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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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Dedicado

a la memoria de mi padre, a mi querida madre y

mi querido amigo Deon Durholtz

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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.

Signed by candidate

Carolina E. Parada Véliz
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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 first year (Fig. 1.2). The first clear evidence that the shelf-edge frontal jet current plays an important role in the transport of ichthyoplankton from the Agulhas Bank to the west coast is provided by Shelton and Hutchings (1982). In spite of a clear funneling of anchovy eggs to the nursery grounds from the Agulhas Bank by the jet current, a substantial offshore egg loss has been suggested along the funnel to unfavorable localities (Boyd *et al.*, 1992).

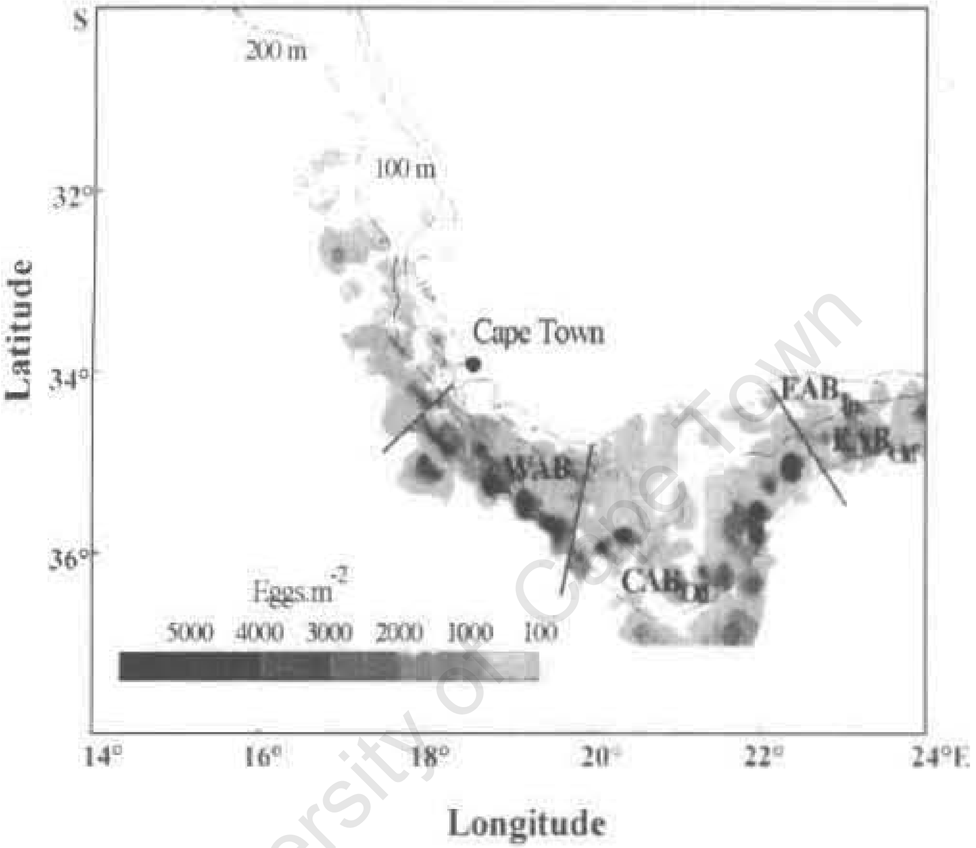

Figure 1.1. Composite distribution map of anchovy eggs collected using a CalVET net during annual pelagic spawner biomass surveys over the period 1983-2000. Data updated from van der Lingen *et al.* (2002). The locations of the WAB (Western Agulhas Bank), CAB$_{\mathrm{Off}}$ (Central Agulhas Bank offshore), EAB$_{\mathrm{In}}$ (Eastern Agulhas Bank inshore) and EAB$_{\mathrm{Off}}$ (Eastern Agulhas Bank offshore) spawning grounds are shown. These areas used in the individual based model (IBM) designs are indicated. The boundaries of each area are based on the 100 and 200 m isobaths.

Several environmental and biological variables are considered to influence the recruitment success of anchovy. These include temperature, wind, food availability, turbulence/stability, predation, competition, population density and gross egg production, as well as localized and widespread oceanographic events (Lasker, 1985; Hutchings and Boyd, 1992; Cochrane and Hutchings, 1995). Recent modeling studies based on ADCP and spawner biomass data have shown that variations in the advective processes that transport anchovy eggs and larvae in the southern

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.

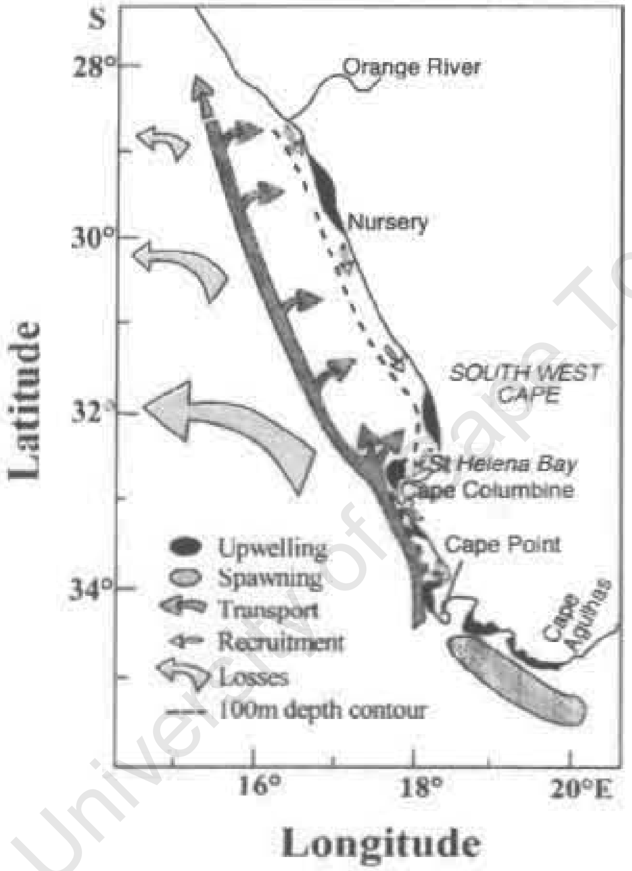

Figure 1.2. Conceptual model of the anchovy's life history (after Hutchings *et al*., 1998).

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

Benguela Currents) and changing winds. The biological response to environmental variability depends on the individual properties of eggs and larvae, and their tolerance to critical environmental values. An important step towards understanding the recruitment process is describing and studying the environmental variables determining the spatial distribution of eggs and larvae (Sundby, 1991). Stratification of the water column is an important feature that influences the adjustment of anchovy eggs and larvae to certain depths, due to the interaction between water density and the intrinsic buoyancy properties of the eggs and larvae. Measurements of the specific gravity of anchovy eggs suggest that eggs are positively buoyant, drastically increasing their density during the few hours before hatching (Tanaka, 1990; Tanaka *et al.*, 1991) so that larvae are neutrally or negatively buoyant after hatching (Tanaka and Oozeki, 1996). Buoyancy has an immediate effect on the vertical distribution of eggs and larvae, which is important for horizontal transport, spreading and survival (Sundby, 1991). The Agulhas Bank, where eggs are spawned, is characterized by intense stratification that gives rise to inshore phytoplankton blooms in early spring (Shannon *et al.*, 1984). During the summer season, upwelling processes dominate and high concentrations of chlorophyll are present inshore (Shannon *et al.*, 1984; Brown, 1992; Pitcher *et al.*, 1992). Upwelling is also a feature of the ocean circulation along the west coast (nursery area) of South Africa characterized by cold, well-mixed nutrient-rich waters during the summer upwelling season (Pitcher *et al.*, 1992).

The jet current that transports the eggs and larvae from the spawning grounds to the nursery grounds is characterized from the south by warm water originating from the Agulhas current and from the north by cold, recently upwelled waters originating in the Benguela region. These diverse temperature regimes affect different aspects of anchovy biology. Spawning success in anchovy has been suggested to be dependent on the extent of a suitable spawning habitat in Agulhas Bank (Shelton 1986; Richardson *et al.*, 1998), both spatially (16-19°C) and temporally (spring). A relation between anchovy egg abundance and the area of 16-19°C has been reported on Western Agulhas Bank (Richardson *et al.*, 1998). In addition, laboratory data indicate that egg and larval developmental rates increase exponentially with increasing temperature (King *et al.*, 1978; Lo, 1985) with warmer temperatures accelerating metabolism and favoring the growth of individuals and their food requirements, while cold water will decrease metabolism, reducing individual growth rates. Therefore, it is possible that anchovy eggs found optimal conditions for development in areas of 16-19°C in Western Agulhas Bank. It has been suggested that the shallow thermocline and cool (<14°C) water associated with the cold ridge on the Eastern Agulhas Bank may preclude extensive spawning in this region (Hutchings, 1994). Studies of several species of fishes show that eggs are generally less tolerant to temperature extremes than larvae (Hempel, 1979; Bunn *et al.*, 2000; Huggett *et al.*, 2003). Laboratory experiments of the temperature tolerance range of *E. encrasicolus* eggs showed that temperatures less than 14°C (King *et al.*, 1978) may be lethal. Temperatures below 14°C inhibit egg development to the extent that larvae fail to develop a functional jaw (King *et al.*, 1978), while larvae are unable to tolerate temperatures below 12°C (Hutchings, per. com.).

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:

(1) To quantify key environmental and biological factors and processes that influence the transport success of early stages of anchovy from the spawning grounds (Agulhas Bank) to the nursery area (west coast).

(2) To quantify key environmental and biological factors and processes that influence the onshore-offshore advection of early stages of anchovy along the jet current and in the nursery area.

(3) To study the relationship between the spawning and nursery areas with regard to the sources of mortality of early stages of anchovy.

(4) To assess an alternative hypothesis describing retention of anchovy in the nursery area for recruitment success in the southern Benguela ecosystem.

(5) To explore physical and biological processes affecting recruitment success.

1.5. HYPOTHESES

Currently accepted hypotheses regarding anchovy recruitment success focus on the importance of the jet current to successfully transport early life stages of anchovy from the spawning area of the Agulhas Bank to the nursery areas on the west coast (Fowler and Boyd, 1998; Hutchings *et al.*, 1998). It is assumed that most of the recruits to the west coast fishery originate from the stratified WAB, which contains the bulk of the spawner population at the peak of the spawning season during November (Hutchings *et al.*, 1998). In this study, four hypotheses related to the life history of anchovy in the southern Benguela region are investigated. I propose that a combination of interactions between the jet current and a suite of biological and environmental variables may influence the overall transport success of early stages of anchovy to the nursery area.

Firstly, early stages of anchovy are characterized by intrinsic buoyancy properties that, together with water density, directly determine their vertical position and indirectly, their horizontal distribution. In this regard, two questions have to be addressed. Is the buoyancy of eggs and early larvae a factor that interacts with physical transport, thereby contributing to affect their horizontal distribution and transport success? Is there any relationship between vertical patterns of egg distribution that is determined by their specific buoyancy, and the jet current intensity and direction (inshore-offshore transport)?

H1 : The buoyancy of eggs and early larvae plays a key role in the successful transport of individuals from the spawning grounds to the nursery area, and in their offshore advection once transported to or near the nursery grounds.

A second key environmental factor that infuences individual anchovy egg and larval mortality and growth is temperature. The Agulhas Bank and the nursery areas are very different environments in terms of temperature, both spatially and temporally. The Agulhas Bank is bounded in the west by cold, nutrient-rich upwelled waters, and in the east by the warm, nutrient deficient

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 the period 1990-1994, roughly half of the anchovy biomass was found west of Cape Agulhas and the other half east of Cape Agulhas. Field studies have shown that since 1994 the spawning habitat of anchovy has displayed a marked change, with anchovy spawning predominantly off the south and east coasts. This is likely to impact egg and larval transport to the nursery grounds, and subsequently the recruitment strength (van der Lingen *et al.*, 2001). After 1994, with the exception of 1995, more than 60% of the spawner biomass was associated with the EAB and CAB_{Off} (van der Lingen *et al.*, 2002). The shift in spawner biomass has also been manifested in shifts in anchovy egg distribution patterns, although these shifts were observed earlier (1989) than the shifts in the spawner biomass (van der Lingen *et al.*, 2002). Recruitment strength of anchovy was low and stable between 1985-1996 and higher and unstable between 1997-2001 (Hutchings *et al.*, 1998; Barange et *al.*, 1999; van der Lingen *et al.*, 2002). The high recruitment of anchovy observed in 2000 (detected during the May/June survey) was four times higher than any recruitment observed over the last 15 years (Barlow *et al.*, 2002). Later in the 2000 season, the November spawner biomass survey showed an adult biomass more than twice the magnitude of any recorded since 1984, confirming the exceptional recruitment of 1999/2000 (van der Lingen *et al.*, 2001; Roy *et al.*, 2002). However, this high recruitment was not reflected by the relatively low numbers of pre-recruits that were observed during the March 2000 pre-recruit survey (which only covers the west coast). Therefore, this paradigm is open to question, because it is possible that recruitment success is not solely determined by the successful transport of anchovy individuals to the nursery area of the west coast. It is therefore suggested that the EAB may play a role as an alternative retention and nursery area. Finally, anchovy larvae employing vertical behavior strategies leading to active retention of the individuals in the nursery area west coast and EAB will be assessed. An alternative hypothesis to the current knowledge status about the early life history of anchovy in southern Benguela system will be discussed in the light of the results of this research:

H4: Retention processes are playing a role on the Eastern Agulhas Bank, allowing the development of a local population that could contribute substantially to overall anchovy recruitment.

1.6. ORGANIZATION OF CHAPTERS

Following this introductory chapter, Chapter 2 outlines the methodology used to implement the different designs of the individual based model (IBM) experiments. The simulation procedures, testing of the hypotheses and the comparisons of the model outputs with available data that are common to the various IBM experiments are described.

Chapters 3 and 4 explore the interaction between the biological properties of anchovy eggs and larvae, the spatial and temporal scales of the spawning process, and two environmental variables, namely water density and temperature, with regard to transport success. Chapter 3 describes an IBM experiment designed to simulate the depth adjustment of anchovy eggs and early larvae to variations 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.

CHAPTER 2: GENERAL MODELING APPROACH AND METHODS

2.1. MODELING EXPERIMENTAL APPROACH

In this research, an experimental modeling approach, using individual based models (IBMs) was employed to test the set of hypotheses described in the previous chapter. This approach is characterized by the design of comparative experiments with an increasing level of complexity to identify the hierarchy of mechanism and factors influencing the system. During the modeling process, I followed the theoretical and practical suggestions proposed by several authors (Grimm *et al.*, 1996; Auyang 1998; Grimm, 1999; Grimm *et al.*, 1999; Railsback, 2001), which have been summarized by Mullon *et al.*, (submitted) as follows:

(1) Maintain the simplicity of the model formulation and avoid over-parameterization (Grimm, 1999).

(2) Find the appropriate level of resolution of the model that solves the problem for which the model was designed. The idea of "scaling down" suggested by Grimm (1999) involves starting with a very coarse model and refining the model step by step, fixing parameters that do not explain an important part of the model variance, and progressively adding further levels of complexity to the model.

(3) Use an experimental approach that starts with formulating hypotheses in terms of processes and then ascertaining the best method of testing the hypotheses. Once results are obtained, these are immediately accepted so as to avoid the never-ending fine-tuning of the model. A sensitivity analysis should then be employed to assess the sensitivity of the model to variations in the parameters.

(4) Apply a pattern-oriented approach (POA) which involves first defining a set of "testing patterns" and then building a model that includes the mechanisms and individual trials as hypotheses that will be tested. Alternative formulations for individuals in the individual based model (IBM) are then used to simulate the condition under which each test pattern has been observed to occur. The final step is to then compare the testing pattern with the response variables (Grimm, 1994; Grimm *et al.*, 1996; Auyang 1998; Grimm, 1999; Grimm *et al.*, 1999; Railsback, 2001).

(5) Keep in mind that the model is heuristic, and not intended to be predictive (Grimm, 1999).

With this framework in mind, the modeling process used an IBM coupled to a hydrodynamic model, and was implemented using the following step-wise approach (Fig. 2.1):

- coupling each IBM to the hydrodynamic model
- definition of the experimental protocol (i.e. assumptions, criteria and response variables)
- analysis of results

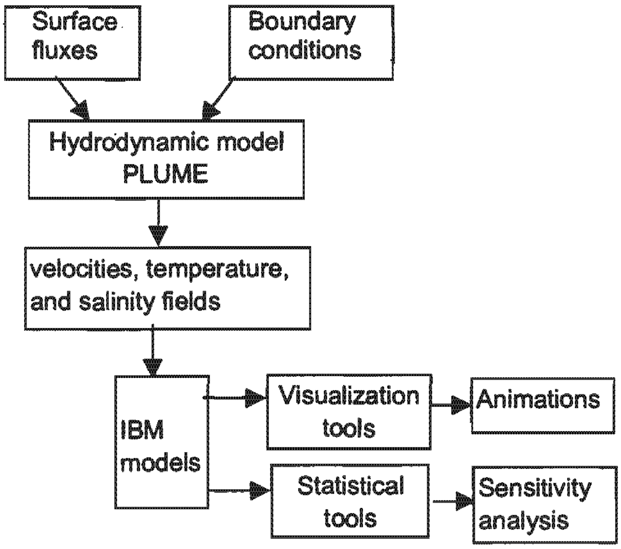

Figure 2.1. Flowchart of the methodological approach (modified after Mullon *et al.*, 2002).

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 approach. Nonetheless, these five years provide sufficiently different scenarios to test the hypotheses presented in chapter 1. The detailed descriptions of the coupling procedure are provided in the relevant chapters.

Table 2.1. Inputs of the IBM using direct and post-processing outputs from hydrodynamic model, and analyses performed using outputs from the hydrodynamic model to explain different scenarios of simulation.

Input of IBM with direct Outputs	**Description**
Water temperature and salinity	Hydrodynamic model (PLUME) (Penven *et al.*, 2001) outputs with a time step of 2 days in the model domain of the Benguela ecosystem
Velocity field	Hydrodynamic model output u,v, and w velocities with time steps of 2 days, used to estimate the Lagrangian trajectory of particles at a given time
Input of IBM with PLUME Post-processing output	**Description**
Water density	UNESCO equations for calculation of water density as a function of water temperature and salinity
IBM Scenarios of simulation with the analysis output PLUME	**Description**
Transport along and across-shore	Transport across- and along-shore (m^3s^{-2}) were estimated in the jet current and nursery area
Temperature profiles	Time series of the temperature profiles were extracted from PLUME outputs in order to study the dynamics of the 12 and 14 °C isotherms both within and between years at various localities on the Agulhas Bank, jet current and nursery area.

2.2.2. Hydrodynamic model

The environmental data used by the IBMs was obtained from the output of a hydrodynamic ocean model (PLUME) of the southern Benguela upwelling subregion (Penven, 2000; Penven *et al.*, 2001). This model is based on the Regional Ocean Modeling System (ROMS) numerical code (see Haidvogel *et al.*, 2000). It solves the free surface, hydrostatic, primitive equations of ocean dynamics over a variable topography using orthogonal curvilinear coordinates in the horizontal and stretched, terrain-following coordinates in the vertical dimension. The curvilinear grid is pie-shaped (Fig. 2.2a) to follow the southwestern corner of the African continent between 28 to 40°S and 10 to 24°E. The topographical input for PLUME was smoothed to prevent instabilities in the model. Horizontal resolution ranges from 9 km at the coast to 16 km offshore and twenty vertical levels preserve a high vertical resolution near the surface (Fig. 2.2b). At the 3 lateral boundaries facing the open ocean, an implicit active radiative boundary scheme, forced by seasonal time-averaged outputs of a basin scale ocean model (Biastoch and Krauß, 1999), connects all of the model's variables to the surroundings (Penven *et al.*, 2001). The model was forced using monthly climatology of wind, heat and salinity fluxes from the COADS ocean surface climatology, which has a spatial resolution of 1° squared (Da Silva *et al.*, 1994).

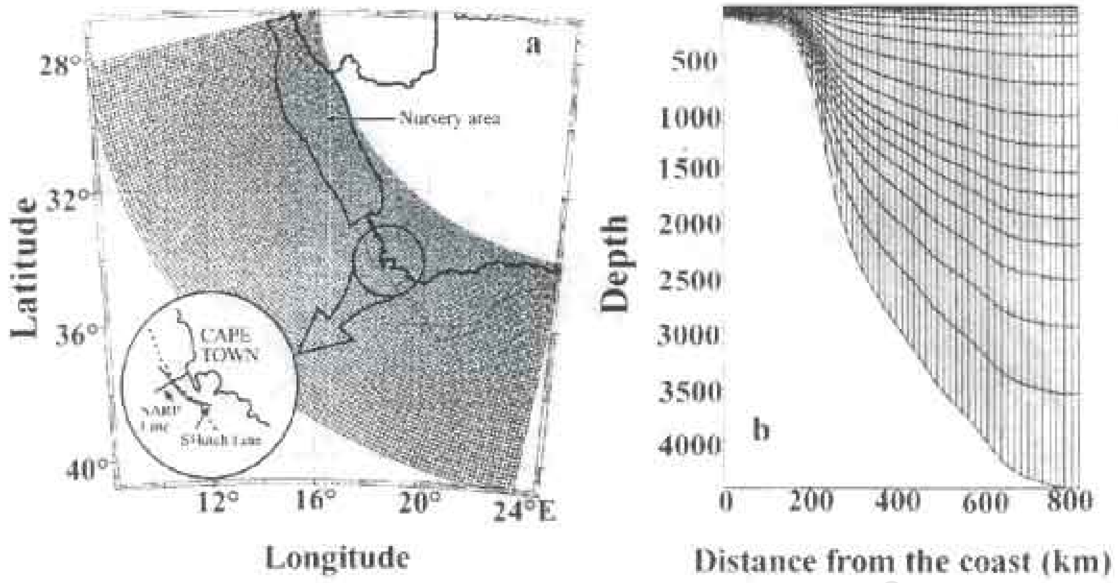

Figure 2.2. (a) The horizontal grid of the hydrodynamic model. The thick line represents the coastline, the thin line the 500 m isobath, and the grid resolution is approximately 10 km at the coast. The location of the west coast nursery grounds and the SARP (Huggett *et al.*, 1998) and SHutch (Shelton 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).

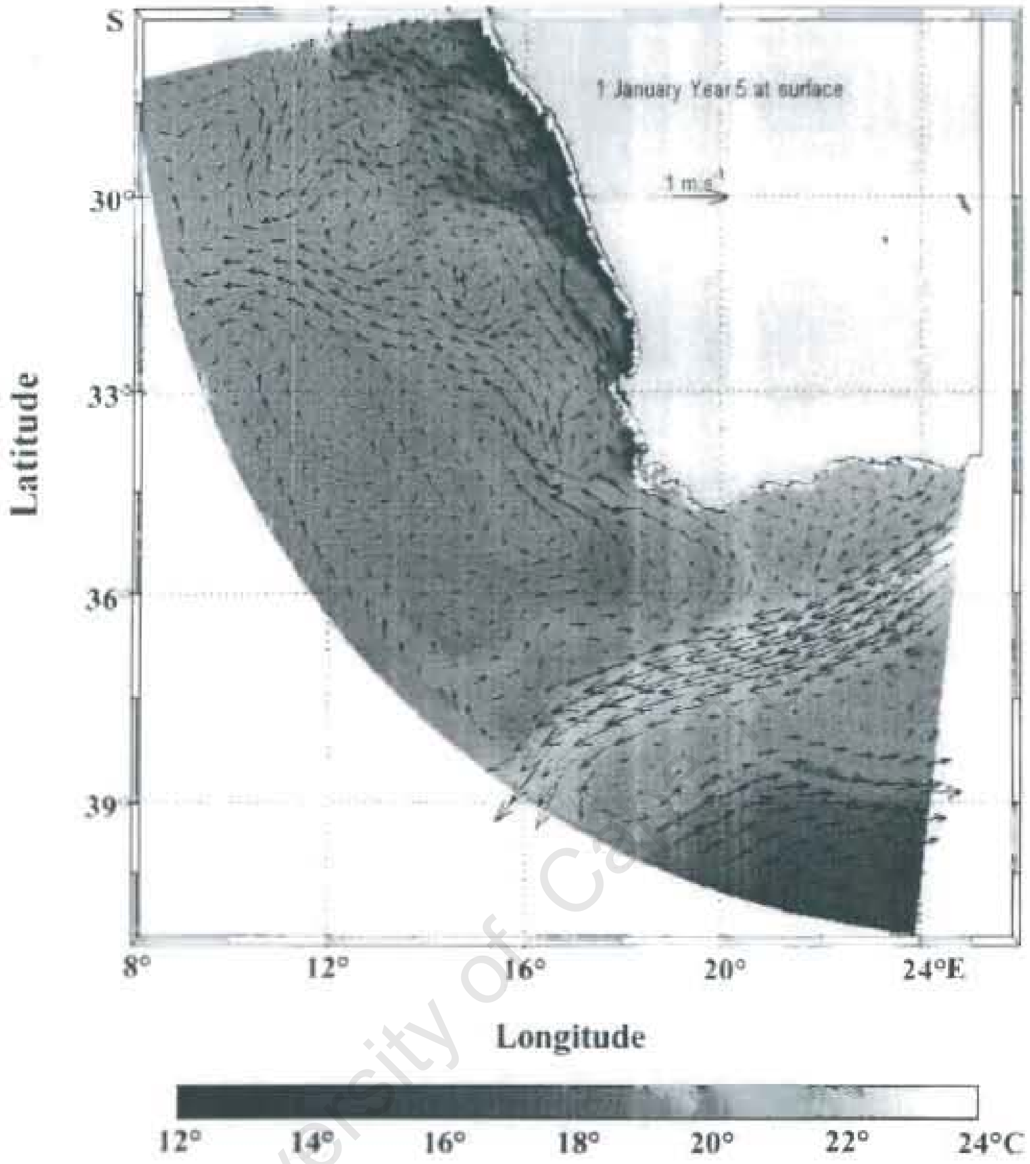

Figure 2.3. A snapshot (1 January of Year 5) of sea surface temperature and currents (arrows, only drawn every 3rd vector) in the southern Benguela region as simulated by PLUME.

2.2.3. Individual based model (IBM)

The individual based modeling technique was used in this study because it offers many advantages for spatially explicit modeling the early life history of marine fish (Hermann *et al.*, 2001). Individual based models (IBMs) are simulation models that use a bottom-up approach incorporating local interactions among individuals and time-varying heterogeneous environments (DeAngelis and Rose, 1992; Lorek and Sonnenschein, 1999) to describe a population. This approach permits a much more detailed examination than does a top-down approach. IBMs are being increasingly used to assess the influence of space on population dynamics, namely the variation of population abundance in time and the pattern formation in their habitats (Grimm, 1999; Grimm *et* *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 value for each response variable being studied (depending on the criteria). Thus each experiment generated a total number of values of each response variable that was equal to the number of combinations of parameters assessed. Furthermore, three replicates of each simulation were run with a random spatial distribution of released (spawned) particles. A multifactor statistical analysis of variance using the GLM module of Statistica (StatSoft, 2000) was employed to assess the performance, significance and the sensitivity of each IBM to changes in the parameter values. A pattern-oriented analysis was then systematically applied to assess the validity of the results of the model. Finally, based on the results of this latter analysis, the realism of each hypothesis was assessed, and the results interpreted in the light of the physical and/or biological processes involved.

2.3.1. Formulating assumptions for the models

Assumptions are statements that are accepted as true by the model without proof. The results and their interpretation are therefore clearly dependent on the validity of the assumptions.

Assumptions of the hydrodynamic model.

(1) It is assumed that after the spin-up of 2 years, equilibrium has been reached. The inter-annual variability observed in the model output is due to mesoscale instability and does not represent inter-annual variability generated by changes in the forcing factors (wind surface, heat fluxes, remote forcing).

(2) The 5 years selected from the total 10 years of the hydrodynamic model output constitutes enough inter-annual variability to properly test the hypothesis with the IBM, considering different scenarios of simulation.

(3) When forced by a monthly wind, solar radiation, climatology and simplistic bathymetry, the hydrodynamic model produces sufficiently realistic circulation patterns.

(4) Short-term (< 1 month) wind events do not significantly affect the transport of spawning products from the spawning grounds to the nursery area.

(5) Turbulence produced by short-term wind variability does not significantly affect the transport of the spawning products from the spawning ground to the nursery area when the buoyancy scheme or/and vertical behavior are incorporated into the models.

(6) Particles representing eggs and larvae are transported mainly in a Lagrangian fashion, and the effects of diffusion are negligible in comparison to this fast mode of transport

Assumptions of the IBMs. Several assumptions that are common with other IBMs developed for the region (for details see Huggett *et al.* 2003) are summarized as follows:

(1) The number of particles used in each simulation (5000) is an adequate number to ensure the stability of the IBM outputs.

(2) Based on field data from spawning surveys, the Agulhas Bank (from Cape Point to Cape St. Francis) from the coast line to the 500 m isobath is considered to be the primary spawning area.

(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.

Transport success criteria and the response variable. The transport success criterion was applied to models 1 to 4, and was defined as those particles older than 14 days (equivalent to 7 model time steps) that arrived on the west coast nursery grounds between Cape Columbine and the Orange River mouth. The nursery area was subdivided into inshore (the continental shelf between 0m and 200m depth) and offshore (200m to 500m depth) regions (Fig. 2.4).

