#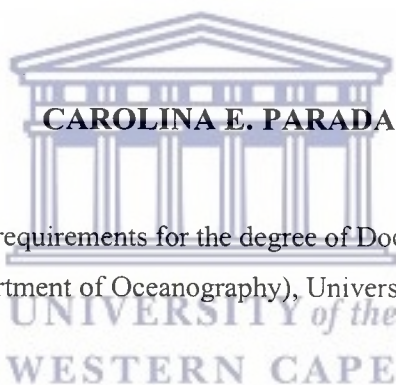 MODELING THE EFFECTS OF ENVIRONMENTAL AND ECOLOGICAL PROCESSES ON THE TRANSPORT, MORTALITY, GROWTH AND DISTRIBUTION OF EARLY STAGES OF CAPE ANCHOVY (*ENGRAULIS ENCRASICOLUS*) IN THE BENGUELA SYSTEM

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CHAPTER 5: MODELING THE VERTICAL BEHAVIOR OF ANCHOVY IN THE NURSERY AREA: IMPLICATIONS FOR RETENTION

DECLARATION

This thesis report is the result of original research that I carried out in the Department of Oceanography, UCT. The ideas and experiments presented in this manuscript are largely my own, but much of this research has been stimulated and conducted by interdisciplinary interaction with scientist from the IDYLE project (Christian Mullon, Pierre Freon, Phillip Cury, Claude Roy, Carl van der Lingen, Larry Hutchings, Jenny Huggett, Frank Shillington, John Field, Coleen Moloney, Lynne Shannon) from Marine Coastal and Management, and the Departments of Oceanography and Zoology of the University of Cape Town. The direct results of this research and the simulation experiments using individual based modeling approach were written and developed under the supervision of Christian Mullon, using the Java tools developed by him. The MATLAB programming was developed using some original programs provided by Pierrick Penven and some modifications of those programs. The sensitivity analysis applied to the output of the IBMs was performed by me, but I received feedback from Christian Mullon, Pierre Freon and Laurent Drapeau in the interpretation of the statistical analysis. Data on distribution of eggs collected by CalVET net during annual pelagic spawner biomass surveys over the period 1983-2000 and the data of the distribution of anchovy pre-recruits using a Methot frame trawl during the March 2000 survey were provided by Carl van der Lingen. Data on the horizontal distribution of eggs along the SARP Line were provided by Jenny Huggett. This work has not been submitted for any other degree at any other University and I fully acknowledge the guidance and assistance received.

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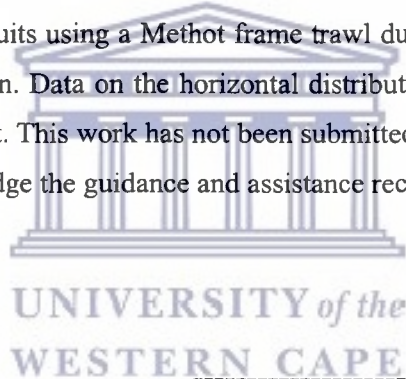
Carolina E. Parada Véliz

March 2003

ABSTRACT

An individual based modeling approach was used to study environmental factors and processes influencing the early life history of anchovy in the southern Benguela region and on the Agulhas Bank. The intention was to then establish the link between these factors and processes and the recruitment success of anchovy in the southern Benguela region. Specific factors that were explored were transport from the spawning grounds to the nursery area, advection, temperature-dependent growth and mortality, vertical migration behavior, retention in the nursery area, as well as the possibility of a second nursery area on the Eastern Agulhas Bank. Eight individual based models were coupled to the output of a 3-D hydrodynamic model to study dispersion processes. Particles representing eggs and larvae were released (spawned) over the Agulhas Bank, and their movements were tracked during their transport to the west coast (the recruitment area). Although the eggs and larvae were initially considered to be neutrally-buoyant, passive particles, increasing levels of complexity were progressively incorporated by adding processes such as particle buoyancy, temperature-dependency of growth and mortality of eggs and larvae, vertical behavior and retention.

A series of experiments was run by setting the parameters representing the factors being investigated by the model, and estimating a primary, quantifiable response variable representing the dynamics of the system (e.g. particles successfully reaching the nursery area). An analysis of variance was employed to assess the significance and the sensitivity of each model to changes in the parameter values. A pattern-oriented analysis was then systematically applied to assess the validity of the results of the model. The results indicate that five processes and their interactions strongly influence the transport of spawning products arriving at and subsequently being retained in the nursery area: (1) the location of the spawning, (2) the buoyancy of the eggs, (3) transport by the jet current and its inter-annual variability; (4) the 3-D structure of the current in the nursery area on the west coast, (5) The swimming abilities of the pre-recruits in both the vertical and the horizontal planes. Two factors appear to be of major importance in effecting mortality during the period leading up to recruitment, namely temperature and offshore losses through advective processes.

A conceptual model of the life history of anchovy in southern Benguela is presented and discussed in the light of the hypothesis proposed by Hutchings *et al.* (1998). A number of modifications to this hypothesis are proposed, specifically an extension of the spawning area, and the addition of several key biological processes. A new element that is proposed in this thesis is the possibility of the Eastern Agulhas Bank as an additional nursery and spawning area.

CHAPTER 1: INTRODUCTION

1.1. THE BENGUELA ECOSYSTEM

The Benguela system off the south-west coast of Africa is one of the major coastal upwelling regions of the eastern boundaries of the world ocean (Parrish *et al.*, 1983; Mann and Lazier, 1991; Shillington, 1998). This system is characterized by relatively high inter-annual and inter-decadal variability in recruitment resulting from large variations in environmental forcing. This natural forcing is compounded by the impact of fishing, resulting in large fluctuations in the abundance of some pelagic fish stocks (Lluch-Belda *et al.*, 1992). The Cape anchovy, *Engraulis encrasicolus* (Linnaeus, 1758), is an important component of the pelagic fishery off South Africa that shows large inter-annual fluctuations in population size. A 25-fold variation in adult anchovy biomass has been observed over the past 17 years (Barange *et al.*, 1999; van der Lingen *et al.*, 2001). This biomass variability is presumably associated with the vulnerability of early life stages to environmental variability that generates fluctuations in the recruitment of juvenile anchovy to the fishery (Hutchings and Boyd, 1992). Cape anchovy formerly called *Engraulis capensis* was considered to be an endemic species of southern Africa. However, now it is considered to be the same species as the European anchovy *E. encrasicolus* (Whitehead, 1990). Throughout this thesis, the *E. encrasicolus* classification will be used.

1.2. LIFE HISTORY OF ANCHOVY

1.2.1. The Agulhas Bank and the spawning process: time and space

The life history of anchovy in the southern Benguela system has been relatively well studied. Anchovy spawn serially over the Agulhas Bank during austral spring/summer (September to March), with a mid-season peak in November (Shelton, 1986; Melo 1994; Huggett *et al.*, 1998; van der Lingen *et al.*, 2001). Egg distribution patterns during the peak spawning season show the importance of the Western Agulhas Bank (WAB) as a major spawning area (Shelton, 1984; Armstrong *et al.*, 1988; Shelton *et al.*, 1993; Roel *et al.*, 1994) (Fig. 1.1). Recent studies, however, indicate a shift in the major spawning areas to the Central (CAB) and Eastern Agulhas Bank (EAB) subsequent to the mid 1990's (van der Lingen *et al.*, 2002). From the Agulhas Bank, eggs are transported via a shelf-edge jet current past the upwelling centers off Cape Point and Cape Columbine (Fig. 1.2) to the variable but productive west coast (Shelton and Hutchings, 1982; Armstrong *et al.*, 1987; Boyd *et al.*, 1992; Hutchings *et al.*, 1998).

1.2.2. The west coast nursery area

The west coast is characterized by an inshore nursery area located between Cape Columbine and the Orange River (Fig. 1.2). Once anchovy have grown to the juvenile stage, they migrate southwards back to the Agulhas Bank from April to September, where they spawn at the end of their

Benguela region may influence the strength of anchovy year-classes (Shannon *et al.*, 1996; Boyd and Nelson, 1998). Studies on recruitment variation in the South African anchovy showed that multiple factors appear to influence recruitment strength. However, in any one year, several different factors appear to operate, making it difficult to generalize (Hutchings *et al.*, 1998). The research described in this thesis investigates the role of various environmental factors and ecological processes on growth, mortality, transport, retention in the nursery area, and distribution of early stages of anchovy in southern Benguela system. The interaction of these factors and processes with individual variation will also be explored.
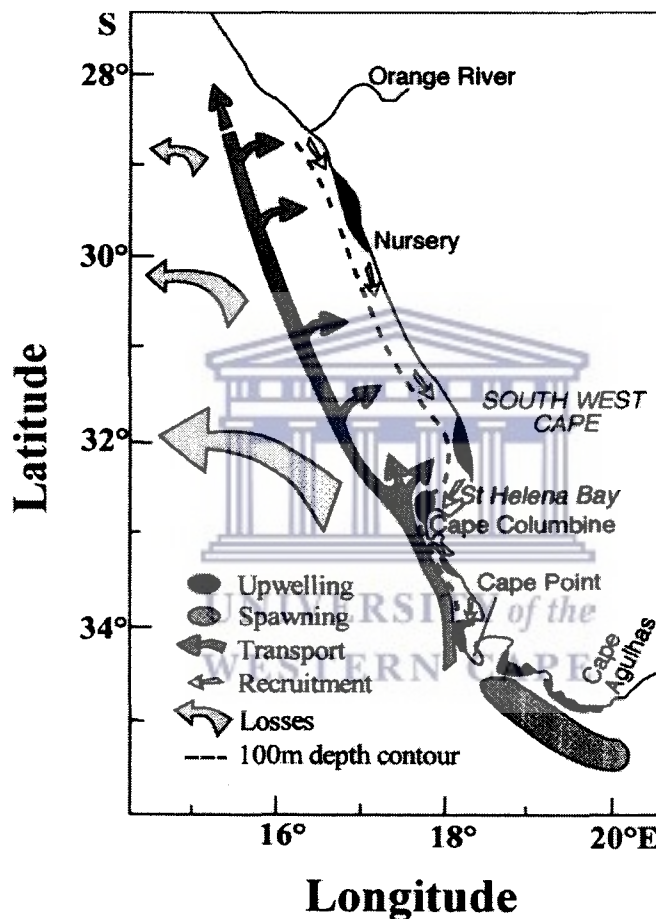
Figure 1.2. Conceptual model of the anchovy's life history (after Hutchings *et al.*, 1998).

1.3. FACTORS INFLUENCING MORTALITY, GROWTH, TRANSPORT OF EARLY STAGES OF ANCHOVY IN BENGUELA ECOSYSTEM

1.3.1. Environmental variables

The physical environment of the Cape anchovy is highly variable, ranging from the warm waters of the Agulhas Bank to the cold waters of the west coast that are strongly influenced by several upwelling cells. This variability is due to the influence of pulsing currents (Agulhas and

1.3.2. Environmental processes

The jet current in the southern Benguela system has been identified as a crucial environmental feature determining the successful transport of early life stages of anchovy from the spawning grounds of the Agulhas Bank to the nursery areas on the west coast (Fowler and Boyd, 1998; Hutchings *et al.*, 1998). Transport success is defined in this context as the proportion of spawning products of anchovy that reach the nursery area. A combination of three other environmental processes has been suggested as determining favorable conditions for fish reproduction, survival and growth of early stages of fishes. These processes, termed "the ocean triad" (Bakun, 1996) are defined as:

(1) Enrichment: processes that input nutrients into the upper water column (e.g. upwelling and vertical mixing).

(2) Concentration: processes that aggregate food for larvae in oceanographic features such as convergence and frontal areas.

(3) Retention: processes that retain early stages of fishes in areas suitable for their survival.

In the Benguela ecosystem, nutrients in cold water upwelled by compensatory flow enrich the upper water column, improving the food conditions for feeding larvae. In an east-west direction, the upwelling process evolves from the formation of clear thermal fronts to filament structures that are frequently associated with the formation of eddies. Enhanced lateral and vertical mixing in upwelling fronts leads to increased primary and secondary production (Olson and Backus, 1985). Similarly, the long filaments of cold water extending offshore have been observed to have higher chlorophyll *a* concentrations compared to the adjacent ocean, implying elevated biological productivity (Shillington *et al.*, 1992; Logerwell *et al.*, 2001). Olson and Backus (1985) suggested that in the frontal areas around eddies, a concentrating mechanism occurs in which individuals can make use of the increased density of their prey. In a system with a double-cell upwelling structure the elements of the Bakun's triad are combined in the coastal cell, allowing early stages of fishes to be retained in productive and relatively stable coastal waters, avoiding advection offshore to oligotrophic areas (Roy, 1998). This process of retention may be enhanced by a biological strategy such as vertical migration that may be the key to improve the survival of early stages of anchovy. Bakun (1996) has pointed out that retention occurs when vertically migrating larvae use the onshore flow in the surface or deep layers to return to the nursery areas.

1.4. OBJECTIVES

The objectives of this research were:

Agulhas Current water (Lutjeharms *et al.*, 1996). Ambient water temperature ranges between 14 and 21°C in spring, and between 10 and 22°C in summer (Mitchell-Innes *et al.*, 1999). For the spawning process, the optimal temperature range appears to be between 16 and 19°C (Anders, 1965; King *et al*, 1978; Shelton, 1986; Richardson *et al.*, 1998). Along the jet current between the Cape Peninsula and Cape Columbine (Fig. 1.2), the temperature of upwelled water fluctuate between 8 and 10°C, while adjacent oceanic waters can reach tempreatures greater than 18°C (Shannon, 1995). A study using self-organizing maps to characterize variability in sea surface temperatures along the west coast of South Africa indicated temperature ranges of 13 to 17°C in spring and 14 to 21°C in summer (Richardson *et al.*, 2000). The question of how the influence of temperature on individual growth and survival interacts with the transport from spawning grounds is addressed by the second hypothesis:

H2: Enhanced transport success depends on a combination of efficient physical transport from the spawning grounds (Agulhas Bank) to the nursery areas (west coast), the stage of development of individuals reaching the nursery area (temperature-dependent growth), and temperatures favorable for survival (temperature acting as a lethal factor).

Once individuals have been successfully transported to the nursery area, they may be subjected to offshore advection resulting from Ekman drift. The transport of anchovy larvae away from the coast to oceanic waters that are characterized by low chlorophyll *a* concentrations may significantly reduce the probability of their survival. However, retention processes can take place due to the double layers of upwelling circulation, and larvae and post-larvae could actively migrate vertically and subsequently be trapped in productive coastal waters. Hypothesis 3 consequently addresses the question of what extent the onshore-offshore circulation that characterizes the upwelling process, as well as active vertical migration, promotes the transport of larvae and post-larvae of anchovy into the nursery area.

H3: Active vertical migration behavior could counteract the offshore advective process and significantly increase the transport success to the nursery area.

The interaction of vertical migration behavior with transport processes in a vertically structured ocean offers a means by which living organisms are potentially able to follow drift trajectories that may in no way resemble those that completely passive particles must undergo (Bakun, 1996). Even though various retention processes are proposed to enhance larval survival, losses of larvae offshore through surface Ekman transport are inevitable. The hypotheses presented above are based on the currently accepted paradigm of the early life history of anchovy in the southern Benguela system, which stresses the importance of the successful transport of eggs and larvae to the nursery areas on the west coast as the key factor regulating recruitment success. During

of water density during the transport from the spawning grounds to the nursery area. The IBM experiment described in Chapter 4 was designed to simulate the effect of temperature on the mortality and growth of eggs and larvae of anchovy, and on the transport success.

In Chapter 5, an IBM experiment is used to examine transport and retention processes (one element of the ocean triad hypothesis of Bakun, 1996) in the nursery area. How passive behavior of early stages of anchovy in the nursery area influences transport and retention is explored using a Lagrangian approximation. Following this, the relationship between the field velocity and the vertical behavior of post-larvae is tested using simulations. Finally, the retention of post-larvae is assessed considering both active behavior and a residence time of >10 days in the nursery area west coast. This retention model is also applied to Eastern Agulhas Bank, assessing the residence time of > 10 days of post-larvae in this area.

Chapter 6 synthesizes concepts and processes, discussing the relevance of the biological and physical processes that enhance survival and affect growth and distribution patterns in the Benguela ecosystem. In addition, the limitations and advantages of the methodology that was employed in this research are discussed, as well as the limitations of the hydrodynamic model (PLUME) outputs and IBM designs, and the importance of this modeling approach. The validity of the assumptions inherent in the approach and a comparative study of the models are discussed. The scope of the results obtained using the individual based modeling approach and their agreement with currently available data as well as the proposed hypotheses are explored. Finally the present status of knowledge of the early life history of anchovy in southern Benguela system is re-visited with reference to future research in this field.
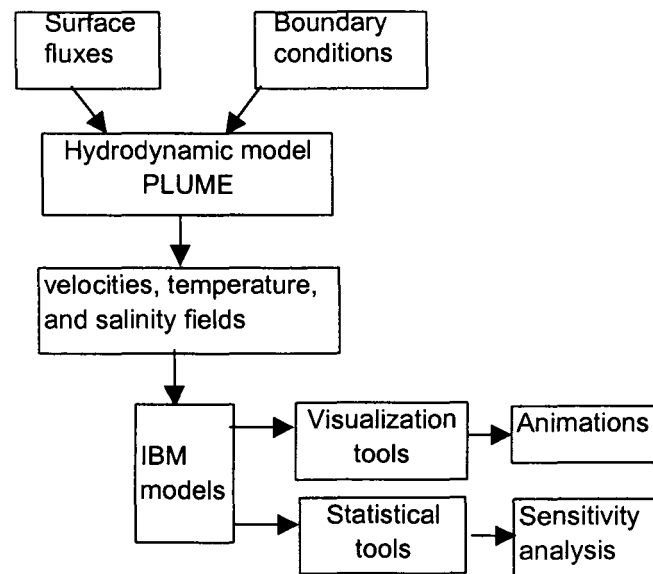
Figure 2.1. Flowchart of the methodological approach (modified after Mullon *et al.*, 2002).

2.2. MODELING

2.2.1. Coupling the IBMs to the hydrodynamic model

The IBMs were coupled to the hydrodynamic model using a Lagrangian framework. This approach implies movements of a discrete parcel of fluid, which is preferable when past history influences the present responses of the environment. The coupling technique employed in this study was that of Hermann *et al.* (2001). The hydrodynamic model was run once and low-pass-filtered decimated time-series of the fields at each grid point of the model were stored (Fig. 2.2). These stored outputs of the hydrodynamic model were then used in the IBM in three ways (Table 2.1.):

(1) As direct inputs into the IBM (e.g. temperature, salinity and velocity fields),

(2) As post-processing inputs into the IBM (e.g. water density), and

(3) To define simulated scenarios (e.g. average transport by the current and series of temperature profiles in determined locations in the domain).

