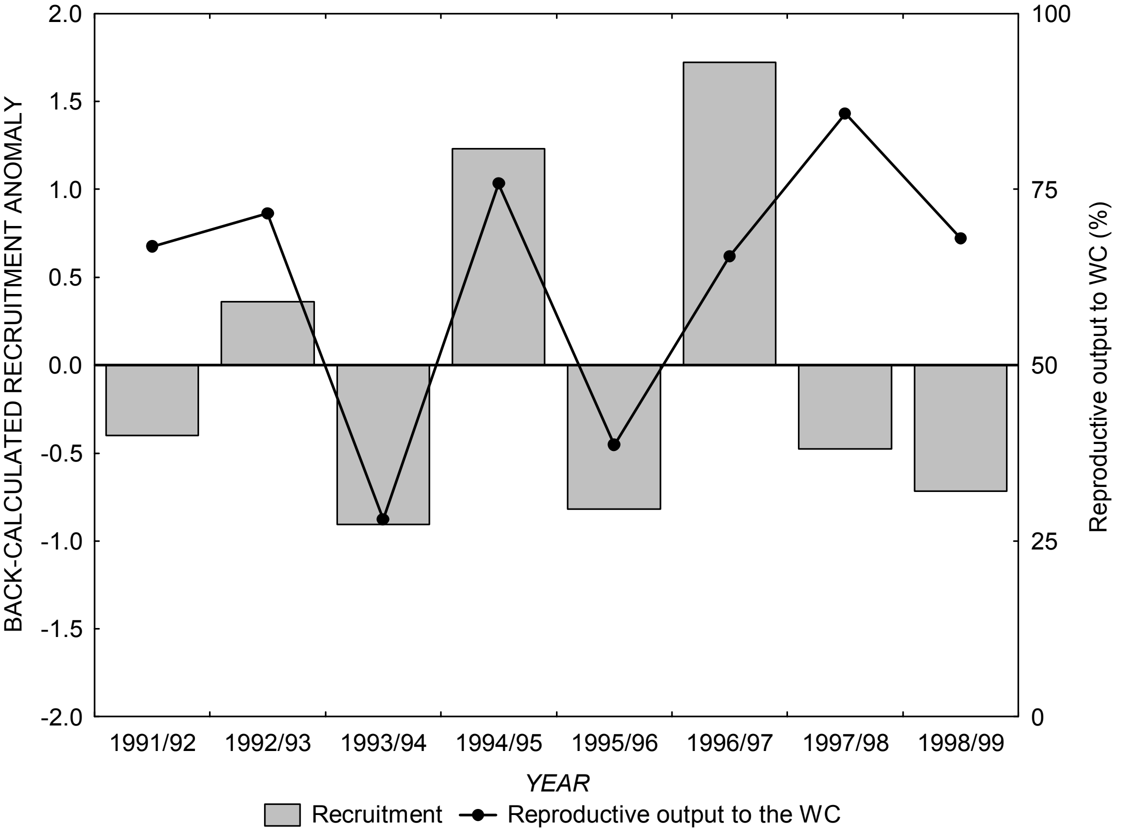

Fig. 6.9: Back-calculated recruitment anomaly (columns) and the percentage contribution of the west coast nursery area to the total recruitment of reproductive output (line plot)

6.4. DISCUSSION

The spatial distribution of the sardine spawning stock in the southern Benguela has been presented for the period 1991-1999, along with the stock size structure by year and area. The results represent the best available data for the region. However, it must be remembered that these observations are derived solely from November spawner biomass surveys, hence the potential changes in the distributions of spawners and size classes during the spawning season cannot be determined. Hence, the assumption has to be made that the distribution of spawners in November accurately represents the distribution of spawners throughout the spawning season. It is also assumed that the size classes chosen represent meaningful divisions. These were the same size classes used in previous studies (e.g. Barange et al. 1999) and are therefore comparable. Using the von Bertalanffy growth equation derived by Baird (1970a), one-year-old fish are found to be roughly 13.2cm in length, growing to 16.6cm the next year. So the chosen size classes include most reproductively active fish, although length at sexual maturity has been shown to change for sardine in the southern Benguela ecosystem (Armstrong et al 1989). First time and young spawners fall into the small (14-18cm) category, whilst repeat spawners are in the medium (>18-21cm) and large (≥21cm) categories.

The time series examined was not long enough to look at age truncation effects of fisheries. To do this properly would require length frequency distributions of landings as well as a benchmark size structure with which to compare current size structure. The fluctuations in relative abundance of each size class observed (Fig. 6.2) are most likely a result of large fluctuations in recruitment. In most years more than half of the spawners were small (i.e. 1-2 year olds) and few were very large. Considering that sardine are believed to live up to 8-10 years of age (Beckley and van der Lingen 1999), this could be an indication that age truncation of the stock has occurred as the result of fishing, but no data of a ‘pristine’ ecosystem state exist with which to make any comparison so no solid conclusions can be drawn.

Results showed that the majority of spawners were located on the WAB (Fig. 6.2) and that most of these were longer than 18cm. This translates to substantial reproductive effort from this area and it appears that the sardine spawning stock favoured this spawning ground over the period examined. The EAB had a higher proportion of large spawners than any other spawning area, but a substantial proportion of small spawners are found there too. Barange et al. (1999) noted that the presence of older fish on the EAB could be the remnants of those that have been along the east coast on the sardine run, when large shoals of medium-sized sardine migrate northwards to the KwaZulu-Natal coast in June or July each year. Despite this the majority of spawners sampled are generally found west of Cape Agulhas (Fig. 6.4).

The location of spawners and the size structure of spawning stock in each stratum changed throughout the short time series (Fig. 6.5). There was no period of relative stability in the spawning stock distribution or size structure of the stock. The separation either side of Mossel Bay for fish longer than 14cm noted by Barange et al. (1999) is clear for fish longer than 18cm but many 14-18cm fish were found all across the Agulhas Bank.