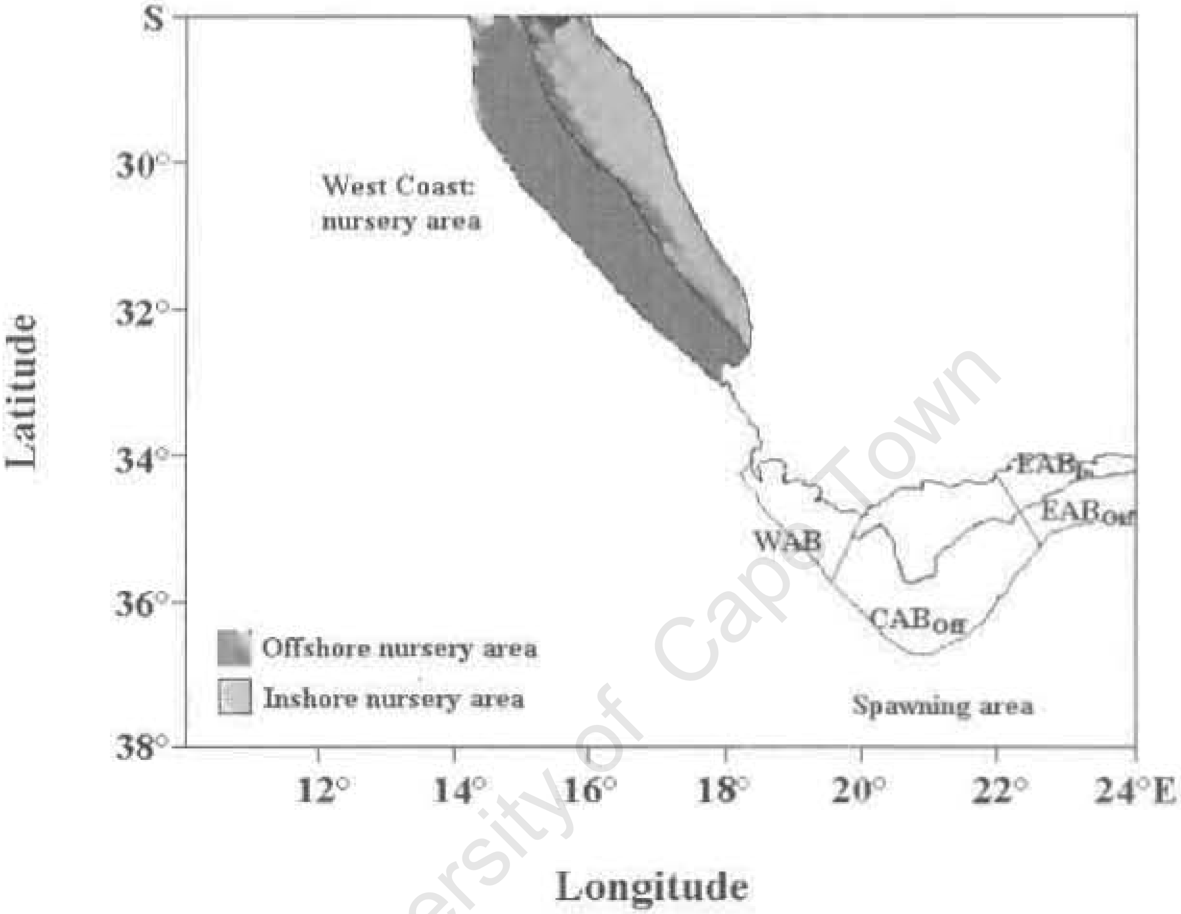

Figure 2.4. Transport success area in the nursery ground west coast (inshore and offshore area). The locations of the WAB (Western Agulhas Bank), $\mathrm{CAB_{Off}}$ (Central Agulhas Bank offshore), $\mathrm{EAB_{In}}$ (Eastern Agulhas Bank inshore) and $\mathrm{EAB_{Off}}$ (Eastern Agulhas Bank offshore) spawning grounds are shown.

The response variable for these models (i.e. models 1 to 4) was measured as the ratio of the number of particles that satisfied the transport success criterion at the end of the simulation to the number of particles released at the beginning of the simulation (Table 2.2). The choice of a 14 days threshold for anchovy arriving successfully in the nursery area was based on the observation that anchovy larvae >7 mm caudal length (corresponding to an approximate age of 14 days; Brownell,

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 temperature thresholds were considered because no information concerning the upper lethal temperature threshold is available for *E. encrasicolus* in the Benguela system. The response variables in the IBM were the egg and larvae mortality indices. The egg mortality index was defined as the ratio between the number of particles representing eggs that died as a result of low temperatures at the end of the simulation to the number of particles released at the beginning of the simulation. The larval mortality index was then defined as the ratio between the number of particles representing larvae that died as a result of low temperatures at the end of the simulation to the number of particles representing surviving eggs (Table 2.3).

Table 2.3. Mortality criteria and response variable used in each model.

Models	Mortality criteria	Mortality (index) response variable
4-8	Egg mortality resulting from the lethal effect of low temperature	Ratio between the number of eggs that died due to the temperature effect by the end of the simulation to the total number of egg (particles) released
4-8	Larvae mortality resulting from the lethal effect of low temperature	Ratio between the number of larvae that died due to the temperature effect by the end of the simulation to number of surviving eggs (particles).

Retention criteria and response variables. The criterion for successful retention in the west coast nursery area (model 7) was that larvae arriving in the nursery area (both inshore and offshore) after they had hatched and reached the active behavior stage, had to remain in the area for a period >10 days (Table 2.4). The response variable was then measured as the ratio of successfully retained larvae to the total number of egg (particles) released (Table 2.4). The same retention criterion and response variable was employed in the EAB model (model 8), but differed in that the success area was considered to be the EAB_{In} and EAB_{Off} (Fig. 1.1).

Table 2.4. Retention criteria and response variable used in each model.

Models	Retention criteria	Retention response variable
7	Larvae that arrive in the inshore nursery area after they hatched and reached the active behavior stage and stayed more than 10 days in this area	Ratio between the number of larvae that stayed more than 10 days in the inshore part of nursery area to the total number of egg (particles) released
8	Larvae that arrive in EAB_{In} and EAB_{Off} area after they hatched and reached the active behavior stage and stayed more than 10 days in these areas	Ratio between the number of larvae that stayed more than 10 days in the EAB areas to the total number of egg (particles) released

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 to the nursery area. The third IBM (model 7) extended this behavioral scheme to assess the retention of anchovy larvae and post-larvae (i.e. individuals between a month to 12 weeks) in the inshore part of the west coast nursery area. The final IBM (model 8) used the same parameters and constants to address the alternative hypothesis of retention on the EAB.

Table 2.6. Constants and parameters set for the second group of IBMs aimed at studying the effects of environmental processes on the growth, mortality, transport success, retention and distribution of 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	**Passive behavior (5)**	**Active behavior (6)**	**Retention (7) applied to west coast**	**Retention (8) applied to EAB**
Constants				
Spawning duration	✓	✓	✓	✓
Tracking duration	✓	✓	✓	✓
Duration of the simulation	✓	✓	✓	✓
Number of particles	✓	✓	✓	✓
Density of particles	✓	✓	✓	✓
Shape of particles	✓	✓	✓	✓
Factor of growth	✓	✓	✓	✓
Lethal temperature for eggs	✓	✓	✓	✓
Lethal temperature for larvae	✓	✓	✓	✓
Time after hatch start active behaviour	-	-	✓	✓
Parameters				
Area of spawning	✓	✓	✓	✓
Date of spawning	✓	✓	✓	✓
Year of simulation	✓	✓	✓	✓
Depth of egg released	✓	✓	✓	✓
Time after hatch start active behaviour	-	✓	-	-
Depth selected after hatch	-	✓	✓	✓

EAB: Eastern Agulhas Bank

The configuration of these groups of experiments and the biological schemes used to define the various models are presented in the relevant chapters. Once the models were initialized and the parameters set for each simulation, a population of 5000 particles (representing eggs) was randomly released in specific regions within the spawning area. The spawning area was subdivided into four regions following Huggett *et al.* (2003):

(1) The Western Agulhas Bank (WAB): extending from Cape Point to Cape Agulhas between the 0 and 500 m isobaths,

(2) The offshore region of the Central Agulhas Bank (CAB_{Off}): extending from Cape Agulhas to Mossel Bay between the 125 and 500 m isobaths,

(3) The inshore region of the Eastern Agulhas Bank (EAB_{In}): from Mossel Bay to Plettenberg Bay between the 0 and 125 m isobaths,

(4) The offshore region of the Eastern Agulhas Bank (EAB_{Off}): from Mossel Bay to Plettenberg Bay between the 125 and 500 m isobaths.

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

parameters that were not significant, or those that were significant but explained less than 2% of the variance were discarded. The GLM was then run again and the error of the new model assessed. In the final assessment of the statistical analyses significant parameters and their interactions were only considered when they explained >5% of the model variance. Following this, different combinations of parameters in the IBMs, including those parameters that had previously been removed, were tested in order to avoid that any interaction of first and second order parameters was significant and explained more than 5% of the variance. The mean least squares was computed for each value of the parameters of the model in order to assess the effect of specific parameter values on the specific dependent variables.

Pattern-oriented analysis. Pattern-oriented analysis (POA) identifies important patterns in the model output (IBM). POA attempts to understand and represent the mechanisms that cause such patterns (Fig. 2.1). This is a way to focus a modeling study, providing guidance on such issues as what processes to include, and what scales are relevant (Grimm *et al.*, 1996). The key benefit of pattern-oriented modeling is that it assures that the model produces predictions suitable for testing. In other words, models can be tested as to whether or not they reproduce the patterns they were designed to address (Grimm *et al.*, 1996). A series of test patterns were selected for each IBM and compared with the patterns identified in the output of each model (Table 2.7).

Table 2.7. Patterns of data used to compare with the IBM model outputs.

Patterns	Description	Model
SARP Line	Egg data collected from the SARP (Sardine Anchovy Recruitment Program) Line, a 34-mile transect of 12 evenly-spaced stations running west-south-west of Slangkop Point off the Cape Peninsula, sampled 1-2 times every month (Huggett *et al.*, 1998).	1-3
SHutch Line	Vertical profiles of egg concentrations along a line off the Cape Peninsula provided by Shelton and Hutchings (1982). (called the SHutch Line in our model Fig. 3a)	3-4
Pre-recruit surveys	Horizontal size-frequency distributions of pre-recruits collected using a Methot frame trawl during March surveys in the years 1983-2000, with exception of year 1993 (van der Lingen and Merkle, 1998; 1999)	5-8

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.

3.2. METHODS

3.2.1. Overview of the experiments and simulations

The IBM was used to track the movement of particles representing anchovy eggs spawned over the Agulhas Bank and transported northwards to the west coast nursery grounds. Both horizontal and vertical movements of particles were modeled: horizontal movement was driven by the outputs of the 3-D hydrodynamic model (PLUME), while vertical movement was regulated by both the PLUME outputs and particle buoyancy properties. The latter were dependent on each particle's density relative to that of the surrounding seawater, the particle's diameter, seawater viscosity and gravitational force. By incorporating the buoyancy component into the model, the IBM generated a variety of vertical and horizontal particle distribution patterns that gave rise to differential transport success.

3.2.2. Setting the constants and parameters of the experiments

Three experiments were conducted. The first (a Lagrangian experiment using model 1), excluded buoyancy and treated eggs and early larvae as purely Lagrangian particles, the vertical and horizontal velocities of which depended only on the flow-field output from the hydrodynamic model. The second and third experiments (the buoyancy experiments using models 2 and 3) incorporated the effect of buoyancy, and computed particle vertical velocity as a function of buoyancy and vertical flow-fields, horizontal velocities depended on the flow-field output from the hydrodynamic model. The buoyancy experiments made use of different assumptions and timing when incorporating buoyancy into the IBM. In the second experiment (the buoyancy experiment applied to particles representing eggs and larvae using model 2), the buoyancy properties of egg and early larvae stages were assumed to be the same, hence the same buoyancy scheme was applied to all particles throughout the simulations. The third experiment (the buoyancy experiment applied only to particles representing eggs using model 3) assumed that only the egg stages were buoyant, and that larvae behaved as Lagrangian particles after hatching. The buoyancy scheme was therefore only applied to particles during the first 3 time steps of PLUME (1 time step = 2 days). The constants set in these experiments and their values are listed in Table 3.1. In the Lagrangian experiment, the set parameters were Date (6 values), Year (5 values), Depth (3 values) and Area of spawning (4 values). It should be noted that all 4 values of the latter parameter where used in each simulation (i.e. eggs were released in all 4 regions of the Agulhas Bank). Three replicates of each simulation were run, generating a total of 6 x 5 x 3 x 3 = 270 simulations (Table 3.1). Both buoyancy models used the same set of parameters as did the previous model, but also included the parameters Particle density (5 values) and Shape of the particles (3 values). This generated a total of 6 x 5 x 3 x 3 x 5 x 3 = 4050 simulations (Table 3.1).

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).

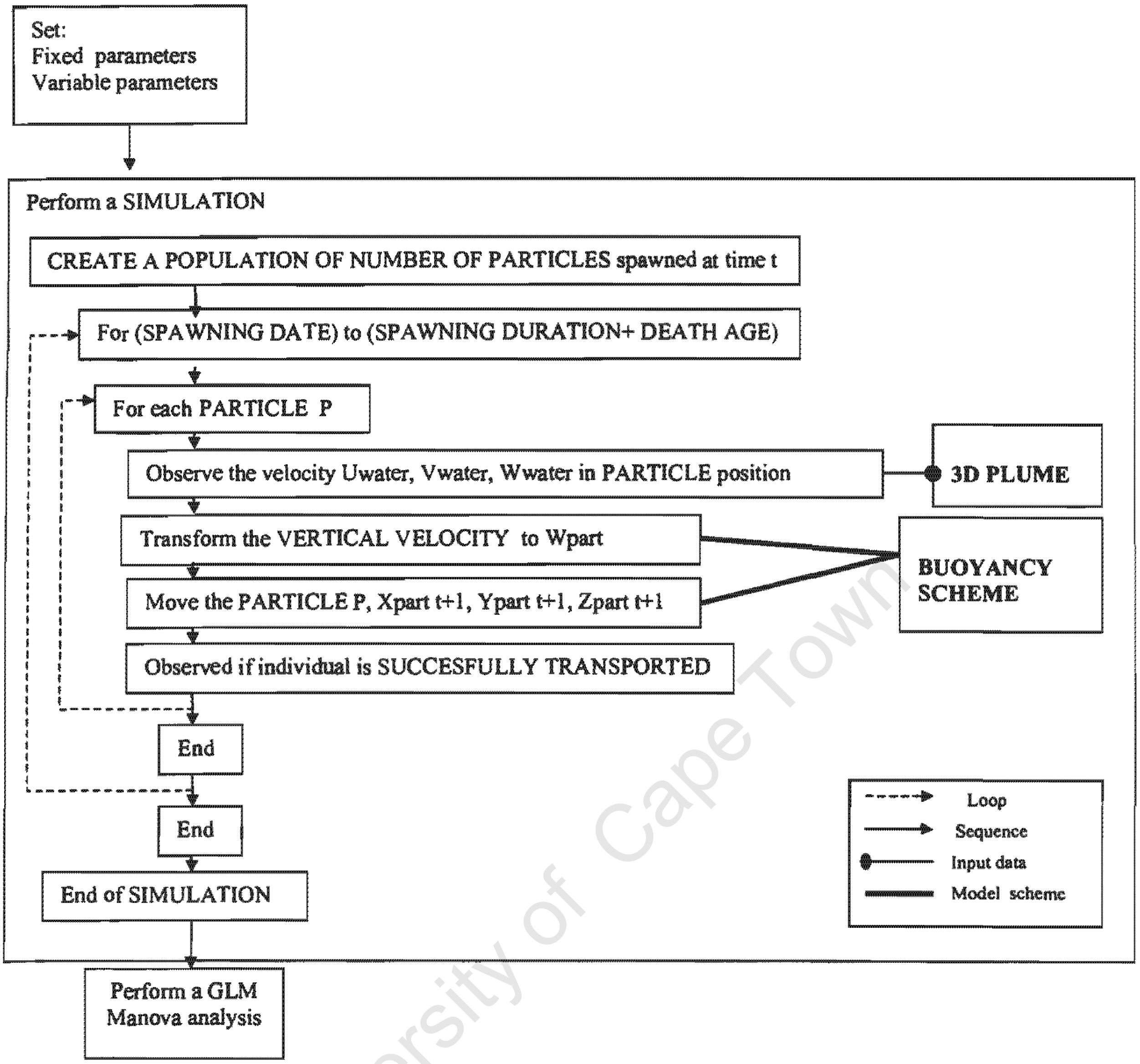

Figure 3.1. Flowchart of experimental simulations of buoyancy model.

3.2.4. Response variable: Transport success

The criteria of transport success used in all three experiments specified that the particles older than 14 days (equivalent to 7 model time steps) that arrived at the west coast nursery grounds (inshore and offshore area, Fig. 2.4) were successfully transported. The response variable in the IBM was then defined as the ratio of the number of particles that satisfied the criterion of transport success at the end of the simulation, to the number of particles released at the start of the simulation. This ratio was considered to be the dependent variable in the subsequent statistical analyses (Table 2.3).

3.2.5. The buoyancy scheme

The terminal velocity of the particles was calculated using the equation of Denny (1993) that computes the force required to propel a prolate spheroid of given weight moving parallel to its long 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 ($\nu = 0.01\ m^2s^{-1}$), minor (d) and major (l) axis length and particle density (ρ_{part}).

$$w_{part} = w_{water} + \frac{1}{24} g d^2 \frac{\Delta\rho}{\rho_w} \nu^{-1} \ln\left(\frac{2l}{d} + \frac{1}{2}\right) \tag{3.1}$$

where :

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

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:

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

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

$$\frac{dz_{part}}{dt} = w_{part} \tag{3.5}$$

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:

$$x_{part(t+1)} = x_{part(t)} + u_{water}dt \tag{3.6}$$

$$y_{part(t+1)} = y_{part(t)} + v_{water}dt \tag{3.7}$$

$$z_{part(t+1)} = z_{part(t)} + w_{part}dt \tag{3.8}$$

3.2.6. IBM outputs and analysis of results

A sensitivity analysis was applied to the response variable of the Lagrangian and the buoyancy experiments using a multiple factor variance analysis from the GLM module of "Statistica" (StatSoft, 2000). The parameters and their first and second order interactions were selected as independent variables (Table 3.1). The values of the response variable of the IBM (transport success) were selected as dependent variables in the sensitivity analyzes. In addition, this analysis included a study of the frequency distribution of residuals in transport success as well as the significance and proportion of variance explained by each of the parameters and their interactions, hence allowing the identification of the main variables in the IBM that impacted on transport success. The full GLM included all parameters and their interactions up to the second level of interaction. The parameters and interactions that explained more than 5% of the variance in the model were then considered to be important influences on transport success.

3.3. EFFECT OF PARTICLE DENSITY UNDER DIFFERENT JET CURRENT SCENARIOS

Three scenarios of jet current strength and possible offshore advective loss were identified from analyses of the PLUME model output, and were used to examine how particle density affected transport success. These scenarios were identified using averaged transport values ($m^3.s^{-1}$) in the jet current over a three months period (corresponding to the duration of the simulation in the IBM) subsequent to the date on which particles representing eggs were released and integrated for the first 50 m. Both along-shore (north-south) and across-shelf (offshore-onshore) cumulative transport values were computed from the PLUME model output. Six along-shore and six across-shelf transport value, corresponding to the six different dates for the initiation of the spawning (see Table 3.1) were computed for each model year used in this analysis (year 4-8), giving a total of 60 values. The cumulative transport values alongshore were calculated along a 100 km line positioned at the location of the SARP (Sardine Anchovy Recruitment Program) Line (Fig. 2.2a) a transect of 12 evenly-spaced stations running west-south-west of Slangkop Point off the Cape Peninsula, sampled 1-2 times every month located at 60 km from the coastline (see Huggett *et al.*, 1998). The across-shore transport was calculated in a line of 100 km across-shelf of the SARP Line. Both transport values were integrated for the upper 50m. These boundaries were chosen to represent the transport region as well as the likely vertical distribution range of anchovy eggs (Shelton and Hutchings, 1982) and the maximum offshore position of the jet current (Boyd and Nelson, 1998).

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 model, and the residual variance was only 2.3% when all other factors are considered (Table 3.2.). Residuals of transport success from the passive Lagrangian experiment appeared to be normally distributed, as required for the GLM analysis.

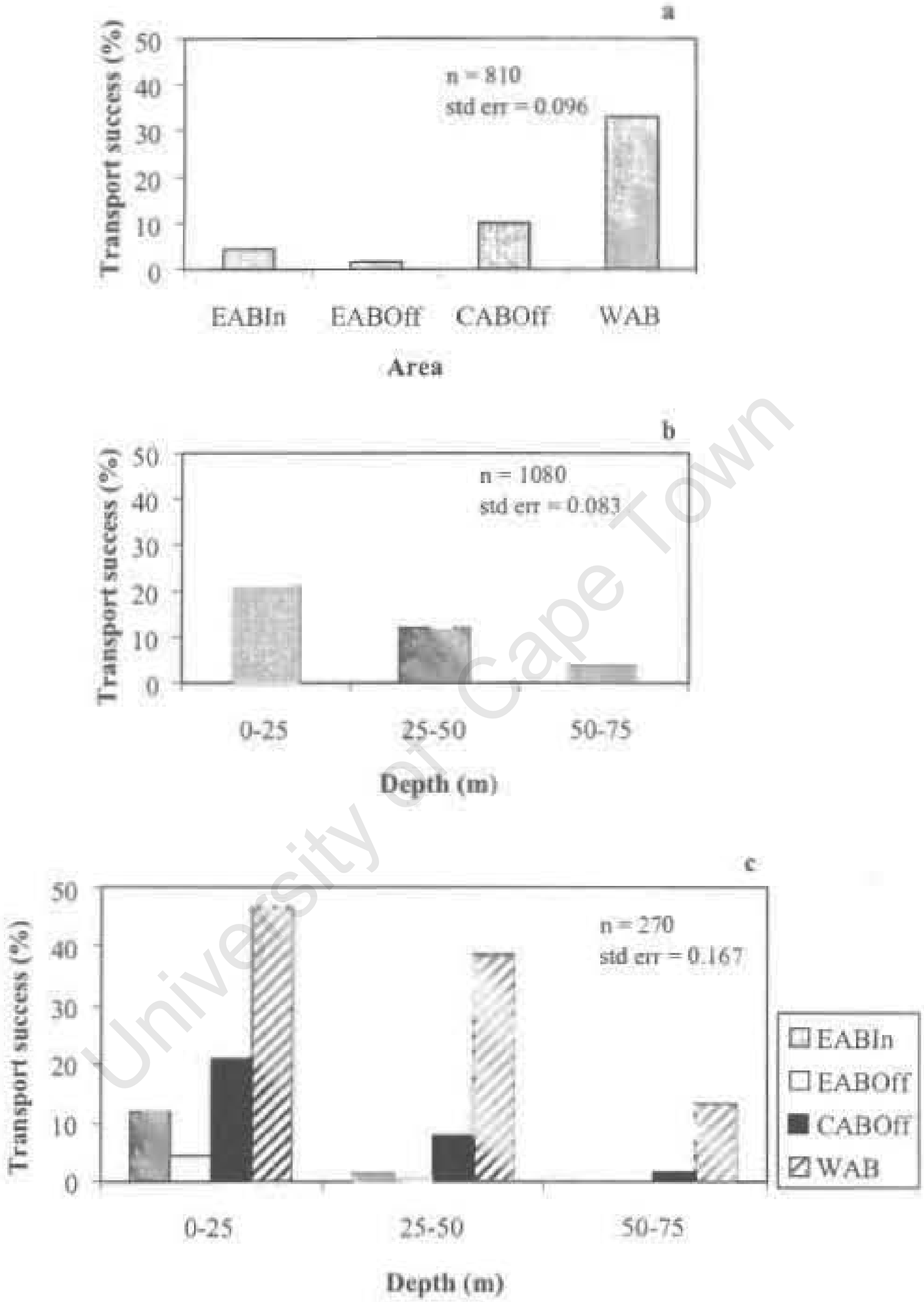

Figure 3.2. Ratio of transport success to the released particles representing eggs for the single parameters used in the Lagrangian experiment: (a) Area of spawning, (b) Depth of particle release, and (c) interaction between Area of spawning and Depth of particle release.

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, $S = P < 0.001$, $NS = P > 0.05$

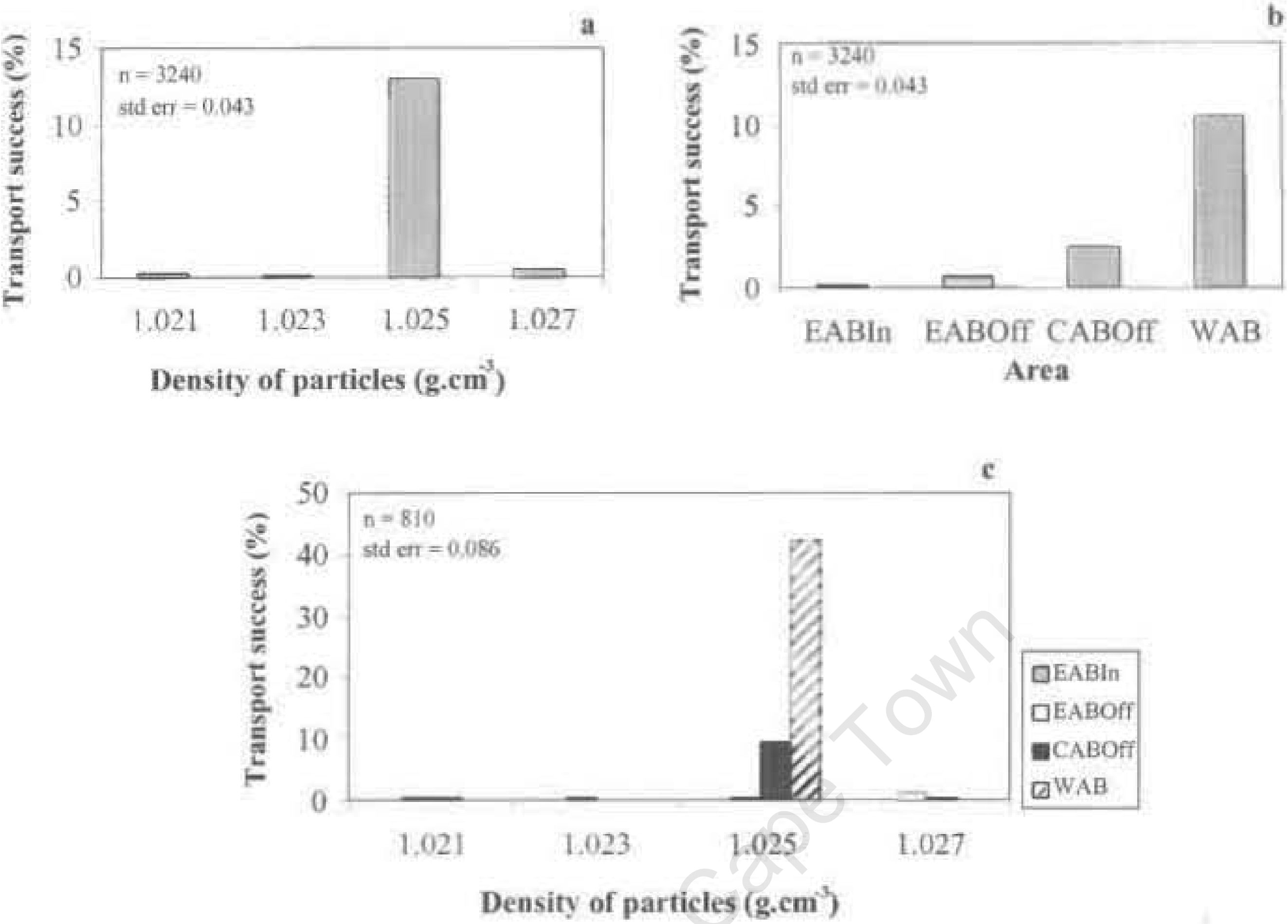

Figure 3.3. Ratio of transport success to the number of released particles representing eggs for the single parameters used in the buoyancy experiment (model 2): (a) Density of the particle, (b) Area of spawning, (c) Interaction between Density of the particle and Area of spawning.

Buoyancy scheme applied only to egg stage (model 3). The results of this experiment were very similar to those obtained from model 2, except that Area explained slightly more of the variance than did particle Density. The first levels of interaction, namely Area*particle Density, Date*particle Density, and the second level of interaction all explained less of the variance relative to model 2 (Table 3.4). The parameters and significant interaction terms of this experiment accounted for 83.9% of explained variance, and the error term was 5.4% for the full model (Table 3.4). Residuals of transport success were normally distributed.

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%).