The configuration of the IBM used stored output from the hydrodynamic model with a time step of two days. The hydrodynamic model was not intended to reproduce any true year in particular, but rather to provide a virtual environment that has a sufficient degree of spatial and temporal realism to be used for the biological model simulations. From the 8 years of post-equilibrium outputs, only 5 years (Years 4-8) were selected for coupling to the IBM. This constraint was imposed because the individual based modeling technique incorporates spatially explicit circulation, water properties and biological behavior that require computationally efficient methods. Solving the equations for every "individual" imposes a computational constraint on this type of modeling
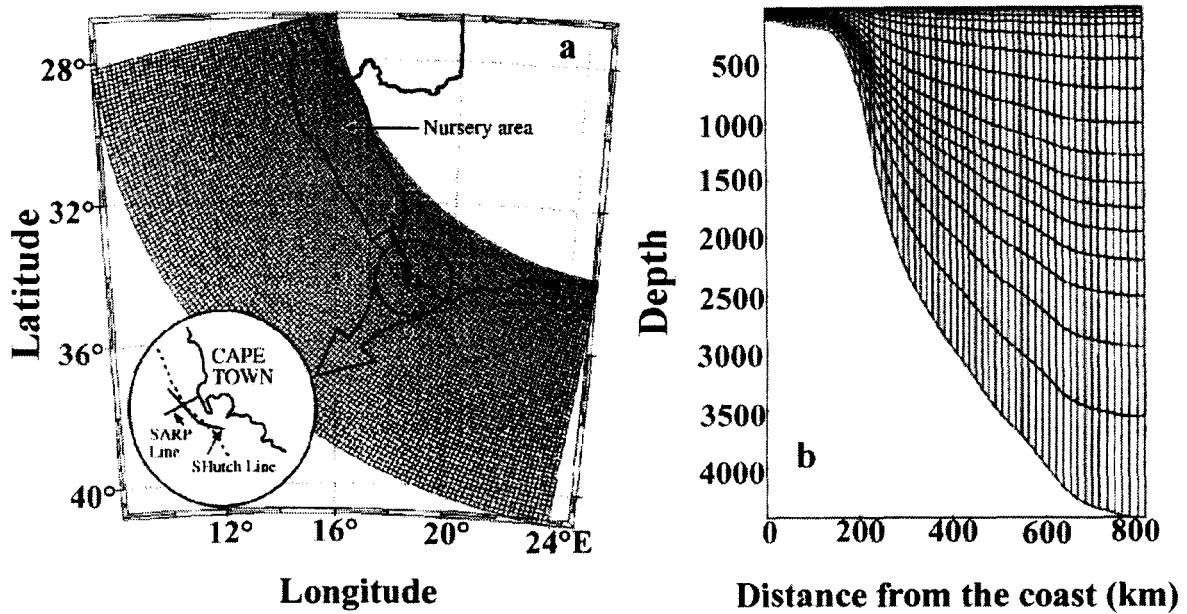
Figure 2.2. (a) The horizontal grid of the hydrodynamic model. The thick line represents the coastline, the thin line the 500 m isobath, and the grid resolution is approximately 10 km at the coast. The location of the west coast nursery grounds and the SARP (Huggett *et al.*, 1998) and SHutch (Shelton and Hutchings, 1982) lines are shown. (b) Vertical S-coordinate levels of the hydrodynamic model following topography. The resolution is 9 m for the first surface levels, and approximately 1000 m for the deepest level offshore.

The hydrodynamic model was started from rest using summer values as initial conditions. Because the model domain is relatively small, the model reaches equilibrium after a spin-up period of about two years (Penven *et al.,* 2001). Although the model was run for 10 years and forced by a repeated climatology (i.e. no inter-annual variability in the forcing fields), there are pronounced differences in the simulation outputs between individual years. This inter-annual variability has been attributed to intrinsic mesoscale activity resulting from oceanic instability processes in the absence of added forced variability (Penven *et al.*, 2001), and is in agreement with previous studies of the dynamics of the California Current upwelling ecosystem (Marschesiello *et al.*, 2001). A snapshot of the surface structure of temperature (SST) and surface currents output by PLUME (Fig. 2.3) shows a high level of realistic, mesoscale activity and some of the main features of southern Benguela system, including the jet current, the generation of Agulhas rings, and the shedding of cyclonic eddies from the southern tip of the Agulhas Bank, Cape Peninsula and Cape Columbine. The average behavior of the model and its variability has been checked against observed data (see Penven *et al.*, 2001 for details).

al., 1999; Lomnicki, 1999, Hermann *et al.*, 2001). Eight IBM designs, of increasing complexity, were developed in Java language and run on a J-Builder platform professional 3.0 (Borland, 1999). These models were aimed at studying the environmental factors and processes influencing the early life history of anchovy in the southern Benguela region and on the Agulhas Bank. To test the hypotheses described in Chapter 1 using the IBMs, a progressively increasing level of realism was employed. Initially, individuals were considered to be passive particles. Subsequently, increased levels of realism in terms of the properties of the individuals were incorporated into the models.

Particles. Initially, simple particle tracking was used to represent eggs in the system. In this approach, simulated current fields from the 3-D hydrodynamic model were used to study dispersion processes. This kind of approach is relatively straightforward and is considered the first step in the formulation of a spatially-explicit IBM, where given flow fields are properly resolved and particle trajectories can be computed (Hermann *et al.*, 1996; Huggett *et al.*, 2003). In the preliminary IBM, eggs and larvae were considered neutral floating particles released (spawned) over the Agulhas Bank. Their movements in time and in space were tracked during their subsequent transport northwards to the inshore areas of the west coast nursery ground (the successful recruitment area). However, in the preliminary IBM no biological or environmental factors were considered, which is clearly unrealistic when the intention is to understand recruitment variability.

Individuals. Following a stepwise approach, different processes such as particle buoyancy, temperature-dependency on growth and mortality for eggs and larvae, vertical behavior for larvae, and retention in the west coast and Eastern Agulhas Bank (EAB) areas were gradually incorporated in the IBM. The IBM not only tracked the movement of particles (representing eggs) released over the Agulhas Bank (with buoyancy properties) and larvae, but also their temperature-dependent growth and mortality. In addition, the last IBM accounts for vertical behavior in order to assess the potential of active migratory behavior by larvae and post-larvae to be transported to, and thereafter retained in, the nursery area of the west coast and EAB.

2.3. EXPERIMENTAL PROTOCOL

Each IBM was used to run a series of experiments, each of which consisted of a set of simulations using constant values and parameters representing the factors being investigated by the model. In keeping with the principles presented in section 2.1 and the steps of an experimental simulation applied to IBMs by Mullon *et al.* (submitted), the experimental procedure was designed and implemented using the following approach. First, a series of assumptions were formulated, and biological and physical processes explicitly defined as the target processes to study the effect on recruitment success. Secondly, the response variable, the quantity used for subsequent statistical analysis, was defined. Thirdly, a set of parameters was selected to represent the response variable. For each individual simulation, a new value of a given parameter was tested, generating a single

(3) The spatial (horizontal plane) and temporal spawning scales set in the model were adequate to explore the variability in reproductive and transport success.

(4) Inherent in the spatial spawning scale was the subdivision of the Agulhas Bank into 4 spawning areas, namely the WAB (Western Agulhas Bank), CAB_{Off} (Central Agulhas Bank Offshore), EAB_{In} (Eastern Agulhas Bank Inshore) and EAB_{Off} (Eastern Agulhas Bank Offshore). In terms of the temporal spawning scale, the spawning season was set from October to March, while the duration of spawning in each simulation corresponded to 30 days.

(5) The particle distribution at each depth interval where particles where released in each simulation is assumed to be homogeneous, and any departure from this assumption would not significantly affect the transport success.

Assumptions that are specific to each IBM used in this study are

(6) The transport success criterion (Table 2.2) defined for each model is assumed to be a good proxy for recruitment success.

(7) The criteria listed in Table 2.3 and Table 2.4 assumed to be a good proxy for mortality and retention respectively.

(8) The buoyancy scheme is the major biological component associated with the vertical movement of the spawning products. It is assumed that the vertical drag of particles is in equilibrium with the buoyancy forces, resulting in a terminal velocity that is a function of the gravitational force, seawater density, kinematic viscosity, minor and major axis length. Although this assumption was implicit in model 2-8 presented in this thesis (Table 2.5 and 2.6), the buoyancy scheme was applied to particles representing both eggs and larvae in model 2, but only to eggs in the remaining models (i.e. models 3 to 8, Table 2.5 and 2.6.).

(9) Temperature is considered to be the main source of mortality of particles representing egg and larvae during the simulation experiments (model 4-8, Table 2.5 and 2.6).

(10) The growth of eggs and larvae up to post-larvae is assumed to be adequately described by a temperature-dependent Gompertz equation (model 4-8, Table 2.5 and 2.6).

(11) The selection of a preferred depth by each larva after it hatches in the nursery area is a suitable proxy for vertical behavior associated with transport to the inshore part of the nursery area and the retention processes (model 6-8, Table 2.6).

(12) It is assumed that the response variables used in the IBMs are proxies of the processes under study (e.g. recruitment success, mortality and retention).

2.3.2. Criteria and response variables in the IBMs

The IBMs generated different values for the response variables depending on the criteria of transport success, mortality and retention. The criteria and the response variables used in each IBM are listed in Tables 2.2, 2.3 and 2.4, and their use justified below.

1983) could avoid a bongo net during the day but not at night (Badenhorst and Boyd, 1980). This suggests that larvae of this size and age are capable of active swimming. It was therefore assumed that anchovy less than 7 mm could be considered as passive particles that would behave in a manner indistinguishable from eggs. Larvae smaller than this size would not be able to retain themselves in the nursery area and would be subject to offshore advective losses; hence it is considered that their transport was not successful. Larvae larger than 7 mm would have sufficiently developed swimming capabilities to maintain themselves within the nursery area. The criterion of transport success and the response variable for model 5 resembles those of models 1 to 4, but only consider the inshore nursery area as the target area (Table 2.2). For model 6, the criterion of transport success (Table 2.2.) was consequently defined as larvae that have hatched and reached the active behavior stage that arrived at the inshore area of the west coast (Fig. 2.4). The response variable was then the ratio between the number of larvae that have hatched and reached the active behavior stage and arrived at the inshore part of the nursery area to the total number of eggs released. It is important to note that transport success is only a proxy for recruitment success. There are many processes associated to mortality such predation, starvation that needs to be solved before speaking of proper recruitment success.

Table 2.2. Transport success criteria and response variable used in each model.

Models	Transport success criteria	Transport success response variable
1-4	Individuals that arrive in the offshore and inshore nursery area within 7 time steps (i.e. older of 14 days of age)	Ratio between the number of successfully transported particles (eggs or larvae) from the spawning to the nursery area (inshore and offshore) by the end of the simulation to the total number of eggs (particles) released
5	Individuals that arrive at the inshore nursery area within 7 time steps (i.e. older than 14 days of age)	Ratio between the number of successfully transported particles (larvae) from the spawning to the nursery area (inshore) by the end of the simulation to the total number of eggs (particles) released
6	Individuals that arrive at the inshore nursery area after they hatched and have reached the active behavior stage	Ratio between the number that have hatched and reached the active behavior stage and reached the nursery area (inshore) to the total number of eggs (particles) released

Mortality criteria and response variables. The criterion of mortality was defined as a function of the minimum temperature thresholds for particles that represent eggs and larvae (Table 2.3). In model 4, a set of values for each threshold was used to test the model sensitivity (see Chapter 3). In models 5 to 8 on the other hand, the lethal temperatures for particles representing eggs and larvae were constant values of <14°C (eggs) and <12°C (larvae). These values were set because these temperature ranges act as a lethal factor for eggs and larvae of anchovy. Egg development is inhibited below 14°C, to the extent that larvae fail to develop a functional jaw (King *et al.*, 1978). Larvae are unable to tolerate temperatures below 12°C (L. Hutchings, per. comm.). No maximum

2.3.3. Setting the parameters

As mentioned above (section 2.3), the configuration of each IBM involved setting a suite of constants and parameters (Tables 2.5 and 2.6). With this framework in mind, two groups of experiments were conducted. The first group, comprised four IBMs (Table 2.5) aimed at understanding the effects of various environmental factors on growth, mortality and distribution of early stages of anchovy. In this group, the first IBM studied the Lagrangian transport of particles from the spawning grounds to the nursery area on the west coast, and assessed the importance of several spatio-temporal variables in determining transport success. The second and third IBMs (see Table 2.5 and Chapter 3) examined the depth adjustment of anchovy egg and early larvae to variations in water density. The fourth IBM examined the effect of temperature on the survival and growth rates of simulated eggs and larvae during their transport from the spawning grounds to the nursery area (Table 2.5).

Table 2.5. Constants and parameters set for the first group of four IBMs that were designed to study the effects of environmental factors on the growth, mortality, transport success and distribution of particles representing early stages of anchovy. The reference number used for each model throughout this thesis is indicated in parentheses. The " ✔ " represent the presence and "-" the absence of the element in the model.

Model	Lagrangian (1)	Buoyancy (2) applied to eggs and larvae	Buoyancy (3) applied only to eggs	Growth and mortality (4) temperature function
Constants				
Spawning duration	✔	✔	✔	✔
Tracking duration	✔	✔	✔	✔
Duration of the simulation	✔	✔	✔	✔
Number of particles	✔	✔	✔	✔
Density of particles	✔	✔	✔	✔
Shape of particles	-	-	-	✔
Parameters				
Area of spawning	✔	✔	✔	✔
Date of spawning	✔	✔	✔	✔
Year of simulation	✔	✔	✔	✔
Depth of egg released	✔	✔	✔	✔
Density of particles	-	✔	✔	-
Shape of particles	-	✔	✔	-
Factor of growth	-	-	-	✔
Lethal temperature for eggs	-	-	-	✔
Lethal temperature for larvae	-	-	-	✔

The second group of experiments, which also comprised four IBMs (Table 2.6) investigated the influence of environmental processes on transport success to the nursery area, the retention processes of Bakun's Triad and the distribution of early stages of anchovy. The first IBM (model 5) excluded any form of active behavior by larvae in the nursery area, treating them as purely passive, Lagrangian particles. The second IBM of this group (model 6) incorporated a vertical movement component into larval behavior to assess the potential effect of this component on transport success

The position of the 125 m and 500 m isobaths in the smoothed topography of the PLUME domain correspond to the positions of the real subdivision of the spawning areas at 100 m and 200 m depth (see Fig. 1.1).

During each simulation, the position of each particle representing an egg or larva was interpolated from the hydrodynamic model input data at five time steps during each 48 hour interval. After each time interval, particles representing eggs and larvae were individually moved to new positions determined by the velocity fields of PLUME and the buoyancy properties specified for each IBM design. The additional biological processes considered in each IBM are discussed in detail in the relevant chapters of this thesis.

2.3.4. Analysis of results

The outputs of the IBMs were analyzed using visualization tools, statistics and pattern oriented analysis.

Visualization tools. The interfaces and programs developed in Java for the IBMs allowed visual analysis of the performance of the IBM by means of on-screen animations (tools developed by C. Mullon, see Fig. 2.1). The screen design of the IBM is divided in 3 areas: (i) The *simulation* area defines the 2-D spatial and temporal domain of the hydrodynamic model, and specifically the areas where particles representing eggs were released, and areas of successful transport. (ii) A *graphic* area, where the model results are displayed in real time (e.g. the distribution individuals according to depth, the number of individuals successfully transported, the number of individuals retained in the nursery area, etc.). (iii) The *parameter* area where the parameters are set.

Statistical analyses. The sensitivities of the IBMs to their parameters were analyzed using a multiple factor analysis of variance that was applied to the outputs of the IBM experiments (response variables values) using the General Linear Model (GLM) module of "Statistica (v. 5.0)" (StatSoft, 2000). The parameters and response variables from each IBM represented the independent and dependent variables in the variance analyses respectively. This analysis computed the normality of the residuals, as well as the significance and proportion of variance explained by each of the parameters and their interactions. Two procedures were used to find the best fit in the GLM:

(1) A full GLM, including up to the first level of interactions, was run. If the error of this model was >20%, a second level of interactions was analyzed. In the final assessment of the statistical analysis, significant parameters and their interactions were only considered when they explained >5% of the model variance.

(2) A sub-optimal GLM was run for those IBM designs that exceeded the maximum number of parameters and interactions that could be analyzed by "Statistica". In these cases, a GLM that included only the first level of interaction was run. If the model error was > 20%, single

CHAPTER 3: MODELING THE EFFECT OF BUOYANCY ON THE TRANSPORT OF ANCHOVY EGGS TO THE NURSERY GROUNDS

3.1. INTRODUCTION

The physical and biological factors that determine the vertical distribution of spawning products are important when predicting egg/larval horizontal drift in relation to their survival and subsequent recruitment (Tanaka, 1992). Although several descriptive studies have investigated the buoyancy of pelagic fish eggs (Coombs, 1981; Coombs *et al.*, 1985; Tanaka *et al.*, 1991; Tanaka and Oozebi, 1996; Stenevik *et al.*, 2001), few investigations have studied the processes that control the vertical distribution of eggs and larvae (Sundby, 1983; 1997; Ådlandsvik *et al.*, 2001). Egg buoyancy is species specific, and varies with the developmental stage of the eggs (Coombs *et al.*, 1985; Tanaka, 1990; Tanaka *et al.*, 1991; Tanaka and Oozeki, 1996). Eggs adjust to certain depths depending on water density and their intrinsic density, stabilizing at depths where their density is equivalent to that of the surrounding water. The depth at which the eggs were originally spawned also plays a role in this adjustment. Cape anchovy eggs on the Agulhas Bank are generally spawned within the first 75 m, with highest concentrations occurring between 10 and 50 m depth (Shelton and Hutchings, 1982). Although anchovy eggs have been described as being positively buoyant (tending to rise to the surface, Tanaka, 1992), recent field experiments have showed that the egg density in the southern Benguela system ranges between 1.021 to 1.027 gcm^{-3} (van der Lingen, unpublished data). These data suggest that in certain cases, eggs can be denser than the surrounding water and would consequently sink deeper into the water column. The spatial distribution of anchovy eggs is therefore affected both directly and indirectly by their intrinsic buoyancy properties. As described above, egg buoyancy directly determines their vertical position and this then indirectly influences their horizontal distribution because of the horizontal field velocity characterizing that part of the water column.