A few assumptions needed to be made to calculate potential reproductive output from each spawning area and potential recruitment to the nursery areas. Modelled recruitment means for August to March only were used, which is considered reasonable because most sardine spawning occurs over this time (Shelton 1986) and both of the two peaks in spawning activity (September-October and February-March) and the month when length frequencies were sampled (November) are included. The assumption of deterministic spawning also implies that there is no spatial or annual variability in the output of eggs. In the Californian system Hunter and Leong (1981) showed as much as 33% of the total egg output in anchovies was supported by current feeding as opposed to accumulated fat stores. This implies that spawners are likely to have improved egg production in better feeding environments. However, in the absence of any spatial indices of production over this time period it is necessary to simplify the model to consider only fish size as the most important determinant of egg production. An exponential increase in fecundity with length was assumed. This is believed to be realistic as it has been reported for numerous fish species before (see Weatherley 1972 and Wootton 1990) and is based on real data (Le Clus 1988, 1989): an 18cm fish produces seven times as many eggs as a 14cm fish, and a 21cm fish produces four times as much as 18cm and more than 30 times as many as a 14cm fish. Hypothesised improvements in egg quality and larval viability with fish size plus the increased likelihood of matching reproductive output with favourable environmental conditions in a variable environment due to a longer spawning season, emphasise the potential importance of large fish to successful recruitment.

The WAB contributes consistently to the potential west coast recruitment because this is an area that has a high level of successful transport to the west coast, lots of spawners and a high proportion of old spawners. Conversely, the UWC contributes far less, and less frequently, due to variable and low numbers of spawners found there from year to year. The LWC contributes less than the WAB to potential west coast recruitment despite similar levels of transport success, because of the smaller number of spawners, which are also generally younger than those on the WAB. The EAB contributes substantially to potential south coast recruitment due to good levels of retention and a high proportion of old spawners. This high proportion of old spawners could also explain why the EAB’s contribution to potential recruitment is consistently high (in years when spawners are found on the EAB) because of the stabilising effect of old spawners in ensuring reproductive output remains high. The CAB contributes very little (3.1%) to the west coast nursery areas mainly because of the lack of large spawners in this area, a clear indication of the importance of the size structure of this stock. However, this area is the source of just over a third of the potential recruitment on the south coast due to the very high levels of retention here.

Discrepancies between the proportion of spawners in a stratum and its contribution to potential recruitment can usually be explained by the size structure. In cases where a greater than expected contribution was made (e.g. UWC 1992/93, LWC 1998/99, CAB 1994/95 and 1997/98, EAB 1991/92 and 1996/97) this is because a greater proportion of large fish or a lesser proportion of small fish were found in that stratum during that year. Conversely, when a less than expected contribution to potential recruitment is made (e.g. LWC 1992/93 and 1994/95, WAB 1997/98) this is due to a lesser proportion of large spawners or a greater proportion of small spawners. Size structure also explains why the contribution to potential west coast recruitment is less closely linked to the proportion of spawners on the LWC than on the UWC because size structure of spawners on the LWC changes more often than on the UWC. In 1994/95 and 1997/98 the CAB contributed more than usual to the modelled south coast recruitment. But, these anomalies are not explained by size structure and are rather the result of spawner distribution. In 1997/98 spawning was localised to a high degree on the WAB with some spawners on the CAB and LWC but negligible amounts on the UWC and EAB. In 1994/95, no spawners were found on the EAB. Therefore, as the EAB usually contributes the most to the potential south coast recruitment, the lack of a contribution from this area during these two years meant that the WAB and CAB between them made up the modelled recruitment there.

No significant relationship between the spawning location index and relative recruitment was found. However, there is an indication of low relative recruitment when spawners are centred east of Cape Agulhas. When this is the case, most reproductive output would be reaching the south coast nursery area. So it appears likely that annual recruitment is more closely linked to potential reproductive output reaching the west coast, an hypothesis supported by Barange et al. (1999) who showed that high abundances of sardine recruits in St Helena Bay corresponded to successful recruitment (and the converse, when few fish were there, recruitment levels were lower). On average, two thirds of the reproductive output over the whole time series reached the west coast nursery area. While the proportion of west coast contribution to potential recruitment was not found to correlate significantly with the back-calculated recruitment anomaly, Fig. 6.9 does show that some relationship exists, as suggested by Barange et al. (1999). But in both 1997/98 and 1998/99 the recruitment anomaly does not relate to the proportion of recruitment to the west coast. 1998/99 was one of the few years when most spawners were located east of Cape Agulhas, so this may explain the discrepancy in that year. However, in 1997/98 the majority of the spawners were on the WAB, and in that year and 1998/99 there were a large proportion of small spawners on the WAB but this was also the case in 1992/93 and 1996/97 and both of these years corresponded with positive recruitment anomalies. However, in 1992/93 and 1996/97 there was also a larger than usual proportion of large spawners but this was not the case in 1997/98 when the lowest proportion of large spawners was found. This would result in an overall reduction in the length of the spawning season that would decrease the likelihood of matching reproductive output with favourable environmental conditions. This may explain the lack of correlation between recruitment anomaly and proportion of potential recruitment on the west coast in 1997/98.

Unfortunately, it is problematic relating modelled recruitment to actual back-calculated recruitment estimates. This is because back-calculated recruitment is estimated from data obtained in the May recruitment surveys. The standard survey area extends from Hondeklip Bay to Cape Infanta, although the eastern extent of these surveys was Wilderness (eastern edge of CAB) in 1996, and Port Alfred in 1994 and 1995 (Barange et al. 1999). Only the surveys in 1994 and 1995 would have accurately captured the impact of south coast retention on recruitment levels (and a sizeable proportion of recruits were found in these areas in those years, although this was not included in the survey estimate of recruitment). Therefore, potentially significant recruitment occurring in the south coast nursery area is often not included in the recruitment estimates. In order to have more comparable recruitment estimates survey cruises would need to extend further east.

It is clear from this brief examination of age/size structure effects that the size distribution of spawners can have a large impact on the level of recruitment and the relative importance of spawning areas. In order for a more thorough investigation to be carried out, monthly estimates of spawner distribution and size/age structure would be necessary to see how these change through the spawning season. High variability in recruitment implies high variability in the relative abundance of each size/age class. This should in turn imply high variability in recruitment unless the older age classes are retained and have a stabilising effect on reproductive output. Therefore the effectiveness of this evolutionary adaptation to variable recruitment is compromised if the age-structure is truncated.

The southern Benguela sardine stock seems to have a constantly shifting spatial distribution through time with no fixed patterns apparent. Only certain features such as the lack of small spawners on the west coast, the lack of large spawners on the CAB and the importance of the WAB seem to persist, at least during the period studied here. It appears that the spatial extent of the sardine stock fluctuates because in some years no spawners were found on the UWC, EAB or both. These are the two extremes of the spawner distribution and the absence of spawners in these areas indicates the restriction of the spawning range for that year. The consistently high numbers of spawners on the WAB indicates that spawning is centred on this region. These fluctuations in distributional range were not related to spawner biomass between 1991 and 1999 (results not shown here), as is the case for anchovy (Barange et al. 1999), so the reasons for this are still uncertain.