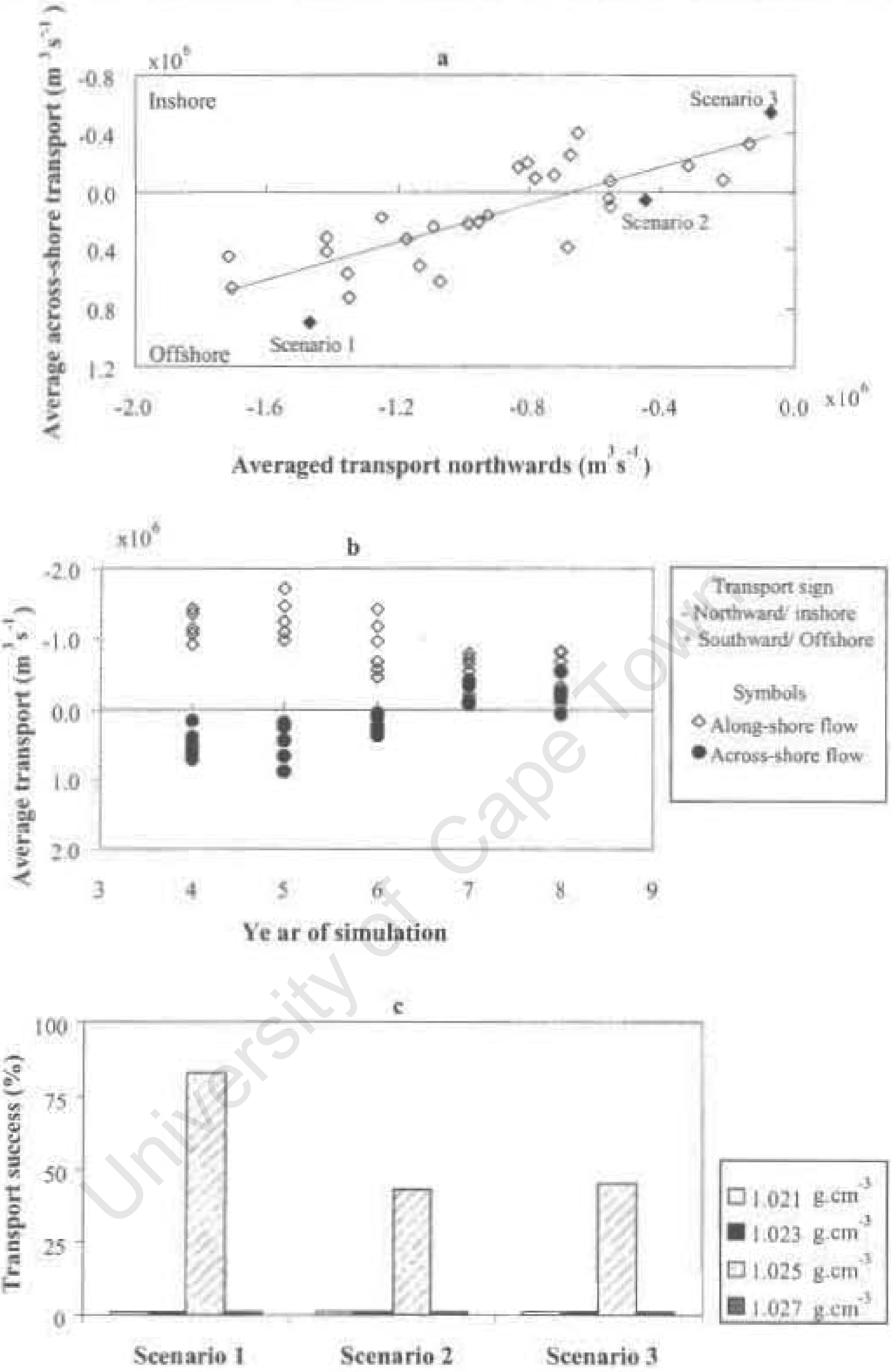

Figure 3.4. (a) Average along-shore and across-shelf transport in the region of the jet current for all simulations, (b) average along-shore and across-shelf transport per year, and (c) transport success as a function of Density for particles released in the upper 25m over the WAB only for each of three scenarios. Each scenario represents a single simulation. The average transport and transport success was calculated over a 3 month periods corresponding to the duration of the IBM simulations.

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).

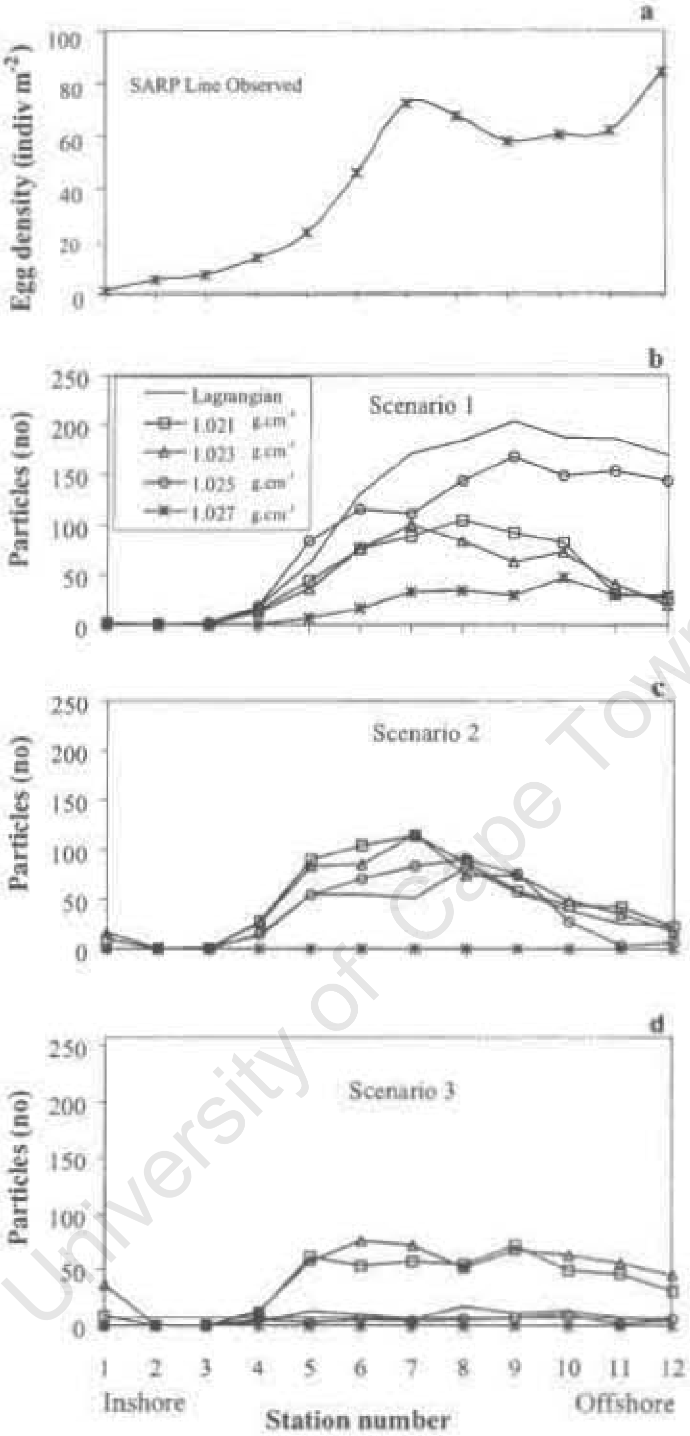

Figure 3.5. (a) Observed (between August 1995 and July 2001; data from J. Huggett, Marine and Coastal Management, pers. comm.) horizontal distribution of anchovy eggs and simulated (b-d for the three jet current scenarios) horizontal distributions of particles along the SARP Line.

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.

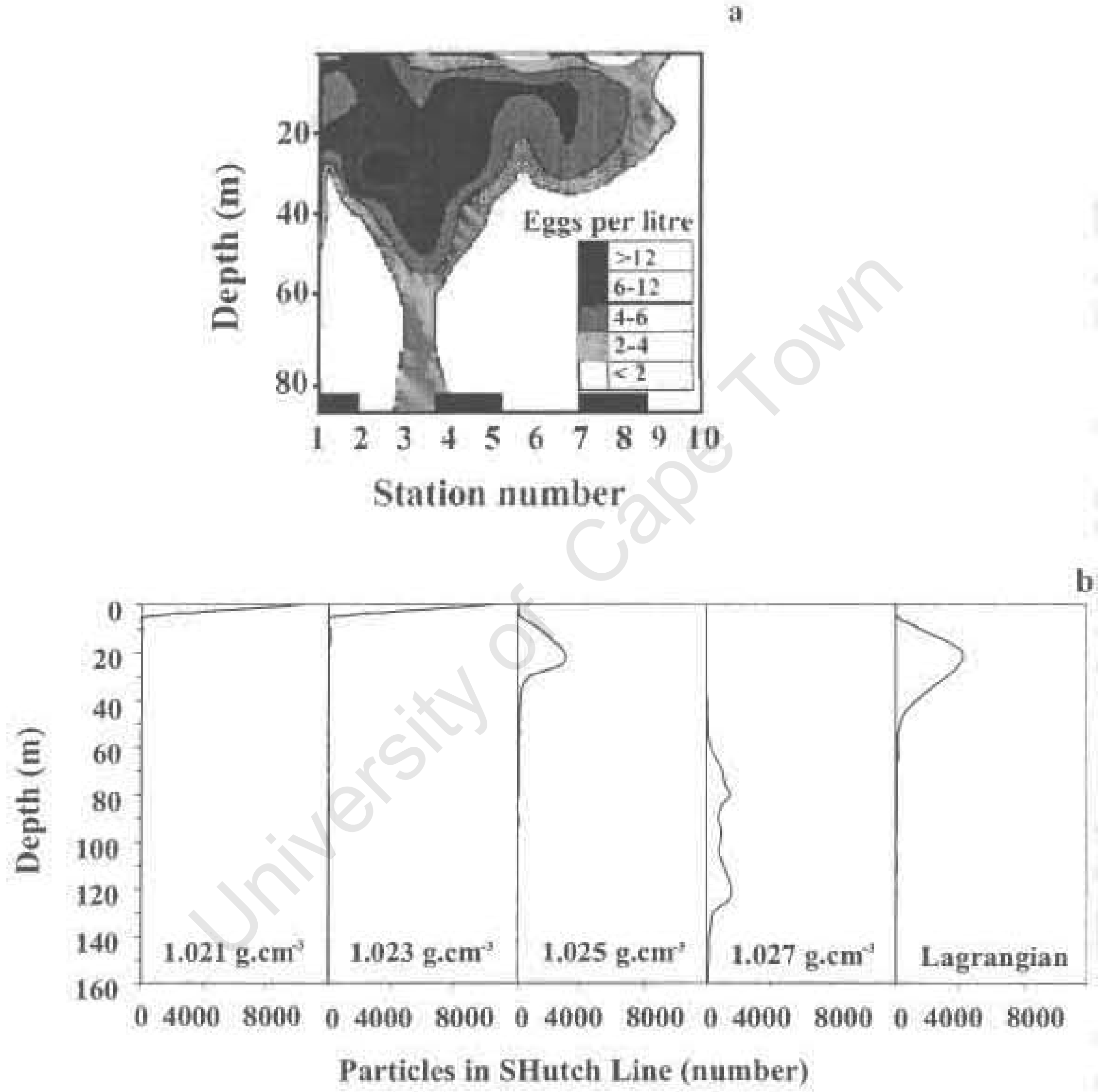

Figure 3.6. (a) Observed vertical distributions of anchovy eggs below the SHutch Line (Shelton and Hutchings, 1982), and (b) simulated vertical distributions of particles of varying densities in the SHutch Line.

3.6. DISCUSSION

An IBM was designed to simulate the transport of anchovy eggs in the southern Benguela upwelling system, from the Agulhas Bank spawning area to the west coast nursery grounds. By positioning particles that represent eggs in a 3-D hydrodynamic model of the region and tracking their transport by a coastal jet to the nursery grounds, and by varying parameters such as density of the particles and the spatio-temporal location of particle release, it was possible to examine the importance of these parameters in influencing transport success. Since the transport of eggs and early larvae is considered to be one of the major factors impacting on anchovy recruitment success (Hutchings *et al.*, 1998), this study may be useful in furthering our understanding of recruitment variability in this economically and ecologically important species. Outputs from the IBM compared well with observed patterns of vertical and horizontal egg distribution from the region, indicating that the IBM provided quasi-realistic simulations. Of the parameters in the simulations, particle Density and spawning Area were the major determinants of transport success, with particles having a density of 1.025 g.cm^{-3} being most successfully transported on average, and the WAB being the most and the EAB the least favorable spawning areas. Both the sensitivity and pattern analyses indicated that particle Density had a significant impact on both the vertical and horizontal distributions, and hence an important effect on transport success. Examination of outputs from the buoyancy experiments has improved our understanding of the factors affecting the transport of particles from the spawning to the nursery area, and has also permitted the characterization of biological and physical properties that are likely to influence transport. The distribution patterns of particles generated by the models compared relatively well with observations in both the vertical and horizontal planes. This, together with the fact that the PLUME model reproduces recognizable mesoscale features such as upwelling filaments and plumes (Penven *et al.*, 2001), gives us confidence concerning the realism of the IBM and the accuracy of inferences made from it concerning transport process.

The results presented here were used to identify the primary determinants of transport success in the various experimental simulations, and examined and compared to field observations. In the passive Lagrangian experiments, Area was the dominant parameter and accounted for more than 50% of the variability in the transport success of particles representing eggs. This finding is consistent with other modeling studies of anchovy egg transport in the southern Benguela system in which buoyancy was not considered (Huggett *et al.*, 2003). Depth of spawning was also an important parameter in the passive Lagrangian experiments, but not in the buoyancy experiments since the particle Density parameter "controls" the depth of particles at any time step during simulations. The inclusion of particle density in our buoyancy experiments showed the importance of this parameter, both in itself and in its interactions with other parameters. Whereas both buoyancy experiments identified density as an important factor, reducing the period during which the buoyancy scheme was applied only slightly reduced the percentage of variance explained by density (from 19.9 to 17.5%)

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 contrast, when the particles are light (1.021-1.023 g cm^{-3}) they tend to be concentrated in the upper 5 m. Dense (1.027 g.cm^{-3}) particles are distributed between 60 m and 140 m, which appears to be too deep compared to field observations from the southern Benguela system, and for anchovy species elsewhere (Motos and Coombs, 1998; Moser and Pomeranz, 1999; Santos *et al.*, 2000).

Results from the various scenarios in terms of the SARP Line indicate another important pattern, namely a relationship between particle density and averaged jet current transport. Particle density had different effects on transport to the SARP Line in three scenarios: strong transport (Scenario 1) promoted Lagrangian particles and those with a density of 1.025 g.cm^{-3} and considerably reduced the transport of particles less than and greater than 1.025 g.cm^{-3}. As northward transport was reduced (Scenario 2), the transport of lighter (1.021 and 1.023 g.cm^{-3}) particles was enhanced. When northward transport was substantially reduced (Scenario 3), only lighter (1.021 and 1.023 g.cm^{-3}) particles arrived at the SARP Line. This suggests that when northward and offshore transport is strong, most of the particles arriving at the SARP line are those with a density of 1.025 g.cm^{-3}. In contrast, when northward and offshore transport decreases, or under conditions of moderate northward and strong onshore transport, lighter particles are more successfully transported to the SARP Line. These results emphasize the importance of the interaction between buoyancy and physical conditions in determining a particular transport success in any given year.

The importance of particle density on transport success may have been underestimated by our analysis because of the vertical scales used in the hydrodynamic model. The minimum vertical resolution of the hydrodynamic model is 9 m (the uppermost layer), which may be too large to capture fine-scale differences (over scales of tens to hundreds of cm) in egg vertical distributions that have been reported for other anchovy species (Motos and Coombs, 1998; Santos *et al.*, 2000; Coombs *et al.*, 2000 for *E. encrasicolus*; Moser and Pommeranz, 1999 for *E. mordax*). Hence it is possible that increasing the vertical resolution in the near-surface domain of the model would have resulted in a higher variability on the stabilization of eggs to determined depths.

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 mortality and growth rates of anchovy eggs and larvae, the interaction of these effects with the temporal and spatial scales of the spawning process, and the consequences on transport success. Annual and seasonal patterns in the temperature profiles generated by the hydrodynamic model PLUME were first identified. Subsequently a simple temperature-dependent growth scheme was selected, threshold values of temperature affecting eggs and larval mortality were defined, and an IBM designed. The temperature approach used in this IBM might seem too simple, however, it is the first attempt to relate and quantify the critical effect of temperature with such spatial and temporal resolution. Next IBMs should include other mortality sources such predation and starvation that could not be included in this study due to the lack of field data to support basic assumptions. The results were analyzed with a multiple factor analysis of variance using the general linear model (GLM) module of Statistica, and were then compared to field data.

4.2. METHODS

4.2.1. Identification of annual and seasonal patterns in the temperature profile outputs of the hydrodynamic model

Annual and seasonal temperature profiles generated by the PLUME model were investigated at 8 stations in southern Benguela region (Fig.4.1): three stations in the nursery area, west coast (Nur1, Nur2, Nur3), one station in the jet current, four stations on the Agulhas Bank (WAB, CAB_{Off}, EAB_{Off} and EAB_{In}).

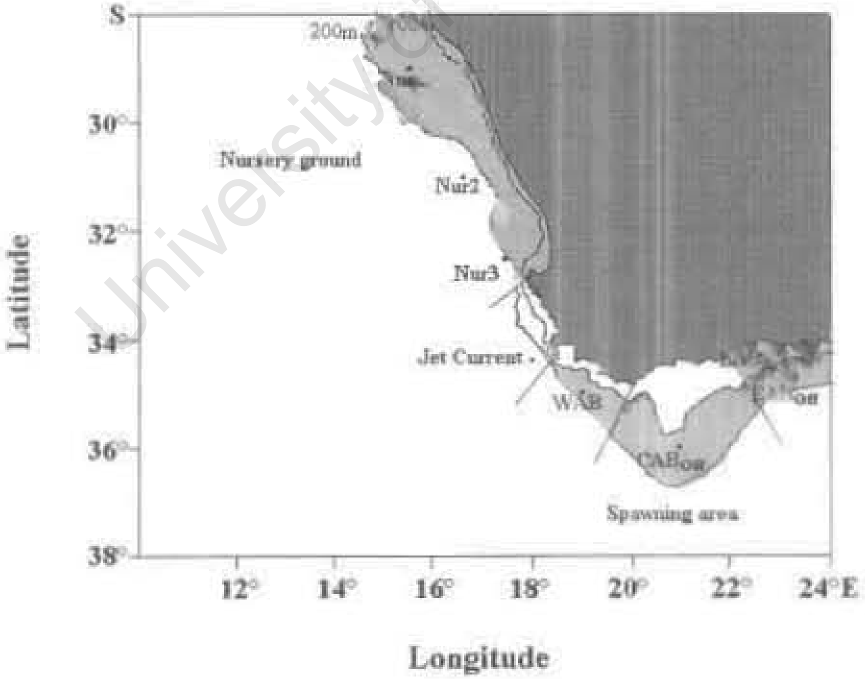

Figure 4.1. Map of the 8 stations where time-series of temperature profiles were extracted from the hydrodynamic model: (i) three stations in nursery area, west coast (Nur1, Nur2, Nur3), (ii) jet current, (iii) four stations in Agulhas Bank (WAB, CAB_{Off}, EAB_{Off} and EAB_{In}).

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 $6 \times 5 \times 3 \times 5 \times 3 \times 3 \times 3 = 12150$ 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 stages: (i) eggs/larvae survive and grow/develop at a rate according to the ambient temperature, (ii) eggs/larvae die because the ambient temperature falls outside of critical limits.

Table 4.1. Constants and parameters used to formulate the individual-based model of growth and mortality as a function of temperature (model 4)

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	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 of the relative size (in km^2) of each area
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 ratio minor to major axis for a prolate spheroid 0.05:0.14 cm

Parameters	Description
Area	Eggs were released in Western (WAB), Central offshore (CAB_{Off}), Eastern Agulhas Bank inshore (EAB_{In}) and offshore (EAB_{Off})
Date	The dates of spawning were set to 1st October, 1st November, 1st December, 1st January, 1st February and 1st March
Year	Years 4-8 from Hydrodynamic model output (Penven, 2000) were used in the IBM
Depth	Eggs 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
Factor of growth	The factor of growth (λ) was set to 1.5, 1.2, 1.0, 0.5 and 0.2
Lethal temperature for eggs	The lethal temperatures for eggs (θ_E) were set to <13°C, <14°C and <15°C
Lethal temperature for larvae	The lethal temperatures for larvae (θ_L) were set to <11°C, <12°C and <13°C

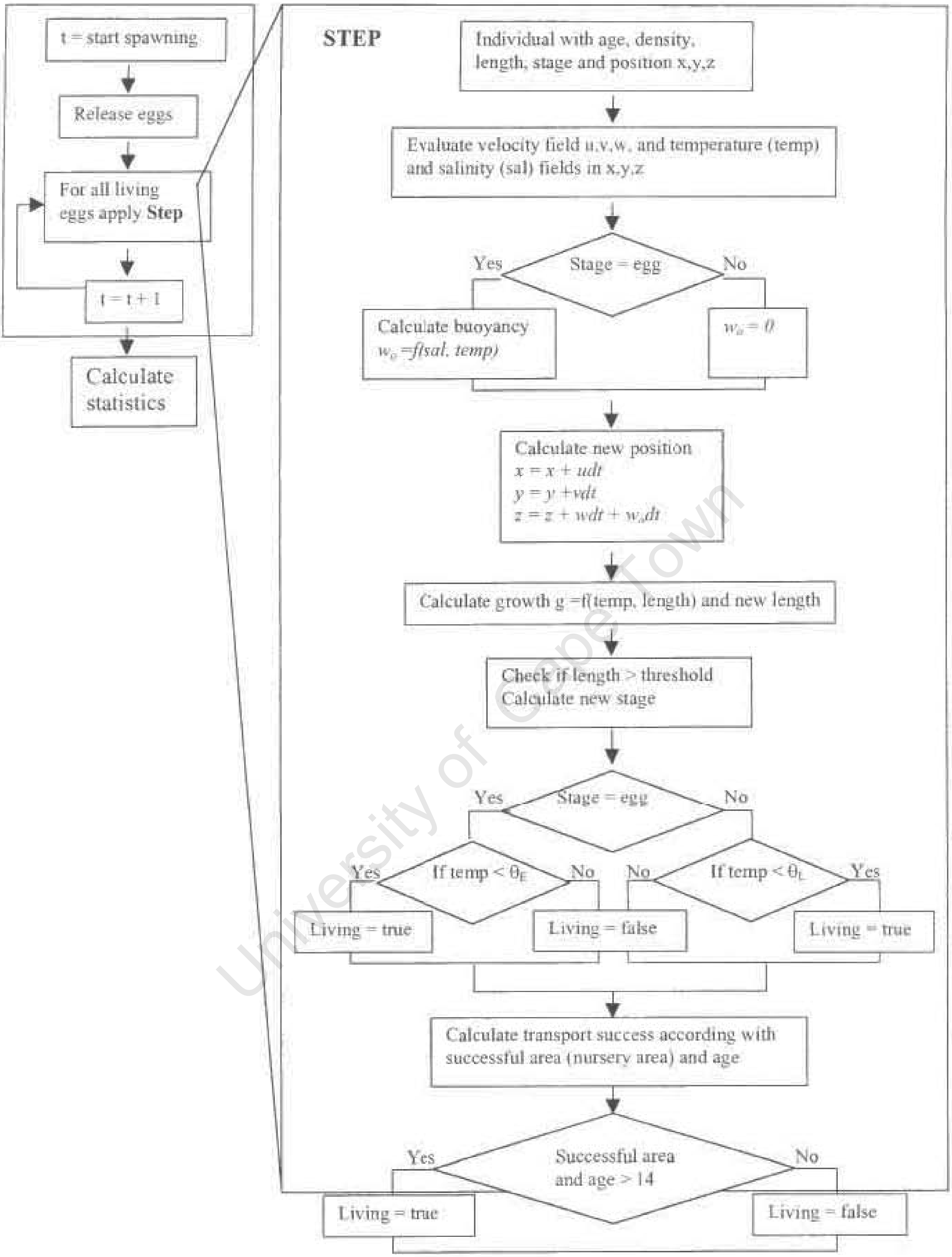

Figure 4.2. Flowchart of experimental simulations of growth and mortality model: general algorithm (left), and the details of the process simulating movement, growth, mortality and transport success (right).

Response variables: egg and larval mortality and transport success. The transport success and egg and larvae mortality criteria used by this growth and mortality model (model 4) have been described in Table 2.3. In this model, three response variables were assessed: (1) egg mortality index, defined as the ratio of the number of eggs that died as a result of the temperature effect to the number of eggs released, (2) larval mortality index, defined as the ratio of the number of larvae that died as a result of the temperature effect to the number of eggs that survived, and (3) transport success, defined as the ratio of the number of larvae that satisfied the criteria of transport success at the end of the simulation to the number of eggs released (Table 2.3). These response variables were the dependent variables used in subsequent statistical analyses.

4.2.3. Growth scheme

The growth equation employed in this model was based on the Gompertz model developed by Zweifel and Lasker (1976) to describe the growth of northern anchovy (*E. mordax*) from before hatching up to first feeding. The model for eggs and larvae of *E.mordax* has an initial length (L_o) value of 0.025 mm, with length increasing exponentially through 12 eggs stages to reach 2.85 mm at hatching, and then gradually converging to 4.31 mm by the time the larvae develop a jaw that allows them to start feeding (Zweifel and Lasker, 1976). Individuals exposed to higher temperatures show faster growth rates than those exposed to lower temperatures. Because the length of eggs and larvae ($L_{t,T}$) is a function of both time (t) and temperature (T) growth was modeled as:

$$L_{t,T} = L_o e^{k(1-e^{-\alpha_T t})} \qquad (4.1)$$

where the temperature-dependent variable α_T is defined as:

$$\alpha_T = \alpha_o e^{m(1-e^{-\beta T})} \qquad (4.2)$$

The parameters L_o, k, α_o, m and β were empirically set according to the values of Zweifel and Lasker (1976).

King *et al.* (1978) showed that although *E. encrasicolus* displays the same temperature-dependent growth pattern as northern anchovy, the incubation times and lengths differ between the two species. Due to this disparity between the model of *E. mordax* and the data of King *et al.* (1978) for Cape anchovy, the model of Zweifel was corrected by modifying the slope of the length versus time curves according to the data of King *et al.* (1978). The correction was incorporated by fitting the parameter α_T for the empirically determined length at hatching of Cape anchovy at different incubation temperatures. Using this approach, a set of equations was developed to describe the growth of early stages of Cape anchovy in the southern Benguela system (Fig. 4.3).

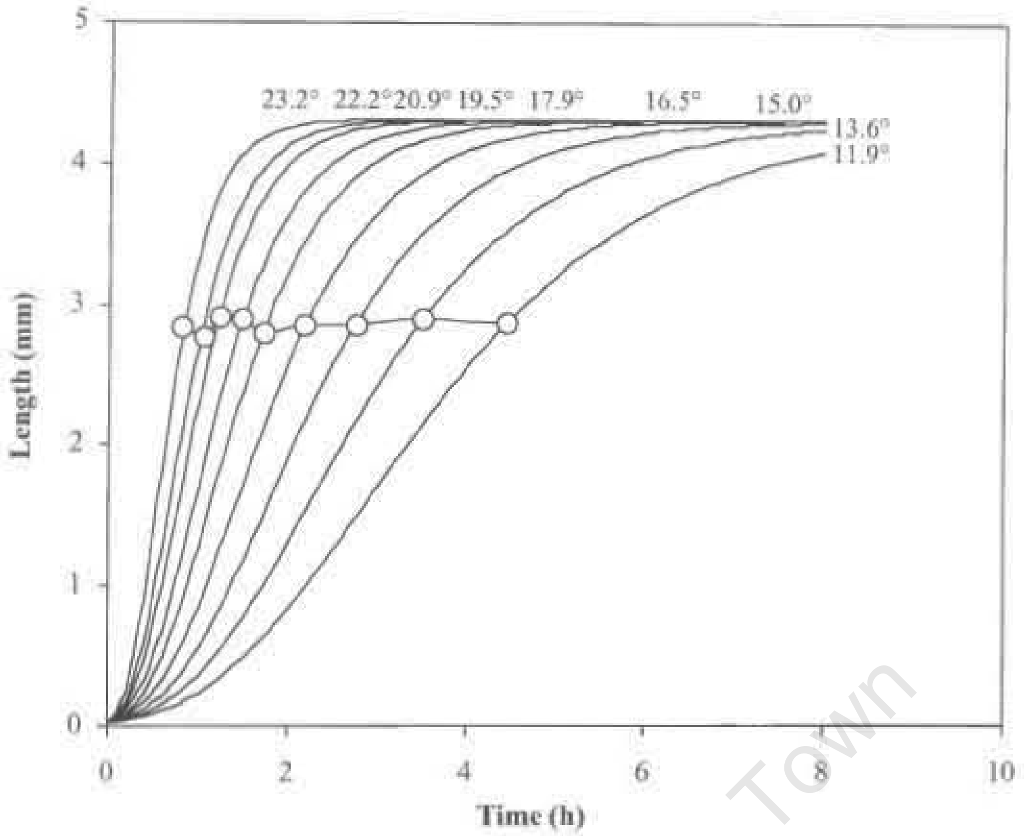

Figure 4.3. Gompertz model of Cape anchovy growth as a function of temperature. Circles indicate the hatching length at incubation time under different temperature conditions according the experiments of King *et al.* (1978).