The research described in this chapter used an individual based modeling approach to address the question of how egg buoyancy affects the transport of eggs from the spawning grounds, and hence their ultimate destiny. An individual based model (IBM) was designed using a buoyancy scheme based on that of Denny (1993), and examined the response of anchovy eggs (of specified density) to variations in water density during their transport by the strong jet current from the spawning grounds to the nursery area on the west coast. The approach also addresses the interactions of egg buoyancy with the temporal and spatial scales of the spawning process in terms of transport success.

Table 3.1. Constants and parameters used to formulate the Lagrangian and buoyancy experiments

Constants	Description
Spawning duration	Spawning is a constant process starting on the first day of simulation and lasting 30 days
Tracking duration	All particles representing eggs were tracked until the age of 60 days
Duration of simulation	Every simulation was run over 90 days (Spawning duration + Tracking duration)
Number of eggs	The number of particles representing eggs was set to 5000 per simulation. These were released continuously over the Spawning duration

Parameters	Description
Area	Particles were released over all 4 spawning areas (Western Agulhas Bank (WAB), Central Agulhas Bank offshore (CAB$_{Off}$), Eastern Agulhas Bank inshore (EAB$_{In}$) and offshore (EAB$_{Off}$), in proportion to the relative size (in km^2) of each area
Date	The dates of release were set to: 1st October, 1st November, 1st December, 1st January, 1st February and 1st March
Year	Years 4-8 from hydrodynamic model (Penven, 2000) were used in the IBM
Depth	Particles were released at 3 depth ranges to 0-25, 25-50 and 50-75 m, and randomly distributed in the water column over the specified range
Particle density*	The range of density for the particles was set in the model to 1.021, 1.023, 1.025, 1.027 (g.cm^{-3})
Shape*	Three shape for the particles were tested in the model according to the relationships between minor and major axes; 0.1:0.1 cm (spherical); 0.07:0.12 cm (intermediate shape) 0.05:0.14 cm (prolate spheroid)

* Lagrangian model excluded the parameters Particle density and Shape of the eggs

3.2.3. Configuration of the experiments

The same basic configuration was employed in all three experiments, differing only in that the Lagrangian model did not incorporate a buoyancy component to calculate vertical velocity, but used only the vertical velocity of the fields from the hydrodynamic model. The configuration of the experimental simulations is illustrated in Figure 3.1. Once the model was initialized and the parameters set for each simulation, outputs from the hydrodynamic model were used as inputs to the IBM. A population of 5000 particles was then randomly released over the Agulhas Bank (i.e. all four sub-regions described earlier) during the 15 time steps of PLUME that reflect a spawning duration of one month. During the 90-day simulation period, the position of each particle was monitored. After every 9.6 h (5 times each 2-day time-step of PLUME), the vertical velocity of each particle was estimated according to the buoyancy scheme (for the buoyancy experiments) and according to the velocity field (for the Lagrangian experiment), and particles were individually moved to their new positions. Throughout the simulation, the IBM recorded the number and age of particles meeting the criteria for successful transport (see Chapter 2). Each individual simulation was run 3 times (i.e. 3 replicate sub-simulations).

axis. In the buoyancy scheme, the vertical velocity of particles are confined to within the Stokes' regime when the Reynolds number is less than < 0.5, indicating that viscous force dominate over frictional forces (Sundby, 1983). It is assumed that the vertical drag of the particle is in balance with the buoyancy forces, resulting in the terminal velocity (w_{egg}) that is a function of gravitational acceleration (g), sea water density (ρ_w), kinematic viscosity ($v = 0.01$ m^{2}s^{-1}), minor (d) and major (I) axis length and particle density (ρ_{part}).

$$w_{part} = w_{water} + \frac{1}{24} gd^2 \frac{\Delta \rho}{\rho_w} v^{-1} ln(\frac{2I}{d} + \frac{1}{2})$$
(3.1)

where :

$$\Delta \rho = \rho_{part} - \rho_w$$
(3.2)

and w_{water} is vertical velocity $\frac{dz}{dt}$ (where z is depth and t is time) of the hydrodynamic model. To assess the effect of variations in particle size and/or shape on vertical movement, a "shape parameter" describing three categories of particle size and shape was derived based on the relationship between their major and minor axes (Table 3.1). The categories selected for this parameter reflect a gradient in shape from prolate spheroids (simulating anchovy egg shape), and intermediate shapes to spherical eggs (simulating sardine eggs shape). The effect of these categories was used to assess the sensitivity of the model, and to link the shape parameter to selective advantages. Field measurements of the density of Cape anchovy eggs obtained using a density-gradient column method (Coombs, 1981) ranged from 1.021-1.027 g.cm^{-3} (van der Lingen, unpublished data). Values of egg density falling within this range were used in the experiments to ensure that the density parameter was a realistic one. The equations solved by the IBM to determine the velocities of particles in every time step were:

$$\frac{dx_{part}}{dt} = u_{water}$$
(3.3)

$$\frac{dy_{part}}{dt} = v_{water}$$
(3.4)

$$\frac{dz_{part}}{dt} = w_{part}$$
(3.5)

where u_{water} and v_{water} are the east-west and north-south components respectively of the velocity output of the PLUME model. The vertical position of the particles is determined by the terminal velocity of the particles and the ω_{water} from PLUME. The position of the particles at a given time was approximated with an Eulerian forward solution where $x_{part}(t)$, $y_{part}(t)$ and $z_{part}(t)$ are the 3-D positions of the particles at time t and $x_{part}(t+1)$, $y_{part}(t+1)$ and $z_{part}(t+1)$ are the positions of particles at time t+1, where:

3.4. COMPARING THE MODEL OUTPUT TO FIELD OBSERVATIONS

Outputs from the IBM experiments were compared with vertical and horizontal anchovy egg distribution patterns observed in the field. Data on the vertical distribution of anchovy eggs in the southern Benguela region is scarce, but IBM outputs were compared to vertical profiles of egg concentration along a line off the Cape Peninsula (called the SHutch Line in our model; Fig. 2.2a) provided by Shelton and Hutchings (1982). Horizontal particle distributions generated by the IBM were compared with egg data collected from the SARP Line. Model-derived patterns that closely resemble those observed in nature should enable a better understanding of the processes that lie behind such patterns (Grimm *et al.*, 1996).

3.5. RESULTS

3.5.1. Sensitivity analyses: Lagrangian experiment (No buoyancy added: model 1)

Area was the primary determinant of transport success (Table 3.2), with the WAB resulting in maximum transport success, followed by CAB_{Off} with the inshore and offshore EAB regions being the least successful (Fig. 3.2a). Depth of particle release had a less marked, but still significant effect on transport (Table 3.2), with maximum success associated with particles released nearest the surface (0-25 m) and decreasing with depth (Fig. 3.2b).

Table 3.2. General linear model applied to Lagrangian experiment output (No buoyancy added: model 1) for dependent variable transport success

General linear model	df	SS	MS	F	P	Explained variance (%)
Intercept	1	482369.2	482369.2	63631.1		
Single variable						
Year	4	8965.6	2241.4	295.7	S	1.0
Date	5	18258.4	3651.7	481.7	S	1.9
Area	3	492052.5	164017.5	21636.2	S	52.1
Depth	2	159505.2	79752.6	10520.5	S	16.9
Shape	2	0.0	0.0	0.0	NS	0.0
First level of interaction						
Area*Depth	6	82097.0	13682.8	1805.0	S	8.7
Second level of interaction						
Year*Date*Area	60	50220.7	837.0	110.4	S	5.3
Error	2828	21438.3	7.6			2.3
Total	3239	943550.2				

df = degrees of freedom, *SS* = Sum of squares, *MS* = Mean squares, *F* = f-ratio, *P* = probability, *S* = *P* < 0.001, *NS* = *P* > 0.05

A significant first order interaction between Depth and Area was also observed. In all spawning areas, a consistent trend of reduced transport success with increasing depth of release was apparent (Fig. 3.2c). This trend was most pronounced in both the inshore and offshore regions of the EAB, followed by the CAB_{off} and the WAB. Area, Depth and the Area*Depth interaction, together with a second order interaction between Year, Date and Area, explained 83.1% of the variance of the

3.5.2. Sensitivity analysis: buoyancy experiments

Buoyancy scheme applied to both egg and larvae stages (model 2). Particle Density was the most important single parameter determining transport success (Table 3.3), with a value of 1.025 g.cm^{-3} resulting in the maximum success (Fig. 3.3a). Area of spawning was the only other important single parameter. The WAB was the most successful spawning area, transport success decreasing as spawning moved eastward, being reduced for CAB$_{Off}$ and close to zero for the inshore and offshore regions of the EAB (Fig. 3.3b). Three important interactions were observed; the first order interactions Area*particle Density, Date*particle Density and a second order interaction between Date, Area and particle Density (Table 3.3). The interaction between particle Density and Area explained over a third of the variance in the GLM output (Table 3.3), indicating that the optimal particle Density was 1.025 (g·cm^{-3}) for the different spawning areas, with the exception of the EAB$_{off}$ where the optimal particle Density was 1.027 (g·cm^{-3}) (Fig. 3.3c). The variables and interaction terms listed below, together with the interactions accounted for 88.6% of explained variance, and the error term of the full model was 3.7% (Table 3.3). Visual examination of the residuals of transport success suggested a normal distribution.

Table 3.3. General linear model applied to the output of buoyancy experiment for egg and larvae stages (model 2) for dependent variable transport success

General linear model	df	SS	MS	F	P	Explained variance (%)
Intercept	1	156220.2	156220.2	25645.7		
Single variable						
Year	4	2316.4	579.1	95.1	S	0.1
Date	5	40315.4	8063.1	1323.7	S	2.0
Area	3	231366.9	77122.3	12660.7	S	11.5
Particle density	3	399150.2	133050.1	21842.0	S	19.9
Depth	2	7.3	3.7	0.6	NS	0.0
Shape	2	35.0	17.5	2.9	NS	0.0
First level of interaction						
Date*Particle density	15	116460.1	7764.0	1274.6	S	5.8
Area*Particle density	9	745782.6	82864.7	13603.4	S	37.2
Second level of interaction						
Date*Area*Particle density	45	241806.5	5373.5	882.1	S	12.1
Error	12200	74316.0	6.1			3.7
Total	12959	2003609.3				

df = degrees of freedom, *SS* = Sum of squares, *MS* = Mean squares, *F* = f-ratio, *P* = probability, *S* = *P* < 0.001, *NS* = *P* > 0.05

Table 3.4. General linear model applied to the output of buoyancy experiment for egg stages (model 3) for dependent variable transport success

General linear model	df	SS	MS	F	P	Explained variance (%)
Intercept	1	290845.5	290845.5	35909.8		
Single variable						
Year	4	6496.9	1624.2	200.5	S	0.4
Date	5	20104.4	4020.9	496.4	S	1.1
Area	3	368320.8	122773.6	15158.5	S	20.2
Particle density	3	319355.2	106451.7	13143.3	S	17.5
Depth	2	480.8	240.4	29.7	S	0.0
Shape	2	424.8	212.4	26.2	S	0.0
First level of interaction						
Date*Particle density	15	47200.8	3146.7	388.5	S	2.6
Area*Particle density	9	569879.2	63319.9	7817.9	S	31.3
Second level of interaction						
Date*Area*particle density	45	197031.1	4378.5	540.6	S	10.8
Error	12200	98811.8	8.1			5.4
Total	12959	1821782.5				

df = degrees of freedom, *SS* = Sum of squares, *MS* = Mean squares, *F* = f-ratio, *P* = probability, *S* = $P < 0.001$, *NS* = $P > 0.05$

3.5.3. Identification of scenarios and of particle density under different jet current scenarios:

Averaged jet current transport for three months calculated from the PLUME hydrodynamic model showed a strong linear relationship between along- and across-shore components. Strong northwards flow was associated with a strong offshore component, while weak northwards flow was associated with stronger inshore transport (Fig. 3.4a). Years 4, 5 and 6 were characterized by strong northwards and offshore transport, whereas onshore transport predominated in Years 7 and 8 (Fig. 3.4b). On the basis of these observations, three jet current scenarios were selected; Scenario 1 was characterized by strong northward offshore flow (January of Year 5), Scenario 2 by weak northward and offshore flow (December of Year 6) and Scenario 3 by weak northwards and strong onshore flow (March of Year 8). IBM simulations were run under each of these scenarios with varied particle Density values (1.021-1.027g.cm^{-3}) but all other values fixed (Area was the WAB and Depth of spawning was 0-25m). Maximum transport success was associated with particles having a density of 1.025 g.cm^{-3} in all three Scenarios (Fig. 3.4c) but was substantially higher for Scenario 1 (80%) than for Scenarios 2 and 3, which generated similar transport success values (~40%).

3.5.4. Comparing the model output to field observations: pattern-oriented analysis

The distribution of eggs along the SARP Line during the period September 1995 to March 2001 is characterized by relatively few eggs at the first five (inshore) stations and higher concentrations at stations 6-12, with peak egg concentrations at stations 6, 8 and 12 (Fig. 3.5a). In general terms, the simulation outputs from the three jet current scenarios showed similar patterns to the field observations, showing low concentrations inshore and high concentrations offshore (Fig. 3.5b-d). Under Scenario 1, a higher number of Lagrangian particles (neutrally buoyant) and virtual individuals having an intermediate density (1.025 $g.cm^{-3}$) would have been recorded at the SARP Line compared to particles either lighter or denser than 1.025 $g.cm^{-3}$ (Fig. 3.5b). Under Scenario 2, the maximum number of virtual individuals crossing the SARP Line was reduced by at least half compared to Scenario 1. Lighter particles (1.021 and 1.023 $g.cm^{-3}$) would dominate and denser particles (1.027 $g.cm^{-3}$) were not recorded there (Fig. 3.5c). The pattern of Scenario 3 is similar to that from Scenario 2 with lighter particles dominant, but with the difference that Lagrangian particles and those of intermediate density (1.025 $g.cm^{-3}$) were poorly represented (Fig. 3.5d).

Shelton and Hutchings (1982) showed that anchovy eggs were mostly distributed in the upper 50m of the water column, with a maximum concentration at 30m depth (Fig. 3.6a). Modeled particle vertical distribution patterns along the SHutch Line differed with particle Density, the lightest particles (1.021 and 1.023 g.cm^{-3}) being concentrated at the surface and the densest ranging between 60 and 130 m depth (Fig. 3.6b). In the model, neutrally buoyant particles and those with a density of 1.025 g.cm^{-3} showed vertical distributions that most closely resembled field observations.
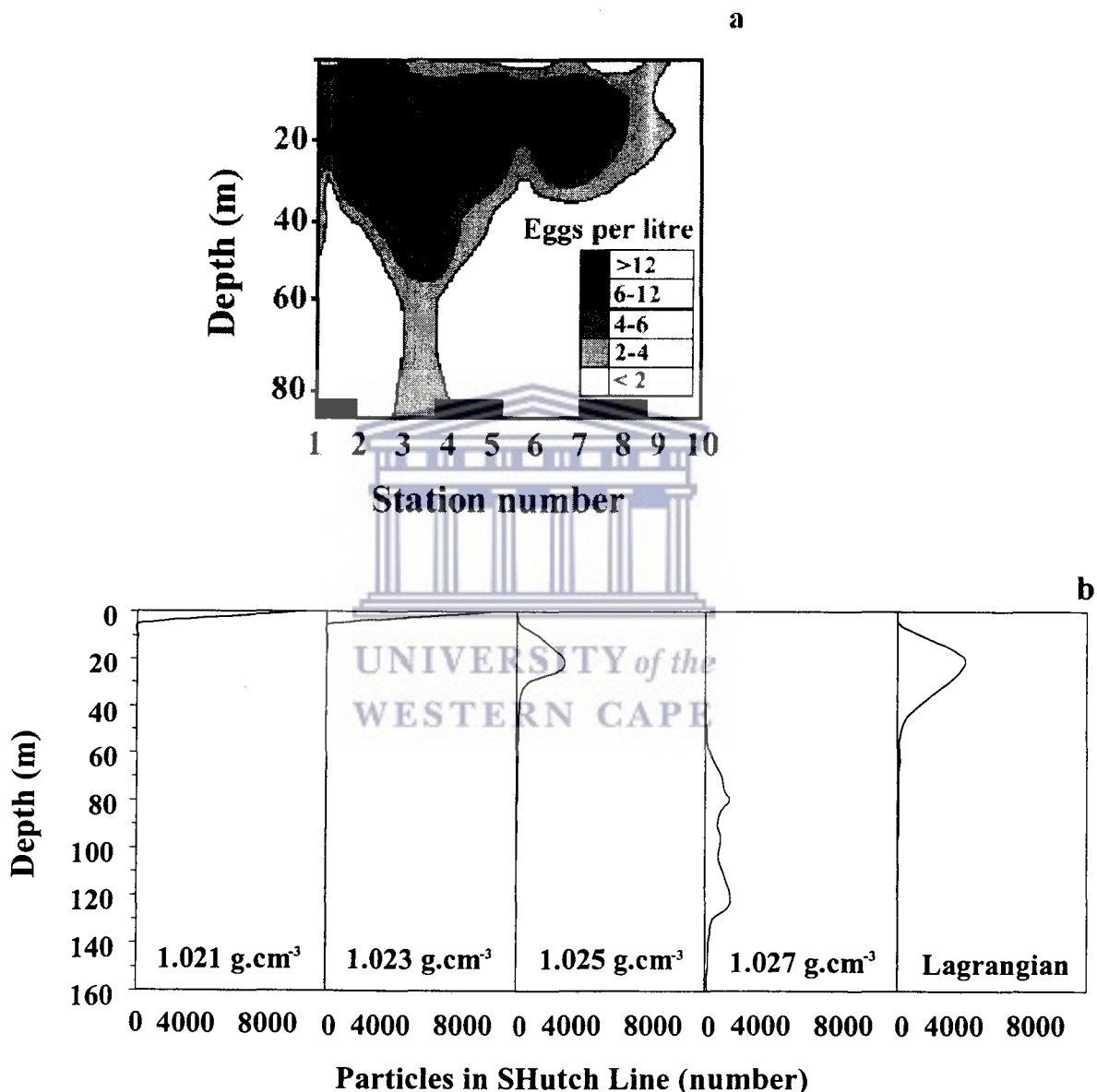

Figure 3.6. (a) Observed vertical distributions of anchovy eggs below the SHutch Line (Shelton and Hutchings, 1982), and (b) simulated vertical distributions of particles of varying densities in the SHutch Line.

and increased the percentage of variance explained by Area (from 11.5 to 20.2%). However, neither experiment is realistic, since larvae are not passive Lagrangian drifters (model 3) and eggs and larvae have variable densities (model 2). Tanaka (1990; 1992) has shown that the density of Japanese anchovy (*Engraulis japonicus*) eggs increases during their development from spawning to hatching, with early eggs being positively buoyant and late eggs/recently hatched larvae negatively buoyant. Similarly, Coombs *et al.* (1985) observed that pilchard (*Sardina pilchardus*) eggs increased in density during the later stages of development, so that by hatching a significant proportion of early larvae were denser than the ambient seawater.