The results of this experiment confirm the WAB as the most important spawning area for the southern Benguela sardine stock during the 1990s, that region having the highest contribution to potential recruitment in the favourable nursery west coast area. Therefore, environmental conditions impacting on the survival of eggs and larvae in the WAB and fluctuations in transport success to the west coast will have important consequences for the strength of recruitment. However, the EAB could well prove to be an important subsidiary spawning ground if recruitment to the south coast can be confirmed.

CHAPTER 7 – SYNTHESIS AND DISCUSSION

The southern Benguela sardine (*Sardinops sagax*) stock has a wide spatial range, with well defined hydrodynamic boundaries beyond which it cannot extend. To the north the powerful Lüderitz upwelling cell acts as a physical boundary to stock expansion (Barange et al. 1992) and to the east the tropical waters beyond the KwaZulu-Natal coast cannot support a productive stock. Even at times of low abundance sardine can be found throughout this range. This vast spatial extent, combined with a broad temporal spawning pattern, makes it difficult to understand the strategy of spawning and the mechanisms of recruitment of sardine in this ecosystem. Because most research on pelagic fish in the southern Benguela ecosystem has in the past has been primarily focussed on anchovy, which was the dominant species in the ecosystem from the mid-1960s to the mid-1990s (Moloney et al. 2004), there are limited field observations to confidently explain sardine spawning behaviour and recruitment. This thesis set out to explore a number of hypotheses regarding sardine spawning strategy and recruitment using an IBM-based approach and correlation analyses that could not necessarily be tested with available data. This was done by starting with a simple initial model and slowly adding complexity (using available data insofar as possible), while keeping the focus on the objectives and hypotheses being tested. Additionally, analysis of size-specific distribution patterns of sardine spawners was conducted to examine the effect of increases in potential reproductive output of large spawners. The model results improve understanding of recruitment of sardine in this complex ecosystem, although they need to be compared with field data. Also, the time series examined in the thesis was short and the actual results are specific to the 1990s. While current knowledge and data suggest that there have not been any major changes in oceanographic conditions that are likely to invalidate the results of this model for retrospective or future applications (C.D. van der Lingen, MCM, pers. comm.), a more thorough examination of historical changes in oceanographic conditions would be required in order to address the problem of the long-term generality of this results presented here.

7.1. HYPOTHESES TESTED

The null hypothesis that all sardine recruitment occurs on the west coast (Chapter 3) can be confidently rejected, since results showed that particles could be retained on the south coast in great quantities. The area of spawning was shown to play a pivotal role in determining the destination of spawned eggs, and patterns of transport to and retention in each area did not vary significantly from year to year. This led to one of the major findings of this thesis (Chapter 3): recruitment of sardine in the southern Benguela ecosystem is effectively divided between two closed systems (the WAB/WC-WC and SC-SC systems), separated at Cape Agulhas by the circulation of the region. This agrees with the accepted view of this point as a boundary between the west coast eastern boundary shelf system (Shannon 1985) and the EAB western boundary shelf system (Swart and Largier 1987). There is some transfer between these systems that prevents the separation into two stocks. A small proportion of eggs and larvae spawned on the CAB are transported to the west coast (the CAB-WC system), although very few from the EAB are lost from the SC-SC system. But, while few eggs and larvae are transported eastward to the south coast recruitment ground from the WAB and the west coast, recruits and adult sardine do migrate further east. Within the two closed systems there is no clear seasonal pattern of retention, other than a slight increase during winter. Only the transport of eggs and larvae from the western and central Agulhas Bank to the west coast seems to have an optimal temporal pattern (spring to early summer).

Water temperatures off the west coast are generally colder than those on the Agulhas Bank, since wind-induced upwelling brings cold water to the surface in the inshore regions of the west coast. The null hypothesis of equal development times across the region (Chapter 4) can be rejected because development times on the west coast were found to be longer than those on the Agulhas Bank, arising from cooler water in the former region. This slow development impacts on recruitment of sardine in the WAB/WC-WC system by increasing offshore loss of individuals before they are able to retain themselves in favourable areas. The hypothesis that temperature-induced mortality has no affect on modelled recruitment (Chapter 4) can also be rejected. Direct temperature induced mortality is higher on the west coast than the south coast. In addition to this, the slower an individual develops, the more time is spent in the mortality prone early stages. This increases the importance of transport in this system (i.e. from the WAB to the west coast) and could in part explain the spatial separation of spawning areas (i.e. the WAB) and nursery grounds in this system. Individuals from the western Agulhas Bank take longer to reach the west coast than they take to develop to a stage at which they are able to recruit. Their swimming ability is such that they should therefore be able to avoid offshore loss from the west coast nursery areas, and may even be able to select the favourable inshore arm of the Cape Columbine jet current to get to the productive nursery grounds. Individuals spawned on the west coast are dependent on circulation patterns for retention in this area. Temperature also impacts on preferred depths for spawning and transport of individuals, trading off greater retention at depth with quicker development and lower mortality in the warmer, shallower water.

The ability of eggs and larvae to move is restricted mainly to changing their vertical position; for sardine eggs their shape and density could have an effect on its terminal velocity. However, the model results presented here (Chapter 5) suggest that observed patterns of the vertical distribution of eggs is more a function of the depth at which eggs are spawned and the vertical flow or turbulence in the water column, rather than characteristics of the eggs themselves. This implies that the depth at which sardine spawn can have an effect on the transport or retention of individuals during the egg, and to a lesser extent the yolk-sac larva, stages. Whereas, the hypothesis that the depth of spawning and vertical movement in the water column determine the vertical position of individuals (Chapter 5) must be accepted for the egg stage, observations indicate that it can be rejected for the larval stages of development. Distinct day and night distributions suggest that larvae are targeting different depths in the water column, resulting in observations not matched by passive drifters. Early larvae, which are not as efficient swimmers as late larvae, have less clear patterns of diel vertical migration than late larvae, which position themselves in very specific depth ranges. Current flow at different depths affects the transport and retention of particles in both recruitment systems. Likewise, the null hypothesis that the vertical position of eggs and larvae significantly increases the level of modelled recruitment to favourable nursery areas (Chapter 5) must be rejected on the findings of this model. While it was thought that the vertical positioning of larvae could be adapted to maximise inshore transport on the west coast, it does not appear to maximise recruitment to this favoured nursery area. It seems more likely that efficient transport and retention are traded-off with other factors such as predator avoidance, prey abundance or energetic activity, or that these other factors alone explain the vertical distributions.