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:

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

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:

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

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 growth rate of 50% and 20% respectively, whereas λ values of 0.8 and 0.5 would represent decreases in the growth rate of 20% and 50% respectively (Fig. 4.4)

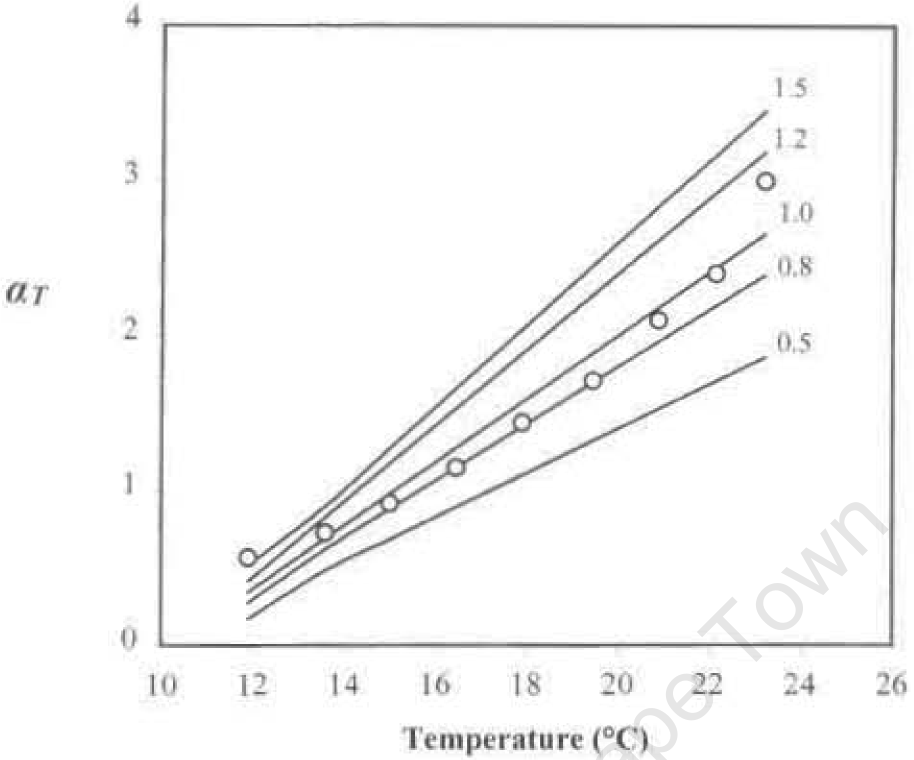

Figure 4.4. Graph illustrating the linearization of α_T as a function of temperature. Each solid line illustrates the linearized relationship at various levels of λ (growth factor). Circles indicate the α_T estimated with equation 4.2 under different temperature conditions according the experiments of King *et al.* (1978).

To compute length at a given time and temperature, an Eulerian approximation was applied (equation 4.5), in which derivatives are calculated by equations 4.6 and 4.7:

$$L_{t+\Delta t} = L_t + \frac{\partial L}{\partial t}\Delta t + \frac{\partial^2 L}{2\partial t^2}\Delta t^2 \tag{4.5}$$

$$\frac{\partial L}{\partial t}(t,T) = L_0 \alpha_T k e^{k(1-e^{-\alpha_T t})-\alpha_T t} \tag{4.6}$$

$$\frac{\partial^2 L}{\partial t^2}(t,T) = L_0 \alpha_T^2 k e^{k(1-e^{-\alpha_T t})-\alpha_T t}(ke^{-\alpha_T t}-1) \tag{4.7}$$

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.

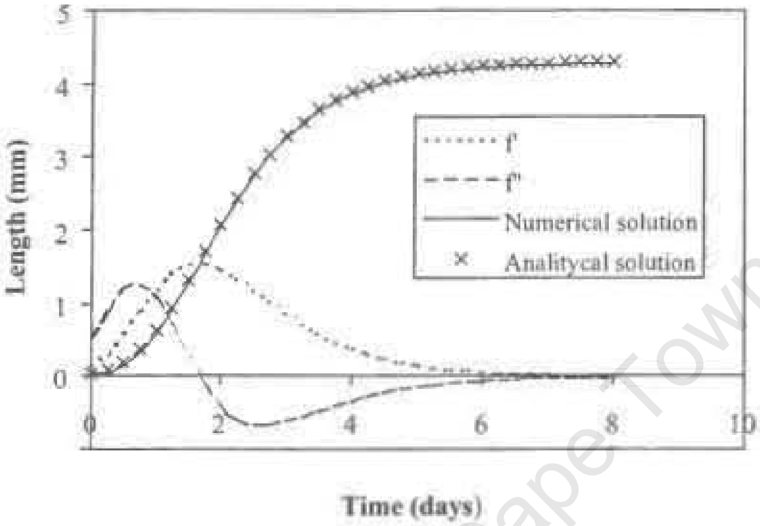

Figure 4.5. The numerical and analytical solution of equation 4.1, the first (f') and the second derivative (f'') for a temperature of 15.1°C using $\Delta t = 0.25$ days.

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 larval mortality as well as transport success in the IBM. The GLM was also used to compute least square means for each model variable in order to assess the effect of specific variable values on the dependent variables.

4.3. RESULTS

4.3.1. Identification of annual and seasonal patterns in the temperature profiles generated by the PLUME model

The analysis of the temperature profiles showed marked seasonal and annual patterns on the Agulhas Bank. From June to October the first 75 m are very well mixed with water temperatures between 16 to 14°C. From late October to March, the water column tends to be more stratified and the isotherms start to deepen toward June. In general, this process is repeated in all the years and for all the stations sampled from PLUME on the Agulhas Bank (Fig. 4.6). The profiles at the stations WAB, CAB$_{Off}$ and EAB$_{Off}$ (Fig. 4.6a, b and c, respectively) showed a similar stratified structure with isotherms less than 16°C associated with depths less than 50 m. The WAB was an exception, however, during the period in which the water column was well mixed, temperatures less than 16°C were observed from the surface. The same pattern is found for EAB$_{In}$ with the difference that the mixing of the water column is more intense and the stations are shallower (maximum 150 m) than elsewhere (Fig. 4.6d).

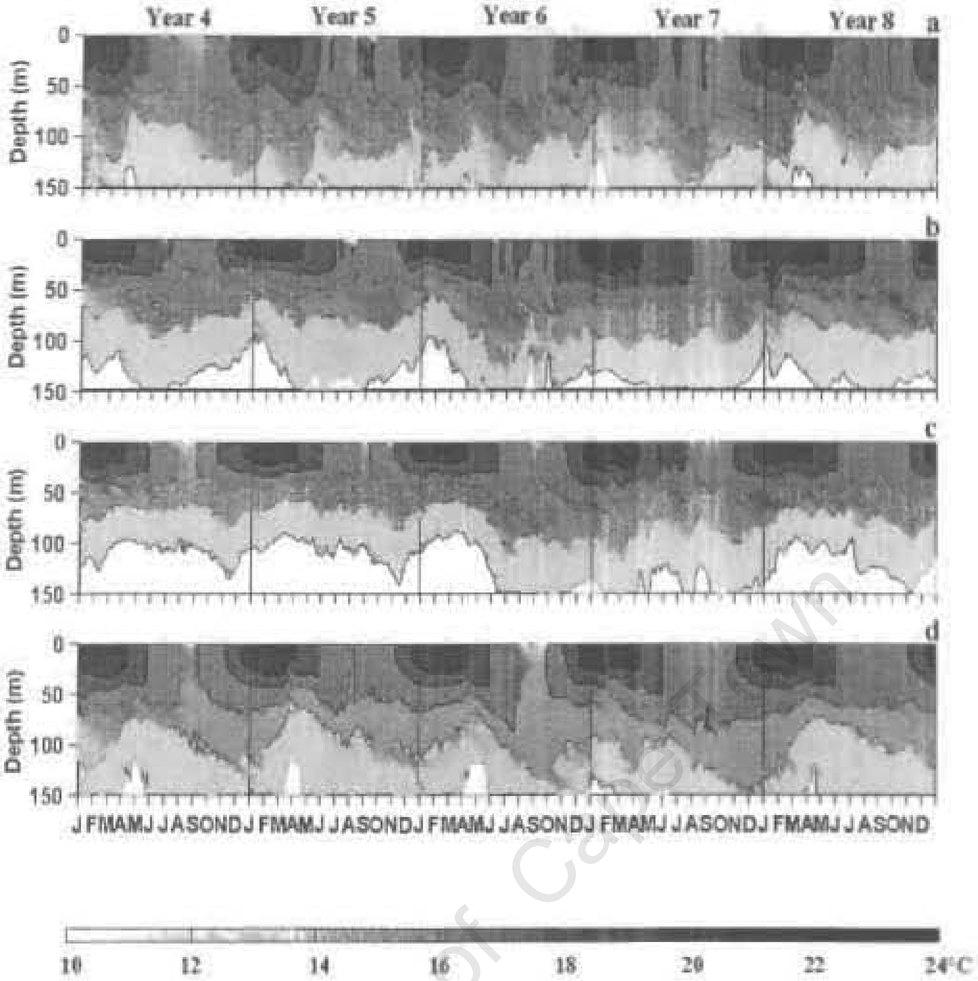

Figure 4.6. Temperature profiles in 4 localities in the Agulhas Bank (a) WAB, (b) CAB_{Off}, (c) EAB_{Off}, (d) EAB_{In} extracted from PLUME. See Fig. 4.1 for localities.

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).

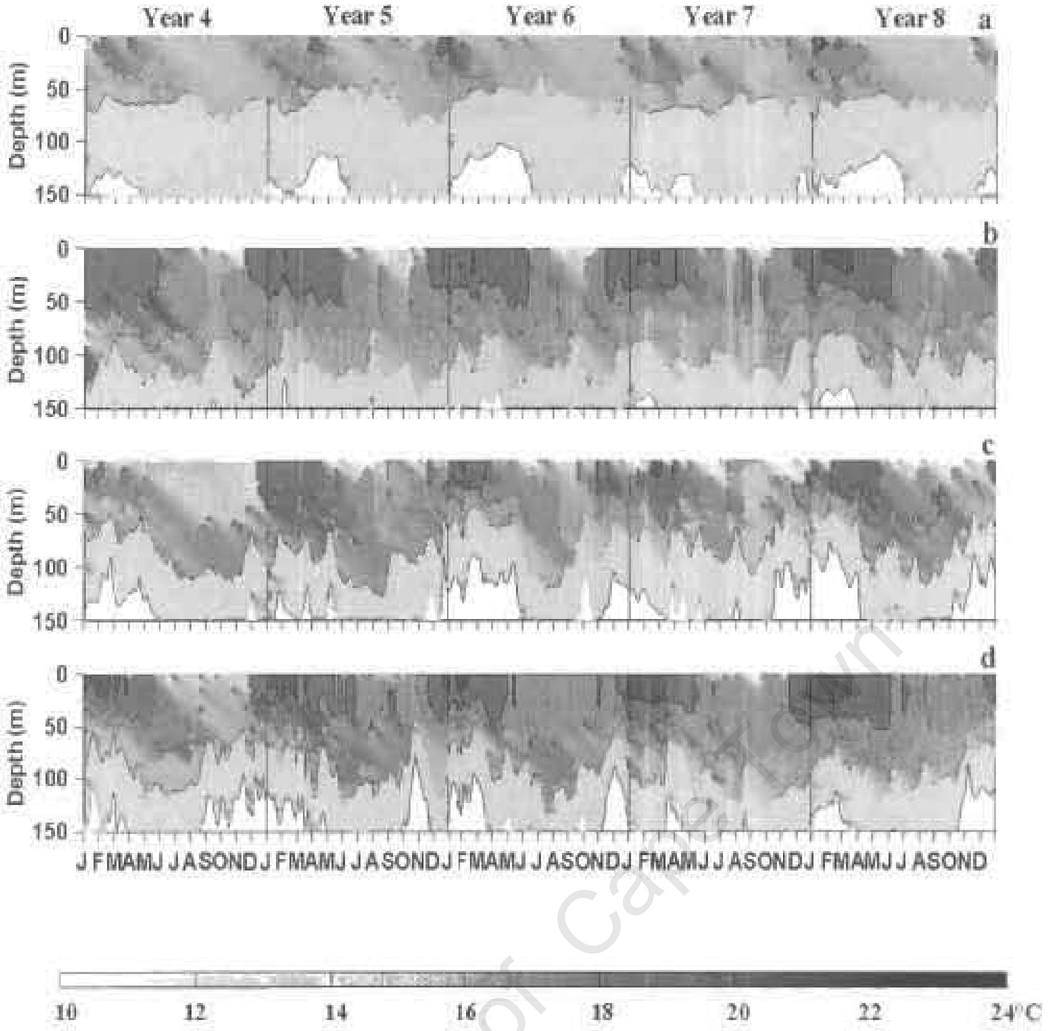

Figure 4.7. Temperature profiles in 4 localities in west coast nursery area: (a) Nur1, (b) Nur2, (c) Nur3 and (d) Jet current, extracted from PLUME. See Fig. 4.1 for localities.

4.3.2. Sensitivity analysis: Egg mortality index

Depth was the primary determinant of egg mortality (Table 4.2), with the depths of 50-75 m resulting in highest egg mortality, followed by surface and subsurface (Fig. 4.8a). Date of spawning and θ_E had a less marked but still significant effect on egg mortality index (Table 4.2). Maximum mortality was associated with eggs spawned in October (Fig. 4.8b) coincident with the onset of the upwelling (Fig. 4.7), and with eggs susceptible to broader lethal temperature ranges (<15°C, Fig. 4.8c). This last result suggests that an increment of 2°C in the susceptibility range of temperature increase the mortality in a 15% (Fig. 4.8c). Year, Area, growth factor and θ_L were all significant parameters, but explained less than 5% of the variance of the model. The Date*Depth and Depth* θ_E first level of interactions explained an important part of the variance (Table 4.2). Collectively, Depth, Date and θ_E and the interactions listed in Table 4.2 explained 74.3% of the variance of the model.

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, $S = P < 0.001$, $NS = P > 0.05$

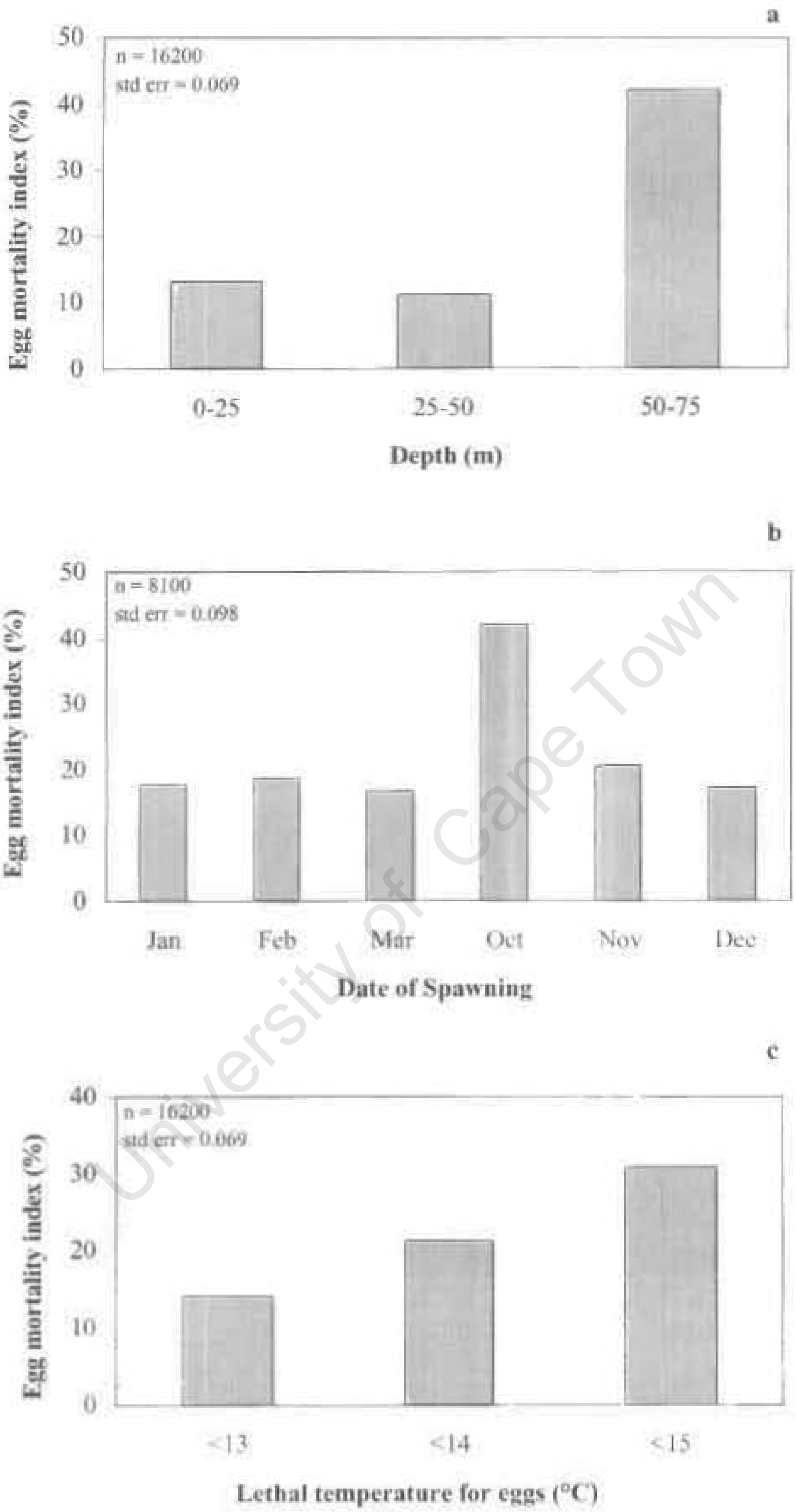

Figure 4.8. Ratio eggs mortality index for the single variables used in the growth and mortality model: (a) Depth, (b) Date of spawning, (c) Lethal temperature for eggs.

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* = $P > 0.05$

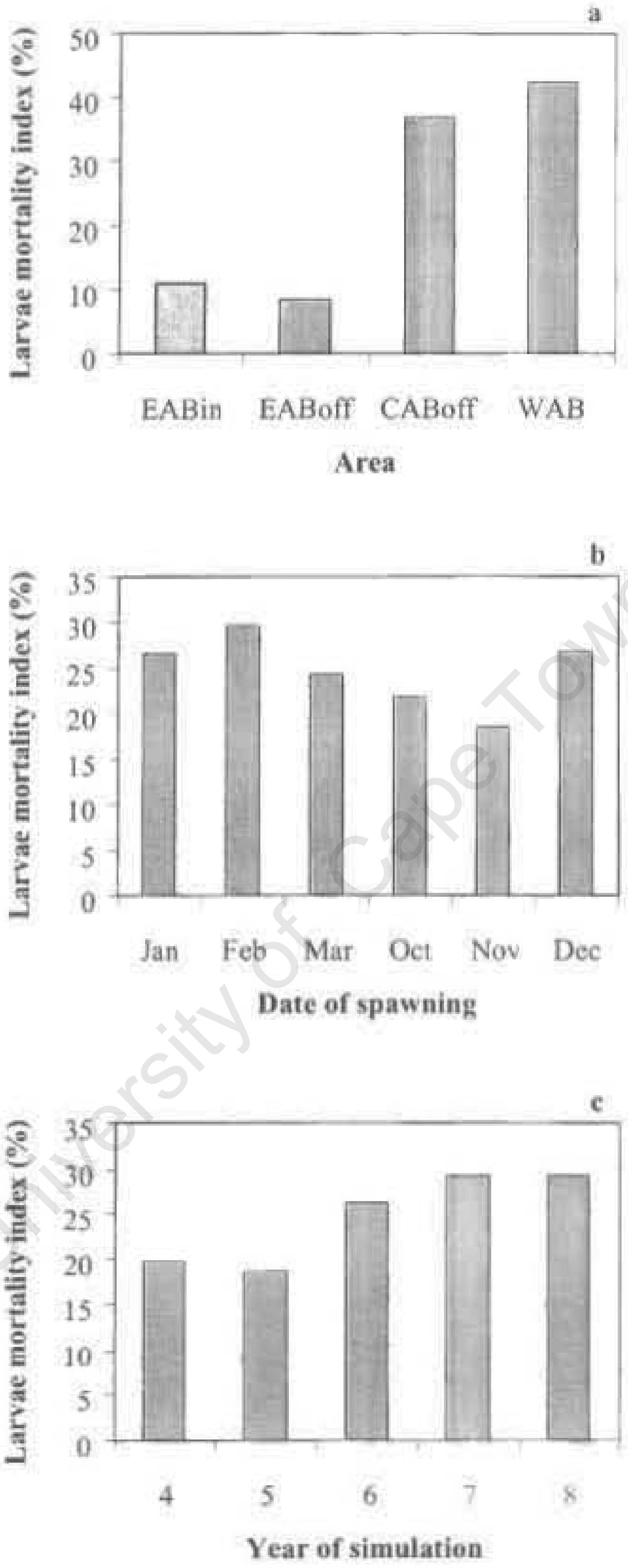

Figure 4.9. Ratio larvae mortality index for the single variables used in the growth and mortality model (model 4): (a) Area, (b) Depth, (c) Date of spawning and (d) Year of simulation.

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* = $P > 0.05$

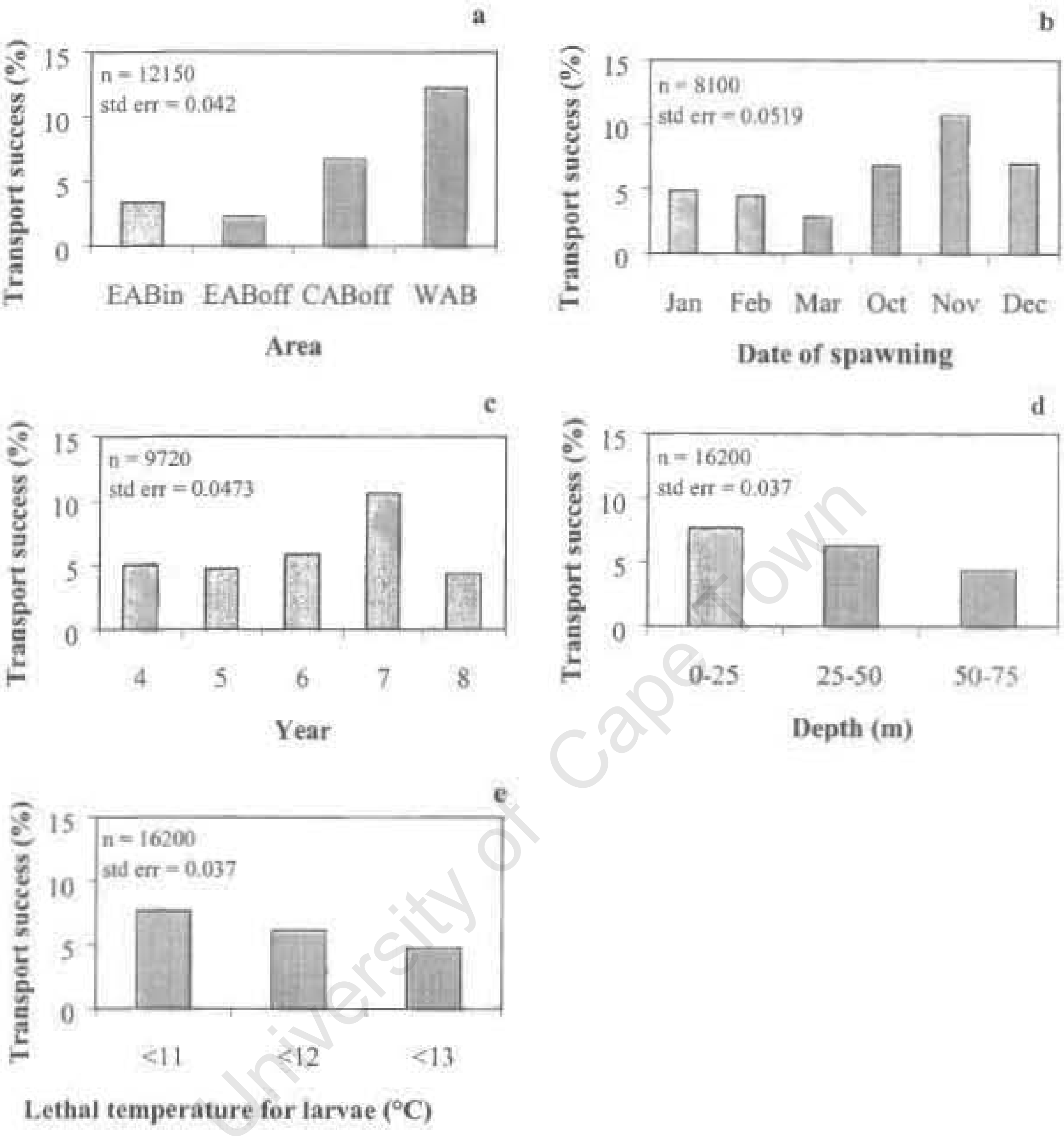

Figure 4.10. Ratio of successful larvae (transport success) to released eggs for the single variables used in the growth and mortality model: (a) Area, (b) Date, (c) Year, (d) Depth and (e) Lethal temperature for larvae.

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 eggs encounter cold upwelled water on the west coast. However, water temperatures at these depths tend to be low enough to kill the eggs. As a result, eggs and larvae that show a low resistance to temperature will be more susceptible to the spatial and temporal components of oceanographic processes that result in low temperatures. These results appear to therefore support the hypothesis that enhanced transport success results from a combination of efficient physical transport from the spawning ground to the nursery area, the stage of development of individuals reaching the nursery area (temperature-dependent growth), and favorable temperatures for survival (temperature acting as a lethal factor).

The time-series of vertical profiles of temperature provided by the hydrodynamic model are in agreement with the time-series of the temperature profiles observed on the CAB (Lutjeharms *et al.*, 1996), and are characterized by surface temperatures varying between 19° to 23°C in summer and between 16° to 18°C in winter. Bottom temperature varied between 11° and 16°C. This seasonal pattern is a result of periodic variations between summer stratification and winter mixing where the thermocline is eroded by the winter storms that create a well mixed water column (Lutjeharms *et al.*, 1996). This observed pattern is reflected in the hydrodynamic model output. The environmental conditions in terms of the temperature reproduced by the hydrodynamic model were used to study the influence of this factor on the mortality and growth of eggs and larvae, and in the success of transport to the nursery area on the west coast.

Growth-mortality IBM outputs showed that larval mortality and transport success depend primarily on the spawning Area parameter, with WAB being the area associated with the highest temperature induced mortality, and at the same time the greatest in terms of transport success. The apparent paradox of these results can be explained by patterns evident in both the PLUME model output and in field data, showing that the WAB displays a general drift pattern of surface waters in a north-west direction, with upwelling occurring inshore in the late summer, exposing eggs and larvae to cold waters (Hutchings *et al.*, 2002). These waters are entrained by the jet current that promotes the transport of eggs and larvae to the nursery area (Boyd *et al.*, 1992). Therefore a trade-off between transport speed and the presence of larvae in upwelling centers and lethal temperatures leading to mortality is hypothesized. Simulated profiles of temperature coincident with field observations (Lutjeharms *et al.*, 1996) showed that in October the water column is still very well mixed, with cold water at the surface increasing the mortality of anchovy eggs and larvae. As a result, maximum mortality of eggs was observed when the spawning date was set to 1st of October.

The depth interval of 50-75 m that resulted in maximum egg mortality in the IBM is consistent with the vertical egg distributions from survey data that show that eggs of anchovy are seldom found at depths greater than 60 m in the southern Benguela region and elsewhere (Shelton and Hutchings, 1982; Motos and Coombs, 1998; Moser and Pomeranz, 1999; Santos *et al.*, 2000). The IBM experiments that considered only the buoyancy and spatio-temporal factors (Chapter 3), showed that eggs with high density (1.027 g.cm^{-3}) displayed a deep vertical distribution (60 to 140 m). However, when adding the biological constraints of growth and temperature biological 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.

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

5.1. INTRODUCTION

Part of the life history of anchovy is associated with the west coast. The nursery area of the west coast of South Africa is characterized by an intense offshore Ekman drift and strong upwelling during summer. Instabilities can lead to the development of filaments capable of transporting shelf waters hundreds of kilometers offshore, resulting in the loss of biota to oligotrophic oceanic areas (Hutchings *et al*., 2002). Anchovy eggs spawned on the Agulhas Bank are transported to the west coast by the jet current that accelerates along the west coast and passes the active upwelling centers off Cape Town and Cape Columbine (Fowler and Boyd, 1998; Hutchings *et al*., 2002). North of Cape Columbine, the jet current develops three components: offshore, along-shore and inshore (Boyd *et al*., 1992). According to the studies of Hewitt and Methot (1982), offshore larval drift is probably responsible for reduced survival of northern anchovy *Engraulis mordax*. Offshore transport in the Benguela region during the peak of the upwelling season (coincident with the spawning period of anchovy) may carry eggs and larvae out of the system. Furthermore, strong winds may dilute food patches through turbulent mixing within the water column (as observed off California by Lasker, 1975), causing increased mortality by decreasing the encounter rate with food particles. Physical transport of pre-recruits out of the spawning/nursery area is considered to be a major cause of mortality (Shannon, 1995; Shannon *et al*., 1996) because the surrounding waters are typically unfavorable for survival although actual mortality may be due to predation and starvation (Smith and Lasker, 1978; Valdés *et al*., 1987).