One of the patterns to emerge from the buoyancy experiments is that on average, a density of 1.025 g.cm^{-3} promoted the most successful transport when particles were released over the WAB. That the WAB was the most successful spawning area in both passive Lagrangian and buoyancy experiments supports previous hypotheses (Shelton and Hutchings, 1982; Armstrong *et al.*, 1988; Boyd *et al.*, 1992; Roel *et al.*, 1994; Hutchings *et al.*, 1998) that anchovy spawn primarily over the WAB because of the increased probability of successful transport of eggs to the west coast nursery grounds. Similarly, other IBM studies examining anchovy egg transport in the southern Benguela system also identified the WAB as the optimum site for successful transport (Mullon *et al.*, 2002; Huggett *et al.*, 2003). However, almost to zero transport success for particles representing eggs released over the EAB was surprising, given that recent field observations have shown an eastward shift in anchovy spawning that has been followed by successful recruitment (van der Lingen *et al.*, 2002). In our simulations only the west coast was considered as a suitable nursery ground, and the failure of successful transport of particles representing eggs released over the EAB was due to advective losses offshore or individual particles remaining over the EAB or at least not reaching the nursery area within the 60-day period of particle tracking. Since anchovy larvae and early juveniles have been found off South Africa's south and east coasts (Anders, 1975; Beckley, 1986; Beckley and Hewitson, 1994), it is possible that these areas may also act as nursery grounds. This idea will be examined and discussed in chapter 5.

Another strong pattern observed was the change through time of jet current characteristics from the hydrodynamic model simulations. Between Years 5 and 8, transport changed from having strong northward and offshore components to having weak northward and strong onshore components. However, this change did not result in marked changes in annual average transport success for particles released over the WAB (Fig. 3.4c). This indicates that whereas strong northward transport moves substantial numbers of particles representing eggs towards the west coast, a large proportion of these are advected offshore. However, when the northward transport is reduced, the associated increased inshore transport means that most of the particles carried to the west coast make it into the nursery area. It appears that the transport success of particles representing eggs released over the CAB$_{Off}$, EAB$_{In}$ and EAB$_{Off}$ is not strongly coupled with jet current strength.

The vertical distributions obtained in simulations compared well with field observations from the SHutch Line for particles having a density of 1.025 g.cm^{-3} and Lagrangian particles. In

CHAPTER 4: MODELING THE EFFECTS OF TEMPERATURE ON THE GROWTH, MORTALITY AND TRANSPORT SUCCESS OF ANCHOVY EGGS AND LARVAE TO THE NURSERY GROUNDS

4.1. INTRODUCTION

According to the current understanding of the life history of *Engraulis encrasicolus,* eggs and larvae of anchovy spawned on the Agulhas Bank are transported to a remote nursery area located on the west coast of South Africa. The link between the Agulhas Bank and this nursery area is provided by a regular frontal jet that develops off Cape Point in spring/summer (Shelton and Hutchings, 1982; Armstrong *et al.,* 1988; Boyd *et al.,* 1992; Hutchings *et al.,* 1998). During transport, eggs and larvae are exposed to fluctuations in temperature resulting from spatial and temporal differences in the oceanographic processes on the Agulhas Bank, in the jet current and in the nursery area. The Agulhas Bank is bounded to the northwest by a cold, nutrient-rich upwelling regime, and to the east by the warm, nutrient-deficient Agulhas Current (Lutjeharms *et al.,* 1996). Temperature on the Agulhas Bank ranges between 14 and 21°C in spring and between 10 and 22°C in summer (Mitchell-Innes *et al.,* 1999). The optimal temperature range for spawning of anchovy has been identified as 16-19°C (Anders, 1965; King *et al,* 1978; Shelton, 1986; Richardson, 1998). In the jet current between Cape Peninsula and Cape Columbine, the temperature of upwelled water fluctuates between 8 to 10°C, while temperatures in excess of 18°C have been recorded in the adjacent oceanic waters (Shannon, 1985; Shillington and Nykjaer, 2002). A study using self-organizing maps to characterize sea surface temperature (SST) variability on the west coast of South Africa (i.e. the nursery area) showed that SST ranged between 13 and 17°C in spring, and between 14 and 20°C in summer (Richardson *et al.,* 2000). Anchovy larvae are unable to tolerate temperatures below 12°C (com. per. Hutchings), while egg incubation temperatures below 14°C inhibit development to the extent that larvae fail to develop a functional jaw (King *et al.,* 1978). The developmental rate of anchovy egg and larvae is temperature-dependent, increasing exponentially with increasing temperature. Warmer water will consequently accelerate metabolism, favoring individual growth but requiring more food. Conversely, cold water decreases metabolism to the detriment of individual growth. Several attempts to model the relationship between incubation time and temperature have been conducted (Smith, 1973; Lo, 1985; 1986; Le Clus and Malan, 1995). The rates of egg development and larval growth of *Engraulis mordax* at different temperatures were best described by a Gompertz-type curve, where growth rates tend to undergo exponential decay with time (Zweifel and Lasker, 1976; Methot and Kramer, 1979; Brownell, 1983).

The research described in this chapter uses an individual based modeling approach to address the question of how the effect of temperature on growth and mortality interacts with the transport of eggs and larvae to the nursery area. An individual based model (IBM), growth and mortality model (model 4), was consequently designed to examine the effects of temperature on the

4.2.2. Overview of the IBM experiments and simulations

The IBM was used to track the movement of particles representing anchovy eggs and larvae of optimal density (1.025 $g.cm^{-3}$) spawned on the Agulhas Bank and transported northwards to the west coast nursery area. This model incorporates a buoyancy scheme applied only to particles representing eggs (see Chapter 3) and retains the algorithm defining successfully transported individuals (i.e. individuals reaching the inshore and offshore areas of the west coast were considered to be successful). Two additional processes were also incorporated, namely growth and mortality of particles representing eggs and larvae as a function of temperature. Because this model distinguishes between stages of development, reference will no longer be made to "particles", but rather to "eggs" and "larvae".

Setting of constants and parameters for the experiment. Before running the experiment, the constants (egg density, shape of eggs, duration of tracking, duration of simulation and number of eggs released) were set (Table 4.1). The parameters in the IBM were changed for each individual simulation so that their effects could be tested using the GLM. The parameters (listed in Table 4.1) were Date (6 values) and Area (4 values) of spawning, Year of simulation (5 values), Depth of spawning (3 values), growth factor (λ= 5 values), lethal temperatures for eggs (θ_E = 3 values) and larvae (θ_L = 3 values). Three replicates of each simulation were run, which, with all the combinations of the parameters (except Area of simulation for which the 4 values of the parameter were tested simultaneously in each simulation) generated a total of 6 x 5 x 3 x 5 x 3 x 3 x 3 = 12150 simulations for the experiment (Table 4.1).

Configuration of the experiment. The configuration of the model is illustrated in Figure 4.2. Prior to each simulation, the model was initialized and the parameters set, after which outputs from the hydrodynamic model (temperature, salinity and velocity field) were used as inputs to the IBM. A population of 5000 eggs was then randomly released in WAB, CAB_{Off}, EAB_{In}, EAB_{Off}, (based on field observations of anchovy egg distribution, see van der Lingen *et al.*, 2001). The spawning duration (30 days) determined the period over which new eggs entered the population (Table 4.1). The six dates retained for each spawning were: 1st October, 1st November, 1st December, 1st January, 1st February and 1st March, corresponding to most of the spawning season. Each simulation was run for a period of 90 days, during which the position, length and stage of development of each individual in the IBM was monitored each 9.6h (5 times each 2-day time step of PLUME, Table 4.1). Once individuals hatched, larval movements were purely Lagrangian. Details of the buoyancy scheme and the model set up are provided in Chapter 3. Eggs and larvae were subjected to mortality resulting from lethal temperature values, and at every 9.6 h temperature-dependent growth scheme was applied to the eggs and larvae. The model recognized two stages of individual: eggs and early larvae (up to the pre-feeding state). The mortality and growth of eggs and larvae is assumed to be purely dependent on temperature. The model therefore allows for two possible events for each of the
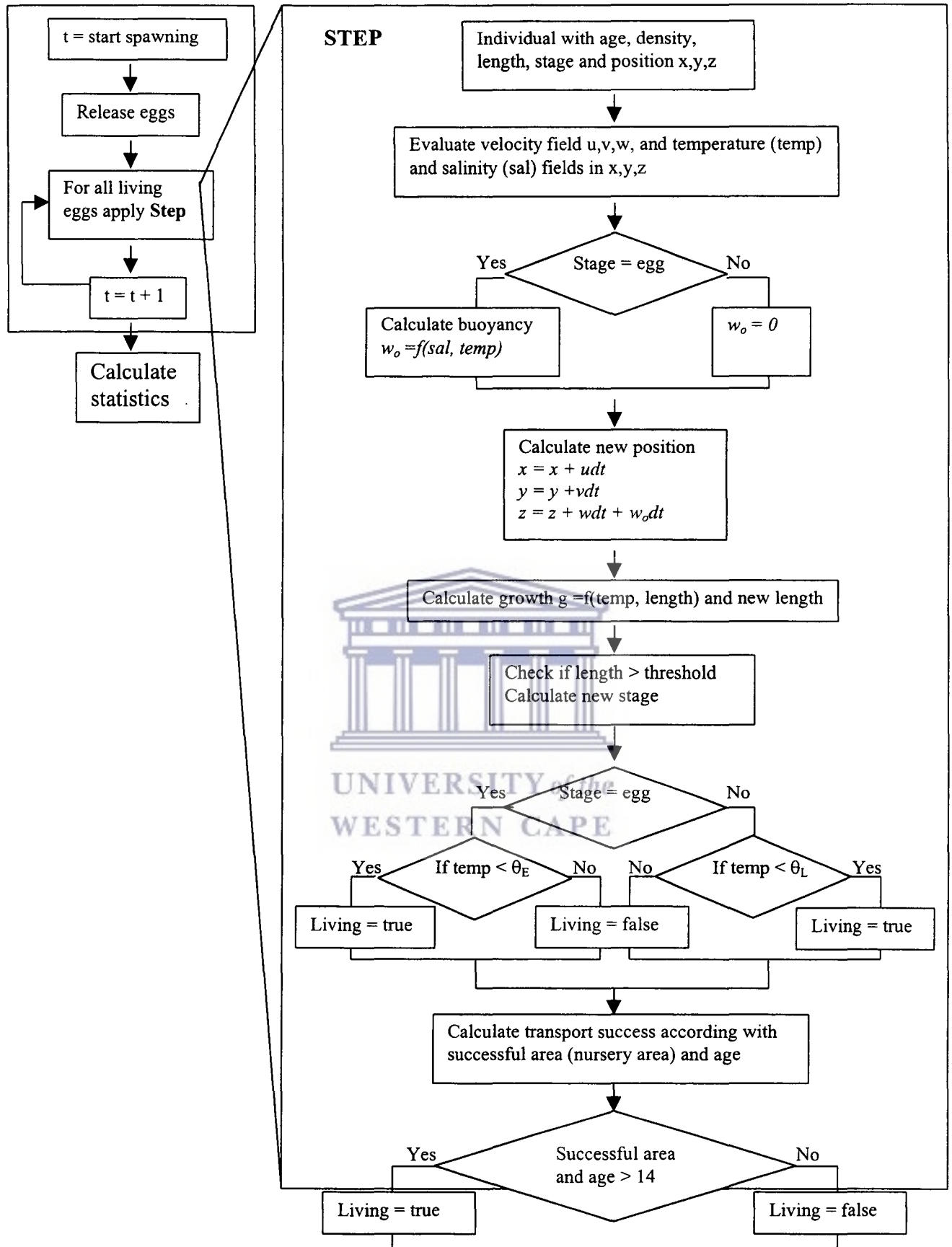
Figure 4.2. Flowchart of experimental simulations of growth and mortality model: general algorithm (left), and the details of the process simulating movement, growth, mortality and transport success (right).
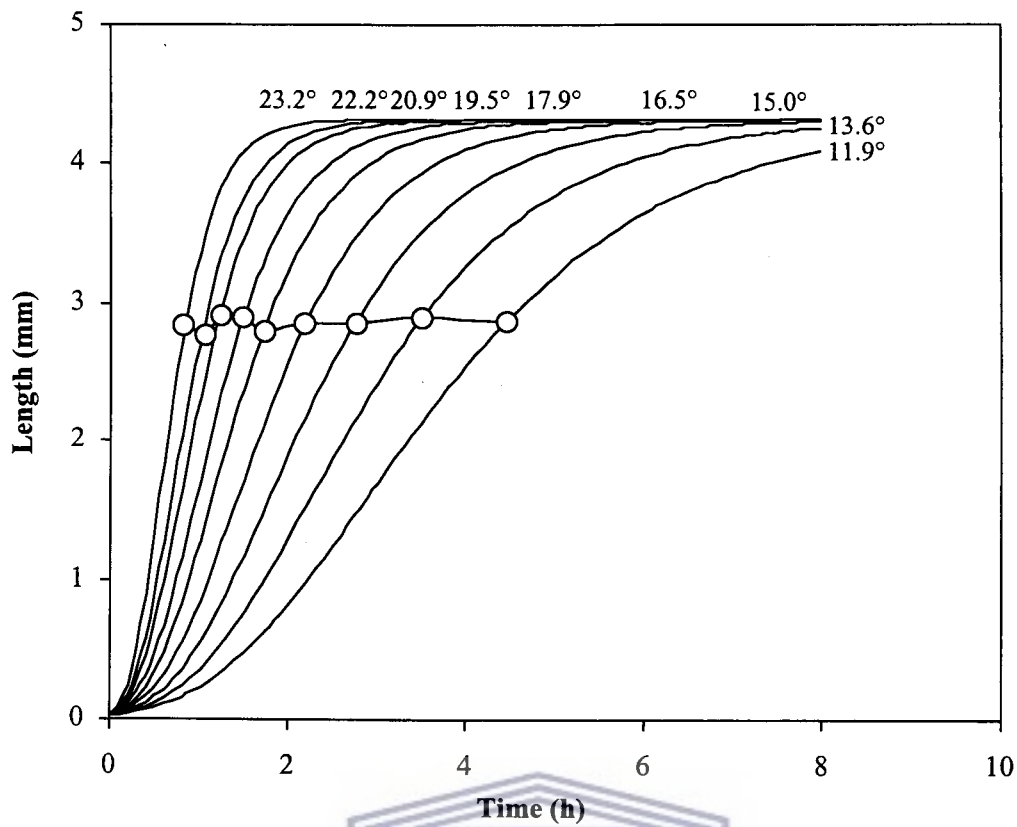
Figure 4.3. Gompertz model of Cape anchovy growth as a function of temperature. Circles indicate the hatching length at incubation time under different temperature conditions according the experiments of King *et al.* (1978).

The equation (Equation 4.1 above) provided by Zweifel and Lasker (1976) has two terms with a double exponential. This equation was simplified by linearization to reduce complexity in the simulation processes. α_T (illustrated with circles in Fig. 4.4) was fitted to a linear relation:

$$\alpha_T = nT - c .$$ (4.3)

The parameters of the equation are $n = 0.2041$ and $c = 2.0833$ with a correlation of $R^2 = 0.95$. Different values of α_T were calculated to test the effect of growth:

$$\alpha_T = \lambda(nT - c)$$ (4.4)

where λ is the growth factor that was assigned 5 different values to either decelerate (0.5, 0.8) or accelerate (1.2 and 1.5) the growth rate, and $\lambda = 1$ represents the original, linearized relationship between α_T and temperature. λ values of 1.5 and 1.2 would consequently represent increases in the

The numerical solution of equation 4.1 (equation 4.5), the first and the second derivative (equations 4.6 and 4.7) for a temperature of 15.1°C, and the analytical solution obtained by equation (4.1) are shown in Figure 4.5. Because the solution of equation 4.5 is dependent on the time step employed, a maximum time step (Δt) of 0.25 days must be selected to ensure good approximation. Using time steps in excess of 0.25 days results in unacceptable deviations of the numerical solution of equation (4.5) from the analytical solution.
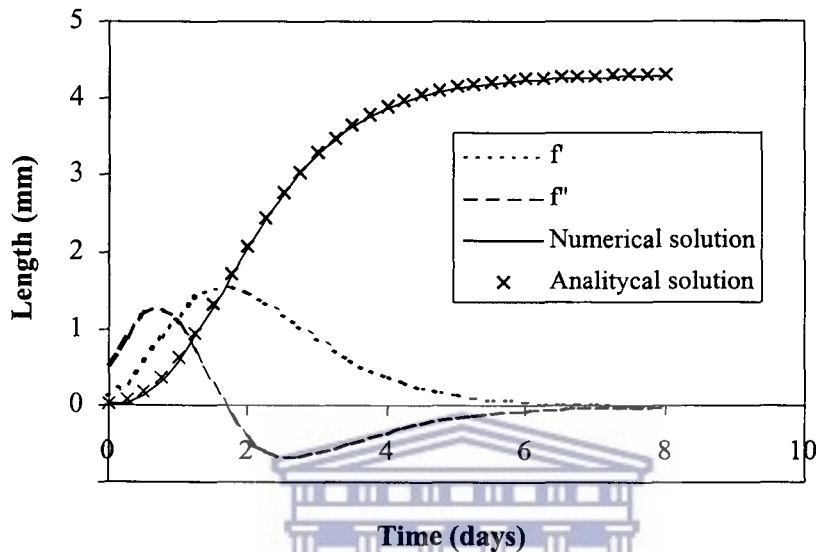

Figure 4.5. The numerical and analytical solution of equation 4.1, the first (f') and the second derivative (f'') for a temperature of 15.1°C using Δt = 0.25 days.