Analysis of available data on the size structure and spatial distribution of sardine spawners during the 1990s confirmed the big interannual changes in location within their occupied range. Nearly two thirds of the reproductive effort of the sardine stock recruited in the WAB/WC-WC system, indicating that the west coast nursery grounds are a preferred destination for larvae. Recruitment estimates were low in years when spawning was centred east of Cape Agulhas, when most larvae would be expected to recruit to the south coast recruitment areas. However, spawning west of Cape Agulhas could not guarantee successful recruitment, so the hypothesis that spawning location does not significantly influence recruitment success (Chapter 6) cannot be completely rejected. However, sardine rarely spawn over a restricted area, and through this bet-hedging spawning pattern successful transport to, and retention in, each of the nursery areas should occur to a greater or lesser extent each year. No significant relationship between reproductive effort reaching the west coast and estimated recruitment could be established but all years of successful recruitment corresponded with years when the majority of reproductive output reached the west coast nursery area. Hence, the hypothesis that the west and south coast nursery areas support equally high levels of recruitment (Chapter 6) can be tentatively rejected. However, the south coast could be a more important recruitment ground than previously thought. At present estimates of annual recruitment are derived from surveys that do not adequately sample the proposed south coast nursery area, and therefore have an inherent bias towards west coast recruitment.

7.2. THE MODEL

The results presented in this thesis are predominantly based on model outputs and are therefore subject to a number of assumptions made in order to simplify the system being explored. All the major assumptions made (Chapter 2, Table 2.1) have been addressed in the relevant experimental chapters. Wherever possible, actual data have been used to set parameters, validate assumptions or to help analyse results. Barange and Hampton (1997) found that the current acoustic survey design, based on the distribution of anchovy, is not well suited to the spatial distribution of sardine. Also, spawner biomass surveys are timed to coincide with peak anchovy spawning in November and therefore do not coincide with either of the two peaks of sardine spawning. No other data exist for comparison, but the estimates made from the spawner and recruit surveys are the only available data and are used in practice for fisheries management procedures (total allowable catch allocations).

The ability of the PLUME hydrodynamic model to accurately reproduce macro- and meso-scale circulation features of the southern Benguela ecosystem is fundamental if the results are to be extrapolated to the real ecosystem. The experiments in this thesis address large-scale, general patterns, and fine-scale features unlikely to be captured by the model are not considered to impact significantly on these patterns. Perhaps the greatest shortcoming of the hydrodynamic model is the weekly averaged wind forcing used. This could potentially hinder the model's ability to accurately capture cross-shelf flow, particularly on the west coast. However, the PLUME model has been shown to be proficient at reproducing satellite measurements of sea surface height, surface kinetic energy and sea surface temperature (Penven et al. 2001a, Blanke et al. 2002). Circulation features correspond very well with *in situ* current measurements (Penven 2000) and the model has also been shown to accurately represent current features such as eddies generated by the Agulhas current (Penven et al. 2001b) and shear edge eddies (Lutjeharms et al. 2003). Numerous other IBM studies have been conducted using the PLUME hydrodynamic output (e.g. Mullon et al. 2002, Huggett et al. 2003, Parada et al. 2003, Lett et al. in press) and it is generally accepted that this modelled environment provides a realistic proxy of the physical southern Benguela ecosystem.

The particle tracking model was individual-based insofar as each individual had its own unique origin in time and space, followed a unique trajectory in the modelled flow field and developed at a rate determined by the immediate environment in which it was found. Even though results were aggregated into modelled recruitment rates, mortality rates or vertical distributions, it is essential for individuals to experience environmental variation in order to study detailed spatial patterns in the life histories of populations (Hinckley et al. 1996). Variance within a population cannot be adequately explained by using identical time series of environmental variables.

IBMs have been applied to life history studies in many ways. For example, reproductive strategies can be examined intrinsically through multi-generational models. Le Page and Cury (1997) used an IBM approach to explain how two differing reproductive strategies, obstinate and opportunistic, may act at the population level given the spatial structure and dynamics of the environment and spawning seasons. Mullon et al. (2002) used a particle-tracking IBM and a set of environmental constraints for successful recruitment to study the ‘evolution’ of spatio-temporal spawning patterns of anchovy in the southern Benguela ecosystem. Broad scale studies combining hydrodynamic models, models of early life stages of fish and NPZD (nutrient-phytoplankton-zooplankton-detritus) models attempt to gain a general understanding of ecosystem dynamics and trophic ecology (e.g. Hermann et al. 2001). On a smaller scale IBMs can be used to examine ecological interactions affecting certain stages of the life history, such as size-dependent predation and behavioural responses to this (e.g. Dekshenieks et al. 1997, De Robertis 2002). Within populations, IBMs can be applied to gain understanding of what environmental, physiological or ecological factors cause observed behavioural patterns and how these control life history strategies. For example, studies of krill (*Euphausia superba*) have focussed on how behaviour of individuals controls processes such as the descent-ascent cycle, a potential reproductive strategy in response to the thermal structure of the environment (Hofmann et al. 1992), and swarm formation, a response to predation pressure (Hofmann et al. 2004). The most common IBM studies of early life stages in the pelagic environment focus on dispersion of individuals as a result of environmental, physiological and behavioural factors. The most straightforward involve tracking individuals, with varying levels of interaction with their environment, and examining resulting distributions (e.g. Heath et al. 1998, Jenkins et al. 1999, Bartsch and Coombs 2004, Bartsch et al. 2004). In many cases nursery areas are pre-defined with the purpose of examining the effects of spatial and temporal differences in spawning on ‘recruitment’ to those areas (e.g. Bartsch and Coombs 1997, Hare et al. 1999, Hinckley et al. 1999, Quinlan et al. 1999). Condie et al. (1999) used a dispersion model to extrapolate the likely ‘advection envelope’ of tiger prawn (*Penaeus esculentus* and *P. semisulcatus*) larvae to specific nursery habitats (i.e. the size and location of the source of larvae). Mortality, in one form or another, is often incorporated into IBMs in order to determine year-to-year survival of early stages and the relative importance of factors contributing to this (e.g. Bartsch and Coombs 2001, Suda and Kishida 2003). Such studies generally conclude that life history strategies are strongly structured by the regional physics of the system.