Many previous efforts to understand the cause of the mortality are focused on single process such as oceanographic transport and retention mechanisms (Hjort, 1914; Parrish *et al*., 1981; Sinclair, 1988). Bakun (1996) has stressed that fish larvae inhabiting the upper ocean layer in coastal upwelling regions would tend to be swept away from their favored coastal habitat by strong, offshore directed Ekman transport. However, offshore transport of near surface water is balanced by onshore transport at depth. Organisms employing appropriate vertical migration behavior could take advantage of this onshore component of upwelling circulation to minimize offshore transport losses (Pillar and Stuart, 1988: Verheye *et al*., 1991; Bakun, 1996), because such organisms are required to be within favorable habitat within some period of time after drifting in the currents (Jackson and Strathmann, 1981; Roughgarden *et al*., 1988; Hill, 1991). The study of a biological mechanism, such as vertical migration, could therefore provide valuable information regarding the transport of spawning products to the nursery area, and hence on recruitment success.

An additional question that should be addressed concerns the current hypothesis regarding the life history of anchovy in the southern Benguela system. It is generally accepted that the west coast is the only (or at least the main) nursery area of anchovy, and successful transport of the spawning 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 migratory behavior by larvae and post-larvae to enhance the successful transport of these individuals to the inshore part of the west coast nursery area. Both models (model 5 and 6) tracked the movement of particles representing eggs of optimal density (1.025 $g.cm^{-3}$) spawned over the Agulhas Bank and the subsequent transport of larvae northwards to the inshore areas of the west coast nursery ground. The models included the effect of temperature on the mortality and growth of eggs and larvae. In contrast with previous models, only the inshore regions of the nursery area were targeted as transport success area because consistently pre-recruit surveys conducted on the west coast (van der Lingen and Merkle, 1998; 1999) have shown that larger individuals occur closer inshore while smaller larvae occur further offshore, suggesting an offshore-onshore progression.

5.2.2. Modeling the effect of vertical migration on retention

With regard to the analysis of retention processes on the west coast and the EAB, a separate model was run for each locality. Model 7 studied the retention in the west coast, while model 8 studied the potential of the Eastern Agulhas Bank as an alternative retention/nursery area. The models tracked the movement of particles representing eggs of optimal density (1.025 $g.cm^{-3}$) larvae spawned over the Agulhas Bank and the subsequent transport of larvae and post-larvae either northwards to the inshore areas of the west coast nursery ground, or eastwards to the inshore areas of the EAB. The models included the effect of temperature on the mortality and growth of eggs and larvae. Both retention models incorporated the vertical migration behavior component to explore the potential for this mechanism to enhance the retention of larvae and post-larvae on the west coast and EAB nursery areas.

5.2.3. Setting constants and parameters for the different experiments

The constants set for both passive (model 5) and active (model 6) behavior models were the same as those set for the previous models described in this thesis (i.e. spawning and simulation duration, tracking duration, number of eggs released, density and shape of the eggs, see Table 5.1). In addition, several of the parameters explaining <5% of the variance for the dependent variable transport success in the previous model (growth and mortality model, see Chapter 4) were set as constants for the IBMs (e.g. lethal temperature for eggs and larvae and factor of growth, see Table 5.1).

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 (τ_L = 4 values) and Depth of active behavior (δ_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

The combination of all the parameters for the passive behavior model resulted in 6 x 5 x 3 x 3 = 270 simulations (model 5), while the combination of parameters for the active behavior model generated 6 x 5 x 3 x 4 x 6 x 3 = 6480 simulations (model 6).

With regard to the retention models (models 7 and 8), the same parameters that constrained the active behavior model (model 6) were incorporated, except that the parameter Lag in the active behavior (τ_L) was set to the value 1 (that is two days) because in previous experiments no significant difference was observed in the response variable when the parameter was assessed set to different values. The retention model for the west coast (inshore and offshore) nursery area evaluated the number of larvae and post-larvae that reached this area and remained there for a period longer than 10 days. In contrast, the active retention model for the EAB evaluated the number of larvae and post-larvae that reached both the inshore (EAB_{In}) and offshore (EAB_{Off}) regions of the EAB, and remained in these areas for >10 days. The parameter combinations of both retention models generated 6 x 5 x 3 x 6 x 3 = 1620 simulations. In all simulations, a population of 5000 eggs was randomly released on the WAB, CAB_{Off}, EAB_{In}, EAB_{Off}, based on field observation of anchovy egg distribution (Fig. 1.1). The spawning duration constant (30 days) determined the period over which new eggs entered the population (Table 5.1).

5.2.4. Configuration of the experiments

Once the models were initialized and the parameters set for the simulation, a population of 5000 eggs was released simultaneously in the four areas on the Agulhas Bank (see above and Table 5.1). Each simulation was set up for a period of 90 days. During this period, the position, length and stage of each individual, the mortality of eggs and larvae due to temperature, transport success and retention (where relevant, Table 5.1) were monitored at 2-day intervals. Although the movements of eggs were defined by the 3-D velocity fields from the hydrodynamic model, the vertical velocity of eggs were dependent on the buoyancy scheme (Chapter 3), assuming a constant egg density of 1.025 $g.cm^{-3}$ (Table 5.1). In the models, the development of eggs to larvae was based on the growth scheme employed in Chapter 4 (see Fig. 4.3). The mortality of eggs and larvae was a function of temperature with constant threshold values set to <14°C for eggs and <12°C for larvae (Table 5.1).

The difference between the passive and the active behavior models is the incorporation of the active behavior component. In the passive behavior model (model 5), the movement of larvae was continuously regulated by the 3-D velocity fields, the larvae therefore moving as Lagrangian particles. In contrast, the active behavior (model 6) and active retention models (models 7 and 8) incorporated a preference by the larvae for a specific depth after hatching that was realized by active swimming behavior. Up to the point that larvae developed active swimming behavior, their movements were regulated by the 3-D velocity fields, after which they actively maintained a preferred depth. In the horizontal plane, their movements were regulated by the 2-D horizontal velocities provided by the hydrodynamic model.

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.

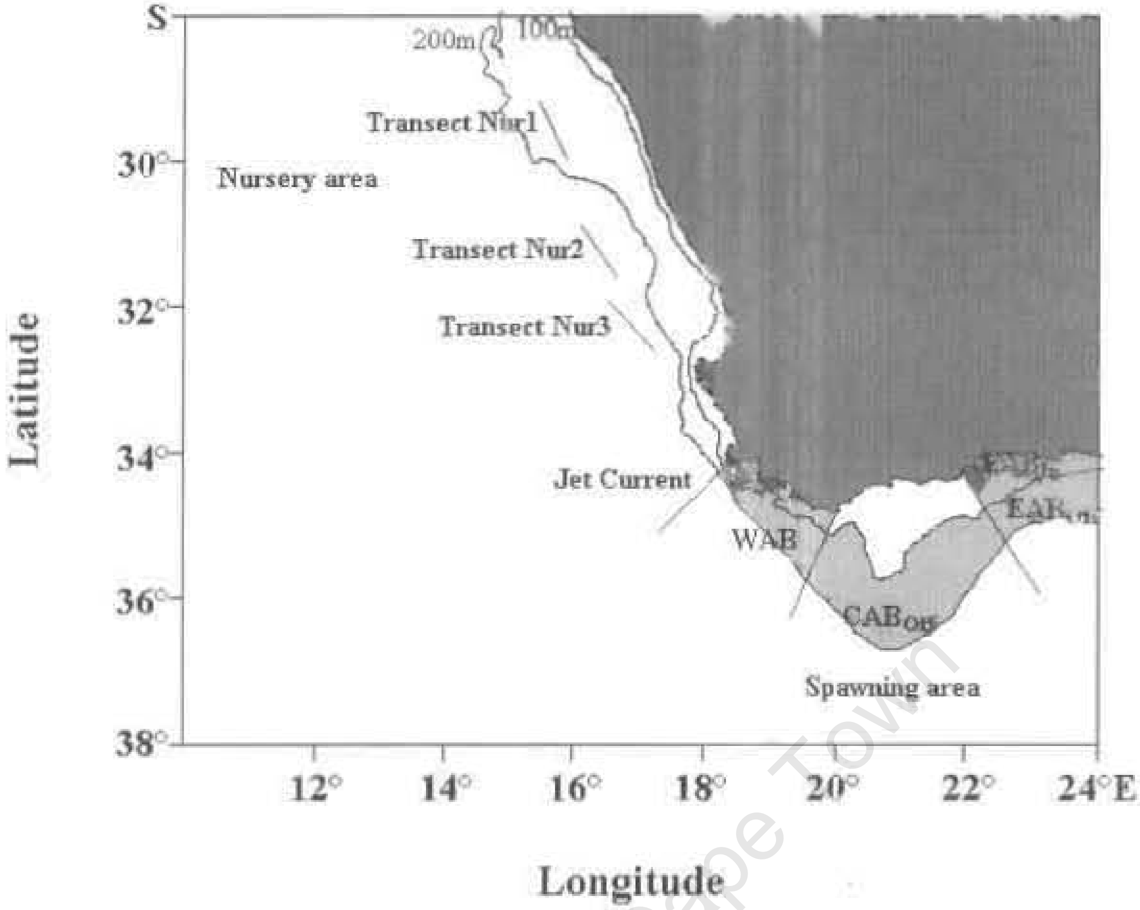

Figure 5.1. Map of the study area showing transects (Nur1, Nur2, Nur3) where across-shore transport was estimated. The locations of the WAB (Western Agulhas Bank), CAB_{Off} (Central Agulhas Bank offshore), EAB_{In} (Eastern Agulhas Bank inshore) and EAB_{Off} (Eastern Agulhas Bank offshore) spawning grounds and the nursery area are shown.

5.2.7. Comparing model output to field observations

The active behavior model was run for 100 days for a set of selected parameters, as an example (Year 6 in October), to compare with the age classes that correspond to the estimated lengths observed in pre-recruits data. The age distributions (days) of larvae and post-larvae in the west coast nursery area obtained from the model output were transformed to length (cm) using the equation of Thomas (1986):

$$Length = 0.147 + 0.0597\ age \tag{5.1}$$

These model data were then compared to field estimates of the size class distribution of larvae and post-larvae along the west coast. These field data were collected during several annual pre-recruit (larvae and post-larvae up to 3 months old) surveys conducted using a Methot frame trawl during March of all years between 1983 and 2000, with the exception of 1993 (van der Lingen and Merkle, 1998; 1999). The field data were divided into size classes defined as "smallest" (<20 mm standard length, SL), "small" (20-34 mm SL), "medium" (35-50 mm SL) and "large" (50 mm SL) pre-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).

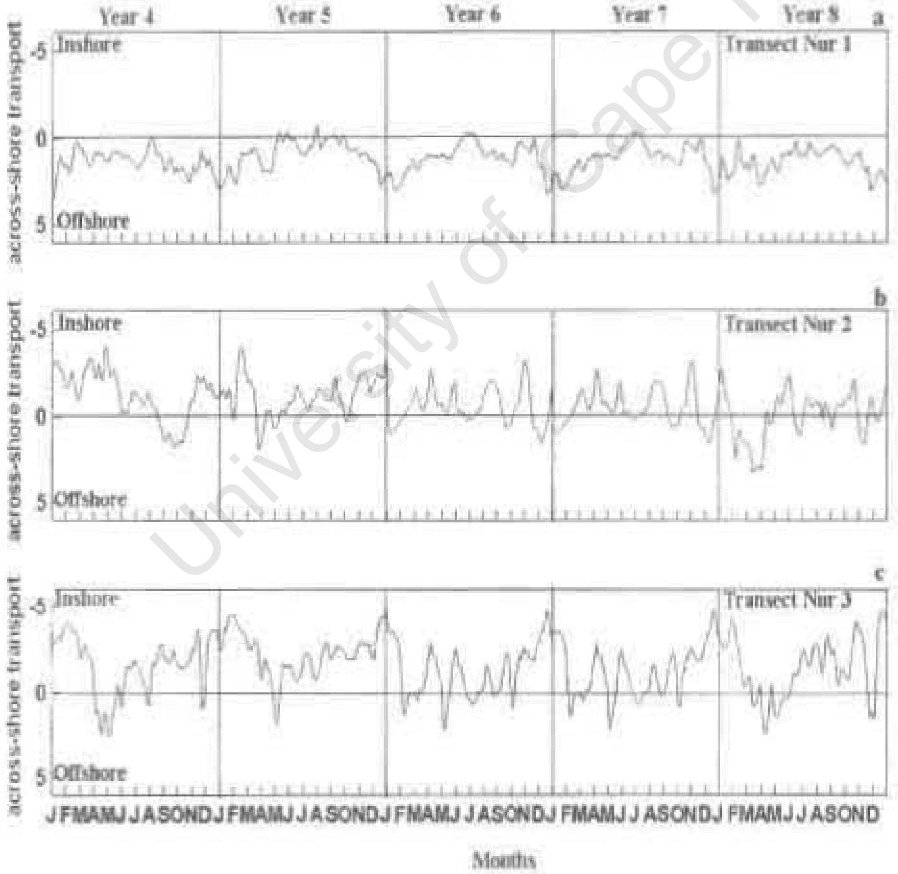

Figure 5.2. Across-shore transport (x 10^6 m^3s^{-1}) estimated from PLUME output in the west coast nursery area along transects (a) Nur1, (b) Nur2 and (c) Nur3 (see Fig. 5.1 for details of position of transects).

5.3.2. Sensitivity analysis of the passive behavior model on the west coast (model 5): transport success

Transport success to the inshore nursery area was, on average, very low (0.6%) with a maximum transport less than 2%, when compared to the figure obtained for the inshore and offshore nursery areas combined (average of 12% and a maximum transport of 32%; Chapter 3 model 1). Year was the primary determinant of transport success, with Year 7 displaying the highest levels of transport success (Fig. 5.3a). Area, Depth of spawning and Date of spawning also had significant effects on transport success (Table 5.3). Maximum transport success was associated with eggs spawned on the WAB (Fig. 5.3b) in surface and sub-surface waters (Fig. 5.3c) in October (Fig. 5.3d). Year*Date, Area*Depth, Year*Depth and Date*Area first level interactions explained a significant component of the variance, while other interactions of less importance are listed in Table 5.3. Area, Date, Year and Depth and the interaction listed in Table 5.3 collectively explained 57.4% of the variance of the model, with a large error term of 34.6% (Table 5.3).

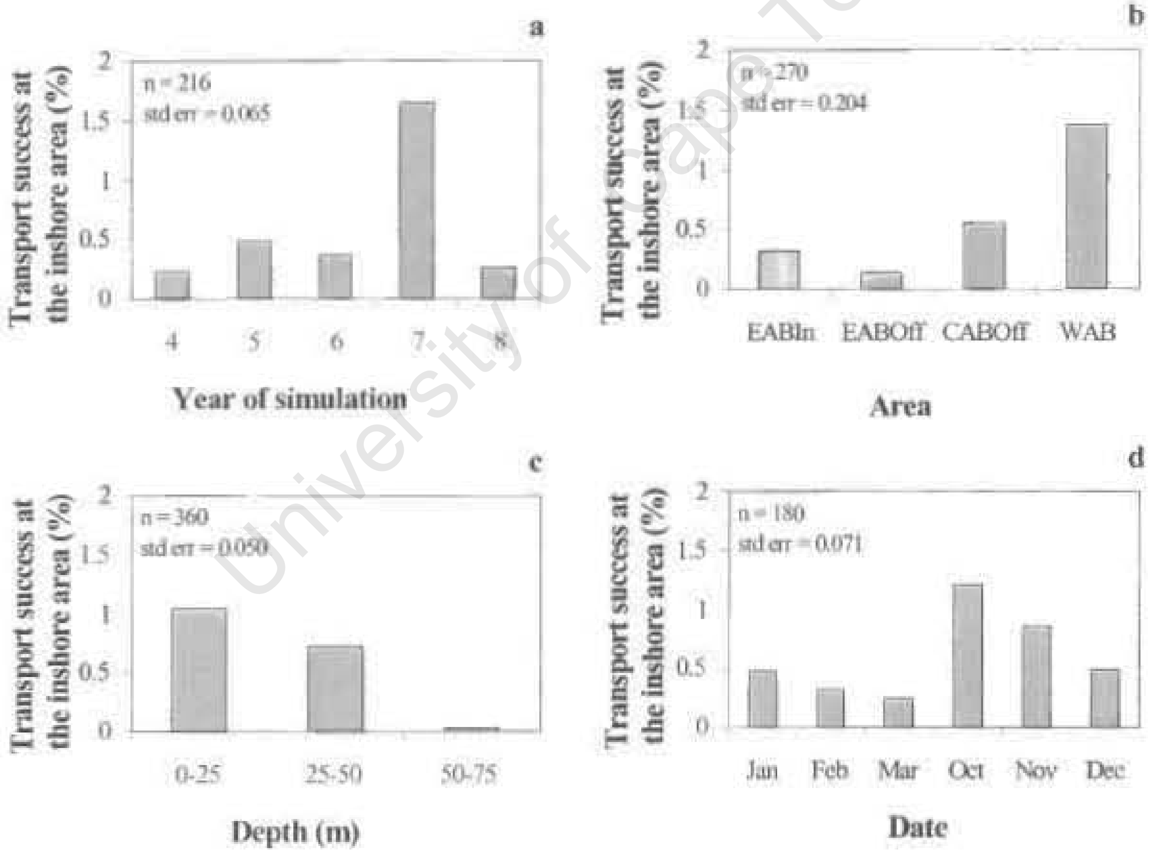

Figure 5.3. Ratio of transport success in the inshore part of the nursery area of the west coast. Success is given by the number of larvae to released eggs for the single variables used in the passive behavior model (model 5): (a) Year of simulation, (b) Area, (c) Depth and (d) Date.

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* = $P > 0.05$

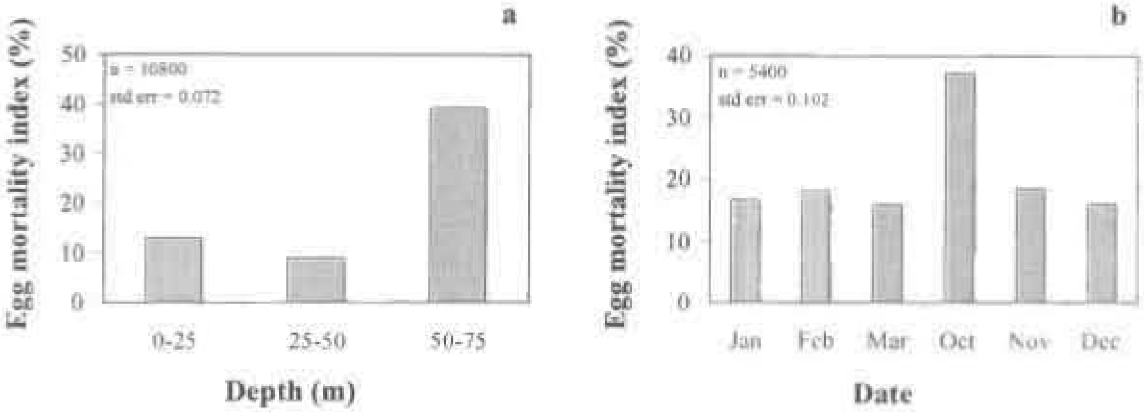

Figure 5.4. Ratio of egg mortality index for the single variables used in the active behavior model (model 6): (a) Depth and (b) Date.

5.3.4. Sensitivity analysis of the active behavior model (model 6): Larval mortality index

Area of spawning was the most important variable determining the mortality of the larvae (Table 5.5). Larvae coming from eggs spawned in the WAB displayed the highest level of larval mortalities, followed by CAB_{Off}, EAB_{In}, and EAB_{Off}, where mortality can occurs between spawning and recruitment grounds (Fig. 5.5a). Larval mortality showed a distinct trend relative to the depth selected after the onset of active behavior (δ_L). Larval mortality remained relatively constant between δ_L of 5 and 40 m (about 8%), but this increased as larvae selected depths deeper than 40 m, the maximum mortality approximately 36% observed when larvae selected depths of 100 m (Fig. 5.5b). τ_L (Lag in the active behavior), Depth, Date, Year all had a significant effect on larval mortality, but explained less than 5% of the variance of the model. No interaction explained > 5% of the model variance (Table 5.5). The combined effects of Area, δ_L, τ_L, Depth, Date, Year explained a total of 59.9% of the variance of the model, with an error term of 19.0% (Table 5.5).

Table 5.5. General linear model applied to the active behavior model output for the dependent variable larval mortality index (model 6).

General Linear Model	*Df*	*SS*	*MS*	*F*	*P*	*Explained variance (%)*
Intercept	1	8404027.0	8404027.0	103713.2		
Single variable						
Year	4	98387.7	24596.9	303.5	*S*	0.7
Date	5	166547.0	33309.4	411.0	*S*	1.2
Area	3	4816511.5	1605503.7	19813.3	*S*	35.1
Depth	2	5561.2	2780.6	34.3	*S*	0.0
δ_L	5	2941940.2	588388.0	7261.2	*S*	21.4
τ_L	4	206363.5	51590.8	636.6	*S*	1.5
Error	32159	26058888.8	81.0			19.0
Total	32399	13720286.8				

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

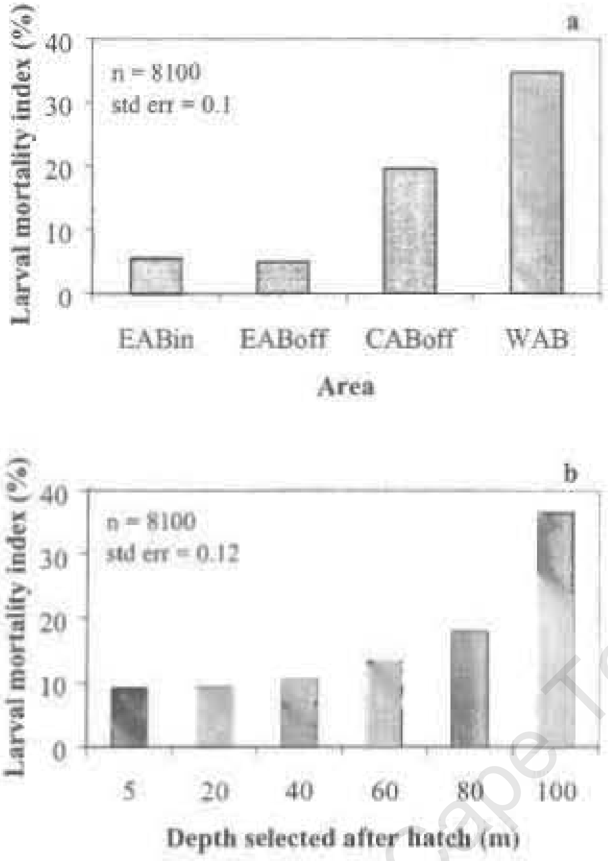

Figure 5.5. Ratio of larval mortality index for the single variables used in the active behavior model (model 6): (a) Area and (b) Depth selected after hatch.

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 and the interaction listed in Table 5.6 explained a total of 56.2% of the variance of the model, with an error term of 14.8% (Table 5.6).

Table 5.6. Optimal general linear model with second level of interaction, applied to the active behavior model output for the dependent variable transport success (inshore) (model 6).

General Linear Model	*Df*	*SS*	*MS*	*F*	*P*	*Explained variance (%)*
Intercept	1	731017.4	731017.4	46415.8		
Single variable						
Year	4	11374.0	2843.5	180.5	*S*	0.3
Date	5	50084.0	10016.8	636.0	*S*	1.5
Area	3	1066890.2	355630.1	22580.7	*S*	32.3
Depth	2	39365.3	19682.7	1249.7	*S*	1.2
δ_L	5	270449.9	54090.0	3434.4	*S*	8.2
τ_L	4	16901.7	4225.4	268.3	*S*	0.5
First level of interaction						
Area*δ_L	15	401873.3	26791.6	1701.1	*S*	12.2
Error	31086	489583.4	15.7			14.8
Total	32399	3305985.4				

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

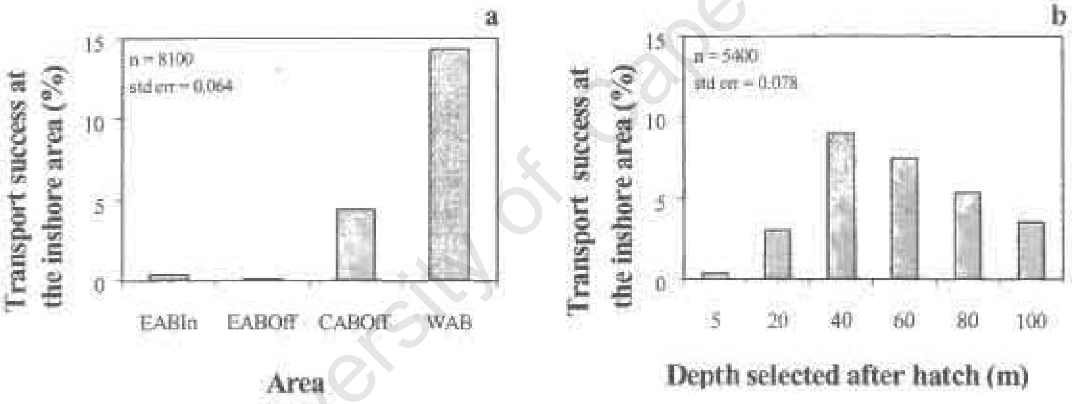

Figure 5.6. Transport success to the inshore part of the nursery area. Success is given by the ratio of the number of larvae to the number of released eggs for the single variables used in the active behavior model (model 6): (a) Area and (b) Depth selected after hatch.

5.3.6. Sensitivity analysis of the active retention model for the west coast nursery area (inshore and offshore)

On average, 5.8% of the larvae were retained in the west coast nursery area with a maximum retention (17.5%) associated to larvae coming from eggs spawned in WAB. The active retention model applied to the nursery area showed the same patterns as the active transport model, with Area of spawning being the most important variable determining the retention of larvae in the nursery area (Table 5.7). Larvae spawned on the WAB were the most successful in terms of being retained in the west coast nursery area, followed by CAB_{Off}. Very few of the larvae spawned on the EAB_{In} and

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* = $P > 0.05$

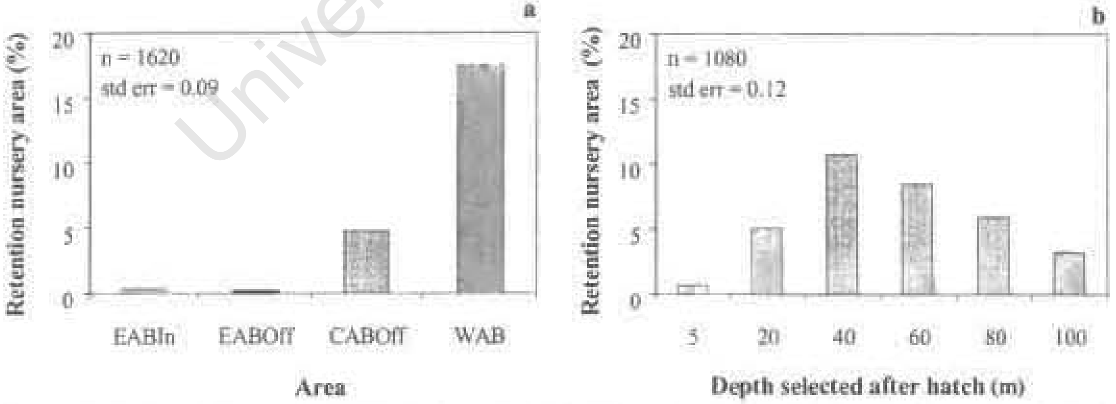

Figure 5.7. Ratio of the number of larvae retained in the nursery area to the number of eggs released for the single variables used in the active retention model for the west coast (model 7): (a) Area and (b) Depth selected after hatch.

5.3.7. Sensitivity analysis of the active retention model of the EAB (inshore and offshore)

The active retention model applied to the EAB area showed that, on average, only 2.8% of the larvae were retained on the EAB (inshore and offshore). The value is less than that observed on the west coast model (5.8%). A different pattern to that of the west coast nursery area was also observed. Although Area of spawning was again the most important variable determining the retention of larvae over the EAB (Table 5.8), larvae spawned on the EAB (both EAB_{In} and EAB_{Off}) were the most successfully retained. The maximum value of retention was associated to larvae coming from eggs spawned in EAB_{In} (8.3%, Fig. 5.8a). Negligible numbers of larvae spawned on the CAB_{Off} and WAB were retained in the EAB region (Fig. 5.8a). The depth at which eggs were released also explained a significant proportion of the variance of the model (Table 5.8) with most of the successfully retained larvae originating from eggs released between 0 to 25 m. This result differs from that of the west coast model where, the most successful release depth was 40 m (Fig. 5.8b). The depth selected after onset of swimming activity (δ_L) was also an important parameter, with larvae that selected depths of about 5m being the most likely to be retained (Fig. 5.8c). The Area*Depth and Area*δ_L first level interactions explained > 5% of the variance, the other important interactions are listed Table 5.8. Area, Depth, δ_L, Date, Year and the interaction listed in Table 5.8 explained a total of 64.7% of the variance of the model, with an error term of 12.0% (Table 5.8).