4.2.4. Statistical analysis of the IBM outputs

A sensitivity analysis was applied to the response (dependent) variables of the IBM, namely egg mortality, larval mortality and transport success (Table 4.1) using a multiple factor variance analysis from the GLM module of the Statistica package (StatSoft, 2000). The parameters and their interactions were considered to be the independent variables in the sensitivity analyses. To analyze the egg and larval mortality variables, a full GLM was run including all the parameters and their interactions up to the second level, and those that explained more than 5% of the variance. For the dependent variable "transport success", two GLMs were run. Firstly, a model that included up to the first level of interactions (full GLM), and secondly a sub-optimal model that included up to the second level of interactions and only single parameters that explained more than 2% of the variance. The reason for this procedure was that the full GLM presented a high degree of error, requiring that a sub-optimal GLM including the second level of interactions be used. The frequency distribution of the residuals of the three dependent variables, as well as the significance and proportion of variance explained by each of the parameters and their interactions were also computed during the sensitivity analysis. These results permitted the identification of the main variables that impacted on egg and
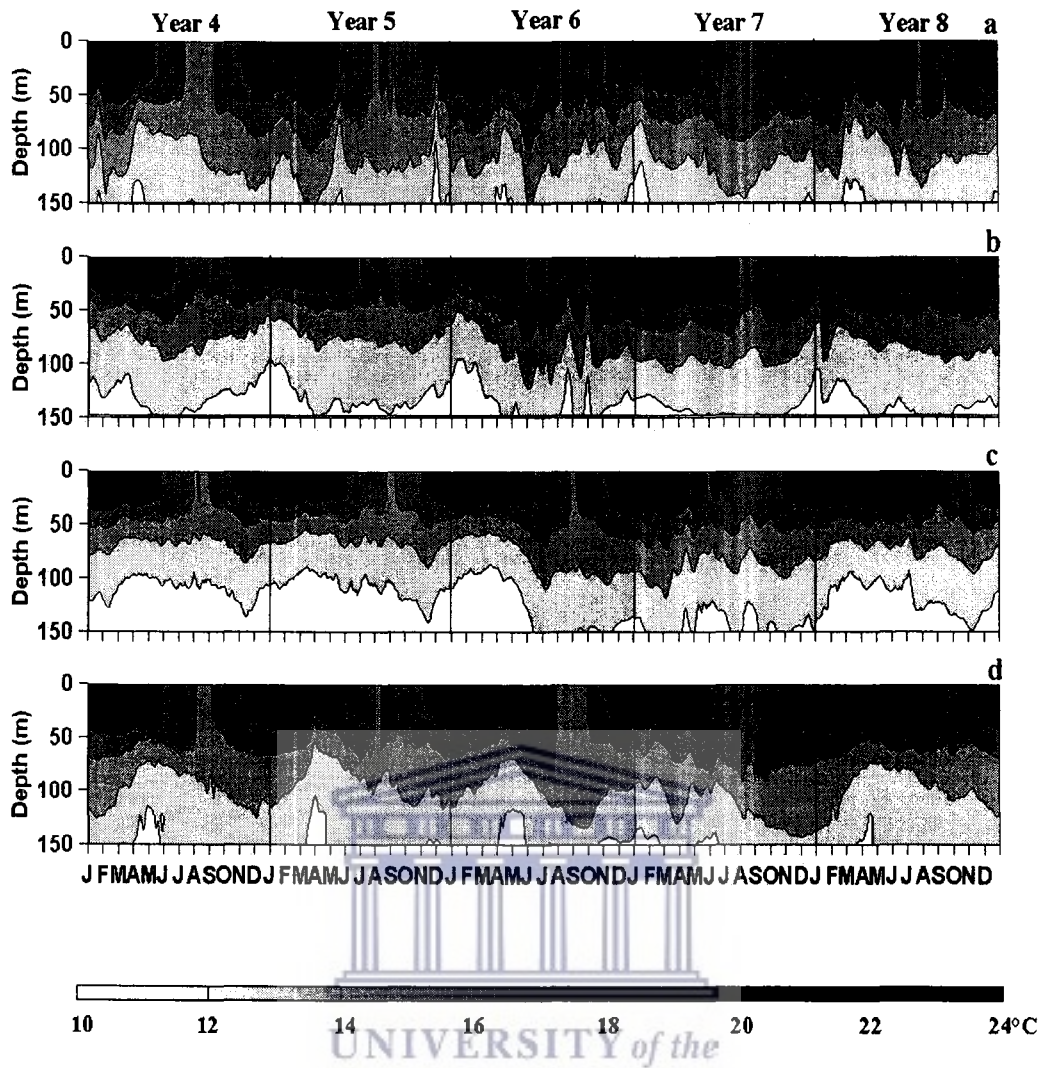
Figure 4.6. Temperature profiles in 4 localities in the Agulhas Bank (a) WAB, (b) CAB_{Off}, (c) EAB_{Off}, (d) EAB_{In} extracted from PLUME. See Fig. 4.1 for localities.

A similar general seasonal and annual pattern was observed at the stations located in the nursery area, west coast and jet current. Stratification of the water column began in late December and lasted until June, earlier than on the Agulhas Bank area, with a well mixed water column between June-December and a deeper extension of the mixing (Fig. 4.7). Nur1 station departs remarkably from the others (Fig. 4.7a), in that the water column was characterized by temperatures less than 14°C at depths greater than 50 m, except during the period of intense mixing where these temperatures are found from the surface (Nur1 station is very shallow with maximum depth of 150 m). In the southern stations (Nur2, Nur3 and the jet current), the temperature increased and the stratification of the water column was more intense (Fig. 4.7b, c and d respectively).

with an error term of only 11.7% (Table 4.2). Visual examination of the residuals of egg mortality index suggested a normal distribution.

Table 4.2. General linear model applied to the output of the growth and mortality IBM (model 4) for dependent variable eggs mortality index

General Linear Model	df	SS	MS	F	P	Explained variance (%)
Intercept	1	23791010.3	23791010.3	308462.6		
Single variable						
Year	4	172073.4	43018.4	557.8	S	0.5
Date	5	3862296.5	772459.3	10015.3	S	12.1
Area	3	111717.9	37239.3	482.8	S	0.4
Depth	2	9837473.6	4918736.8	63773.9	S	30.9
Growth factor λ	4	204663.7	51165.9	663.4	S	0.6
Lethal temp. for eggs θ_E	2	2306624.9	1153312.4	4953.3	S	7.2
Lethal temp. for larvae θ_L	2	0.0	0.0	0.0	NS	0.0
First level of interaction						
Date*Depth	10	4764164.6	476416.5	6177.0	S	14.9
Depth* θ_E	4	2441725.8	610431.4	7914.6	S	7.7
Error	48374	3730974.7	77.1			11.7
Total	48599	31875186.1				

df = degrees of freedom, SS = Sum of squares, MS = Mean squares, F = f-ratio, P = probability, S = $P < 0.001$, NS = $P > 0.05$

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4.3.3. Sensitivity analysis: Larval mortality index

Area of spawning was the primary determinant of larval mortality (Table 4.3), with the WAB having the maximum effect on larval mortality, followed by CAB_{Off}, EAB_{In} and EAB_{Off} (Fig. 4.9a). Depth, Date of spawning and Year of simulation had a less marked, but still significant, effect on the larval mortality (Table 4.3), with the maximum mortality associated with larvae that develop from eggs from December to March (Fig. 4.9b) in Years 6 to 8 (Fig. 4.9c). θ_L, λ and θ_E were all significant variables, but explained less than 5% of the variance of the model. The Year*Date and Date*Area first level of interactions explained an important part of the variance (Table 4.3), while Area, Depth, Date, Year and the interactions listed in Table 4.3 collectively explained 70.0% of the variance of the model, with an error term of only 17.0% (Table 4.3). Visual examination of the residuals of larval mortality index suggested a normal distribution.

Table 4.3. General linear model applied to the output of the growth and mortality IBM (model 4) for dependent variable larval mortality index

General Linear Model	df	SS	MS	F	P	Explained variance (%)
Intercept	1	29390949.6	29390949.6	331795.7		
Single variable						
Year	4	1019292.3	254823.0	2876.7	S	4.1
Date	5	642280.3	128456.0	1450.1	S	2.6
Area	3	11246471.1	3748823.7	42320.6	S	44.7
Depth	2	182833.6	91416.8	1032.0	S	0.7
λ	4	46744.0	11686.0	131.9	S	0.2
θ_E	2	88113.6	44056.8	497.3	S	0.4
θ_L	2	475053.9	2375326.9	2681.4	S	1.9
First level of interaction						
Year*Date	20	2377014.1	118850.7	1341.7	S	9.4
Date*Area	15	1468277.9	97885.1	1105.0	S	5.8
Error	48374	4285039.9	88.58			17.0
Total	48599	25160980.7				

df = degrees of freedom, *SS* = Sum of squares, *MS* = Mean squares, *F* = f-ratio, *P* = probability, *S* = *P* < 0.001, *NS* = *P* > 0.05

4.3.4. Sensitivity analysis: Transport success (optimal GLM)

Area (of spawning) was the primary determinant of transport success (Table 4.4), with the WAB being the most important area for successful transport, followed by CAB_{Off}, EAB_{In} and EAB_{Off} (Fig. 4.10a). Date of spawning, Year of simulation, Depth and θ_L had less marked, but still significant effects on the transport success (Table 4.4). Maximum transport success was observed for eggs spawned from October to December (with a peak in November, Fig. 4.10b) in Year 7 (Fig. 4.10c) at the surface (Fig. 4.10d) with a high resistance to low temperatures (threshold <11°C, Fig. 4.10e). The growth factor λ and temperature threshold for eggs θ_E were significant parameters, but explained less than 5% of the variance of the model. The Year*Date and Date*Depth first level of interactions explained an important part of the variance (Table 4.4). Collectively, Area, Date, Year, Depth and θ_L and the interaction listed in Table 4.4 explained 56.6% of the variance of the model, with a relatively high error term of 32.9% (Table 4.4). Due to the large error of this optimal model, a sub-optimal model was used, retaining only the single variables that explained more than 2% of the model and adding a second level of interaction (see section 4.2.4).

Table 4.4. General linear model for applied to the output of the growth and mortality IBM (model 4) for the dependent variable transport success

General Linear Model	df	SS	MS	F	P	Explained variance (%)
Intercept	1	1813601.7	1813601.7	83186.4		
Single variable						
Year	4	257548.0	64387.0	2953.3	S	8.0
Date	5	303570.0	60714.0	2784.8	S	9.5
Area	3	725241.3	241747.1	11088.5	S	22.6
Depth	2	91064.9	45532.5	2088.5	S	2.8
λ	4	10683.1	2670.8	122.5	S	0.3
θ_E	2	5145.6	2572.8	118.0	S	0.2
θ_L	2	69519.0	34759.5	1594.4	S	2.2
First level of interaction						
Year*Date	20	191250.1	9562.5	438.6	S	6.0
Date*Depth	10	159612.5	15961.2	732.1	S	5.0
Error	48374	1054634.1	21.8			32.9
Total	48599	3206130.1				100

df = degrees of freedom, *SS* = Sum of squares, *MS* = Mean squares, *F* = f-ratio, *P* = probability, *S* = *P* < 0.001, *NS* = *P* > 0.05

4.3.5. Sensitivity analysis: Transport success (sub-optimal GLM)

This sub-optimal model showed the same pattern as the previous model. However adding the second levels of interaction Year*Date*Area and Date*Area*Depth explained 14.4% and 6.3% of the variance respectively (Table 4.5). Collectively, Area, Date, Year, Depth and θ_L and the first and second level of interactions listed in Table 4.5 explained a total of 76.8% of the variance of the model, with a lower model error of 11.8% (Table 4.5).

Table 4.5. Sub-optimal General linear model applied to the output of the growth and mortality IBM (model 4) for the dependent variable transport success

General Linear Model	Df	SS	MS	F	P	Explained variance (%)
Intercept	1	1813601.7	1813601.7	231220.6		
Single variable						
Year	4	257548.0	64387.0	8208.9	S	8.0
Date	5	303570.0	60714.0	7740.6	S	9.5
Area	3	725241.3	241747.1	30820.9	S	22.6
Depth	2	91064.9	45532.5	5805.0	S	2.8
θ_L	2	69519.0	34759.5	4431.6	S	2.2
First level of interaction						
Year*Date	20	191250.1	9562.5	1219.1	S	6.0
Date*Depth	10	159612.5	15961.2	2034.9	S	5.0
Second level of interaction						
Year*Date*Area	60	460088.1	7668.1	977.6	S	14.4
Date*Area*Depth	30	201517.2	6717.2	856.4	S	6.3
Error	48188	377967.4	7.8			11.8
Total	48599	3206130.1				100

df = degrees of freedom, *SS* = Sum of squares, *MS* = Mean squares, *F* = f-ratio, *P* = probability, *S* = *P* < 0.001, *NS* = *P* > 0.05

4.4. DISCUSSION

The effect of temperature on the mortality and growth of anchovy egg and larvae during transport from the spawning grounds on Agulhas Bank to the nursery area on the west coast was studied using an individual based modeling approach. By varying biological parameters such as the lethal temperature threshold for eggs and larvae and the growth factor as well as the spatio-temporal location of the particle released, it was possible to examine the importance of these parameters on the mortality of eggs and larvae and the subsequent transport success of larvae. There is an apparent contradiction in the results: the conditions that favor the transport success of larvae, such as Area of egg released (WAB) and spawning Date (October), are the same parameters that increase the larvae mortality index. This is because there is a spatio-temporal component associated with larval survival that is related to processes that characterize the temperature of the water column. Eggs released in the surface layers (<25m) of the WAB are rapidly transported to the nursery areas where the low temperatures associated with the upwelling centers are lethal for them. In contrast, if eggs are released too deep in the water column (>50 m), transport to the nursery area is slow, preventing that

constraints in the IBM, the egg and larvae vertical profiles resulting from the simulations showed a more realist distribution, demonstrating the importance of temperature as a factor controlling the distribution and mortality of eggs and larvae. Field observations of the northern part of the west coast between Cape Columbine (32°30'S) and the Cunene river (17°30'S), showed that daily growth rates were positively correlated with temperature. Larval growth was slower at inshore stations where cool upwelled waters were present (Thomas, 1986). The advection of larvae offshore may be beneficial in increasing the growth rate, but may also contribute to increased mortality as a result of dispersal (Parrish *et al.*, 1981). Other modeling attempts have demonstrated the importance of spawning location and timing in successful transport to nursery areas for anchovy as well as other species (Hinckley *et al.*, 2001; Mullon *et al.*, 2002; Huggett *et al.*, 2003; Parada *et al.*, in press). IBMs run for other regions have also included the relationship between length-specific growth rate, age, and environment using temperature as a proxy, but mortality was not taken into account (Heath and Gallego, 1997). Bartsch (2002) used a logistic growth curve aiming to incorporate a temperature dependent function into this curve. This growth formulation was used to model mackerel larval growth in a biophysical transport model, but mortality was excluded. Our study represents one step forward because not only we considered buoyancy of eggs and the effect of temperature on individual growth, but also the mortality effects due to temperature for eggs and larvae. Other source of mortality for eggs and larvae in the southern Benguela region have been attributed to factors such as predation (Fraser, 1970; Hunter and Kimbrell, 1980), starvation, disease and cannibalism (Brownell, 1983; Lasker, 1985; Alheit, 1987; Brownell, 1987; Valdés *et al.*, 1987). However, the problem is to devise a representation that retains sufficient of the spatial and temporal dynamic of the system and also a simplified configuration in the model to permit a comprehensive sensitivity analysis. The inclusion of mortality and growth as a function of temperature is an innovation of the IBM that permits an insight into environment effects on both individuals and the entire population in the southern Benguela system. Furthermore, the simplicity of the IBM design and the step by step approach make it possible to discriminate factors and processes really fundamental in the IBM, reducing the number of variables tested in the GLM analysis and thereby simplifying the interpretation process. This model might seem simplistic, because the effect of temperature on many pelagic species has been well documented in literature. However, this is the first attempt using a spatially-explicit individual-based model that considers both temperature-dependent growth and mortality. The contribution of this study arises from the analysis of the individual temperature effects assessed for the whole modeled population, in a context where temperature has a high spatial and temporal resolution. Furthermore, the mortality effect on eggs and larvae due to temperature can be linked to oceanographic features that have particular spatial and temporal characteristics.

products from the spawning ground on the WAB to the nursery area will result in enhanced recruitment. Recent studies have, however, indicated a shift in the major spawning area of anchovy from the WAB to the Central (CAB) and Eastern Agulhas Bank (EAB) since the mid 1990's (van der Lingen *et al.*, 2002). It should also be noted that anchovy recruitment during the period 1999 to 2001 has been exceptionally high (van der Lingen *et al.*, 2001; Barlow *et al.*, 2002; Roy *et al.*, 2002) in spite of the shift in spawning areas to regions generally considered to be unfavorable. An interesting paradox is apparent in this regard (Wilhelm, 2002) in that the high levels of recruitment that were detected during the 2000/2001 recruit surveys (conducted along the west and south coasts in May-June each year) were not reflected in the relatively low densities of pre-recruits observed during the 2000 pre-recruit survey (conducted only along the west coast in March each year). This observation suggests the presence of an alternative nursery area other than the west coast, the most obvious candidate being the inshore areas of the EAB.

The research presented in this chapter consequently has two objectives: (1) to study the potential benefits of vertical migration behavior in the context of the onshore-offshore circulation on the west coast upwelling area for the transport of larvae and post-larvae to the nursery area, (2) to study the effects of vertical migration behavior on the retention of larvae and post-larvae on both the west coast and the Eastern Agulhas Bank.

5.2. METHODS

In the previous chapters, the combined effect of spawning date, location, and the influence of the egg buoyancy on transport success were explored, after which, the impact of temperature on the growth, and mortality of eggs and larvae were incorporated. In this chapter, a new process simulating vertical behavior of larvae (from 3 days) and post-larvae (up to 3 months) on the west coast is incorporated into the design of the IBM. Two comparative analyses were performed:

(1) The first was directed at assessing the potential effects of vertical migration behavior on the transport success of larvae and post-larvae to the nursery areas, west coast, coming from eggs spawned in Agulhas Bank,

(2) The second analysis focused on the effects of such behavior on the retention of larvae and post-larvae in both the west coast and potential Eastern Agulhas Bank (EAB) nursery areas.