The IBM in the present study also focussed primarily on dispersion. Other similar IBM studies have been conducted on the early stages of fish in the southern Benguela, but these focussed primarily on anchovy (Table 7.1, see Mullon et al. (2003) for a full review of these).

Table 7.1: Similarities and differences between transport IBM experiments conducted in the southern Benguela ecosystem

	Model			
	Huggett et al. (2003)	**Parada et al. (2003)**	**Parada (2003)**	**Present study**
Species	Anchovy	Anchovy	Anchovy	Sardine
Physical Model	PLUME – repeat forcing	PLUME – repeat forcing	PLUME – repeat forcing	PLUME – real weekly wind fields
Parameters:				
Spawning Area	5 – south coast	4 – south coast	4 – south coast	9 – west and south coast
Year	4-8	4-8	4-8	1991/92 – 1998/99
Month	Jul-Jun	Oct-Mar	Oct-Mar	Jul-Jun
Depth	0-60	0-25, 25-50, 50-75	0-25, 25-50, 50-75	0-25, 25-50, 50-75
Patchiness of spawning	Variable	No	No	No
Frequency of spawning	Variable	No	No	No
Density	No	Variable	Fixed/ Variable	From observed distribution
Particle shape	No	Prolate spheroid	Prolate spheroid	Spherical
Growth factor	No	No	Variable	No
Time to active behaviour	No	No	Variable	No
Buoyancy	No	Eggs and larvae	Eggs and larvae	Eggs and larvae
DVM	No	No	Fixed position	Light mediated and empirical positioning
Growth	No	No	Gompertz equation	Bělehrádek curve fit to laboratory temperature-growth data
Mortality	No	No	Minimum lethal thresholds (eggs and larvae)	Minimum lethal thresholds (yolk-sac larvae)
Recruitment criteria:				
Age/stage	14 days	14 days	14 days/Active behaviour	14 days/Late larva stage
Area(s)	West coast	West coast	West coast	West and South coast

While those IBMs also examined dispersion of eggs and larvae, they differed from the present study in a number of ways. Different configurations of the PLUME model were used (notably, monthly rather than weekly wind forcing) and the construction of these models, being geared towards anchovy, produced results that cannot be used to draw conclusions on the life history of sardine. In particular, the spatial extent of spawning was less expansive (no spawning on the west coast), south coast recruitment was not considered, apart from a brief mention by Parada (2003), and a fixed age recruitment criterion was employed in those IBMs. In effect those studies only examined part of the WAB/WC-WC system and the CAB-WC system considered here, and temporal and spatial patterns of transport success in these systems corresponded closely to those reported in this study.

7.3. LIFE HISTORY OF SARDINE IN THE SOUTHERN BENGUELA ECOSYSTEM

Sardine populations around the world commonly display considerable fluctuations in stock size (Schwartzlose et al. 1999), due primarily to interannual variations in recruitment. Factors controlling the level of recruitment include the reproductive potential of the stock (e.g. spawner biomass, age structure, fecundity, length of spawning season etc.), ecological interactions (e.g. predation, productivity) and physical limitations (e.g. drift, fine-scale turbulence, temperature). Various stages of the life history are often termed ‘critical periods’, including vulnerable stages (e.g. egg and yolk-sac larva) often associated with high mortality rates, and stages that rely heavily on favourable conditions to ensure success (e.g. matching of spawning with favourable conditions for growth and reduced predation). No one factor alone determines the strength of recruitment but single factors can limit the potential for recruitment. Bakun’s fundamental triad of processes necessary for good recruitment (Bakun 1996a) includes retention in favourable nursery grounds, which would need to incorporate transport in the WAB/WC-WC and CAB-WC systems where some spawning occurs outside of the nursery areas, as observed by Lett et al. (in press).

The IBMs presented in this thesis are not able to accurately predict recruitment of sardine in the southern Benguela ecosystem. However, they can contribute to the management of this species by demonstrating the effect of transport and retention on recruitment. Transport and retention of eggs and larvae did not correlate positively with observed recruitment estimates yet there was only one year (1994/95) when a positive back-calculated recruitment anomaly resulted despite poor transport and retention of larvae in any of the three systems considered. Therefore while efficient transport and retention cannot guarantee recruitment success, it could set an upper bound, and could limit recruitment despite other conditions being favourable. Standardised anomalies of modelled recruitment in all three recruitment systems show much less interannual variability than observed recruitment estimates in all three IBM experiments. The physical characteristics (current features) of the system (Chapter 3) or the addition of temperature-dependent development (Chapter 4) and vertical movement of individuals (Chapter 5) does not significantly increase the interannual variability in modelled recruitment. Observed interannual variability could be because of small-scale or event-scale changes in current velocity or temperature that are not accurately represented by the hydrodynamic model because of the weekly wind forcing used. Alternatively, it is other processes impacting on recruitment (e.g. enrichment, concentration, predation) that account for the observed interannual recruitment variability.

A conceptual model of the early life history of sardine in the southern Benguela ecosystem can be constructed in light of limitations imposed by transport and retention of individuals (Fig. 7.1). Traditional views of the southern Benguela ecosystem as one in which pelagic fish have spatially distinct spawning and nursery areas (e.g. Crawford 1980, Nelson and Hutchings 1987) do not necessarily apply to sardine. Their spawning behaviour is best visualised by dividing the area into two main recruitment systems and a third system of with limited exchange between them: the eastern boundary WAB/WC-WC system, the western boundary SC-SC system, and the CAB-WC system. A fundamental difference between the WAB/WC-WC and SC-SC systems is that of retention versus transport. Recruitment success in the WAB/WC-WC system is both transport- (from lower west coast, WAB) and retention-based (from the upper west coast), whereas the SC-SC system is purely retention-based. Spawning is frequently observed in the area between 18°E and 22°E, particularly on the WAB, and transport from this area leads predominantly to the west coast nursery area. This transport is seasonal, peaking during spring. Colder temperatures on the west coast make this a sub-optimal spawning ground but retention here, centred offshore away from the more productive upwelled waters, is surprisingly high year round. However, there is an increase in offshore loss during the upwelling season, November to March, which implies the optimal period for transport to, and retention on the west coast is from September to November. In the SC-SC system most spawning occurs on the edge of the Agulhas Bank and eggs and larvae are retained on the offshore edge of the quasi-permanent cool ridge. Again, retention is high year round, but here peak retention is during winter, showing the opposite pattern to transport to the west coast. In both recruitment systems, transport and retention are best for