Table 5.8. Optimal general linear model with second level of interaction applied to the active retention model output over the EAB for dependent variable retention (model 8)

General Linear Model	***df***	***SS***	***MS***	***F***	***P***	***Explained variance (%)***
Intercept	1	49403.8	49403.8	6766.7		
Single variable						
Year	4	720.0	180.0	24.7	*S*	0.2
Date	5	3873.3	774.7	106.1	*S*	1.1
Area	3	69761.5	23253.8	3185.0	*S*	19.7
Depth	2	32292.5	16146.2	2211.5	*S*	9.1
δ_L	5	18381.8	3676.4	503.5	*S*	5.2
First level of interaction						
Area*Depth	6	54397.7	9066.3	1241.8	*S*	15.4
Area*δ_L	15	28164.6	1877.6	257.2	*S*	8.0
Second level of interaction						
Year*Date*Area	60	21208.0	353.5	48.4	*S*	6.0
Error	5810	42418.9	7.3			12.0
Total	6479	353833.1				

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

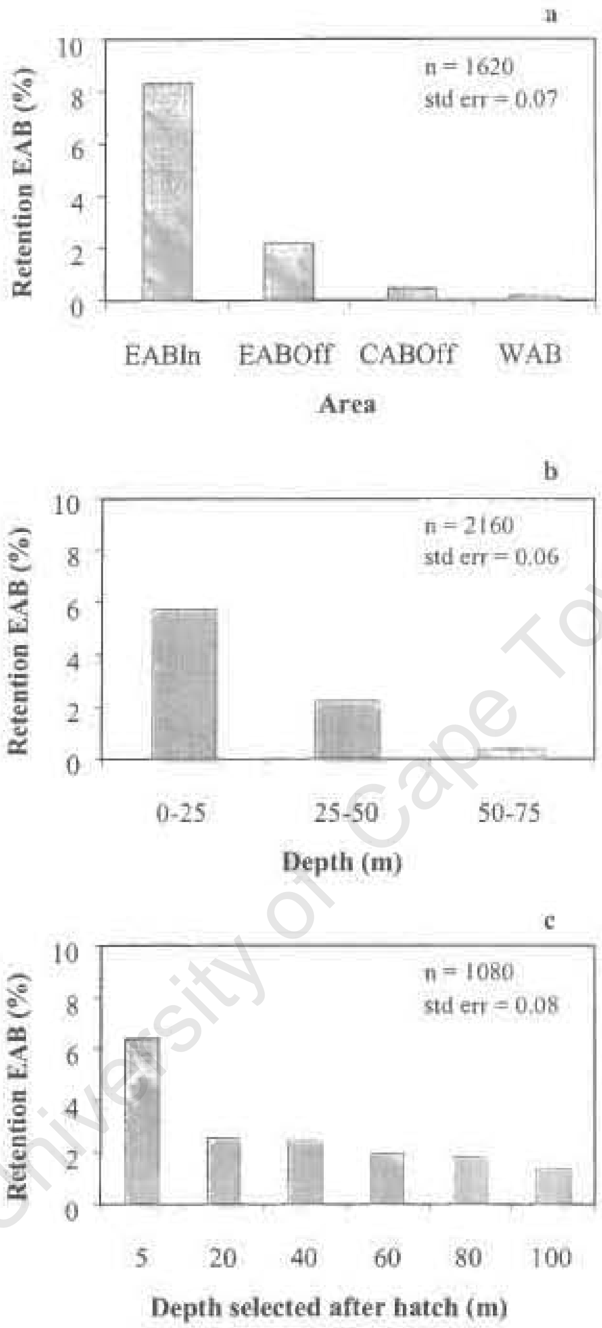

Figure 5.8. Ratio of the number of larvae retained over the EAB to the number of released eggs for the single variables used in the active retention model for EAB (model 8): (a) Area, (b) Depth of eggs released and (c) Depth selected after hatch.

5.3.8. Pattern-oriented analysis: distribution of pre-recruits in the nursery area

The distribution of larvae and post-larvae along the west coast displays a characteristic pattern that has been identified during several of the pre-recruit surveys conducted from 1983-2000 (with the exception of 1993, van der Lingen and Merkle, 1998). The size distribution of anchovy pre-recruits collected using a Methot frame trawl during the March pre-recruit surveys indicated that the smallest fish (<20 mm standard length, SL) occurred offshore along the edge of the continental shelf, generally reaching their highest concentrations in the southern regions of the west coast. Small pre-recruits (20-34 mm SL) were found across-shore, and extended offshore of the continental shelf, whereas the medium (35-50 mm SL) and large (50 mm SL) pre-recruits were primarily found inshore, with the highest concentrations of medium-sized fish generally located south of Hondeklip Bay and the larger individuals around Lambert's Bay (van der Lingen and Merkle, 1998). This pattern is clearly illustrated by the data collected during 2000 (see Fig. 5.9). The distribution of larvae and post-larvae (corresponding to the sizes classes of the pre-recruits surveys) during transport from spawning to nursery area that was generated by the IBMs is illustrated in Figure 5.10. The simulation was run for 100 days (Year 6 in October) to compare with the age classes that correspond to the estimated lengths observed in pre-recruits data (<31 days, 31 to 54 days, >54 to 81 days and >81 days respectively according to ageing done by Thomas, 1986). The simulation showed that in the first 20 days most of the smallest fish (<31 days, Fig. 5.10a) are associated with the jet current, whereas from 30 days there is some transport of this age class just offshore of the nursery area (Fig. 5.10b). The first onshore transport to the nursery area is observed from 40 days for the smallest fish and small pre-recruits (31 to 54 days; Fig. 5.10c), which is enhanced from day 50 with some northward transport close to the coast (Fig. 5.10d). At days 60 and 70, an offshore transport of individuals of the medium size/age class (>54 to 81 days old) was apparent (Fig. 5.10e and f). Between 80 and 90 days, a new input of individuals (small and smallest classes as defined in section 5.2.5) to the inshore part of the nursery area is observed with some northward transport of medium sized fish to the nursery area, and an offshore transport at the level of the jet current area (Fig. 5.10g and h). Finally, at 100 days most of the medium and large individuals (> 81 days) are no longer in the domain, while some smallest and small pre-recruits are still present in the jet current and offshore of the nursery area (Fig. 5.10i). The model results are consequently in good agreement with field data, with the exception of the fact that the model indicates that large pre-recruits are lost to the system, a clearly unrealistic result. This could be explained by the stronger swimming abilities of large pre-recruits (i.e. their horizontal position is no longer determined purely by the ambient hydrodynamics), a feature that is not accounted for the model design.

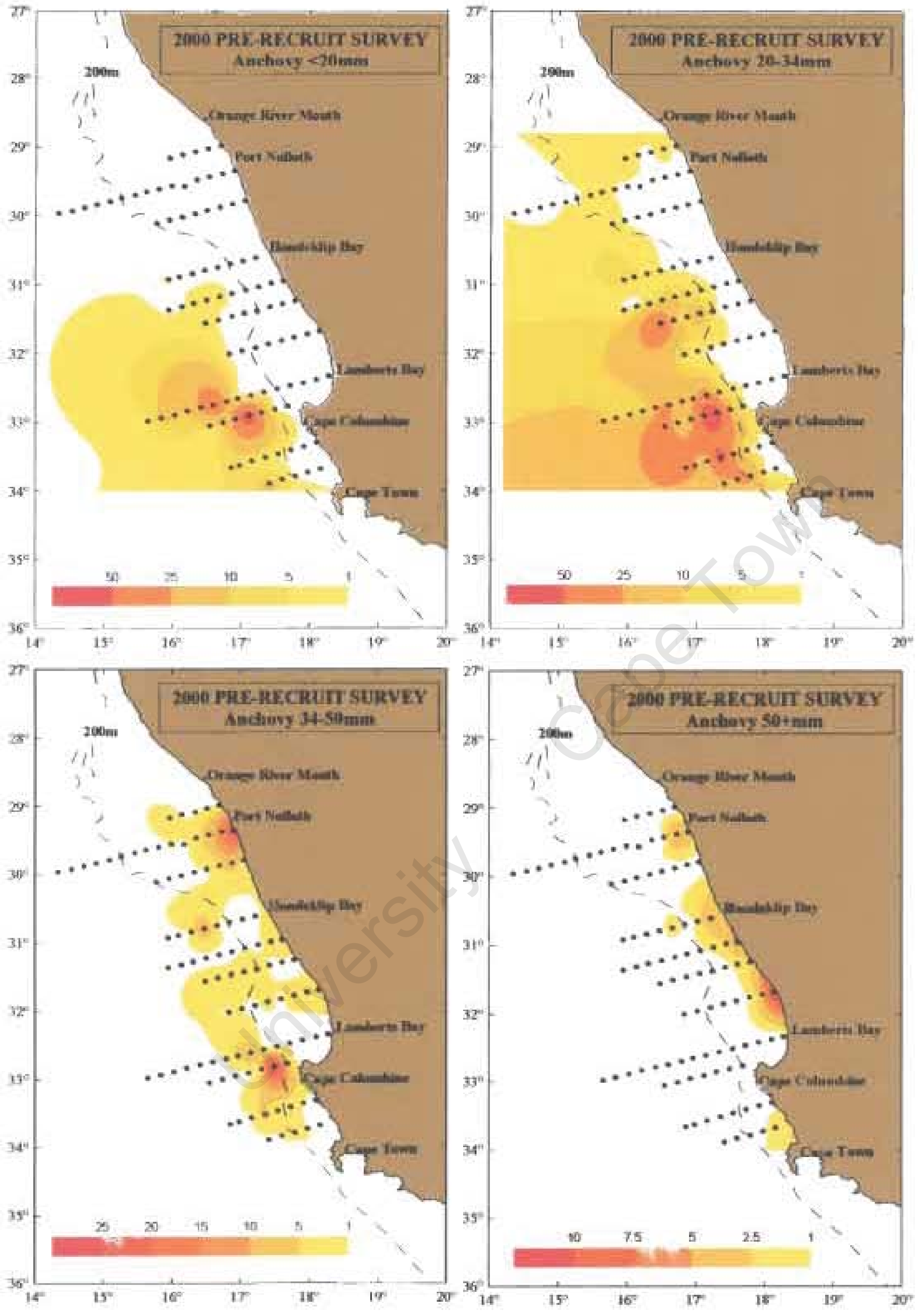

Figure 5.9. Distribution by class of anchovy pre-recruits collected using a Methot frame trawl during March 2000 survey. Dots indicate the positions of the Methot stations from van der Lingen and Huggett (in press).

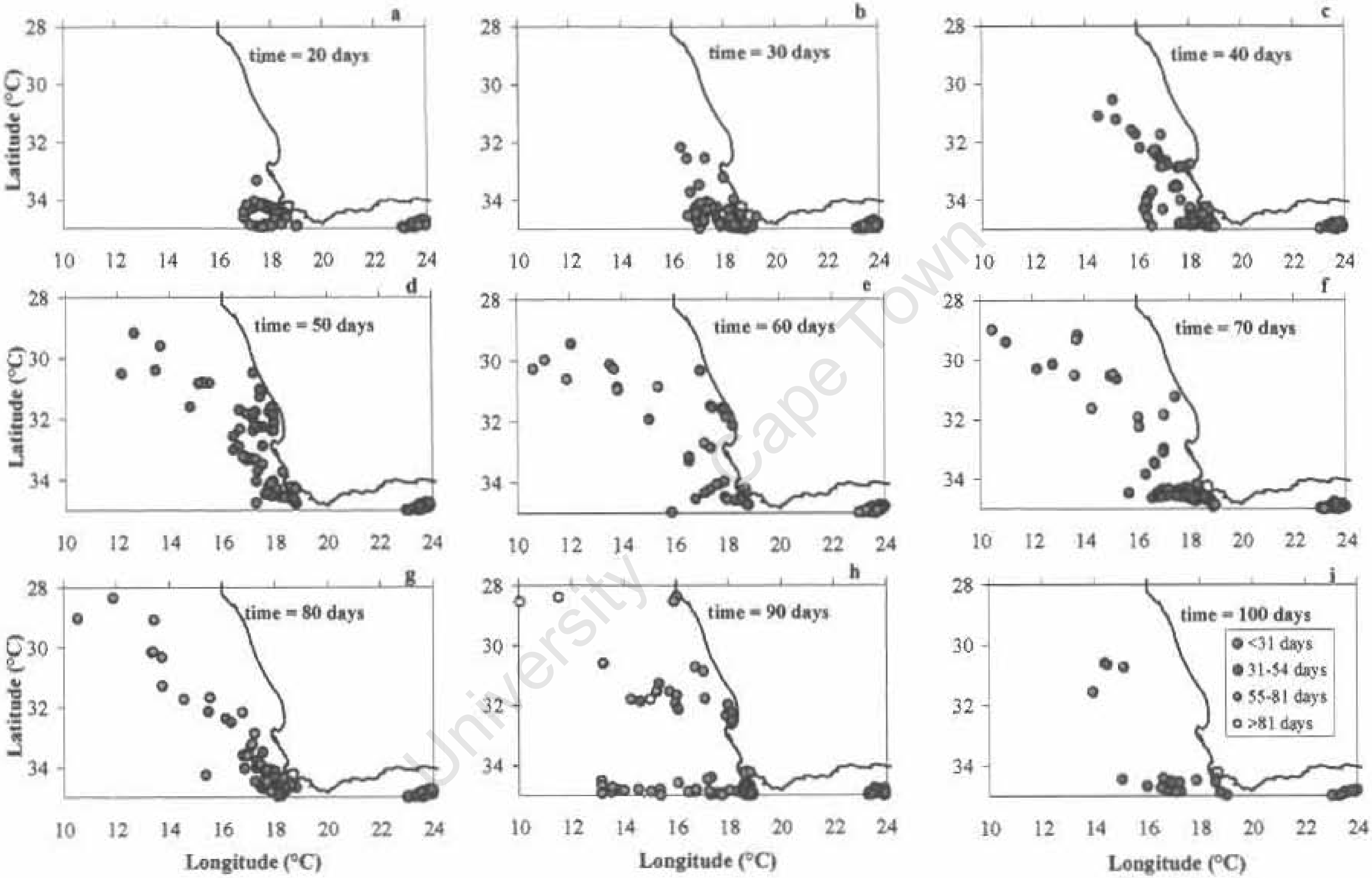

Figure 5.10. a-i. Modeled distribution of anchovy larvae and post-larvae in nursery area for a 100 day simulation, separated into four age classes: <31 days, between 31-54, between 55-81 and >81 days.

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 that actively selected a depth of 40 m tended to be more successfully retained in the nursery area for periods of >10 days (10% retention, Fig. 5.7b). It is important to note that lengthening the time criterion for successful retention (i.e. larvae were only considered to be successfully retained when remaining in the nursery area for periods longer than 10 days) tended to reduce the proportion of successfully retained larvae. This is because water currents in the nursery area showed a latitudinal tendency to move further offshore from south to north (Fig. 5.2). Individuals transported inshore would consequently tend to be move northwards over time, and then be advected offshore in the region of transect Nur1 (Fig. 5.10). Consequently, unless larvae make use of an appropriate vertical migration behavior to counteract this effect (coupled with the development of strong swimming capability), they will not be retained in the nursery area. A secondary objective of the models described in this chapter was to assess the potential of the EAB as a retention area for anchovy larvae and post-larvae. The active retention model for the EAB showed a maximum retention (8.3%) resulting when eggs were released inshore at the surface and larvae actively selected surface water subsequent to the onset of active vertical behavior. Comparatively, the retention in EAB is a half of the retention in west coast showing the potentiality of EAB as a retention/nursery area.

Coastal upwelling areas are characterized by a cross-shelf, vertically stratified water flow that directly affects the horizontal movement of particles (Cronin, 1982; Epifanio *et al.*, 1984; Brink, 1998; Hill, 1998; Batchelder *et al.*, 2002). Circulation patterns therefore impact larval transport patterns, which depend on how the vertical distribution of larvae is interacting with the structure of the flow (Hare *et al.*, 1999). The results obtained in this chapter support these ideas, and specifically hypothesis 3 (see Chapter 1), which proposes that active vertical behavior can counteract the offshore advective processes and increase the likelihood of successful transport to the nursery area. However, it should be noted that with regard to the hydrodynamic model that was coupled to the IBMs, the response of the thermal structure and current fields to intra-annual atmospheric fluctuations has not been fully resolved (Penven *et al.*, 2001). By using averaged monthly wind data, the high frequency signal observed in the wind time-series set is smoothed out. However, superficial frontal features within the southern Benguela region are highly responsive to changes in physical forcing by local wind field (Andrews and Hutchings, 1980; Nelson, 1992). Consequently, the surface manifestation of the upwelling front is spatially highly variable and responds rapidly to changes in wind stress, moving offshore during upwelling-favorable winds and onshore during periods of reversal (Nelson and Walker, 1984; Armstrong *et al.*, 1987). In contrast, the shelf-break front off the Cape Peninsula appears to be a more enduring feature, capable of persisting for longer than a year (Hutchings *et al.*, 1984). In view of these observations, the absence of wind relaxation in the hydrodynamic model does not account for the response of the upwelling front to local winds fluctuations. This is a limitation of the model, considering the generally-held belief that fronts play an important role in the local transport dynamics of anchovy on the west coast (Roy pers. com.). However, being aware of this limitation, using the approach of simplicity and various simulation scenarios, it was possible to test the hypothesis under controlled conditions.

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, future studies should assess the retention success lengthening the criterion of retention using a proper vertical migration scheme. It is possible that the EAB might represent both a spawning and nursery area for anchovy, as has been documented for other species in the southern Benguela system (Hutchings *et al.*, 2002) and elsewhere (e.g. Mackenzie, 1990). However, the question of how many of the individuals that are retained on the EAB would survive remains to be addressed. Additional factors such as starvation, cannibalism and predation are important processes (Brownell, 1983; Lasker, 1985, Alheit, 1987; Brownell, 1987; Valdés *et al.*, 1987) that should be assessed in future IBMs investigating retention success over longer time periods.

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 consistent with the assumption of equilibrium of the hydrodynamic model after the spin-up (see details in Penven 2000; Penven *et al.*, 2001).

Regarding the realism of the model output and its inter-annual variability, the PLUME model was not forced with short-term wind events, however, the model displays a high level of realism, accurately simulating mesoscale activity and several of the main features of the 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, off the Cape Peninsula and off Cape Columbine (Penven *et al.*, 2001). The inter-annual variability of the hydrodynamic model output has been attributed to intrinsic mesoscale activity resulting from oceanic instability processes in the absence of added forced variability (Penven *et al.*, 2001), which is consistent with earlier studies developed for the California upwelling system (Marschesiello *et al.*, 2001). Recent modeling attempts have shown that, the variability observed in the output of the hydrodynamic model PLUME was considerably lower than that obtained when the forcing factors incorporate an inter-annual signal (Blanke *et al.*, 2002). Therefore, we have an important degree of confidence on the generation of enough variability in the modeled system, which enables tests of the IBMs under different known scenarios.

Partial validation of the hydrodynamic model (PLUME) used in this research was achieved by comparing the SST output of the model with satellite images by Penven *et al.* (2001). The major discrepancy between the output of PLUME and hydrological conditions in the field was lower temperatures than expected on the west coast (normally 13 to 17°C in spring and 14 to 21°C in summer, Richardson *et al.*, 2000). This is considered to be a result of the smoothing effect of the monthly forcing of wind stress that is incorporated into the model (Penven *et al.*, 2001).

In addition, intense turbulence induced by wind events appears to be a dispersive process detrimental for larval survival (Lasker, 1978, 1981). For instance, turbulence involved in "Lasker events" may contribute to decrease the food concentrations for fish larvae (Lasker, 1975). In contrast, small-scale turbulence increases the food encounter rate of planktonic organisms (Rothschild and Osborn, 1988).

Several modeling studies using differential wind forcing showed the effect of turbulence on vertical distributions of the eggs of pelagic and mesopelagic fish species and the relation with encounter rates (Sundby, 1983; 1991; 1997; Stenevik *et al.*, 2001). Some of the experiments developed for these models displayed profiles in which it is observed how eggs ascend from spawning depth and finally reach the steady state solution when there is a balance between buoyancy and eddy diffusion fluxes (Sundby, 1997). The equilibrium of the vertical profile is reached, under windless condition, after about 48 h, and after 30 hrs when the wind condition was strong (15 ms^{-1}). In consequence, our assumption concerning the turbulence and the relation with transport should be reviewed in further modeling attempts incorporating a turbulent scheme to assess the effect on the buoyancy of eggs and the vertical behavior of larvae. Regarding the diffusion effect, modeling studies including horizontal diffusion on spatial distribution of favorable hatching locations showed 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 for eggs. In this study, I employed the modified buoyancy scheme of Denny (1993) that incorporates the buoyancy of prolate spheroid eggs. The buoyancy scheme applied during the experiments assumed that there is equilibrium between the vertical drag of particles and opposing buoyancy forces when the Reynolds number is less than < 0.5 (Sundby, 1983). This implies that viscous forces dominate over frictional forces. This assumption has been used for the previously mentioned modeling studies, with the exception of cases in which the wind stress is sufficiently strong that frictional forces dominate. As mentioned before, experiments developed by Sundby (1997) showed that during strong wind conditions (22 ms^{-1}) vertical mixing dominates over ascending velocity of the eggs. Wind intensities derived from the QuickSCAT satellite data showed maximum values of 8 to 9 ms^{-1} between September and March in the southern Benguela region (Riesen, 2002). Although these values suggest that vertical mixing is not dominating, the influence of these wind intensities on the vertical depth adjustment of the eggs should be assessed.

With regard to the mortality of eggs and larvae, the IBMs used in this research adopted a relatively simple approach, in that mortality was attributed only to temperature. In reality, other sources may also contribute to the mortality of anchovy eggs and larvae in the southern Benguela system such as starvation, disease and predation, including cannibalism (Brownell, 1983; Alheit, 1987; Brownell, 1987; Valdés *et al.,* 1987). On the other hand, the growth scheme employed in the models used the temperature-dependent Gompertz equation developed by Zweifel and Lasker (1976) on the basis of extensive experimental studies. The temperature dependency of anchovy growth has subsequently been confirmed by numerous experimental studies conducted in the laboratory (King *et al.,* 1978; Lo, 1985; 1986). Although this approach can be considered to be an oversimplification of the system, the inclusion of both mortality and growth as a function of temperature is an innovative approach in the IBM. This approach permits an understanding of purely physical environmental effects on both the individual eggs and larvae, as well as the entire population in the southern Benguela region.

Several modeling studies have employed a similar approach and incorporated temperature mediated growth equations to model larval fish growth. Bartsch (2002) used a logistic curve to model larval mackerel growth in a biophysical transport model. An interesting study that incorporated an individual based modeling approach developed a simple holistic model of temperature-mediated individual growth coupled to the particle tracking model, but the influence of temperature on mortality was not taken into account (Heath and Gallego, 1997). Other studies using the individual based modeling approach have studied the early life history of walleye pollock (Hinckley *et al.*, 1996; 2001) and transport of fish larvae such as English sole (Walters *et al.*, 1992), cod and haddock (Werner *et al.*, 1996).

The simplicity of the IBM design used in this research and the step by step approach enables the identification of factors and processes that are of fundamental importance in the IBM, and also facilitates the interpretation process by reducing the number of variables that were tested in the GLM analyses. The active behavior component incorporated into the experiments is clearly not as realistic 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 buoyancy model, however, egg Density replaced Depth of spawning as a significant parameter explaining transport success, while the importance of the Area of spawning was reduced (Table 6.1).

Table 6.1. Inter comparison between of the explained variance given for the GLM for the single parameters considering transport success as the dependence variable for different models. The "-" indicates that the parameter is not used and "c" that the parameter is fixed to a constant value.

	Variance explained (%)					
Parameter	**Model 1***	**Model 2***	**Model 3***	**Model 4***	**Model 5***	**Model 6***
Area	52.1	11.5	20.2	22.6	9.2	32.3
Depth	16.9	0.0	0.0	2.8	7.2	1.2
Date	1.9	2.0	1.1	9.5	4.7	1.5
Year	1.0	0.1	0.4	8.0	11.7	0.3
Density	-	19.9	17.5	C	C	c
Shape	-	0.0	0.0	c	C	c
λ	-	-	-	0.3	C	c
θ_E	-	-	-	0.2	C	c
θ_L	-	-	-	2.2	C	c
δ_L	-	-	-	-	-	8.2
τ_L	-	-	-	-	-	0.5
Sum of variance'	71.9	33.5	39.2	45.6	32.8	44.6

Models: (1) Lagrangian, (2) buoyancy applied to eggs and larvae, (3) buoyancy applied only to eggs, (4) growth and mortality as a temperature function, (5) passive behavior, (6) active behavior.
' The sum of variance only considers the variance explained by single variables.
*Only optimal models (from GLM) used in the comparisons

Even when the buoyancy scheme was applied for a short period (i.e. only during the egg stage, model 3), egg density still explained almost 18% of the variance (Table 6.1). The buoyancy model identified an optimal value egg density (1.025 g.cm^{-3}) that maximized transport success, and also resulted in the most realistic vertical distribution of eggs when compared with field data (Shelton and Hutchings, 1982). Recent measurements at sea indicate that the average observed egg density (1.025 gcm-3) matches very well the optimal value in the model (C. van der Lingen, per. comm.) Lighter eggs were more susceptible to offshore advection. Apart from providing further evidence for the importance of the WAB as the main center of spawning (Huggett *et al.*, 2003), these results support hypotheses 1 that points out that buoyancy of eggs and early larvae plays a key role in the successful transport of individuals from the spawning grounds to the nursery area, and in their offshore advection once transported to or near the nursery grounds. This emphasizes the relevance of the density parameter, indicating that an optimal buoyancy of eggs and early larvae significantly enhances the successful transport to the nursery area, with individuals positively buoyant being advected offshore as a result of unfavourable depth distribution.

These findings raise interesting considerations such as the parental effects on egg and subsequent larval quality, and the role of egg density as an adaptive strategy. Variables such as the food condition on the spawning grounds and the age of spawning adults may influence parental condition, which will then affect the size and quality of the eggs, and subsequently the larvae. There 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

Ekman layer and thereby increasing transport success to the nursery area as hypothesized previously by Stenevick *et al.*, (in press). The modeling output seem to be coherent with the larval and post-larval (pre-recruits) distribution data on the west coast. However, short term wind events which are not incorporated in the PLUME model could induce warming of the surface layers and relaxation of the upwelling front. This relaxation-intensification process of the upwelling front could be critical for the transport of spawning products to the nursery area. Future studies considering short term wind variability should explore the influence of frontal feature dynamics on the transport of spawning products.

6.2.2. The effect of temperature-dependent growth and mortality on transport success

The influence of temperature was assessed by incorporating two temperature-dependent processes into the growth and mortality model (model 4) namely, a temperature-dependent growth rates for both eggs and larvae (λ) and temperature acting as a lethal factor for eggs (θ_E) and larvae (θ_L). The major determinant of transport success in this model was the parameter Area of spawning. As in previous models, eggs spawned on the WAB tended to be the most successfully transported. The parameters Year, Depth and Date were of secondary importance in explaining the variance in transport success (Table 6.1). Among the temperature-effect parameters, only the critical temperature for larvae (θ_L) explained more than 2% of the variance, suggesting that larvae more tolerant to low temperatures will be slightly more successfully transported. The influence of the lethal temperature on eggs and the growth factor do not have a major effect when considering overall transport success (Table 6.1). However, when the dependent variables mortality of eggs and mortality of larvae are analyzed separately, the influence of these parameters is significant and explained an important percentage of the variance as explained below.

6.2.3. The effect of temperature on the mortality of eggs and larvae

The two temperature-dependent processes (i.e. the temperature-dependent growth scheme for eggs and larvae, and the lethal temperature limits for eggs and larvae) were incorporated into both the growth and mortality (model 4) and the active behavior models (model 6). Both of these models indicated that egg mortality is highly dependent on both the Depth and the Date of spawning (Table 6.2), while larval mortality is primarily dependent on the Area of spawning. The temperature-dependent parameters tend to be of minor importance in explaining egg and larva mortality in both models, with the possible exception of the lethal temperature for eggs (θ_E) parameter in model 4, which explained 7.2% of the variance in egg mortality. Even though this is a relatively substantial value in comparison with variance explained by other parameters, the parameter θ_E was fixed in model 5 because it is not important with regard to the main dependent variable transport success. With regard to the active behavior component incorporated into model 6, the preferred depth (δ_L) and time of active behavior (τ_L) parameters obviously had no influence on eggs mortality because these processes only began operating after hatching. The mortality of larvae was, however, influenced by 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 coast (Hampton, 1992). The concept of the EAB as a favorable spawning and nursery area is explored below, taking into account the constraint that the hydrodynamic model domain has an eastern boundary at 24°E, while the EAB extends to approximately 29°E.

Optimal density and the jet current transport. One of the patterns that clearly emerged was that an optimal egg density of 1.025 g.cm^{-3} favored successful transport to the nursery area. Smaller and greater values of density substantially reduced transport success. This pattern may be explained by lighter eggs being advected offshore, while heavier eggs descend into slower water currents resulting in reduced transport success (Fig. 6.1).

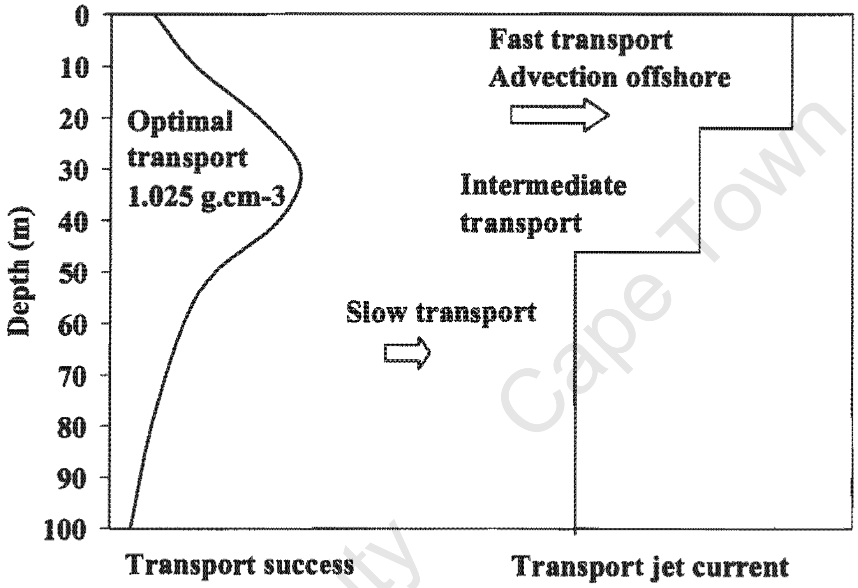

Figure 6.1. Hypothetical scheme of the relation between optimal density and the jet current transport for eggs of optimal density (1.025 g.cm^{-3}).