5.2.1. Modeling the effect of vertical migration on transport success.

To study the influence of vertical migration behavior on transport success, two individual based models (IBMs) were employed, namely a passive and an active behavior model. The passive behavior model (model 5) was used to study the link between the vertical current structure associated with upwelling and the passive transport of larvae and post-larvae to the inshore part of the west coast nursery area. In contrast, the active behavior model (model 6) assessed the potential of active

Table 5.1. Constants set to the passive and active behavior IBMs (models 5 and 6) and active retention IBMs applied to the west coast nursery area (model 7) and the EAB (model 8)

Constants	Description
Spawning duration	Spawning is a constant process starting on the first day of simulation and lasting 30 days
Tracking duration	All particles representing eggs were tracked until the age of 60 days
Duration of simulation	Every simulation was run over 90 days (Spawning duration + Tracking duration)
Number of eggs	The number of particles was set to 5000 per simulation. These particles were released continuously over the Spawning duration
Egg density	The density of eggs was set in the model to 1.025 $(g.cm^{-3})$
Shape	The shape of the eggs tested in the model was using the relationship of minor to major axis for a prolate spheroid to 0.05:0.14 cm
Lethal temperature for eggs	The lethal temperature (θ_E) for eggs were set to <14°C
Lethal temperature for larvae	The lethal temperature (θ_L) for larvae were set to <12°C
Factor of growth	The factor of growth (λ) was set to 1

For both the passive and active behavior models, the parameters Area (4 values), Date of spawning (6 values), Year (5 values), Depth of spawning (3 values), and trials (each simulation was launched 3 times) were employed (Table 5.2). Two additional parameters were incorporated into the active behavior model, specifically: Lag in active behavior $(\tau_L = 4$ values) and Depth of active behavior $(\delta_L = 6$ values) (see Table 5.2 for details).

Table 5.2. Parameters set for the passive and active behavior (models 5 and 6) and active retention IBMs applied to the west coast nursery area (model 7) and the EAB (model 8)

Parameters	Description	Model
Area	Eggs were released over all 4 spawning areas (Western Agulhas Bank (WAB), Central Agulhas Bank offshore (CAB_Off), Eastern Agulhas Bank inshore (EAB_In) and offshore (EAB_Off), proportional to the relative size (in km^2) of each area	5-6
Date	The dates of spawning were set to 1st October, 1st November, 1st December, 1st January, 1st February and 1st March	5-8
Year	Years 4-8 from PLUME (Penven, 2000) were used in the IBM	5-8
Depth	Eggs were released at 3 depth ranges (0-25, 25-50 and 50-75 m), and randomly distributed in the water column over the specified range	5-8
Lag in the active behavior	The initiation of active behavior (τ_L) subsequent to hatching was set at 4, 6,8, and 10 days	6,7*, 8*
Depth of active behavior	Preferred larval depth (δ_L) is fixed after the start of active behavior, and is set to 5, 20,40,60,80 and 100 m	6-8

*Active retention models (models 7 and 8) use a parameter τ_L as a constant with a value equal to 1 day

5.2.5. Response variables: transport success, mortality of eggs and larvae, and retention

In both the active and passive behavior transport models, the primary response variable was transport success, defined as the ratio of the number of larvae that satisfied the criteria for transport success at the end of the simulation, to the number of eggs released (Table 2.3). Note that transport was only considered to be successful when the larvae reached the "inshore part" of the nursery area (Fig. 2.4). The active behavior model also incorporated two other response variables, namely egg mortality and larval mortality indices. The former was defined as the proportion of released eggs that died as a result of lethal temperatures during the simulations, relative to the number of eggs released, while the latter was defined as the number of larvae that died due to the temperature effect relative to the number of surviving eggs to temperature effects (Table 2.3). These three response variables were used as the dependent variables in the subsequent statistical analyses.

In the active retention models (models 7 and 8) the primary response variable was the dependent variable "retention", defined as the number of larvae and post-larvae with active behavior that were retained in the specified area for longer than 10 days relative to the total number of eggs released.

5.2.6. Averaged transport across-shore in the nursery area

Across-shore transport in the nursery area was analyzed from the output of the hydrodynamic model (PLUME). Time series of across-shore transport, integrated over the first 10 m depth, were computed along three transects located 100 km from and parallel to the coastline of the west coast, for each model year (Years 4-8). In the absence of high variability of winds, the integration of transport over the first 10 m intends to monitor the direction and the volume of water per second associated to Ekman transport. Transects located from the northern to the southern part of the nursery grounds were named transects Nur1, Nur2, and Nur3 (Fig. 5.1), and were selected to represent the transport region associated with the upwelling centers of the west coast.

recruits, the size classes corresponding to age intervals of <31 days, 31 to 54 days, >54 to 81 days and >81 days respectively.

5.3. RESULTS

5.3.1. Time series of across-shore transport on the west coast

Across-shore transport (integrated over the first 10 m depth) appears to increase with latitude, characterized by offshore transport in the northern part of the nursery area and onshore transport further south (Fig. 5.2). Transect Nur1 shows the strongest offshore transport, intensifying from December to February in all the simulated years (Fig. 5.2a). In contrast, transects Nur2 and Nur3 generally display onshore transport with brief periods of offshore transport (Fig. 5.2b and c). Transect Nur2 shows an intensification of offshore movement during the periods September to November in Year 4, February to April in Years 5 and 8, and January-March in Years 6 and 7 (Fig. 5.2.b). Transect Nur3 shows a pattern characterized by a weakening of inshore transport during the period March to June, with the peak of offshore transport in May (Fig. 5.2c).
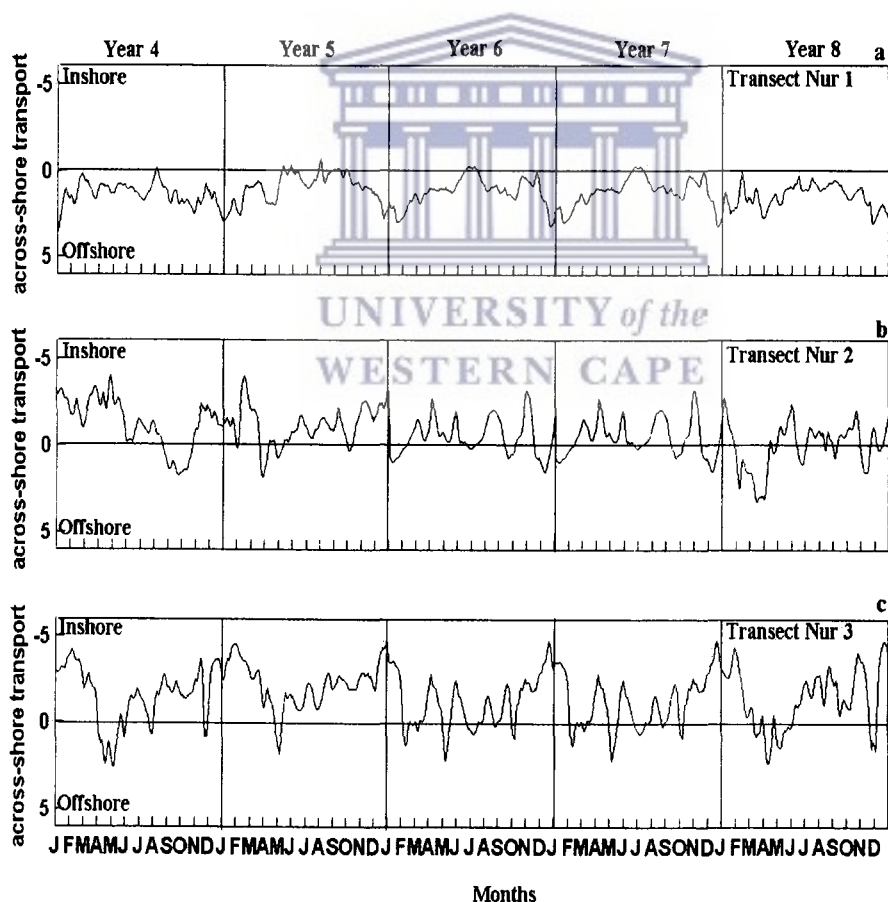
Figure 5.2. Across-shore transport (x 10^6 m^{3}s^{-1}) estimated from PLUME output in the west coast nursery area along transects (a) Nur1, (b) Nur2 and (c) Nur3 (see Fig. 5.1 for details of position of transects).

Table 5.3. General linear model applied to passive behavior model output for the dependent variable transport success in the inshore area (model 5).

General Linear Model	df	SS	MS	F	P	Explained variance (%)
Intercept	1	383.8	383.8	418.6		
Single variable						
Year	4	307.1	76.8	83.7	S	11.7
Date	5	123.1	24.6	26.9	S	4.7
Area	3	242.8	80.9	88.3	S	9.2
Depth	2	189.7	94.9	103.5	S	7.2
First level of interaction						
Year*Date	20	196.6	9.8	10.7	S	7.5
Date*Area	15	133.7	8.9	9.7	S	5.1
Year*Depth	8	153.7	19.2	21.0	S	5.8
Area*Depth	6	163.0	27.2	29.6	S	6.2
Error	994	911.4	0.9			34.6
Total	1079	2631.8				

df = degrees of freedom, SS = Sum of squares, MS = Mean squares, F = f-ratio, P = probability, $S = P < 0.001$, $NS = P > 0.05$

5.3.3. Sensitivity analysis of the active behavior model (model 6): Egg mortality index

Depth of spawning was the primary determinant of egg mortality (Table 5.4), with spawning depths between 50-75 m resulting in the highest egg mortalities (Fig. 5.4a). Date of spawning was the second most significant factor, with the highest mortalities apparent in eggs spawned in October (Fig. 5.4b). Year and Area also had significant effects, but did not explain much of the model variance (Table 5.4). Neither Depth of active behavior (δ_L) nor Lag of active behavior (τ_L) had a significant effect, and neither parameter explained an important proportion of the variance. The Date*Depth interaction explained close to 26% of the variance (Table 5.4). In combination, Depth, Date and the interaction Date*Depth explained a total of 75.1% of the variance in the model, with an error term of 11.2% (Table 5.4).

Table 5.4. General linear model applied to active behavior model for the dependent variable egg mortality index (model 6).

General Linear Model	df	SS	MS	F	P	Explained variance (%)
Intercept	1	13526670.5	13526670.5	242591.8		
Single variable						
Year	4	149394.4	37348.6	669.8	S	0.9
Date	5	1880828.8	376165.8	6746.3	S	11.7
Area	3	74977.9	24992.6	448.2	S	0.5
Depth	2	5843387.1	2921693.6	52398.6	S	36.5
δ_L	5	2.5	0.5	0.0	NS	0.0
τ_L	4	4.8	1.2	0.0	NS	0.0
First level of interaction						
Date*Depth	10	4086416.3	408641.6	7328.7	S	25.5
Error	32159	1793152.9	55.8			11.2
Total	32399	16007870.7				

df = degrees of freedom, SS = Sum of squares, MS = Mean squares, F = f-ratio, P = probability, $S = P < 0.001$, $NS = P > 0.05$
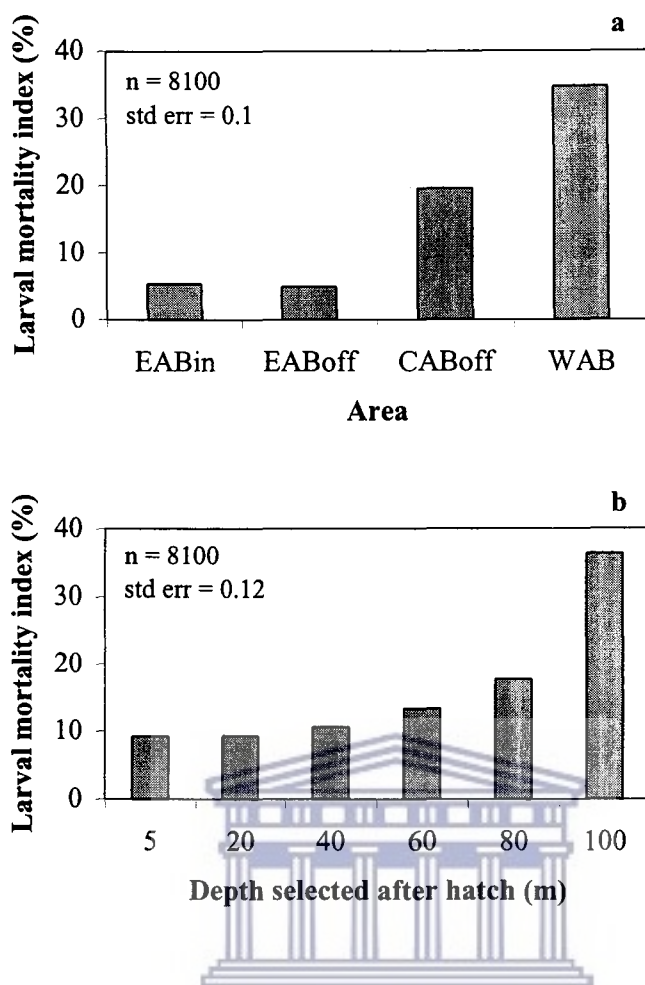
Figure 5.5. Ratio of larval mortality index for the single variables used in the active behavior model (model 6): (a) Area and (b) Depth selected after hatch.

5.3.5. Sensitivity analysis of the active behavior model (model 6): Transport success

Transport success to the inshore nursery area was, on average, 4.7% with a maximum transport of 14.3% when considering the inshore nursery area. Area of spawning was the most important variable influencing the transport success of larvae to the inshore nursery area (Table 5.6), with eggs spawned on the WAB being the most successfully transported, followed by those spawned on the CAB_{Off}. Eggs spawned on the EAB_{Off} and EAB_{In} were the least successful in terms of transport to the inshore areas of the west coast nursery areas (Fig. 5.6a). Transport success of the larvae was most influenced by the depth selected after onset of active swimming (Table 5.6), the most beneficial being a Depth of active behavior (δ_L) of 40m (about 9% of the larvae were successfully transported; Fig. 5.6b). For values of δ_L larger and smaller than 40 m, transport success was reduced, particularly in cases where larvae selected depths closer to the surface (Fig. 5.6b). Date, Depth of egg release, Lag of active behavior (τ_L) and Year had significant effects on transport success, but explained less than 5% of the variance of the model. The Area*δ_L interaction explained > 5% of the model variance (Table 5.6), while the combination of Area, δ_L, τ_L, Depth, Date and Year

EAB$_{Off}$ were successfully retained (Fig. 5.7a). The depth selected after the onset of active behavior was the second most significant variable explaining larval retention success, (Table 5.7), with those larvae associated to 40 m depth (Fig. 5.7b) being most successful. Date, Depth of egg released and Year had a significant effect on the retention, but explained less than 5% of the variance of the model. The Area*δ_L first level interaction and Year*Date*Area second level of interaction explained > 5% of the model variance (Table 5.7). The combination of Area, δ_L, τ_L, Depth, Date and Year and the interactions listed in Table 5.7 explained a total of 68.1% of the variance of the model, with an error term of 10.4% (Table 5.7).

Table 5.7. Optimal general linear model with second level of interaction applied to the active retention model output in the west coast nursery area for the dependent variable retention (model 7).

General Linear Model	*df*	*SS*	*MS*	*F*	*P*	*Explained variance (%)*
Intercept	1	207761.9	207761.9	13005.9		
Single variable						
Year	4	1131.5	282.8	17.7	S	0.1
Date	5	7949.8	1589.9	99.5	S	0.9
Area	3	326184.4	108728.1	6806.3	S	36.7
Depth	2	4730.9	2365.4	148.0	S	0.5
δ_L	5	70478.4	14095.6	882.3	S	7.9
First level of interaction						
Area*δ_L	15	120482.9	8032.2	502.8	S	13.6
Second level of interaction						
Year*Date*Area	60	74310.3	1238.5	77.5	S	8.4
Error	5810	92811.4	15.9			10.4
Total	6479	889112.3				

df = degrees of freedom, *SS* = Sum of squares, *MS* = Mean squares, *F* = f-ratio, *P* = probability, *S* = *P* < 0.001, *NS* = *P* > 0.05
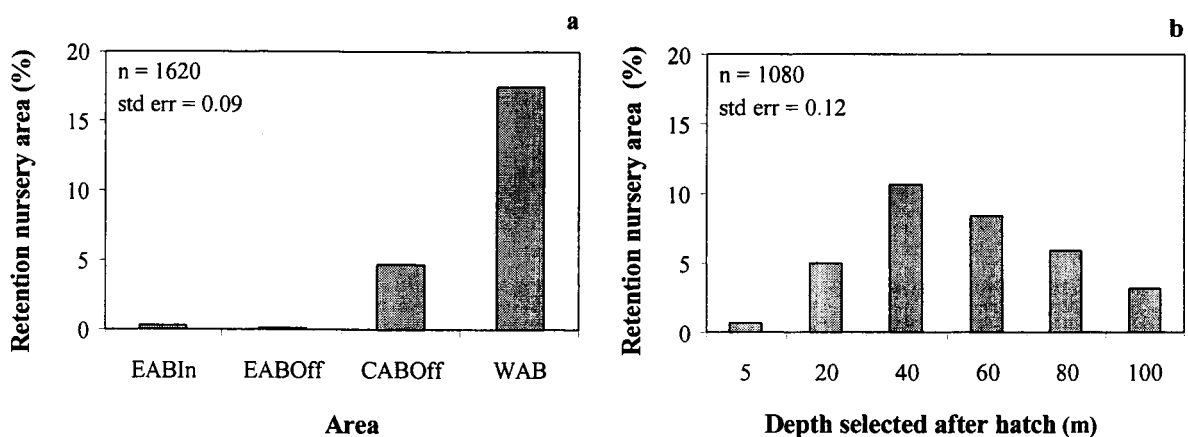