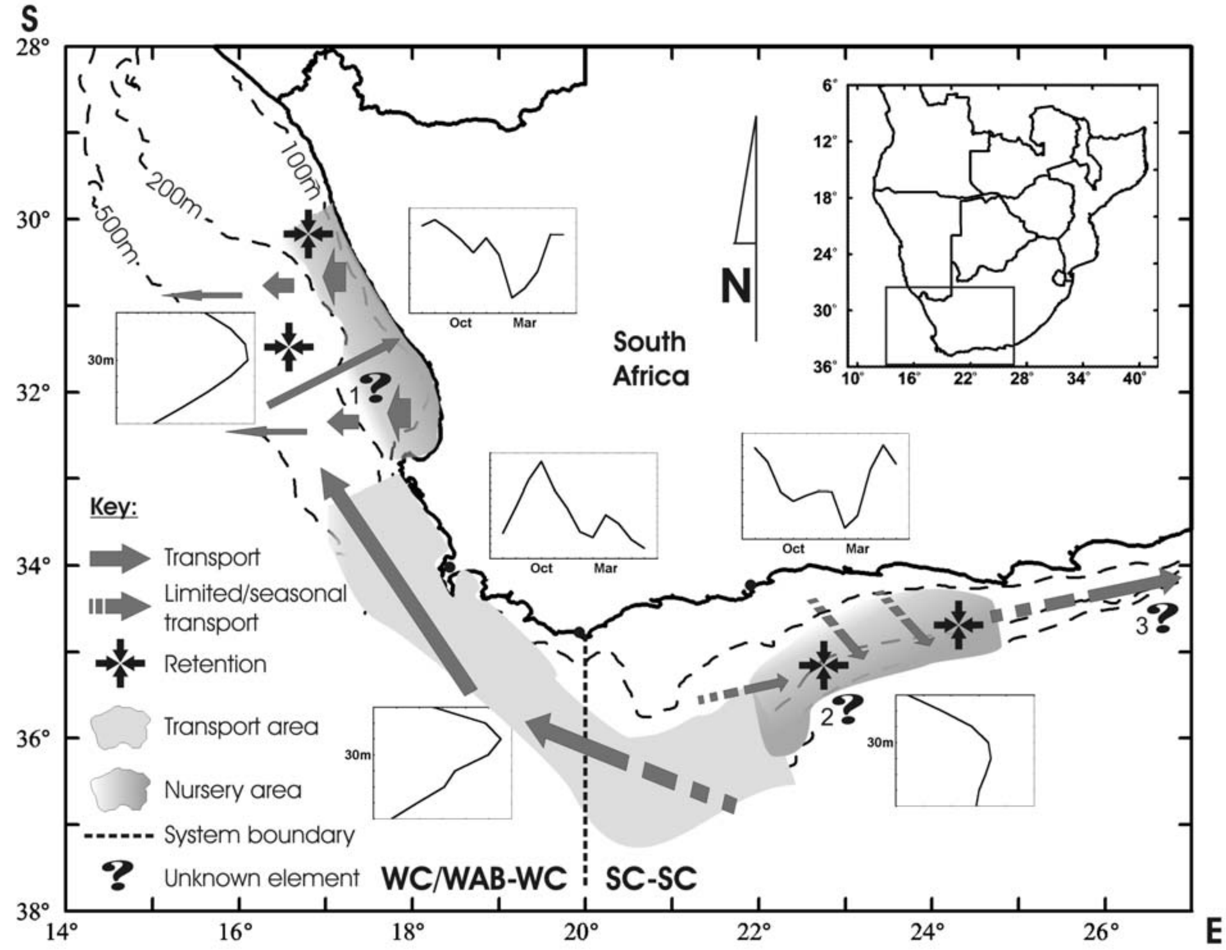

Fig. 7.1: A conceptual model of the early life history of sardine (*Sardinops sagax*) in the southern Benguela ecosystem. Inserted plots show seasonal and depth patterns of modelled recruitment for each area. 1? = onshore movement on the west coast, 2? = recruitment supported on the south coast, 3? = the sardine run

eggs and larvae below the surface layers between 20 and 40m. Eggs are observed frequently in the surface layers as they are positively buoyant and often spawned near the top of the water column. After this short stage, larvae soon begin to display vertical migratory behaviour, possibly making a trade-off between feeding time in the surface layers where prey are more abundant, and more efficient transport or retention and predator avoidance at depth. The spatial and temporal pattern of spawning each year plays an important role in determining both the quantity and location of potential reproductive output.

Three notable aspects of the early life history of sardine that remain poorly understood. The inshore waters of the west coast have high levels of production due to wind-induced upwelling and observations show late stage sardine larvae on the west coast to be near the shore in these productive waters. Model results indicate good transport to, and retention in, the region offshore of the 200m isobath, but transport inshore is poor (marked 1? in Fig. 7.1). It has been proposed that the shelf-break, which usually is offshore of upwelling fronts (though in periods of continued upwelling the two can merge), could be a potential longshore boundary in the Benguela system (Barange et al. 1992). By effectively creating a two-celled, offshore/onshore circulation pattern (Bang and Andrews 1974) the shelf-break could retain individuals inshore and act as a barrier to passive onshore movement from offshore waters. It has been estimated that, given the distances involved and estimated swimming speeds of sardine larvae, it would take more than 100 days for larvae to swim to the inshore nursery area (C.D. van der Lingen, Marine and Coastal Management, pers comm.). This excludes time that would have to be spent feeding, making this scenario implausible. While the offshore area is less productive, the water temperatures are warm and would perhaps favour more rapid development through the larval stages till the juvenile stage, when individuals and may be able to actively swim inshore to the more productive feeding grounds. There is thought to be substantial onshore movement of surface waters from March to May as the upwelling season draws to a close and wind direction starts to change form predominantly south-easterly to north-westerly. The upwelling front moves shorewards and this could provide a mechanism by which sardine larvae could get onshore (L. Hutchings, Marine and Coastal Management, pers comm.), but this was not clear from model results and needs to be examined further.