Inter-annual variability in the transport of the jet current was observed between Years 5 and 8 in the model. A shift from a strong northward and offshore flow to a weak northward and strong onshore flow did not result in marked changes in the average annual transport success of particles released over the WAB. This indicates that although strong northward transport moves substantial numbers of eggs towards the west coast, a large proportion of these are advected offshore. However, when the northward transport is reduced, the associated increased onshore transport means that most of the particles carried to the west coast make it into the nursery area. Although no field data are available to assess the variability of the jet current, the model does appear to reproduce the main features characterizing the transport of spawning products by the jet current.

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).

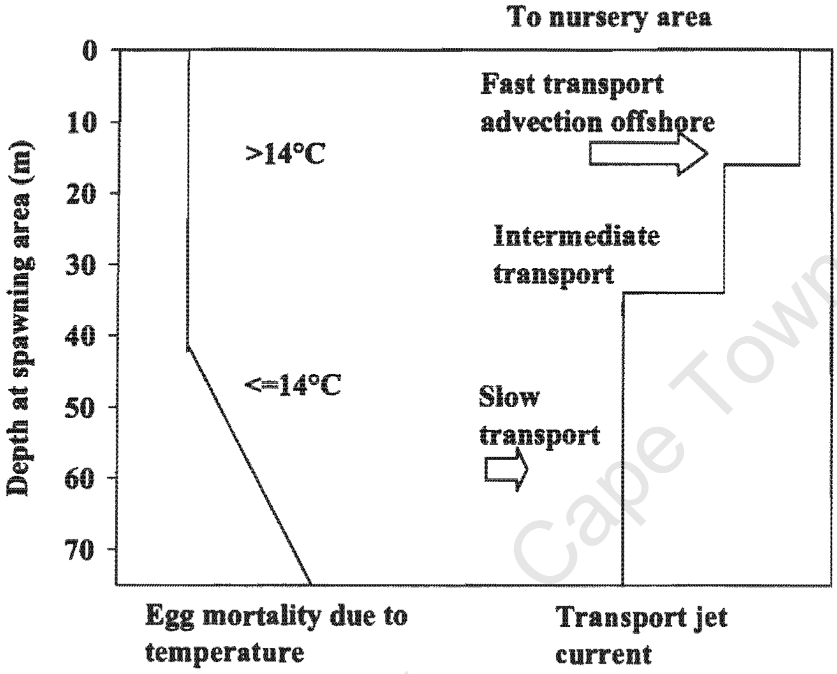

Figure 6.2. Hypothetical scheme of the trade-off between mortality of eggs released at different depth in the spawning area and the transport of the jet current to the nursery area.

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 mortality that is related to the oceanographic processes regulating the temperature of the water column. Larvae spawned on the WAB (together other conditions indicated in the figure such as being spawned between October and December, in Year 7 at Depths <= 25 m) are rapidly transported to the nursery area (i.e. a positive effect in terms of enhanced transport), where low temperatures associated with the upwelling centers can be lethal (i.e. a negative effect in terms of increased mortality; Fig. 6.3).

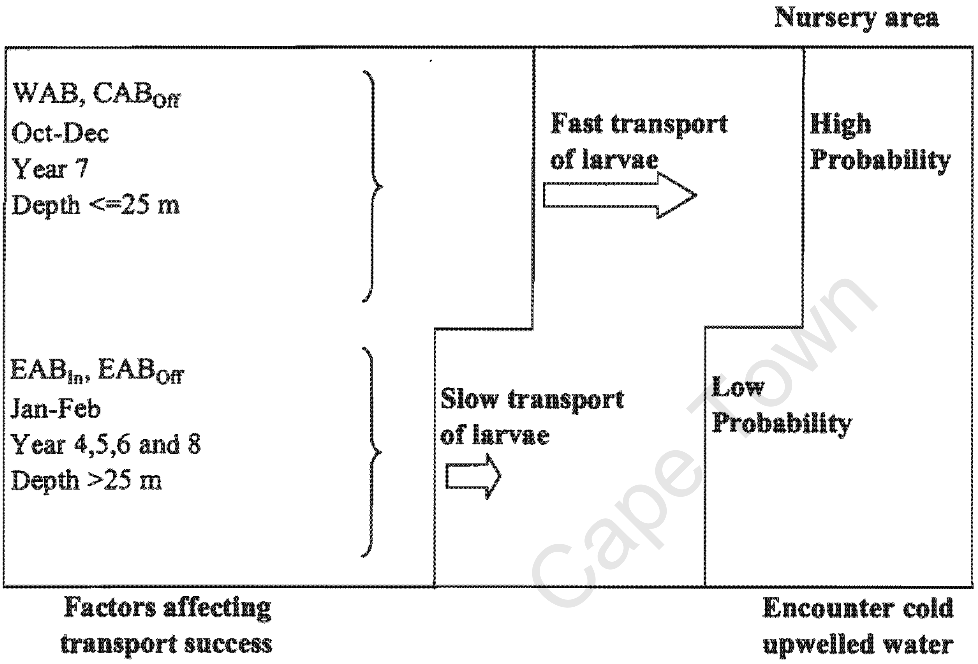

Figure 6.3. Hypothetical scheme of factors determining the transport success and the trade-off between the larval transport and the effect of the water temperature in the nursery area.

Optimal depth of active behavior in the nursery area and the trade-off between current transport and temperature. Another feature that emerged from the models was that larvae maintaining themselves at a depth of 40 m were the most successful in being transported to the inshore section of the nursery area (Fig. 6.4). Larvae maintaining depths shallower or deeper than 40 m showed a decrease in transport success in the IBM. As mentioned above, a possible explanation for this feature is that there is a depth-dependent interactive effect between the direction of across-shore transport of the current and temperature. During upwelling events for example, across-shore transport shows a strong offshore component in the upper layers of the water column (~25m) associated with the Ekman layer (and hence increased advective loss), but this flow becomes progressively more onshore orientated (with increased transport success) as depth increases (Fig. 6.4). The lethal effect of temperature on the larvae, however, is characterized by low mortality over 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).

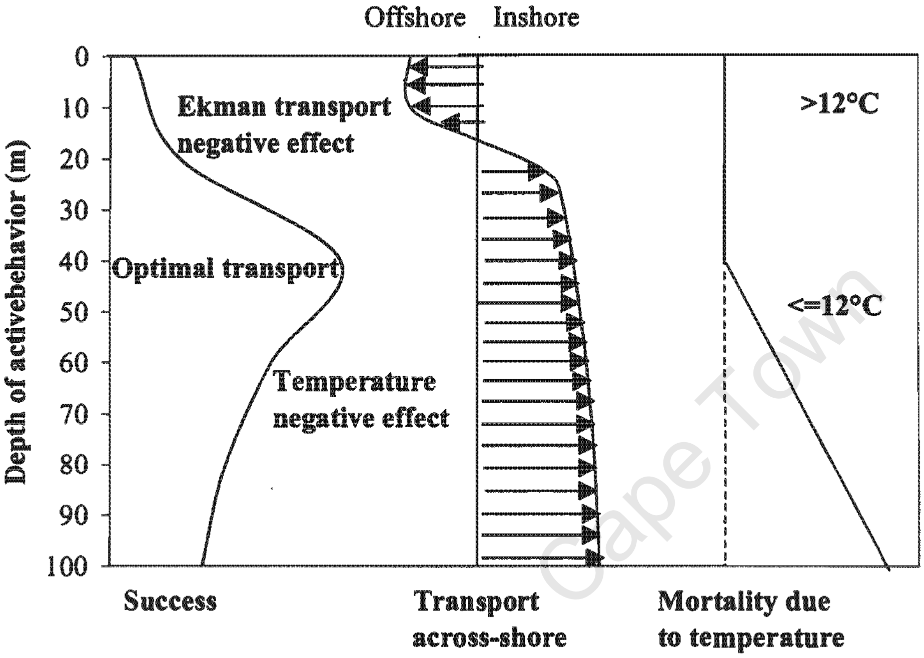

Figure 6.4. Hypothetical scheme showing "optimal transport success" and the tradeoff between Ekman transport and mortality of larvae due to cool temperatures during upwelling.

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 increased upwelling and consequent offshore transport is unrealistic, because of the wind forcing used in the PLUME model, specifically the lack of wind relaxation. In support of this argument, unexpectedly low temperatures are generated by the model when compared to hydrological data (Penven *et al.*, 2001). The retention of individuals in the nursery area is consequently apparent for only a short period in the model. Diel vertical migration behavior could potentially facilitate the maintenance of larvae and post-larvae in the nursery area for longer periods. Similarly, although the model applied to EAB resulted in a significant proportion of spawning products being retained on the EAB, they were again only retained for a short period. However, it is difficult to assess results obtained for the EAB because of its proximity to the eastern boundary of the domain.

The west coast and EAB models differed, however, in the optimal depth that maximized retention success. In the case of the EAB, this was 5 m, as opposed to 40 m in the model applied to the west coast nursery area. Although both models are comparable in the proportion of larvae retained, it is difficult to establish if the 8% retention on the EAB can generate the recruitment of a significant proportion of the population in the long term, particularly in view of the highly dynamic system associated with the Agulhas Bank as well as biological processes such as predation, cannibalism and lower abundance of prey compared to the west coast. It can be speculated, however, that the EAB does in fact contribute to recruitment success but further studies using a vertical migration scheme combined with a hydrodynamic model with greater temporal resolution (output every 3 to 6 h) and strong wind variability are required to determine to what extent this does occur.

6.2.6. Synopsis

With reference to the objectives listed at the beginning of this chapter and how the hypotheses were proved or disproved, the points discussed above can be summarized as follows:

- The transport of anchovy spawning products to the nursery area is primarily influenced by the location of egg release (spawning area), the buoyancy of the eggs (regulated by the interaction between egg and ambient water density), and the direction and intensity of the jet current. The buoyancy of eggs and early larvae plays a key role in the successful transport from the spawning grounds to the nursery area, and in their offshore advection once transported to or near the nursery grounds.
- During their transport in the jet current, and on arriving in the nursery area, the advection of the eggs and larvae (either inshore or offshore) is primarily regulated by the strength and direction of water flow, although behavioral mechanisms (particularly vertical migration) appear to be able to counteract this to a certain extent.
- In terms of mortality, eggs were mostly influenced by the date and depth of spawning, while larval mortalities were primarily attributable to unfavorable spawning locations, coupled to the likelihood of encountering lethal temperatures.
- With regard to the retention of larvae in both the west coast nursery area and on the EAB, spawning location and depth of active behavior (i.e. the preferred depth

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:

(1) The location of the spawning products (spawning grounds),

(2) The buoyancy of the eggs,

(3) Transport by the jet current and its inter-annual variability,

(4) The vertical cross- and along-shore structure of the current associated with the nursery area on the west coast influenced by upwelling,

(5) The swimming abilities of the pre-recruits in both the vertical (i.e. maintaining a preferred depth) and the horizontal (i.e. swimming against "unfavorable" currents) planes.

The precise location of spawning on the Agulhas Bank appears to play a major role in determining whether they are advected offshore (and lost to the system), or moved to the jet current area and subsequently transported to the west coast (Fig. 6.5). In this regard, the WAB appears to be the most favorable spawning area, closely followed by the offshore region of the CAB.

Both on the spawning grounds and during transport in the jet current, the buoyancy of the eggs determines their depths, depending on ambient water density. Because the jet current itself, in terms of the velocity and direction of flow, is the primary transport mechanism, the buoyancy and concomitant depth of the eggs plays an important role in the transport success, with maximum transport success apparently associated with an optimal egg density of 1.025 $g{\cdot}cm^{-3}$ (Fig.6.1). When the northward and subsequently offshore transport is strong, most of the particles crossing the SARP Line are those with a density of 1.025 $g.cm^{-3}$. In contrast, when northward and offshore jet current transport decreases, or under conditions of moderate northward and strong inshore transport, less-dense particles (1.021 – 1.023 $g{\cdot}cm^{-3}$) reach the SARP Line. These results emphasize the importance of the interaction between buoyancy and physical conditions in determining the transport success in any given year.

Larvae and post-larvae that are capable of maintaining a depth of 40 m appear to be the most successful in terms of transport to the inshore part of the west coast nursery area. It would seem, therefore, that appropriate active vertical migration has the potential to significantly increase their chances of being successfully transported to the nursery area.

The output of the hydrodynamic model displays a northward current flow close to the coast, coupled with a tendency for offshore water movement in the northern part of the nursery area. The implication of this finding is that larvae and post-larvae that have been successfully transported to the inshore parts of the nursery area (either passively, or by active vertical migration to the optimal depth of 40 m) will subsequently be transported northwards and ultimately offshore (possibly becoming lost to the system) when reaching the northern part of the nursery area. Although it is unlikely that vertical migration can counteract the strong offshore transport, it is possible that pre-recruits reaching this stage of development (coincident with the schooling behavior) have developed sufficient swimming ability to swim against the offshore flow and actively maintain themselves in the nursery area. However, in view of the constraints imposed on the input of the hydrodynamic 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).

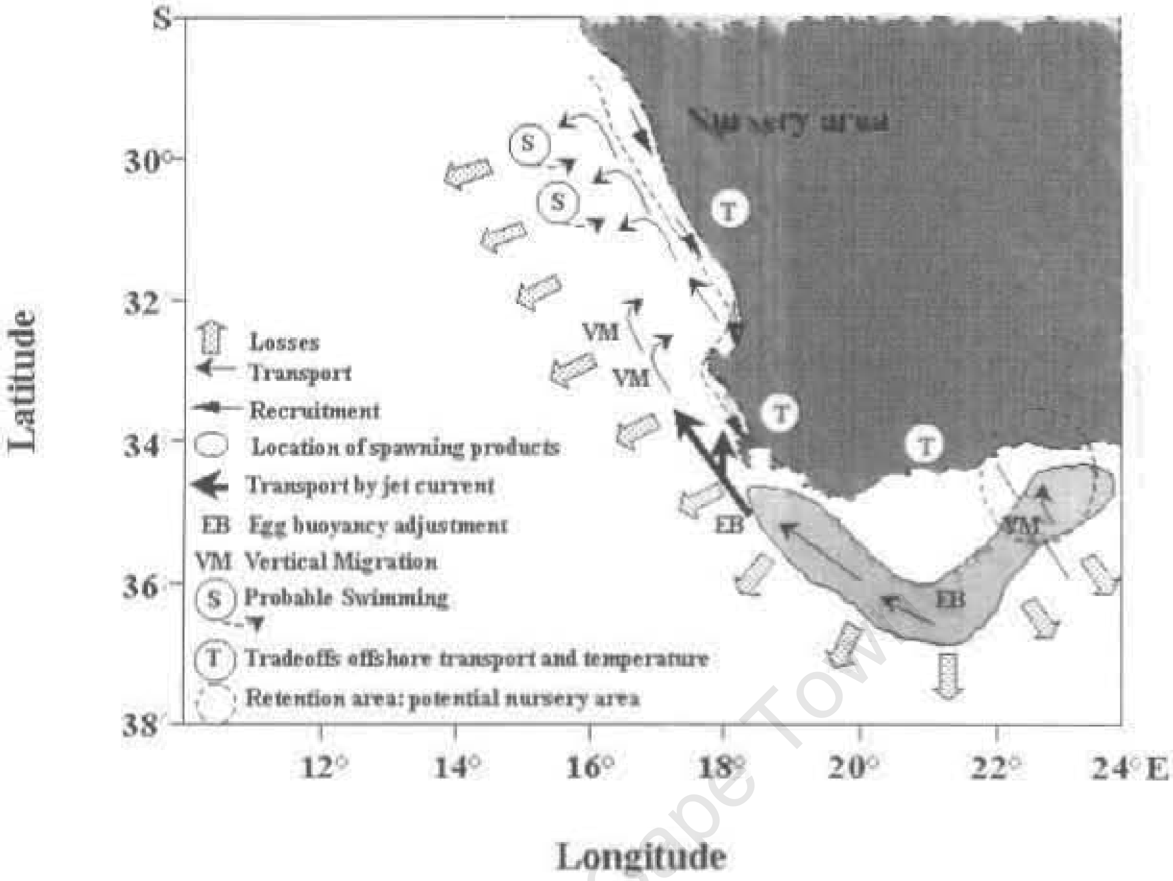

Figure 6.5. A conceptual model of the life history of anchovy in southern Benguela system

Several modeling and field studies focused on fishes such as pollock in the Gulf of Alaska (Hermann *et al.*, 1996), sand eel in the North Sea (Berntsen *et al.*, 1994), cod and haddock early life stages on Georges Bank (Werner *et al.*, 1993), and spot and Atlantic menhaden larvae in the east coast of United States (Hare *et al.*, 1999; Werner *et al.*, 1999) have provided substantial understanding into larval transport processes which has been linked to the inter-annual recruitment variability. Physical and biological factors influencing recruitment have been studied and the variability of the habitats linked to recruitment variability (Nelson *et al.*, 1977; Checkley *et al.*, 1988). Recent field studies of anchovy egg distribution carried out in southern Benguela system have suggested a marked eastwards shift in the anchovy spawner biomass since 1994, with anchovy spawning predominantly off the south and east coasts (van der Lingen, *et al.*, 2002). This shift is likely to have a major impact on the transport of eggs and larvae to the nursery grounds, and subsequently on the recruitment strength (van der Lingen *et al.*, 2001). Recruitment strength appears to have been relatively low but stable between 1985 and 1996, and higher but more variable between 1997 and 2001, coincident with the shift in spawning area (Hutchings *et al.*, 1998; Barange et *al.*, 1999; van der Lingen *et al.*, 2002). The very strong recruitment of anchovy in 2000 (detected during the May/June survey) was corroborated by the high spawner biomass observed during the November 2000 survey (van der Lingen *et al.*, 2001; Barlow *et al.*, 2002; Roy *et al.*, 2002). The relatively few 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.

- Improvement of the active behavior model for testing the hypothesis of avoidance by larvae of the Ekman layer and the retention on the west coast and the EAB. In a later phase, this would involve studies of the schooling and swimming capabilities of pre-recruits.
- Incorporation of processes such as feeding, predation and competition to improve estimates of the mortality of early stages of anchovy in the southern Benguela system. This would require a representation of food availability, either by modeling (e.g. NPZ models) or by collating existing data.

Further field work should be conducted to improve our understanding of the biological and physical mechanisms involved in vertical migration, the swimming abilities of pre-recruits and the retention process. As pointed by Huggett *et al.* (2003), the IBM results provide directions for specific sampling, for example :

- investigations of spawner distribution during the early and late phases of the spawning season,
- surveys to locate pre-recruits older than two months remaining on the Agulhas Bank after the spawning season,
- and multi-layer sampling of larvae to determine their depth distribution at different times of the day.

Experimental studies could also be used to contribute to improve the output of the models. These include:

- Laboratory experiments to assess the incubation times of eggs of *Engraulis encrasicolus* under different temperature conditions.
- Experiments to assess the vertical migration of larvae and post-larvae and the swimming abilities of anchovy pre-recruits.

Such studies will provide vital information to re-assess the models, and the subsequent innovations will no doubt generate new questions and hypotheses to be tested in the field (Mullon *et al.*, submitted). The primary challenge remains to quantify the relationship between the successful transport, retention of anchovy eggs and larvae and recruitment variation (Nelson *et al*, 1977; Hare *et al.*, 1999). In order to address this key issue, one would need to make use of realistic inter-annual forcing of the hydrodynamic model, which is not yet available (work in progress). The connection between the effects of environmental factors and processes on the life history of anchovy in the southern Benguela region and recruitment variability is clearly not straightforward. However, IBMs present a valuable tool to address the life history of pelagic fishes (Woods, 2002), particularly with regard to recruitment issues.

REFERENCES

Ådlandsvik, B., Coombs, S., Sundby, S. and Temple, G. (2001). Buoyancy and vertical distribution of eggs and larvae of blue whiting (*Micromesistius poutassou*) observations and modelling. *Fish. Res.* **50**:59-72.

Alheit, J. (1987). Egg cannibalism versus egg predation: their significance in anchovies. In: The *Benguela and Comparable Ecosystems.* A.I.L. Payne, J.A. Gulland, and K.H. Brink (eds) *S. Afr. J. mar. Sci.* **5**:467-470.

Anders, A.S. (1965). Preliminary observations on anchovy spawning off the South African coast. *S. Afr. Shipp. News Fishing. Ind. Rev.* **20**(11):103-107.

Anders, A. S. (1975). Pilchard and anchovy spawning along the Cape Town east coast. *S.Afr. Shipp. News Fishing Ind. Rev.* **30**(9):53,55,57.

Andrews, W.R.H. and Hutchings, L. (1980). Upwelling in the Southern Benguela Current. *Prog. Oceanogr.* **9**(1):1-81.

Armstrong, D.A., Mitchell-Innes, B.A., Verheye-Dua, F., Waldron, H. and Hutchings, L. (1987). Physical and biological features across and upwelling front in the southern Benguela. In: The *Benguela and Comparable Ecosystems.* A.I.L. Payne, J.A. Gulland, and K.H. Brink (eds) *S. Afr. J. mar. Sci.* **5**:171-190.

Armstrong, M.J., Chapman, P., Dudley, S.F.J., Hampton, I. and Malan. P.E. (1991). Ocurrence and population structure of pilchard *Sardinops ocellatus*, round herring *Etremeus whiteheadii* and anchovy *Engraulis capensis* off the east coast of Southern Africa. *S. Afr. J. mar. Sci.* **11**:1227-1250.

Armstrong, M.J., Shelton, P.A., Hampton, I., Jolly, G. and Melo, Y. (1988). Egg production estimates of anchovy biomass in the southern Benguela system. *Calis. Coop. Oceanic. Fish. Rep.* **29**:137-156.

Armstrong, M.J. and Thomas R.M. (1989). Clupeoids. In: *Oceans of Life off Southern Africa.* A.I.L. Payne and R.J.M. Crawford (eds) *Vlaeberg Publishers*, Cape Town, p 105-129

Auyang, S.Y. (1998). Foundations of complex-system theories in economics, evolutionary biology, and statistical physics, New York, Cambridge University Press. 416 pp.

Badenhorst, A. and Boyd A.J. (1980). Distributional ecology of the larvae and juveniles of anchovy *Engraulis capensis* Gilchridt in relation to the hydrological environment off South West Africa, 1978-1979. *Fish. Bull. S. Afr.* **13**:83-106.

Bakun, A. (1996). Patterns in the oceans. Ocean processes and marine population dynamics. California Sea Grant College System, USA., in cooperation with Centro de Investigaciones biológicas del Noroeste, La Paz, Baja California Sur, Mexico. 323 pp.

Barange, M., Hampton, I. and Roel, B.A. (1999). Trends in the abundance and distribution of anchovy and sardine on the South African continental shelf in the 1990s, deduced from acoustic surveys. *S. Afr. J. mar. Sci.* **21**:367-391.

Barlow, R., Roy, C., Weeks, S., Fréon, P., van der Lingen, C.D., Rouault, M. and Nelson, G. (2002). The unusual 1999-2000 summer season in the southern Benguela: Implications for anchovy recruitment. In: *Report of a GLOBEC-SPACC/IDYLE/ENVIFISH workshop on Spatial Approaches to the Dynamics of Coastal Pelagic Resources and their Environment in Upwelling Areas.* C.D. van der Lingen, C. Roy, P. Fréon, M. Barange, L. Castro, M. Gutierrez, L. Nykjaer and F. Shillington (eds) *GLOBEC Rep.* **16**:49-51.

Bartsch, J. (2002). Modelling the temperature mediation of growth in larval fish. *Fish. Oceanogr.* **11**(5):310-314.

Batchelder, H.P., Edwards, C.A. and Powell, T. (2002). Individual-based models of copepod populations in coastal upwelling regions: implications of physiologically and environmentally influenced diel vertical migration on demographic success and nearshore retention. *Prog. Oceanogr.* **53**:307-334.

Beckley, L.E. (1986). The ichthyoplankton assemblage of the Algoa Bay nearshore region in relation to coastal zone utilization by juvenile fish. *S. Afr. J. Zool.* **21**:244-252.

Beckley, L.E. and Hewitson, J.D. (1994). Distribution and abundance of clupeoid larvae along the east coast of South Africa in 1990/91. *S. Afr. J. Mar. Sci.* **14**:205-212.

Berntsen, J., Skagen, D.W. and Svendsen, E. (1994). Modelling the transport of particles in the North Sea with reference to sandeel larvae. *Fish. Oceanogr.* **3**:81-91.

Biastoch, A. and Krauß, W. (1999) The role of mesoscale eddies in the source regions of the Agulhas current. *J. Phys. Oceanogr.* **29**:2303-2317.

Blanke, B., Roy, C., Penven, P., Speich, S., McWilliams, J. and Nelson, G. (2002). Assessing wind contribution to the southern Benguela interannual dynamics. *GLOBEC International Newsletter* **8**(1):15-18.

Borland (1999). Developer's guide, Borland Jbuilder for Windows 95, Windows 98 and Windows NT. Version 3. A division of inprise corporation, USA.

Boyd, A. J. and Nelson, G. (1998). Variability of the Benguela Current off the Cape Peninsula, South Africa. In: *Benguela Dynamics, Impacts of Variability on Shelf-sea Environments and Their Living Resources.* S.C. Pillar, C.L. Moloney, A.I.L. Payne and F.A. Shillington (eds) *S. Afr. J. mar. Sci.* **19**:15-39.

Boyd, A.J. and Shillington, F.A. (1994). Physical forcing and circulation patterns on the Agulhas Bank. *S. Afr. J. Sci.* **90**:114-123.

Boyd, A.J., Taunton-Clark, J. and Oberholster, G.P.J. (1992). Spatial features of the near-surface and midwater circulation patterns off western and southern Africa and their role in the life histories of various commercially fished species. In: *Benguela Trophic Functioning.* A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn (eds) *S. Afr. J. mar. Sci.* **12**:189-206.

Brink, K.H. (1998). Wind-driven currents over the continental shelf. *The Sea* **10**:3-20.

Brown, P.C. (1992). Spatial and seasonal variation in chlorophyll distribution in the upper 30 m of the photic zone in the Southern Benguela/Agulhas ecosystem. In: *Benguela Trophic Functioning.* A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn (eds) *S. Afr. J. mar. Sci.* **12**:515-525.

Brownell, C. L. (1983). Laboratory rearing of Cape anchovy *Engraulis capensis* and South African pilchard *Sardinops ocellata* through metamorphosis. *S. Afr. J. Mar. Sci.* **1**:181-188.

Brownell, C.L. (1987). Cannibalistic interactions among young anchovy: A first attempt to apply laboratory behavioural observations to the field. In: The *Benguela and Comparable Ecosystems.* A.I.L. Payne, J.A. Gulland, and K.H. Brink (eds) *S. Afr. J. mar. Sci.* **5**:503-511.

Bunn, N.A., Fox, C.J. and Webb, T. (2000). A literature review of studies on fish egg mortality: implications for the estimation of spawning stock biomass by the annual egg production method. *Sci. Ser. Tech. Rep., CEFAS*, Lowestoft. **111**:1-37.

Checkley, D.M., Raman, S., Maillet., G.L. and Manson, K.M. (1988). Winter storm effects on the spawning and larval drift of a pelagic fish. *Nature* **335**:346-348.

Cochrane, K.L. and Hutchings, L. (1995). A structured approach to using biological and environmental parameters to forecast anchovy recruitment. *Fish. Oceanogr.* **4**:102-127.

Coombs, S.H. (1981). A density-gradient column for the determining the specific gravity of fish eggs, with special references to eggs of mackerel *Scomber scombrus. Mar. Biol.* **63**:101-106.

Coombs, S.H., Fosh, C.A. and Keen, M.A. (1985). The buoyancy and vertical distribution of eggs of sprat (*Sprattus sprattus*) and pilchard (*Sardina pilchardus*). *J. Mar. Biol. Ass. U.K.* **65**:461-474.

Coombs, S.H, Sundby, S. and Ådlandsvik, B. (2000). Modelling the vertical distribution of eggs in relation to CUFES sampling. In: *Report of a workshop on the use of the continuous, underway fish egg sampler (CUFES) for mapping spawning habitat of pelagic fish.* D.M. Jr. Checkley, J.R. Hunter, L. Motos and C.D. van der Lingen (eds) *GLOBEC Rep.* **14**:60-62.

Cronin, T.W. (1982). Estuarine retention of larvae of the crab *Rhithropanopeus harisii. Estuar. Coast. Shelf Sci.* **15**:207-220.

Da Silva, A.M., Young, C.C. and Levitus, S. (1994). Atlas of surface marine data 1994. Algorithms and procedures. NOAA atlas NESDIS 6, U.S. Department of Commerce, NOAA, USA. Vol.1, 74 pp.