Figure 5.7. Ratio of the number of larvae retained in the nursery area to the number of eggs released for the single variables used in the active retention model for the west coast (model 7): (a) Area and (b) Depth selected after hatch.
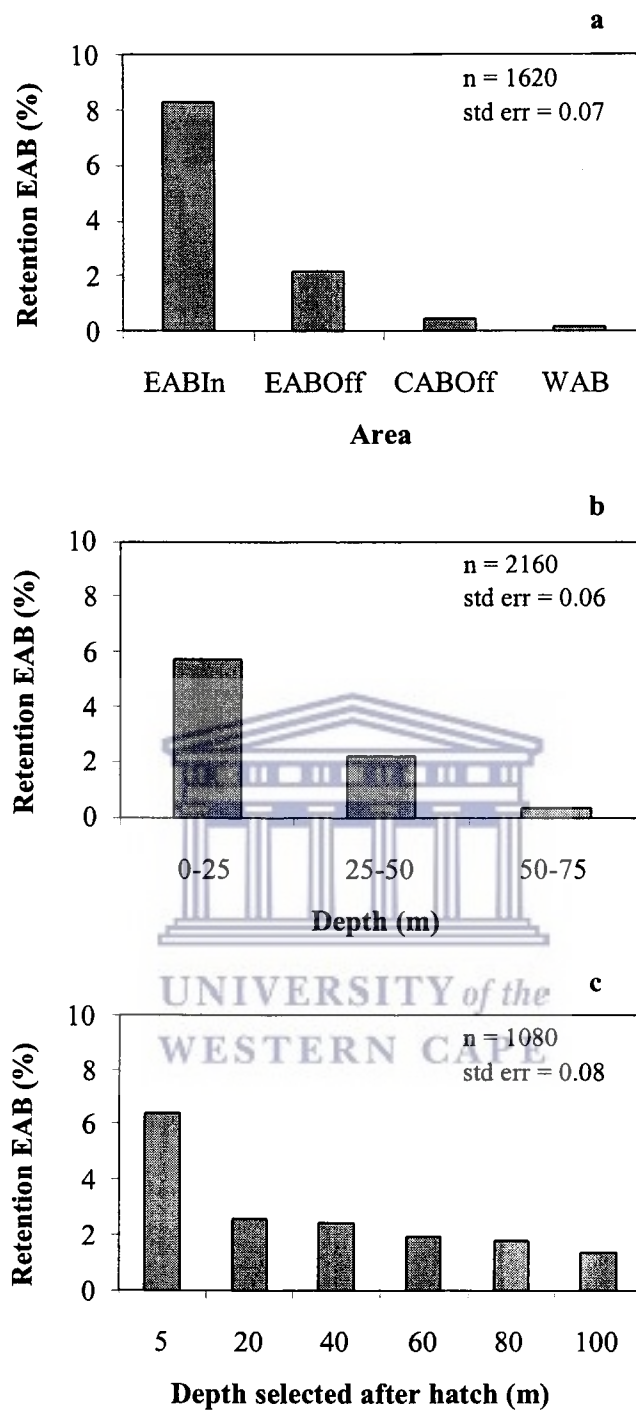
Figure 5.8. Ratio of the number of larvae retained over the EAB to the number of released eggs for the single variables used in the active retention model for EAB (model 8): (a) Area, (b) Depth of eggs released and (c) Depth selected after hatch.
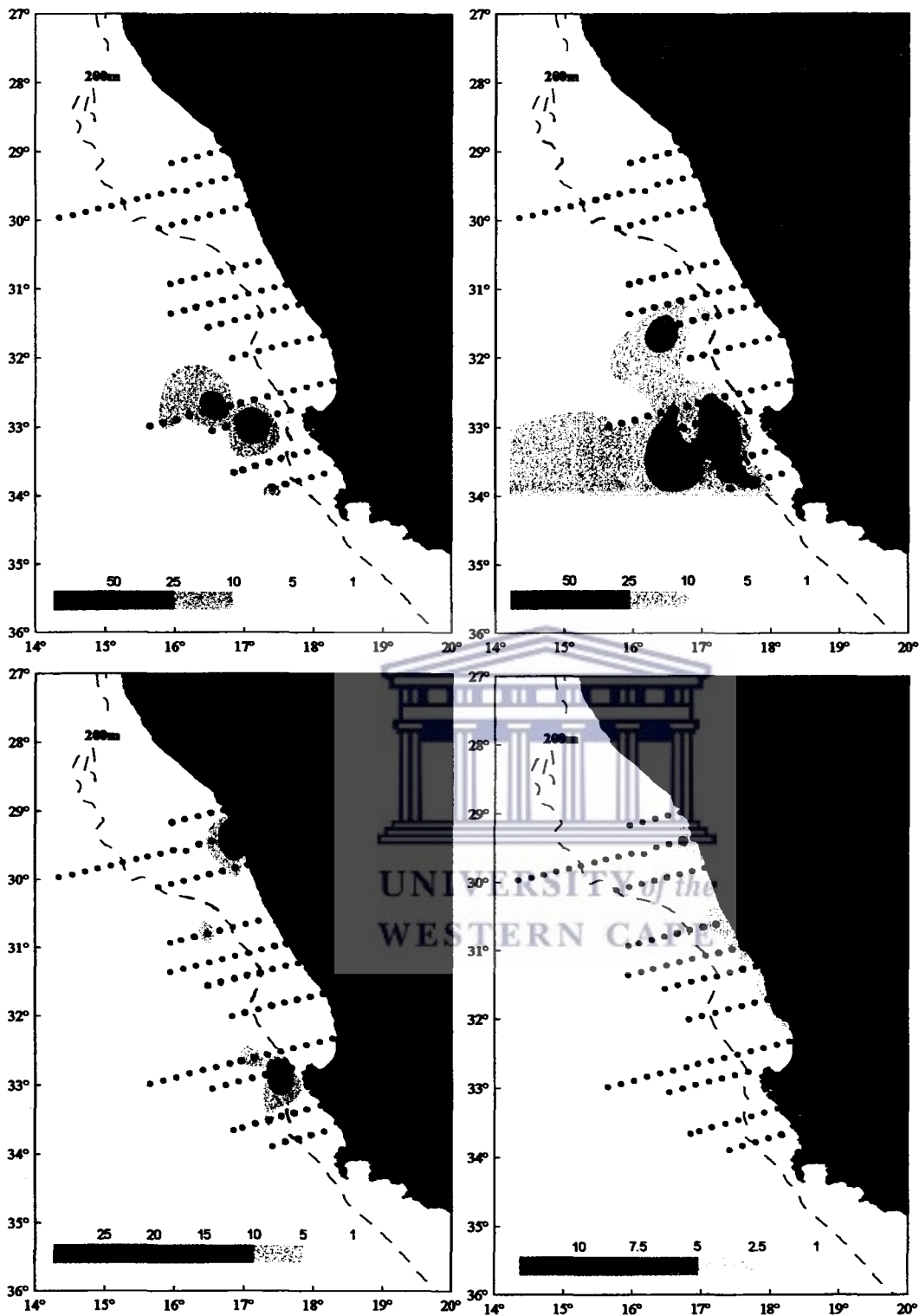
Figure 5.9. Distribution by class of anchovy pre-recruits collected using a Methot frame trawl during March 2000 survey. Dots indicate the positions of the Methot stations from van der Lingen and Huggett (in press).

5.4. DISCUSSION

The primary objective of the modeling exercise described in this chapter was to assess the potential effects of active vertical migration behavior by anchovy larvae on their transport to and retention in the nursery area on the west coast. In the passive model, eggs movements were vertically driven by the buoyancy scheme, while larvae were treated as Lagrangian particles (i.e. their movements were entirely regulated by the 3-D current velocity fields generated by the hydrodynamic model). In contrast, the active behavior model incorporated active vertical behavior by larvae that started at set times after hatching. Prior to this phase, the eggs movements were determined by the buoyancy scheme and larvae were treated as Lagrangian particles, but subsequent to the onset of the active vertical behavior, the larvae were capable of actively moving to a preferred depth, regardless of the vertical current velocity field imposed by the hydrodynamic model.

With regard to the Lagrangian experiments, the averaged transport to both the inshore and offshore nursery area was 12% with a maximum of 32%. When considering only the inshore area the averaged transport was 0.6% with a maximum transport less than 2%. These modeled results indicated that a low proportion of particles arrived passively to the offshore part of the nursery area implying that a passive mechanism does not explain the distribution pattern of older larvae in the inshore area. Incorporating the active behavior component (i.e. active depth selection by the larvae) into the model, however, the maximum value increased to 14.3%. This difference suggests that the vertical current structure plays an important role in the transport of larvae, and that behavioral mechanisms (specifically vertical migration) employed by larvae after the onset of the active swimming can significantly enhance their chances of successful transport to the nursery area. In the active behavior model, the mortality of eggs showed a similar pattern to that observed in the previous model (growth and mortality model, chapter 4) with mortalities largely dependent on the Depth and the Date of spawning parameters. Larval mortalities in the active behavior displayed a different pattern, with Area of spawning being the most influential parameter in terms of transport success (the WAB being the most favorable spawning area) and the parameter depth of active behavior (δ_L) showing that the movement of the larvae to a depth of 40 m maximized transport success, rather than the pattern showed for the growth and mortality model where the parameters Area and Depth are the most influential. The selection of depths deeper or shallower than 40 m tended to result in higher larval mortalities and reduced transport success. This could be explained by temperature-induced mortalities in deeper water (i.e. low temperatures acting as a lethal factor), while larvae that selected depths shallower than 40 m tended to be advected offshore into unfavorable areas (leading to reduced transport success) as a result of Ekman drift of surface and near-surface water. These results therefore support the hypothesis that vertical migration may counteract the offshore advective process and enhance the chances of successful transport to the nursery area. The second comparative study of retention in west coast nursery area generated similar results to those described above, in that maximum retention was associated with eggs spawned in WAB (17.5% of retention). Larvae

. One of the most interesting results generated by the active behavior model was that the selection of an optimal depth of 40 m after hatching favors maximum transport success to the inshore nursery area on the west coast. The selected depth therefore appears to represent a trade-off between the effects of transport by water currents, and mortality due to low temperature. These results are consistent with those of other field studies and modeling attempts that confirmed the relevance of the interaction between a vertical behavior process and vertically stratified currents on the transport to favorable areas (Lenarz *et al.*, 1991; Hermann, *et al.*, 1996; Hare *et al.*, 1999; Batchelder *et al.*, 2002).

In terms of the pattern oriented analysis, the distribution of the modeled age classes of anchovy in the nursery area appears to be partially in agreement with the length class distribution of anchovy pre-recruits (from the surveys). The three first age classes showed a good agreement with the data. However, in the model the individuals corresponding to the large pre-recruits class were advected offshore. A justification of this finding could be that the swimming abilities of large pre-recruits allow them to maintain themselves in the northern part of the nursery area, a process that is not modeled, either in the active behavior or retention models. The retention model for the west coast nursery area generated the same pattern as did the active behavior model. This result is consistent with that of a modeling exercise performed for the northern Benguela system, which showed that particles released at 40 m had a much higher retention rate because of their location below the offshore-moving Ekman layer (Stenevik *et al.*, in press). The proportion of successfully retained larvae in the retention model for the west coast nursery area was reduced when the criterion for successful retention (> 10 days) was lengthened. This can be explained by water movements in the region. Modeled currents in the nursery area showed a latitudinal tendency to increasingly move offshore from south to north, indicating that individuals transported inshore are advected northward and then offshore at the latitude of the transect Nur1. The active behavior component incorporated into the model (effectively confining individuals to a certain depth) was useful in clarifying the importance of vertical current structure in explaining inshore transport, but did not explain the decreased retention over extended periods. The incorporation of a proper diel vertical migration behavior and realistic swimming capabilities of older pre-recruits, coupled to a hydrodynamic model that stores current velocities in a shorter time steps than PLUME (2 days time step) may, in this case, provide this explanation, as has been observed in other modeling attempts (Hill, 1991; Hare *et al.*, 1999; Batchelder *et al.*, 2002).

The comparison of the EAB and west coast as retention areas showed that retention success on EAB (8% of the total eggs released) is half that of west coast. In spite of this, 8% represents a substantial proportion of the total population. On the Agulhas Bank, complex circulation patterns appear where the Agulhas current moves away from the coast (Boyd *et al*, 1992; Boyd and Shillington, 1994). Eggs and larvae may be entrained or displaced offshore, but countercurrents enable those eggs and larvae spawned in the shelf-edge to be retained in the shallows areas of the Bank (Hutchings *et al.*, 2002). Although the EAB seems to display relatively high levels of retention,

CHAPTER 6: SYNTHESIS

The results of the modeling exercises described in this thesis will be discussed with reference to the objectives that were set out in the opening chapter. The research set out to identify and assess the importance of a number of key factors (both environmental and biological, as well as their interactions) that influence:

- the transport of early stages of anchovy from the spawning grounds (Agulhas Bank) to the nursery area (west coast)
- the advection (in both onshore and offshore directions) of early stages of anchovy
- the growth and mortality of early stages of anchovy related to temperature
- the vertical migration behavior and its effect on the transport and the retention of early stages of anchovy (in the nursery area on the west coast, as well as on a potential second nursery area on the Eastern Agulhas Bank)
- ultimately the recruitment success

In an effort to attain these objectives, eight IBMs were designed and coupled to the stored output of a 3-D hydrodynamic model of the region (PLUME). By varying a suite of parameters, a series of values for transport success, mortality indices (of both eggs and larvae) and retention was generated, with random spatial distribution of the spawning products within each area at the start of each simulation. The parameters incorporated into the models were the location and timing of spawning, buoyancy properties of the eggs, temperature-dependent growth and mortality of both eggs and larvae, and active vertical behavior of the larvae. Sensitivity analyses were conducted to identify which parameters were the primary determinants of mortality of eggs and larvae, transport success and retention in the various experimental simulations. The outputs of the models were then compared to field observations to assess the validity of the results.

Before exploring these results (section 6.2) and their implications for our understanding of the early life history of anchovy in the southern Benguela region (section 6.3), the methodological constraints of the IBM approach employed during this research are discussed (section 6.1), emphasizing the limitations of the approach and forming the basis of the recommendations for future research that are provided at the end of this chapter (section 6.4).

6.1. METHODOLOGICAL CONSTRAINTS

6.1.1. Validity of the assumptions of the models

Hydrodynamic model. In general, the assumptions of the hydrodynamic model are valid with the exception of the potential effect of short term wind events. The analysis of the 10 years output of the hydrodynamic model of both the volume averaged kinetic energy (cm^2s^{-2}) and volume averaged potential temperature (°C) of the model indicated an equilibrium reached the second year, which is

that the effect of the diffusion was enlarge the areas already identified by deterministic runs, rather than identify new favorable areas (Heath and Gallego, 1997). In consequence we have certain confidence that the exclusion of horizontal diffusion in our model will not incorporate fundamental errors in our model solution.

Spatial and temporal scales of the spawning process. We have a good degree of confidence of the IBM assumptions related to the spatial and temporal scales of the spawning process. The selection criteria to define the number of particles considered the stability of the model solution and the computational constraints. In this regard, 5000 particles was a reasonable number to reach these requirements and to represent the process and mechanism under study.

Regarding the spatial scales of the spawning, limiting the spawning area of anchovy to the Agulhas Bank in the model is based on several field observations of adult anchovy concentration over the Bank during summer, coinciding with the major anchovy spawning season in the southern Benguela region (Armstrong *et al.* 1987; 1988; 1991; Hampton 1987; 1992; Barange *et al.*, 1999). The subdivision of the spawning ground into 4 areas (WAB, CAB_{Off}, EAB_{In} and EAB_{Off}) was based on the egg distributions reported by van der Lingen *et al.* (2001), and corresponds to the divisions currently used by Marine Coastal and Management (MCM). The suitability of these areas was studied by Huggett *et al.* (2003) who mapped the transport success of particles released on the whole Agulhas Bank subdivided into multiple small areas. The analysis of Huggett *et al.* (2003) showed that the spatial variability of transport success within the 4 areas was substantially less than the variability among the areas indicating the suitability of the areas selected.

The depths at which eggs were released during the experiments were based on field observations indicating that anchovy eggs are generally distributed in the upper 50 m of the water column (Shelton and Hutchings, 1982), while larvae tend to be distributed in the upper 75 m (Motos and Coombs 1998; Moser and Pomeranz 1999; Santos *et al.*, 2000). The temporal range of spawning was defined in accordance with field observations indicating that anchovy spawn mainly between October and February (Shelton 1986; Hutchings *et al.*, 1998). The tracking duration of 60 days defined in the models corresponds to the mean estimated time until metamorphosis (Armstrong and Thomas, 1989), when larvae is 20-35 mm (Wilhelm, 2002) and the swimming capabilities are already well developed. In future studies modeled individuals older than 2 month will require an appropriate biological scheme for swimming.

Biological schemes. Several descriptive researches have highlighted the importance of buoyancy of pelagic fish eggs (Coombs *et al.*, 1985; Tanaka, 1992; Tanaka and Oozebi, 1996; Stenevik *et al.*, 2001). Few investigations have been oriented to understand the processes controlling the vertical distribution of eggs and larvae due to buoyancy (Sundby, 1983; 1997; Ådlandsvik *et al.*, 2001). The most relevant modeling studies testing the effect of buoyancy on the vertical distribution of eggs have been the ones of Sundby (1983; 1991; 1997) and Stenevik *et al.* (2001) using spherical shape

a process as diel vertical migration, but the approach does assess the importance of vertical current structure, and hence the potential benefits of active vertical swimming behavior.

Transport success. A critical assumption in this study concerns the validity of the three transport success criteria that were defined in the models (see chapter 2). The first criterion (applied to models 1 to 4) and second (applied to model 5) (i.e. that individuals reaching the nursery area while older than 14 days are transported successfully) were based on the results of Badenhorst and Boyd (1980). These authors demonstrated that anchovy larvae longer than 7 mm caudal length (corresponding to an approximate age of 14 days according to Brownell, 1983) may avoid a bongo net during the day but not during the night, implying that larvae of this size are capable of active swimming. Therefore, larvae larger than 7 mm are able to maintain themselves within the nursery area and would be considered to be successfully transported. The same argument is used for the third criterion of success (model 6 : active behavior model), with the difference that the onset of active swimming behavior of the larvae was not constrained to occur at a specific age, but varied according to the temperature-dependent growth of each individual after hatching. Therefore, this assumption is supposedly more realistic than that used for the previous experiments.

6.2. MODEL COMPARISONS AND INTEGRATION OF THE RESULTS

6.2.1. From Lagrangian models to IBMs incorporating a biological component

The Lagrangian (model 1) and passive behavior (model 5) models were designed to study transport success to the nursery area using a purely Lagrangian approximation. The aim was then to contrast these models with those that incorporated additional biological "movement" components, namely the buoyancy (model 2 and 3) and active behavior (model 6) schemes. The potential influence of egg density on transport success was consequently assessed by a comparison of models 1 against 2 and 3, while the potential for active behavior to enhance transport success involved a comparison of models 5 and 6. In terms of the dependent variables, these two comparisons differed in that the Lagrangian-buoyancy models defined transport success in terms of both the inshore and offshore areas of the nursery ground, whereas the passive-active behavior models only considered the inshore area for the definition of the transport success. Note that the comparison of two models is based on the analysis of the variance explained for each single parameter presenting the same number of degrees of freedom in both models. The effect of a new parameter added to a model is assessed regarding the variance explained for this new parameter and the re-arrangement of the variance for the previous parameters.

From Lagrangian to buoyancy model. When individuals were treated as passive particles in the Lagrangian model (model 1), the spatial spawning parameters (Area and Depth) were the primary determinants of transport success (Table 6.1). During the evolution from the Lagrangian to the

is evidence for an increase in offspring quality with increasing parent age or reproductive experience. Length and the condition of female anchovy have been positively correlated with egg diameter and buoyancy (Parker and Begon, 1986; Sargent *et al.*, 1987; Marteinsdottir and Steinarssom, 1998; Vallin and Nissling, 2000), and hence could have an impact on recruitment success (Vallin and Nissling, 2000). In support of these observations, examination of the succession of multiple batches of anchovy within a spawning season has shown that the size of adult anchovy is related to the time of spawning, and that eggs decrease in size toward the end of the spawning season (Melo, 1994; Gordina *et al.*, 1997). IBMs incorporating the buoyancy algorithm (chapter 3) applied in this study present a useful tool to explore these ideas further.