Despite model results showing a large proportion of larvae being retained in the south coast nursery area, it is not known what the level of actual recruitment this area could support (marked 2? in Fig. 7.1). Nutrient concentrations on the EAB are substantially lower than on the west coast. While small scale upwelling does occur off some of the capes along the south coast (Schumann et al. 1982) and along the eastern edge of the Agulhas Bank (et al. 1996), this production is very localised and unlikely to supply nutrients over the majority of the Agulhas Bank. Semi-continuous upwelling occurs at the far eastern edge of the Agulhas Bank, just east of Algoa Bay, where the Agulhas Current diverges from the coast, and this semi-continous upwelling supplies nutrient rich water to the whole EAB (Lutjeharms et al. 1996). The EAB is characterised by strong stratification of the water column with well-defined thermoclines during the summer (Carter et al. 1987), and the surface waters are extensively influenced by the nutrient deficient Agulhas Current (Lutjeharms et al. 1989), resulting in sub-surface chlorophyll maxima (Probyn et al. 1994a). These concentrations are close to the 1% light level and are therefore unlikely to be very productive (van der Lingen et al. 2005a). During winter the water column becomes less stratified and cold, deeper water mixes upwards, breaking down thermoclines and providing more nutrients to the surface layers (Lutjeharms et al. 1996), potentially increasing available production. Another disadvantage of this potential nursery ground is the high level of predation that could be expected here. The Agulhas Bank has a large number of fish stocks (Japp et al. 1994), many of which use this area as a spawning ground (Hutchings et al. 2002). Many of the pelagic species are planktivorous and are likely to prey on sardine eggs and larvae because zooplankton are less abundant on the Agulhas Bank than on the west coast. In the Californian upwelling system an abundance of alternative prey has been shown to significantly affect the level of fish predation on sardine larvae (Butler 1991). Anchovy, sardine, red eye and horse mackerel, all of which are abundant on the Agulhas Bank, commonly prey upon euphausiids. Euphausiids, which behave similarly to sardine larvae and to visual predators appear almost identical, are an order of magnitude more abundant on the west coast than on the EAB (Pillar 1986). The absence of this “prey background” on the Agulhas Bank could lead to substantially higher levels of predation mortality in this region (L. Hutchings, Marine and Coastal Management, pers comm.). This evidence of lower production and the possibility of higher predation suggests that some recruitment could be supported on the EAB, but that this is unlikely to be as plentiful as that on the west coast.

Another phenomenon of the sardine life history that is not fully understood is the ‘sardine run’ (Davies 1956, Baird 1970b, Beckley and van der Lingen 1999; marked 3? in Fig. 7.1). Shoals of two- to four-year old sardine regularly migrate up the Transkei and KwaZulu-Natal coasts in June or July (winter) each year. Few of these (less than 5% during the period 1951-1969) are sexually active and this section of coastline with a very narrow coastal shelf is unlikely to be able to support significant numbers of sardine. While it seems unlikely that this phenomenon plays an important role in the early stages of the sardine life history, a better knowledge of this phenomenon could increase our understanding of the potential implications of this migration.

The sardine life history strategy described above leads one to assume that sardine rely less on synchronizing the timing of spawning with optimal conditions and more on a ‘hedging of bets’ strategy. Sardine are generalist spawners (Twatwa et al. 2005), and not relying on optimal conditions for spawning allows extensive spawning across broad regions. This makes sardine robust to short term variability, and implies that it would require a three to four month environmental anomaly to significantly impact on spawning success and hence recruitment (Shelton 1986). Using a stock-market analogy, sardine have been likened to bear markets: able to turn adversity into opportunity (Bakun and Broad 2003). When conditions are favourable, other more specific spawners such as anchovy are likely to benefit, and in sub-optimal conditions, the sardine’s generalist strategy and an absence of competition allow them to prosper.

Extensive, expanded spawning can enhance successful recruitment of eggs and larvae to additional nursery areas, such as the south coast nursery ground, which could be beneficial to a stock as it increases in size (Kobayashi and Kuroda 1991). Sardine stocks become more migratory when abundant (Lluch-Belda et al. 1992a), and offshore expansion of spawners during times of high abundance has been reported for the Pacific sardine (MacCall 2002) and the Japanese sardine (Watanabe et al. 1996, 1997). In the case of the Japanese sardine, this is thought to provide optimal rearing conditions for eggs and larvae. During the late 1990s and early 2000s sardine biomass increased greatly. This was followed by an eastward shift of the sardine stock (van der Lingen et al. 2005a) and intense sardine spawning has been observed over the central and eastern Agulhas Bank (CAB and EAB) during each November survey conducted in the last five years (Fig. 7.2). Sardine have also been observed to be spawning in this area in mid-winter with high concentrations of eggs being found on the offshore edge of the Agulhas Bank south of Mossel Bay during a survey conducted in July 2005 (van der Lingen et al. 2005b). This coincides with the period of best retention on the south coast and may have led to increased recruitment east of Cape Agulhas. In 2005, sardine recruitment was very low and the majority of recruits were found east of Cape Agulhas (J. Coetzee, Marine and Coastal Management, pers comm.).

Five years after the eastward shift occurred the sardine population showed a substantially decline (Fig. 7.3) supporting the view of the south coast as a sub-optimal recruitment ground and raising questions as to why this eastward shift has occurred. It is possible that during the

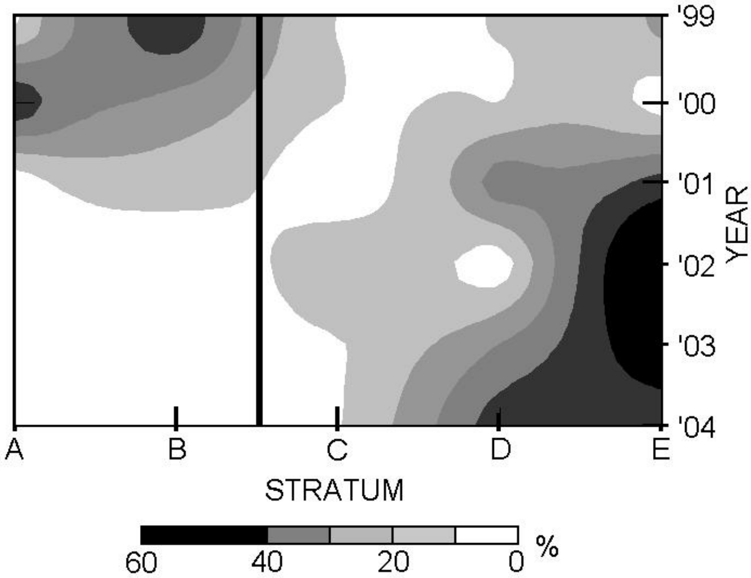

Fig. 7.2: Changes in distribution patterns of sardine eggs for the last five reported years (1999-2004) showing the percentage of total egg numbers by stratum. Contouring is used to interpolate between years and strata. The vertical line indicates the approximate position of Cape Point (from van der Lingen et al. 2005a). Strata: A = west coast, B = southwest coast, C = western Agulhas Bank, D = central Agulhas Bank, E = eastern Agulhas Bank