DeAngelis, D.L. and Rose, K.A. (1992). Which individual-based approach is most appropriate for agiven problem? In: *Individual-based Models and approaches in Ecology.* D.L. DeAngelis and L.J. Gross. Chapman and Hall, New York, p. 67-87.

Denny, M.W. (1993). Air and water: the biology and physics of life's media. New Jersey: Princeton University Press, 341 pp.

Epifanio, C.E., Valenti, C.C. and Pembroke, A.E. (1984). Dispersal and recruitment of blue crab larvae in Delaware Bay. *Estuar. Coast. Shelf Sci.* **18**:1-12.

Fowler, J.L. and Boyd, A.J. (1998). Transport of anchovy and sardine eggs and larvae from the western Agulhas Bank to the West coast during the 1993/94 and 1994/95 spawning seasons. In: *Benguela Dynamics. Impacts of Variability on Shelf-Sea Environments and their Living Resources*. S.C. Pillar, C.L. Moloney, A.I.L. Payne and F.A. Shillington (eds) *S. Afr. J. mar. Sci.* **19**:181-195.

Fraser, J.H. (1970). The ecology of the ctenophere *Pleurobrachia pileus* in Scottish waters. *Journal du Conseil Permanent International pour l'Exploration de la Mer.* **33**:149-168.

Gordina, A.D., Nikolskiy, V.N., Niermann, U., Bingel, F. and Subbotin, A.A. (1997). New data on the morphological differences of anchovy eggs (*Engraulis encrasicolus L*) in the Black Sea. *Fish. Res.* **31**:139-145.

Grimm, V. (1994). Mathematical models and understanding in ecology. *Ecol. Modelling* **75/76**:641-651.

Grimm, V. (1999).Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecol. Modelling* **115**:129-148.

Grimm, V., Frank, K., Jeltsch, F., Brandl, R., Uchmariski, J. and Wissel, C. (1996). Pattern-oriented modelling in population ecology. *The Science of the Total Environment* **183**:151-166.

Grimm, V., Wyszomirski, T., Aikman, D. and Uchmanski, J. (1999). Individual-based modelling and ecological theory synthesis of a worshop. *Ecol. Modelling* **115**:275-282.

Haidvogel, D.B., Arango, H.G., Hedström, K.S., Beckmann, A., Malanotte-Rizzoli, P. and Shchepetkin, A.F. (2000). Model evaluation experiments in the North Atlantic Basin: simulations in nonlinear terrain-following coordinates. *Dyn. Atm. Oceans.* **32**:239-281.

Hampton, I. (1987). Acoustic study on the abundance and distribution of anchovy spawners and recruits in South African waters. In: The *Benguela and Comparable Ecosystems.* A.I.L. Payne, J.A. Gulland, and K.H. Brink (eds) *S. Afr. J. mar. Sci.* **5**:901-917.

Hampton, I. (1992). The role of acoustic surveys in the assessment of pelagic fish resources on the South African continental shelf. In: *Benguela Trophic Functioning.* A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn (eds) *S. Afr. J. mar. Sci.* **12**:1031-1050.

Hare, J.A., Quinlan, J.A., Werner, F.E., Blanton, B.O., Govoni, J.J., Forward, R.B., Settle, L.R. and Hoss, D.E. (1999). Larval transport during winter in the SABRE study area: results of a coupled vertical larval behaviour- three dimensional circulation model. *Fish. Oceanogr.* **8**(Suppl.2):57-76.

Heath, M. and Gallego, A. (1997). From the biology of the individual to the dynamics of the population: bridging the gap in fish early life studies. *J. Fish Biol.* **51**(Suppl.A):1-29.

Hempel, G. (1979). Early life history of marine fish - the egg stage. University of Washington Press, Seattle. 70 pp.

Hermann, A., Hinckley, S., Megrey, B. and Napp, M. (2001). Applied and theoretical considerations for constructing spatially explicit individual-based methods of marine fish early life history which include multiple trophic levels. *ICES J. Mar. Sci.* **58**:1030-1041.

Hermann, A., Hinckley, S., Megrey, B. and Stabeno, P. (1996). Interannual variability of early life history of walleye pollock new Shelikof Strait as inferred from a spatially explicit, individual-based model. *Fish. Oceanogr.* **5**(Suppl.1):39-57.

Hewitt, R.P., Methot, R.D. (1982). Distribution and mortality of northern anchovy larvae in 1978 and 1979. *CalCOFI Rep.* **23**:226–245

Hill, A.E. (1991). Advection-diffusion-mortality solutions for investigating pelagic larval dispersal. *Mar. Ecol. Prog. Ser.* **70**:117-128.

Hill, A.E. (1998). Diel vertical migration in stratified tidal flows: Implications for plankton dispersal. *J. Mar. Res.* **56**:1069-1096.

Hinckley, S., Hermann, A.J. and Megrey, B.A. (1996). Development of a spatially explicit, individual-based model of marine fish early life history. *Mar. Ecol. Prog. Ser.* **139**:47-68.

Hinckley, S., Hermann, A.J., Meir, K.L. and B.A. Megrey. (2001). The importance of spawning location and timing to successful transport to nursery areas: a simulation modeling study of Gulf of Alaska walleye pollock. *ICES J. Mar. Sci.* **58**:1042-1052.

Hjort, J. (1914). Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research. *Rapports et Procès-Verbaux des Rèunions, Conseil International pour l'Exploration de la Mer.* **20**:1-228.

Huggett, J.A., Boyd, A.J., Hutchings, L. and Kemp, A.D. (1998). Weekly variability of clupeioid eggs and larvae in the Benguela jet current: Implications for recruitment. In: *Benguela Dynamics. Impacts of Variability on Shelf-Sea Environments and their Living Resources*. S.C. Pillar, C.L. Moloney, A.I.L. Payne and F.A. Shillington (eds) *S. Afr. J. mar. Sci.* **19**:197-210.

Huggett, J.A., Fréon, P., Mullon, C. and Penven, P. (2003) Modeling the recruitment success of anchovy (*Engraulis encrasicolus*) in the southern Benguela: the effect of spatio-temporal spawning patterns on egg and larval transport. *Mar. Ecol. Prog. Ser.* (in press)

Hunter, J.R. and Kimbrell, C.A. (1980). Egg cannibalism in the northern anchovy, *Engraulis mordax*, *Fish. Bull. U.S.* **78**:811-816.

Hutchings, L. (1994). The Agulhas Bank: a synthesis of available information and a brief comparison with other east-coast shelf regions. *S. Afr. J. Sci.* **90**:179-185.

Hutchings, L., Barange, M., Bloomer, S.F., Boyd, A.J., Crawford, R.J.M., Huggett, J.A., Kerstan, M., Korrubel, J.L., De Oliveira, J.A.A., Painting, S.J., Richardson, A.J., Shannon, L.J., Schulein, F.H., van der Lingen, C.D. and Verheye, H.M. (1998).

Multiple factors affecting anchovy recruitment in the spawning, transport and nursery areas. In: *Benguela Dynamics. Impacts of Variability on Shelf-Sea Environments and their Living Resources*. S.C. Pillar, C.L. Moloney, A.I.L. Payne and F.A. Shillington (eds) *S. Afr. J. mar. Sci.* **19**:211-225.

Hutchings, L., Beckley, L.E., Griffiths, M.H., Roberts, M.J., Sundby, S., van der Lingen, C., (2002). Spawning on the edge: spawning grounds and nursery areas around the southern African coastline. *Mar. Freshwater Res.* **53**:307-318.

Hutchings, L. and Boyd, A. (1992). Environmental influences on the purse seine fishery in South Africa. *Invest. Pesq.* (Chile) **37**:23-43.

Hutchings, L., Holden, C.J. and Mitchell-Innes, B. (1984). Hydrological and biological shipboard monitoring of upwelling off the Cape Peninsula. *S. Afr. J. Sci.* **80**:83-89.

Jackson, G.A., and Strathmann, R.R. (1981). Larval mortality from offshore mixing as a link between precompetent and competent periods of development. *Am. Nat.* **118**:16-26.

King, D.P.F., Robertson, A.A. and Shelton, P.A. (1978). Laboratory observations on the early development of the anchovy *Engraulis capensis* from the cape peninsula. *Fish. Bull. S. Afr.* **10**:37-45.

Lasker, R. (1975). Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *Fish. Bull. Nat. Mar. Fish. Serv. U.S.* **73**(3):453-462.

Lasker, R. (1978). The relation between oceanographic conditions and larval anchovy food in California Current: Identification of the factors leading to recruitment *failure Rapp. P.-v.Réun. Cons .int .Explor. Mer.* **173**: 212-230.

Lasker, R. (1981). Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: Contrasting year 1975 through 1978. *Rapp. P.-v.Réun. Cons .int .Explor. Mer.* **178**: 375-388.

Lasker, R. (1985). What limits clupeoid production? *Can. J. Fish. Aquat. Sci.* **42**(Suppl.1):31-38.

Le Clus, F. and Malan, P.E. (1995). Models of temperature-dependent rate of development of pilchard *Sardinops sagax* eggs, to be used in routine procedures for estimating daily egg production. *S. Afr. J. mar. Sci.* **16**:1-8.

Lenarz, W.H. (1991). Depth distribution of late larvae and pelagic juveniles of some fishes of the California current. *CalCOFI Rep*. **32**:41-46.

Lluch-Belda, D., Lluch-Cota, D.B., Hernández-Vásquez, S. and Salinas-Zavala, C.A. (1992). Sardine population expansion in eastern boundary systems of Pacific Ocean as related to sea surface temperature. In: *Benguela Trophic Functioning*. A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn (eds) *S. Afr. J. mar. Sci.* **12**:147-155.

Lo, N. (1985). A model for temperature-dependent northern anchovy egg development and automated procedure for the assignment of age to staged eggs. In: *An Egg Production*

Method for Estimating Spawning Biomass of Pelagic Fish: Application to the northern anchovy, Engraulis mordax. R. Lasker (ed) *US Department of Commerce, NOAA Technical Rep. NMFS,* **36**:43-50.

Lo, N. (1986). Modelling life-stage-specific instantaneous mortality rates, as an application to northern anchovy, *Engraulis mordax*, eggs and larvae. *Fish. Bull.* **84**(2):395-407.

Logerwell, E.A., Lavaniegos, B., and Smith, P. (2001). Spatially-explicit bioenergetics of pacific sardine in the southern California bight: are mesoscale eddies areas of exceptional prerecruit production? *Prog. Oceanogr.* **49**:391-406.

Lomnicki, A. (1999). Individual-based model and individual-based approach to population ecology. *Ecol. Modelling* **115**:191-198.

Lorek, H. and Sonnenschein, M. (1999). Modelling and simulation software to support individual-based ecological modelling. *Ecol. Modelling* **115**:199-216.

Lutjerhams, J.R.E., Meyer, A., Ansorge, I.., Eagle, G.A. and Orren, M.J. (1996). The nutrient characteristics of the Agulhas Bank. *S. Afr. J. mar. Sci.* **17**:253-274.

MacKenzie, C. L., Jr. (1990). History of the Fisheries of Raritan Bay, New York and New Jersey. *Mar. Fish. Rev.* **52**(4):1-45.

Mann, K.H. and Lazier, J.R.N. (1991). Dynamics of marine ecosystems: biological-physical interactions in the oceans. Blackwell Scientific Publications. 466 pp.

Marchesiello, P. McWilliams, J.C. and Shchepetkin, A.E. (2001). Open boundary conditions for long-term integration of regional ocean models. *Ocean modelling*. **3**:1-20.

Marteinsdottir, G. and Steinarsson, A. (1998). Maternal influence on the size and viability of Icelan cod *Gadus morhua* eggs and larvae. *J. Fish.Biol.* **52**:1241-1258.

Melo, Y. (1994). Spawning frequency of the anchovy *Engraulis capensis*. *S. Afr. J. mar. Sci.* **14**:321-331.

Methot, R.D. Jr. and Kramer, D. (1979). Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. *Fish. Bull.* **77**:413-423.

Mitchell-Innes, B.A., Richardson, A.J. and Painting, S.J. (1999). Seasonal changes in phytoplankton biomass on the western Agulhas Bank, South Africa. *S. Afr. J. mar. Sci.* **21**:217-233.

Moser, H.G. and Pommeranz, T. (1999). Vertical distribution of eggs and larvae of northern anchovy, *Engraulis mordax*, and of the larvae of associated fishes at two sites in the southern California Bight. *Fish. Bull.* **97**:920-943.

Motos, L. and Coombs, S. (1998). Vertical distribution of anchovy eggs and field observations of incubation temperature. Proceedings of the VI Colloquia of Oceanography of the Bay of Biscay. San Sebastian, April 1998. *Ozeanografika* No. 2, San Sebastian, Spain.

Mullon, C., Fréon, C., Parada, P., van der Lingen, C., and Huggett, J. (submitted). From particles to individuals: modeling the early stages of anchovy in the Southern Benguela. *Fish. Oceanogr.*

Mullon, C., Parada, C., Cury, P., Huggett, J., Fréon, P., van der Lingen, C., Penven, P., Moloney, C. and Richardson, A. (2002). Individual Based Modelling (IBM) of the early stages of anchovy in the southern Benguela system. In: *Report of a GLOBEC-SPACC/IDYLE/ENVIFISH workshop on Spatial Approaches to the Dynamics of Coastal Pelagic Resources and their Environment in Upwelling Areas.* C.D. van der Lingen, C. Roy, P. Fréon, M. Barange, L. Castro, M. Gutierrez, L. Nykjaer. and F. Shillington (eds) *GLOBEC Rep.* **16**:87-89.

Nelson, G. (1992). Longshore wind variation on the west coast of southern Africa and its influence on the shelf sea. *S. Afr. J. Sci.* **88**:418-424.

Nelson, G. and Walker, N. (1984). Comparison of summer winds on the West Coast of South Africa between 1979 and 1983 and the response of coastal upwelling. *S. Afr. J. Sci.* **80**:90-93.

Nelson, W.R., Ingham, M.C. and Schaaf, W.E. (1977). Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus. Fish. Bull.* **75**:23-41.

Olson, D. B. and Backus, R.H. (1985). The concentrating of organisms at fronts: A cold-water fish and a warm-core Gulf Stream ring. *J.Mar.Res.* **43**:113-137.

Parada, C., van der Lingen, C.D., Mullon, C. and Penven, P. (in press). Modeling the effect of buoyancy on the transport of *anchovy (Engraulis capensis)* eggs from spawning to nursery grounds in the southern Benguela: an IBM approach. *Fish. Oceanogr.*

Parker, G.A. and Begon, M. (1986). Optimal egg size and clutch size effects of environment and maternal environment. *Am. Nat.* **128**:173-192.

Parrish, R.H., Bakun, A., Husby, D.M. and Nelson, C.S. (1983). Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. In: *Proceedings of the Expert Consultation of Neritic Fish Resources.* G.D.Sharpe and J. Csirke (eds) *FAO Fisheries Rep.* **291**:731-777.

Parrish, R.H., Nelson, C.S. and Bakun, A. (1981). Transport mechanisms and reproductive success of fishes in the California Current. *Biol. Oceanogra.* **1**:175-203.

Penven, P. (2000). A numerical study of the southern Benguela circulation with an application to fish recruitment. *Thèse de doctorat de l'Université de Bretagne Occidentale,* 189 pp.

Penven, P., Roy, C., Brundrit, G., Colin de Verdière, A., Fréon, P., Jonhson, A., Lutjeharms, J.R.E. and Shillington, F.A. (2001). A regional hydrodynamic model of upwelling in the Southern Benguela. *S. Afr. J. Sci.* **97**:472-475.

Pillar, S.C. and Stuart, V. (1988). Population structure, reproductive biology and maintenance of *Euphausia lucens* in the southern Benuela Currents. *J.Plankton Res.* **10**(6):1083-1098.

Pitcher, G.C., Brown, P.C. and Mitchell-Innes, B.A. (1992). Spatio-temporal variability of phytoplankton in the Southern Benguela upwelling system. In: *Benguela Trophic Functioning.* A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn (eds) *S. Afr. J. mar. Sci.* **12**:439-456.

Railsback, S. (2001). Getting "results": The pattern-oriented approach to analyzing natural systems with Individual-based Models. *Natur. Resour. Model.* **14**(3):465-475.

Richardson, A.J. (1998). Within-season variability of copepod abundance and growth in the southern Benguela upwelling system and implications for the spawning of the Cape anchovy. PhD Thesis, University of Cape Town. 208 pp.

Richardson, A.J., Mitchell-Innes, B.A., Fowler, J.L., Bloomer, S.F., Verheye, H.M., Field, J.G., Hutchings, L. and Painting, S.J. (1998). The effect of sea temperature and food availability on the spawning success of Cape anchovy *Engraulis capensis* in the Southern Benguela. In: *Benguela Dynamics. Impacts of Variability on Shelf-Sea Environments and their Living Resources.* S.C. Pillar, C.L. Moloney, A.I.L. Payne and F.A. Shillington (eds) *S. Afr. J. mar. Sci.* **19**:275-290.

Richardson, A., Stachlewska, E. and Shillington, F.A. (2000). Using self-organizing maps to characterize variability in sea surface temperature. Poster C2-12, *28th International Symposium on Remote Sensing of Environment*, Somerset West, Cape Town, 27-31 March.

Risien, C. (2002). Wind-stress variability over the Benguela upwelling system. MSc. Thesis, University of Cape Town. 144 pp.

Roel, B. A., Hewitson, J. Kerstan S., and Hampton, I. (1994).The role of the Agulhas Bank in the life cycle of pelagic fishes. *S. Afr. J. Sci.* **90**:185-196.

Rothschild, R.T. and Osborn, T.R. (1988). The effects of turbulence on planktonic contact rates. *J. Plankton Res.* **10**:465-474.

Roughgarden, J., Gaines, S. and Possingham, H. (1988). Recruitment dynamics in complex life cycles. *Science* **241**:1460-1466.

Roy, C. (1998). An upwelling-induced retention area off Senegal: A mechanism to link upwelling and retention process. In: *Benguela Dynamics. Impacts of Variability on Shelf-Sea Environments and their Living Resources.* S.C. Pillar, C.L. Moloney, A.I.L. Payne and F.A. Shillington (eds) *S. Afr. J. mar. Sci.* **19**:89-98.

Roy, C., Fréon, P. and van der Lingen, C.D. (2002). An empirical model of anchovy recruitment variability in the Southern Benguela. In: *Report of a GLOBEC-SPACC/IDYLE/ENVIFISH workshop on Spatial Approaches to the Dynamics of Coastal Pelagic Resources and their Environment in Upwelling Areas.* C.D. van der

Lingen, C. Roy, P. Fréon, M. Barange, L. Castro, M. Gutierrez, L. Nykjaer and F. Shillington (eds) *GLOBEC Rep.* **16**:52-54.

Santos, M., Uriarte, A. and Motos, L. (2000). A preliminary outlook at the relationship between CUFES and PairoVET/Bongo. In: *Report of a workshop on the use of the continuous, underway fish egg sampler (CUFES) for mapping spawning habitat of pelagic fish.* D.M. Jr. Checkley, J.R. Hunter, L. Motos and C.D. van der Lingen (eds) *GLOBEC Rep.* **14**:31-33.

Sargent, R.C., Taylor, P.D. and Gross, M.R. (1987). Parental care and the evolution of egg size in fishes. *Am. Nat.* **129**:32-46.

Shannon, L.J. (1995). Modelling the oceanographic transport of young Cape anchovy *Engraulis capensis* by advective processes. *Msc Thesis*. University of Cape Town, South Africa. 121 pp.

Shannon, L.V. (1985). The Benguela Ecosystem Part I. Evolution of the Benguela, physical features and process. *Oceanogr. Mar. Biol. Annu. Rev.* **23**:105-182.

Shannon, L.V., Hutchings, L., Bailey, G.W. and Shelton, P.A. (1984). Spatial and temporal distribution of chlorophyll in southern African waters as deduced from ship and satellite measurements and their implications for pelagic fisheries. *S. Afr. J. mar. Sci.* **2**:109-130.

Shannon, L.V., Nelson, G., Crawford, R.J.M. and Boyd, A.J. (1996). Possible impacts of environmental change on pelagic fish recruitment: Modeling anchovy transport by advective processes in the southern Benguela. *Global Change Biol.* **2**:407-420.

Shelton, P.A. (1984). Notes on the spawning of anchovy during summer of 1982-3. *S. Afr.J. Sci.* **80**:69-71.

Shelton, P.A. (1986) Fish spawning strategies in the variable southern Benguela Current region. PhD thesis, University of Cape Town. 327 pp.

Shelton, P. A., Armstrong, M. J. and Roel, B. A. (1993). An overview of the application of the daily egg production method in the assessment and management of anchovy in the Southeast Atlantic. *Bull. Mar. Sci.* **53**:778-794.

Shelton, P.A. and Hutchings, L. (1982). Transport of anchovy, *Engraulis capensis* Gilchrist, eggs and early larvae by a frontal jet current. *J. Cons. int. Explor. Mer.* **40**:185-198.

Shillington, F.A. (1998). The Benguela upwelling system off southwestern Africa. *The Sea.* **11**:583-604.

Shillington, F.A., Hutchings, L., Probyn, T.A., Waldron, H.N. and Peterson, T. (1992). Filaments and the Benguela frontal zone: offshore advection or recirculating loops? In: *Benguela Trophic Functioning.* A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn (eds) *S. Afr. J. mar. Sci.* **12**:207-218.

Shillington, F.A. and Nykjaer, L. (2002). Environmental conditions and fluctuations in distribution in small pelagic fish stocks (ENVIFISH) 1998. In: *Report of a GLOBEC-*

SPACC/IDYLE/ENVIFISH workshop on Spatial Approaches to the Dynamics of Coastal Pelagic Resources and their Environment in Upwelling Areas. C.D. van der Lingen, C. Roy, P. Fréon, M. Barange, L. Castro, M. Gutierrez, L. Nykjaer and F. Shillington (eds) *GLOBEC Rep.* **16**:79-80.

Sinclair, M. (1988). Marine Populations: an Essay on Population Regulation and Speciation. Washington Sea Grant/University of Washington Press, 252 pp.

Smith, P.E. (1973). The mortality and dispersal of sardine eggs and larvae. *Rapp. P.-v Reun. Cons. Int. Explor. Mer.* **154**:282-292.

Smith, P.E. and Lasker, R. (1978). Position of larval fish in an ecosystem. *Rapp. P.-v. Réun. Cons. Perm. Int. Explor. Mer* **173**:77-84.

StatSoft, Inc. (2000). STATISTICA for Windows [Computer program manual]. Tulsa, OK, USA.

Stenevik, E.K., Skogen, M., Sundby, S. and Boyer, D. (in press). The effect of vertical and horizontal distribution on retention of sardine (*Sardinops sagax*) larvae in the northern Benguela- observations and modelling. *Fish. Oceanogr.*

Stenevik, E.K., Sundby, S. and Cloete, R. (2001). Influence of buoyancy and vertical distribution of sardine *Sardinops sagax* eggs and larvae on their transport in the Northern Benguela Ecosystem. In: *A Decade of Namibian Fisheries Science.* A.I.L. Payne, S.C. Pillar and R.J.M. Crawford (eds) *S. Afr. J. mar. Sci.* **23**:85-97.

Sundby, S. (1983). A one-dimensional model for the vertical distribution of pelagic fish eggs in the mixed layer. *Deep-Sea Res.* **30**(6A):645-661.

Sundby, S. (1991) Factors affecting the vertical distribution of eggs. *ICES mar. Sci. Symp.* **192**:33-38.

Sundby, S. (1997). Turbulence and ichthyoplankton: influence on vertical distributions and encounter rates. *SCI. MAR.* **61**(Supl.1):159-176.

Tanaka, Y. (1990). Change in the egg buoyancy of Japanese anchovy *Engraulis japonicus* during embryonic development. *Bull. Japan. Soc. Sci. Fish.* **56**(1):165.

Tanaka, Y. (1992). Japanese Anchovy Egg accumulation at the sea surface or picnocline - observations and model. *J. Oceanogr.* **48**:461-472.

Tanaka, Y., Mukai, Y., Takii, K. and Kumai, H. (1991). Chemoreception and vertical movement in planktonic yolk-sac larvae of red sea bream *Pagrus major. J.Appl.Ichthyol.* **7**:129-135.

Tanaka, Y. and Oozeki, Y. (1996). Where are the eggs of the Pacific saury, *Cololabis saira*? *Ichthyol.Res.* **43**(3):329-333.

Thomas, R.M. (1986). Growth of larval pelagic fish in the South-East Atlantic from daily otolith rings in 1982/83 and 1983/84. *S. Afr. J. mar. Sci.* **4**:61-77.

Valdés, E.S., Shelton, P.A., Armstrong, M.J. and Field, J.G. (1987). Cannibalism in South African anchovy: Egg mortality and egg consumption rates. In: The *Benguela and*

Comparable Ecosystems. A.I.L. Payne, J.A. Gulland, and K.H. Brink (eds) *S. Afr. J. mar. Sci.* **5**:613-622.

Vallin, L. and Nissling, A. (2002). Maternal effect on egg size and egg buoyancy of Baltic cod, *Gadus Morhua*. Implications for stock structure effect on recruitment. *Fish. Res.* **49**:21-37.

van der Lingen, C.D. (1999). Pelagic pre-recruits survey F.R.S.Algoa VOYAGE 063. *Cruise Rep.* 24 pp.

van der Lingen, C.D., Coetzee, J.C. and Hutchings, L. (2002). Temporal shifts in the spatial distribution of anchovy spawners and their eggs in the Southern Benguela: Implications for recruitment. In: *Report of a GLOBEC-SPACC/IDYLE/ENVIFISH workshop on Spatial Approaches to the Dynamics of Coastal Pelagic Resources and their Environment in Upwelling Areas.* C.D. van der Lingen, C. Roy, P. Fréon, M. Barange, L. Castro, M. Gutierrez, L. Nykjaer and F. Shillington (eds) *GLOBEC Rep.* **16**:46-48.

van der Lingen, C.D. and Huggett J.A. (in press). The role of ichthyoplankton surveys in recruitment research and management of South African anchovy and sardine. In: *The Big Fish Bang: Proceedings of the 26th Annual Larval Fish Conference.* H. I. Browman and A. B. Skiftesvik (eds).

van der Lingen, C.D., Hutchings, L., Merkle, D., van der Westhuizen, J.J. and Nelson, J. (2001). Comparative spawning habitats of anchovy (*Engraulis capensis*) and sardine (*Sardinops sagax*) in the Southern Benguela upwelling ecosystem. In: *Spatial Processes and Management of Marine Populations*. G.H. Kruse, N. Bez, T. Booth, M. Dorn, S. Hills, R. Lipicius, D. Pelletier, C. Roy, S. Smith and D. Witherell (eds.). University of Alaska Sea Grant, Fairbanks, AK-SG-01-02:185-209.

van der Lingen, C.D. and Merkle, D. (1998). The pelagic pre-recruit surveys. In: *Report on the pelagic working group workshop on biological research.* van der Lingen, C.D. and R. Cooper (eds) WG/AUG98/PEL/2.

van der Lingen, C.D. and Merkle, D. (1999). Predicting anchovy and sardine recruitment from pelagic pre-recruit surveys. *S. Afr. Shipp. News Fish. Ind. Rev.* p. 24-27.

Verheye, H.M., Hutchings, L. and Peterson, W.T. (1991). Life history and population maintenance strategies of *Calanoides carinatus* (Copepoda: Calanoida) in the southern Benguela ecosystem. *S. Afr. J. mar. Sci.* **11**:179-191.

Walters, C.L., Hannah, C.G. and Thomson, K. (1992). A microcomputer program for simulating effects of typical transport processes on fish larvae. *Fish. Oceanogr.* **1**:11-19.

Werner, F.E., Blanton, B.O., Quinlan, J.A. and Luettich, R.A. (1999). Physical oceanography of the North Carolina continental shelf during the fall and winter season: implications to the transport of larval menhaden. *Fish. Oceanogr.* **8**(Suppl.2):7-21.

Werner, F.E., Page, F.H., Lynch, D.R., Loder, J.W., Lough, R.G., Perry, R.I., Greenberg, D.A. and Sinclair, M.M. (1993). Influences of mean advection and simple behavior on the distribution of cod and haddock early stages on Georges Bank. *Fish. Oceanogr.* **2**:43-64.

Werner, F.E., Perry, R.I., Lough, R.G. and Naimie, C.E. (1996). Trophodynamic and advective influences on Georges Bank larval cod and haddock. *Deep-Sea Res. II* **43**:1793-1822.

Whitehead, P.J.P. (1990). Engraulidae. In: Checklist of the fishes of the eastern tropical Atlantic. J.C. Quero, J.C. Hureau, C. Karrer, A. Post and L. Saldanha (eds) *(CLOFETA) JNICT Lisbon, SEI Paris and UNESCO Paris*. **1**:228-229.

Wilhelm, M.R. (2002). Hatchdate distributions and growth rates of anchovy (*Engraulis encrasicolus*) in the Southern Benguela ecosystem. Thesis presented for the degree of Master of Science, department of Zoology, Faculty of Science, University of Cape Town. 108 pp.

Woods, J. (2002). Primitive equation modelling of plankton ecosystem. In: ocean forecasting. Conceptual basis and applications. N. Pinardi and J. Woods (eds).Springer-Verlag Berlin Heidelberg, Germany. 472 pp.

Zweifel, J.R., Lasker, R. (1976). Prehatch and posthatch growth of fishes. A general model. *Fish. Bull.* **74**(3):609-621.

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