From passive to active behavior model. The overall transport success to the inshore area quantified by the passive behavior model was <5%, but this value increased to approximately 15% when the behavior component (specifically the maintenance of a preferred depth after hatching) was added in the active behavior model. In the passive behavior model, where recently hatched larvae were treated as Lagrangian particles, the spatial and temporal spawning parameters (Year, Area, Depth, and Date) were of similar importance. With the incorporation of the active behavior component (model 6), however, only the Area of spawning remained as an important parameter explaining transport success, the other spatial and temporal spawning parameters becoming of negligible importance.

Highest levels of transport success recorded in this study were associated with larvae maintaining an optimal depth of 40 m after hatching. It is interesting to note that this is the same as the 40 m depth corresponding to highest retention rates of sardine in the northern Benguela region identified by the models of Stenevik *et al.* (in press). The authors suggested that particles at this depth were located below the offshore-moving Ekman layer. This hypothesis has been supported by field data showing that the spatial distribution of eggs and larvae of sardine is characterized by the oldest larvae being found closest inshore, suggesting that they have drifted toward inshore areas (Stenevik *et al.*, in press). Field data of the distribution of anchovy on the west coast of South Africa showed a similar pattern in that the distribution of pre-recruits over several years displayed a repeated trend of increasing fish length closer to the coast (van der Lingen and Merkle, 1998; 1999). This pattern is reproduced by the active behavior model, implying that a biological mechanism is operating (possibly vertical migration) facilitating the inshore transport of larvae. However, current field data of the vertical migration anchovy pre-recruits based on Methot net catches and echosounder traces is inconclusive (van der Lingen, 1999). What is clear is that the passive behavior model (i.e. Lagrangian approach) cannot explain the distribution of pre-recruits on the west coast, and specifically the inshore distribution of the larger pre-recruits. By incorporating a behavioral component associated with the vertical plane, however, the model explains a significant proportion of the inshore transport and distribution. This result supports hypothesis 3, which proposes that active vertical behavior could counteract the offshore advective process, presumably avoiding the

the preferred depth parameter (depth after hatch, δ_L) (Table 6.2). The time of active behavior parameter (τ_L) appeared to be of minor importance in accounting for larval mortality. These comparisons suggest that the mortality of eggs and larvae occur in different spatial planes during the life history, depending on the individual locations (i.e. spawning grounds or nursery area). On the spawning grounds, egg mortality is primarily associated with the vertical dimension of particle release while larval mortality is associated with the horizontal distribution of particle release. In the nursery area, on the other hand, egg mortality is more dependent on the timing of the original spawning while larvae mortality is strongly associated with the vertical dimension.

Table 6.2. Inter comparison between the explained variances given for the GLM for the single parameters considering egg and larval mortality index as the dependent variable for all models. The "-" indicates that the parameter is not used and "c" that the parameter is fixed to a constant value.

	Variance explained (%)			
	Egg mortality index		Larval mortality index	
Parameter	Model 4	Model 6	Model 4	Model 6
Area	0.4	0.5	44.7	35.1
Depth	30.9	36.5	0.7	0.0
Date	12.1	11.7	2.6	1.2
Year	0.5	0.9	4.1	0.7
λ	0.6	c	0.2	c
θ_E	7.2	c	0.4	c
θ_L	0.0	c	1.9	c
δ_L	-	0.0	-	21.4
τ_L	-	0.0	-	1.5
Sum of variance	51.7	49.6	54.6	39.9

Models: (4) growth and mortality as a temperature function and (6) active behavior.

6.2.4. Optimal biological-physical features and trade-offs

The results of the models have indicated that there are a number of physical and biological features that maximize successful transport to the nursery area.

Optimal spawning ground. The WAB appears to be the most favorable spawning ground in terms of spawning products being successfully transported to the nursery area. This result is consistent with field studies that indicate that anchovy spawn primarily over the WAB (Shelton and Hutchings, 1982; Armstrong *et al.*, 1988; Boyd *et al.*, 1992; Roel *et al.*, 1994; Hutchings *et al.*, 1998). Other IBM studies have also identified the WAB as the optimum site for successful transport (Mullon *et al.*, 2002; Huggett *et al.*, 2003). However, the eastward shift in anchovy spawning and subsequent successful recruitment that has been observed in recent years (van der Lingen *et al.*, 2002) is not explained by the IBMs presented in this research. Field data have revealed the presence of anchovy larvae and early juveniles off the south and east coasts of South Africa (Anders, 1975; Beckley, 1986; Beckley and Hewitson, 1994), suggesting the presence of suitable nursery grounds in these areas. However, the abundance of pre-recruits is at least an order the magnitude low than on the west

Trade-off between the effect of temperature on the mortality of anchovy and transport success to the nursery area. The contribution of Depth parameter to transport success can be attributed to a negative effect (in terms of increased mortality) resulting from the lethal effect of critical temperatures for eggs (<14°C) in the water column below 40 m (Fig. 6.2).
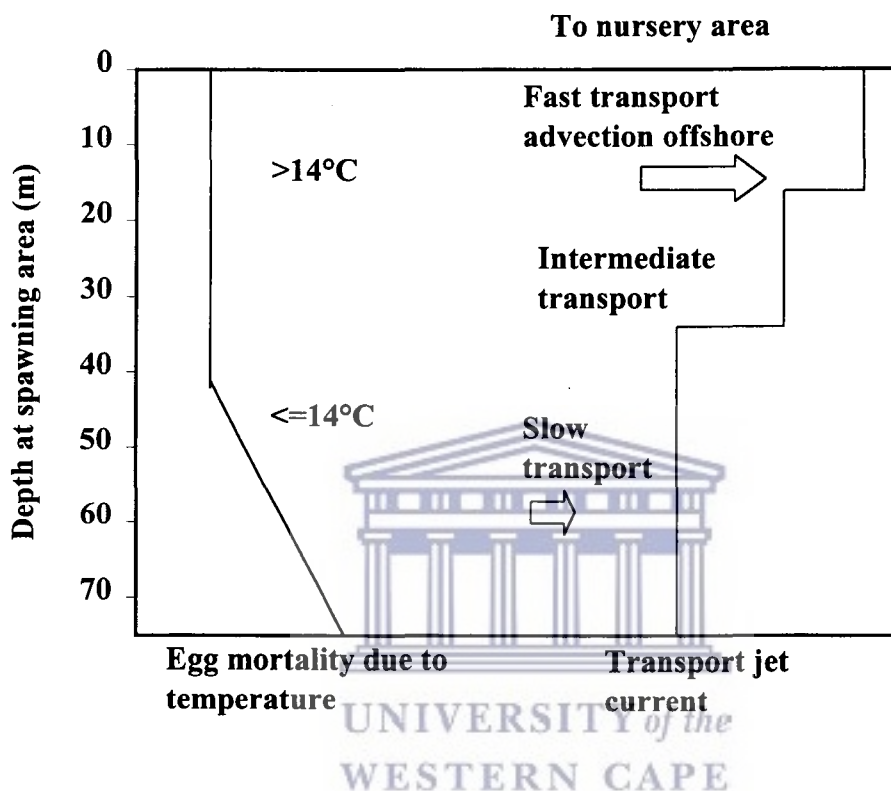

Figure 6.2. Hypothetical scheme of the trade-off between mortality of eggs released at different depth in the spawning area and the transport of the jet current to the nursery area.

If the eggs are spawned too deep in the water column, transport to the nursery area is slow (i.e. a negative effect on transport), which can contribute to delayed encounters of the larvae with cold recently upwelled water on the west coast. During this delay, eggs have more time to develop into larvae that are more resistant to low temperatures (i.e. a positive effect in terms of decreased mortality). In contrast, eggs spawned close to the surface are exposed to non lethal temperatures, but experience an increase in offshore transport/advection (Fig.6.2).

An interesting paradox that emerged from the analysis of the growth and mortality model (model 4) is that the conditions favoring successful transport of anchovy larvae may also contribute to the mortality of the larvae. This is because there is a spatio-temporal component associated with

the top 40 m, but this increases with increasing depth. The trade-off is thus favorable temperatures but unfavorable current flow in the surface layers, as opposed to favorable current flow but potentially lethal temperatures in deeper water. The optimal depth of 40 m layer consequently appears to be the depth at which these opposing effects (i.e. temperature-dependent mortality versus losses resulting from offshore advection) balance out to result in maximal transport success (Fig. 6.4).
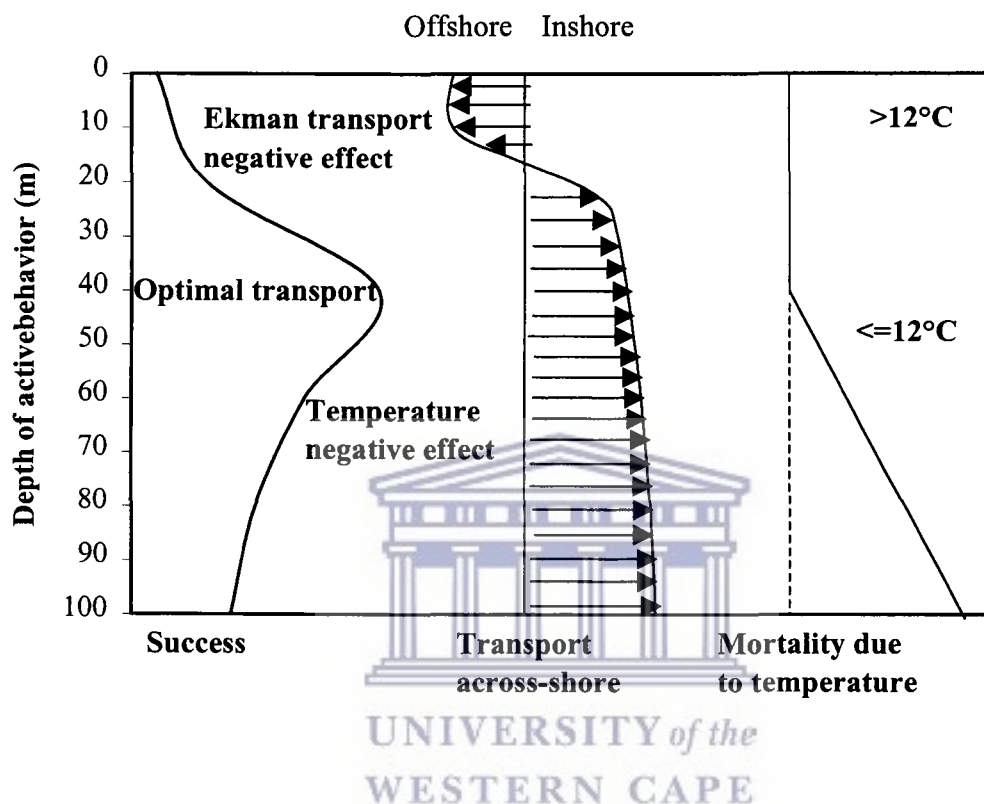
Figure 6.4. Hypothetical scheme showing "optimal transport success" and the tradeoff between Ekman transport and mortality of larvae due to cool temperatures during upwelling.

6.2.5. Retention on the west coast versus the EAB

The retention model applied to the nursery area on the west coast identified the same important parameters as the active behavior model, but it should be emphasized that the active behavior component only explained enhanced retention for a criterion of 10 days (but *a posteriori* experiments showed that a reduced number of individuals was retained when using a criterion of 20 days). This may be attributed to the current patterns characterizing the nursery area. The output of the hydrodynamic model in the nursery area displayed an increasing tendency for offshore transport in the northern parts of the nursery area, and this was compounded by a strong northward flow close inshore through the nursery area. The result of this pattern is that individuals that are successfully transported to the inshore part of the nursery area are moved northwards by the inshore flow, and then are progressively subjected to increasing levels of offshore flow, increasing the probability of offshore advection in the northern parts of the nursery area. It is likely that the intensity of the

maintained by the larvae) were the key factors influencing successful, short-term retention. An additional factor, namely depth of spawning, also played an important role in contributing to retention success on the EAB.

- The final objective aimed to link the physical and biological processes and the potential effect on the recruitment success. Although their relative importance could not be quantified, it is clear that spawning location, egg buoyancy, the direction and intensity of the jet current, the effects of temperature on growth and mortality and behavioral mechanisms employed by the larvae are the key factors regulating successful transport and retention of early life stages of anchovy. The discussion has been limited to transport, retention and mortality because the attempts to link the processes to recruitment rely on data and analyses which are not available. However, the implications of these findings for our understanding of the early life history and recruitment of anchovy in the southern Benguela region are explored in the next section.

6.3. TOWARD A CONCEPTUAL MODEL OF THE EARLY LIFE HISTORY AND RECRUITMENT OF ANCHOVY IN SOUTHERN BENGUELA SYSTEM

The research described in this thesis identified several physical and biological mechanisms that appear to be important for the transport, mortality and retention of the spawning products of anchovy in the southern Benguela region. In the light of these new results, the current hypothesis regarding the life history of anchovy in southern Benguela region proposed by Hutchings *et al.* (1998) is revisited, and several additions are proposed (Fig. 6.5) in which the spawning area is extended and key biological processes added to this hypothesis. One element that is really conceptually different in this proposal is the potential of the Eastern Agulhas Bank as a nursery/spawning area. Distinct spawning, transport and nursery regions characterize the hypothesis of Hutchings, which assumes that most of the recruits to the west coast fishery originate from the stratified WAB that contains the bulk of the spawner population during the peak spawning season in November (Hutchings *et al.*, 1998). Recent studies have, however, documented an apparent eastwards shift in the location of both spawning adults and highest egg densities on the Agulhas Bank (Hutchings *et al.*, 1998; van der Lingen *et al.*, 2001). The connection between the spawning grounds on the Agulhas Bank and nursery area on the west coast, established through the jet current, is the primary factor that determines whether or not spawning products are successfully transported to the nursery area (Figure 2.4).

Based on the results of the IBM modeling studies described in this thesis, it is proposed that five different factors/processes and their interactions strongly influence the transport of spawning products arriving in and subsequently being retained in the west coast nursery area (see Fig. 6.5). In brief, these processes are:

model, specifically the lack in the relaxation in the wind forcing (see section 6.1.1.), further discussion of this point would be largely speculative.

An additional issue to consider in the period leading up to recruitment is that of egg and larval mortality, and the factors/processes influencing it. Two factors appear to be of major importance in this regard:

(1) Mortality due to temperature and,

(2) Offshore losses.

Firstly, the influence of temperature differs both spatially (i.e. whether the spawning grounds or nursery area are being considered) and temporally (in terms of the life stage of anchovy). On the spawning grounds, temperature-induced egg mortality is associated with the vertical distribution of particle release, whereas larval mortality is associated with the horizontal distribution of particles. In contrast, temperature-induced egg mortality in the nursery area is more dependent on the timing of the original spawning, while larvae mortality is strongly associated with the vertical dimension. Secondly, a major factor to consider is offshore losses which are dependent on the horizontal dimension (spawning ground, Cape Peninsula to Cape Columbine, nursery area) and the associated oceanographic processes (Agulhas Current, jet current transport, onshore-offshore transport at upwelling regions).

Specifically, there is a relationship between the depth of eggs and larvae, the associated probability of advective losses, and the mortality due to ambient temperature. The analysis of the egg mortality identified a trade-off between the mortality of eggs released at different depth in the spawning area, and the transport success to the nursery area (Fig. 6.2). On the other hand, the analysis of larval and post-larval mortality showed that the factors affecting transport success are the same as those affecting their mortality. A trade-off therefore exists between the chances of successful larval transport by the jet current and the high probability of encountering the potentially lethal effect of cold upwelled waters on the west coast (Fig. 6.3).

The optimal depth of 40 m for larvae in the west coast involves a trade off between the chances of offshore transport by the Ekman layer and the potentially lethal effect of temperature (Fig. 6.4). Within the framework of successful recruitment of anchovy on the west coast, the biological and physical factors and their interactions, as well as the tradeoffs described above, are proposed as potential key mechanisms for the understanding of the mortality and successful transport of spawning products to the west coast nursery area. However, because this is a modeling approach, it is fundamental to conduct empirical studies to test these hypotheses (see below).

numbers of pre-recruits that were observed during the March 2000 pre-recruit survey (which only covers the west coast) therefore represents an interesting paradox (Wilhelm, 2002). The possibility that recruitment success is not solely determined by conditions on the west coast consequently needs to be addressed. Retention processes could play a role on the EAB, allowing the development of a local population or a delay in the transport to west coast (older individuals may be more able to cope with conditions on the west coast) that could contribute substantially to the overall anchovy recruitment. The results of the modeling study indicated that the proportion of spawning products that is retained on the EAB is substantial (~8% versus ~18% on the west coast). The simulations clearly indicate that for spawning products to be successfully retained on the EAB, they have to be released either on the EAB_{In} or the EAB_{Off}. Moreover, those spawning products released on the EAB were not transported to, or retained in the west coast nursery area in appreciable numbers. These findings suggest that the EAB could play an important role as a spawning and nursery area, contributing substantially to the total recruitment when conditions on the EAB are suitable such as favorable food and low predation. However, it is likely that retained larvae on the south coast are subject to intense predation by the adult pelagics such as red eye, anchovy and sardine (L. Hutchings, per. comm.).

6.4. RECOMMENDATIONS FOR FUTURE RESEARCH

This study should not be considered to be the endpoint in investigations of transport, mortality and retention of early life stages of anchovy. Further modeling studies should be performed and additional field data is required to address some of the questions raised by the model results. Of primary importance are the constraints (section 6.1.1) of the hydrodynamic model (PLUME) that was coupled to the IBMs. It is likely that these constraints lead to some inaccuracies in the representation of the physical dynamics of the system, and the processes involved. These limitations could be addressed by:

- Incorporation of smaller temporal and spatial scales of wind variability to test the influence of wind relaxation on the across-shore transport of larvae and post-larvae in the nursery area. This aspect is currently being addressed (Blanke *et al.*, 2002).
- Extension of the domain of the grid eastward to test the feasibility of the east coast as a nursery area for anchovy. This will address the problem of the boundary conditions of the hydrodynamic model that currently limit its reliability in the eastern regions of the grid.
- Incorporation of an explicit turbulence diffusion scheme for a mixing layer in the IBM. This would account for the influence of the turbulent diffusion effect on the buoyancy of eggs and the vertical behavior of larvae, improving the model's representation of the spatial-temporal distribution of anchovy in southern Benguela region.

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