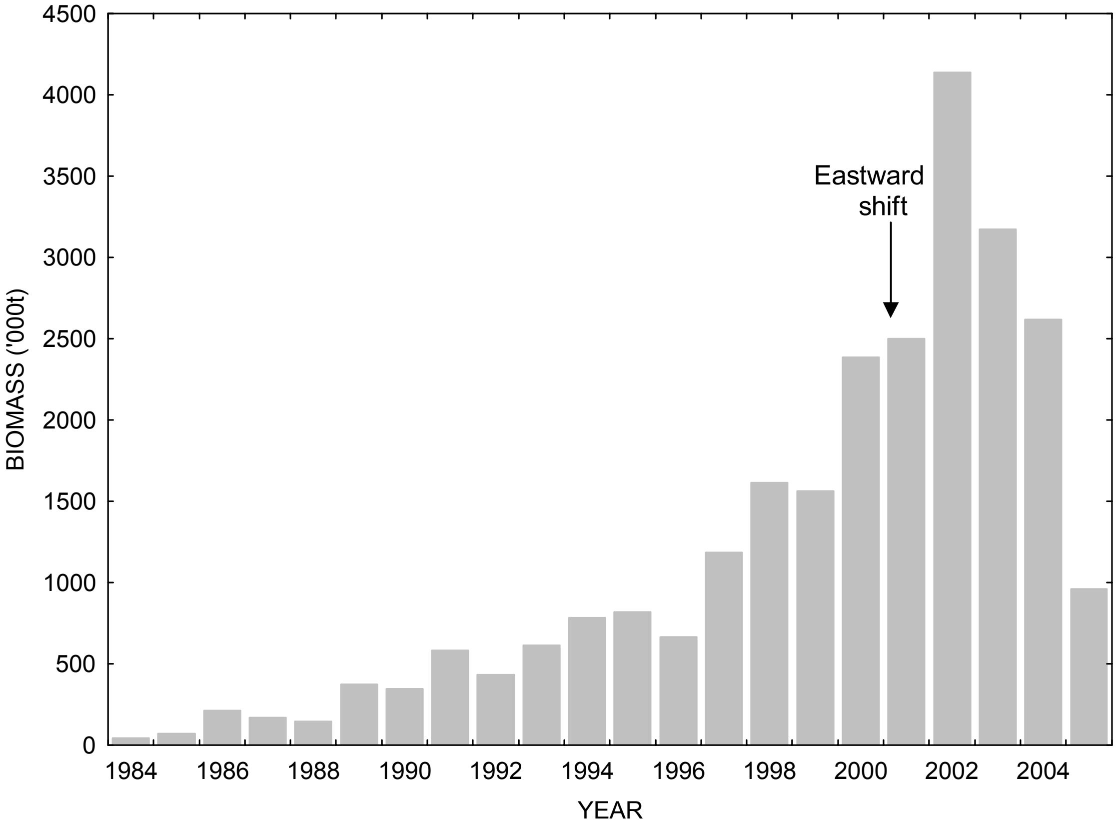

Fig. 7.3: Sardine spawner biomass from acoustic surveys of the southern Benguela ecosystem, 1984-2005. Estimates are corrected for target strength, capping and attenuation by dense sardine schools (data from J. Coetzee, Marine and Coastal Management, pers comm.)

period of high biomass sardine spawners expanded their spawning area onto the EAB where conditions are better for rearing of larvae. If this were followed by a period of poor transport to the west coast but good retention on the south coast, the majority of reproductive output would recruit to the south coast. Because this area appears unable to support a large amount of recruitment, however this would have lead to a decrease in sardine biomass, as observed in 2005. Cury (1994) put forward a theory of 'extended homing' in which individuals might home to specific locations to spawn at specific times, these being imprinted when they were spawned. This was the premise behind the evolutionary IBM of anchovy in the southern Benguela (Mullon et al. 2002) and could explain why spawning persists on the EAB, during optimal months for retention, despite low levels of recruitment. Another possible reason for the eastward shift could be that the sardine stock consists of two sub-stocks, one per closed system, and the prolific west coast sub-stock has been depleted, possibly through overfishing (van der Lingen et al. 2005a). Gaughan et al. (2001, 2002) noted that the Australian sardine stock has distinct centres of spawning, with little exchange in reproductive output between them. It was proposed that early life history of that stock could derive from functionally distinct adult assemblages (FDAAs), the distinctiveness of which is maintained by fitness related ties to suitable areas in this oligotrophic area or potentially to natal homing. This idea of FDAAs could be applied to the southern Benguela sardine stock in light of the two separate closed recruitment systems proposed here.

7.4. FUTURE RESEARCH

The results presented in this thesis have significant implications for understanding the life history of the southern Benguela sardine stock. Viable hypotheses were tested using available data but the findings could be supported by more field data. The thesis has also suggested further avenues for research that could help in developing a better understanding of the sardine life history in this system. Literature on the early stages of sardine in this system is scarce, and experimental work on the growth, mortality, swimming ability and food requirements of sardine larvae, and field observations of vertical migration patterns of larvae, would aid in the construction of IBMs such as this. More field data are required to better understand the dynamics of the sardine population along the south and east coasts of South Africa and to assess the potential of the EAB as a nursery ground. Changes in the timing of research surveys would create a better picture of the full extent of sardine spawning and the implications of this. But just as this thesis explored hypotheses that could not feasibly be tested experimentally, there exist numerous other questions that could be explored further by models of the region. A closer examination of the west coast region could be done, focusing on questions such as how sardine pre-recruits get inshore or why spawning no longer occurs here given the potential retention of the area. An improved hydrodynamic model of the region has been developed with a greater eastern extent and the potential to zoom in on specific areas with increased spatial resolution (P. Penven, Institut de Recherche pour le Développement, pers comm.). This would allow for a more thorough investigation of south coast recruitment, which is topical at present. The incorporation of a NPZD model would aid in this regard and one has recently been developed for this region (Koné et al. 2005, Machu et al. 2005). A means of incorporating realistic levels of predation would also improve understanding of the early stages of sardine in this system. Models of later life stages could be developed to examine the migratory patterns of sardine in the system and explore phenomena such as the annual sardine run.

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LIST OF FIGURES

LIST OF TABLES