

Modelling the effects of spatio-temporal spawning variability on the transport and retention success of sardine (*Sardinops sagax*) eggs and larvae around South Africa

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A. McGrath

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Abstract

The transport and retention of sardine (*Sardinops sagax*) eggs on the west and south coasts of South Africa were investigated using a Lagrangian, particle tracking, individual-based model (IBM), coupled with two 3-D hydrodynamic Regional Ocean Modeling System (ROMS) model configurations of different generations. The same IBM is coupled with PLUME, a older ROMS model configuration used in a previous sardine IBM for the southern Benguela, as well as BENGSAFE, a more recent, better resolved ROMS model configuration. Results from the two runs were compared to see if and how the underlying ocean model affects modelled retention and transport. An updated IBM, extended spatially and temporally to better represent sardine spawning and recruitment, was then coupled with the BENGSAFE model configuration, and assessed. The effects of spawning area, and month, year and depth of particle release, were investigated for each coupled 3D-IBM simulation using linear models. The portion of particles transported from the south coast to the west coast was a focus throughout, as this is of great importance to the management of the sardine fishery. In all simulations, three main systems were identified depending on where particles were released and recruited. Two of these systems were retention-based: particles released on the west coast and retained in the west coast recruitment area (WC-WC), and particles released on the south coast and retained in the south coast recruitment area (SC-SC). The other system is transport-based and represents particles released on the south coast and transported by ocean dynamics to recruit in the west coast recruitment area. Results were similar for the west coast when either hydrodynamic model configuration was used; depth of release proved to be important in this system with its effect varying depending where on the west coast particles were released. Differences occurred on the south coast, with more transport to the west coast and more offshore loss in the higher resolved BENGSAFE IBM than the PLUME IBM. The difference was attributed to the positioning of the PLUME model's boundary in close proximity to the Agulhas Current, and the conditions at this boundary not properly resolving the current. The initial BENGSAFE IBM was spatially restricted to match the PLUME IBM, and therefore south coast spawning and recruitment was not fully represented. Therefore the BENGSAFE IBM was spatially extended on the south coast and run for a longer time period. Similar results were obtained in the extended BENGSAFE IBM and the initial BENGSAFE IBM. However south coast retention increased and the average percentage of particles transported to the west coast decreased slightly. Spawning area proved to be an important determinant of retention and transport success in all recruitment systems, and the further east a particle was spawned the less likely it was to be transported to the west coast, and the more likely it was to be retained on the south coast. Transport to the west coast was most successful in late winter; a significant monthly effect on transport success was present. Correlations between standardised anomalies for stock assessment model estimated recruitment and IBM modelled retention/transport for the west and south coast

were not significant, highlighting that retention and transport are not the only determinants of recruitment success. The extended BENGSAFE IBM can act as a base level to which extra layers of biological complexities can be added, such as horizontal and vertical egg distribution matching observations, incorporating gonadosomatic index (GSI) values, diurnal vertical migration and buoyancy.

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Chapter 1

Introduction

The productive waters of coastal upwelling systems provide a suitable habitat where small pelagic fishes (sardine, anchovy, herring) can thrive. Their large biomasses in these ecosystems has enabled their exploitation by fisheries around the world for many years. Small pelagic fish have short lifespans, fast growth rates and are highly fecund, hence they respond rapidly to environmental conditions, such as temperature and food availability causing large fluctuations in the level of recruitment (Hutchings et al., 2012). Small pelagic fish are forage food for a number of marine species and therefore predation levels also cause high population and recruitment variability. Although upwelling systems are productive they are also extremely dynamic, and advective loss of larvae and eggs from suitable nursery grounds has been identified as a mechanism contributing to poor recruitment in these areas (Iles and Sinclair, 1982; Bakun, 1996). The Optimal Environmental Window (OEW) hypothesis (Cury and Roy, 1989) suggests that recruitment in upwelling areas is maximised at intermediate levels of upwelling, when upwelling-induced productivity is at a sufficient level but upwelling intensity is not strong enough to cause great offshore loss of eggs and larvae. Retention of eggs and larvae was also identified as one of the major environmental processes important for recruitment, along with nutrient enrichment and food availability, in the Ocean Triad hypothesis (Bakun, 1996). Its importance is reflected in sardine's variable inter-annual population sizes in upwelling-dominated and dynamic ecosystems and, as a result, management of these fisheries has proven to be challenging. Effective and suitable management plans are vital to ensure sustainability of the stock and hence the benefitting industries.

The initial aim of this dissertation is to investigate the differences in modelled transport and retention success of sardine (*Sardinops sagax*) eggs and larvae that arise using two different bio-physical models. The second is to better spatially represent the spawning and recruitment areas of sardine in one such model, and therefore improve model results

and contribute to the understanding of stock structure and spawning strategies of sardine in the Southern Benguela, which will prove useful for fisheries management.

1.1 *Sardinops sagax* in southern Africa

1.1.1 Biology and ecology

In southern Africa there are 13 species that fall into the globally and commercially important family, Clupeidae, one of which is the small epipelagic species, sardine (Beckley and van der Lingen, 1999). *Sardinops* is a monotypic genus found in the Clupeidae family, and contains the species found in South African waters, *Sardinops sagax*, hereafter referred to as sardine.

As seen in many of the world's major upwelling systems, sardines and anchovies (*Engraulis encrasicolus*) dominate the small pelagic fish component in the Benguela system and around South Africa, contributing 90% of the total South African pelagic purse-seine catch (van der Lingen, 2002; Department of Agriculture, Forestry and Fisheries, 2014). Sardine is considered to be an omnivorous filter-feeder, consuming both phytoplankton and zooplankton (van der Lingen, 2002). However, stomach content analysis from samples in the Southern Benguela suggested they are mostly zoophagous, feeding mainly on small zooplankton (van der Lingen, 2002). Due to their short life span and planktivorous diets, this species characteristically responds rapidly to environmental conditions and shows long-term fluctuations in catch trends (Checkley et al., 2009). Sardine serve as forage for various marine mammals, birds and fish predators (Cury et al., 2000; Checkley et al., 2009), and have an important position in pelagic food webs, affecting both their prey and predators (Cury et al., 2000). Sardine spawn over a wider temperature range than anchovy, spawning in cool water (15.2-20.5°C) typical of shallow, coastal waters around southern Africa (van der Lingen et al., 2001; Mhlongo et al., 2015). Sardine spawn in austral spring/summer with two spawning peaks (September/October and February/March), but can spawn throughout the year. They are batch spawners, meaning that females spawn individual batches several times in a spawning season (Le Clus, 1987; Akkers et al., 1996).

1.1.2 Distribution and population structure

The distributional range of southern African sardine extends from northern Namibia on the west coast of Africa, to Kwazulu-Natal on the north-east coast of South Africa (Beckley and van der Lingen, 1999) (Figure 1.1). The large upwelling cell at Luderitz acts

as an environmental barrier that prevents large-scale mixing between the South African stock and the Namibian stock, which extends northwards to southern Angola (Lett et al., 2007; Coetzee et al., 2008b).

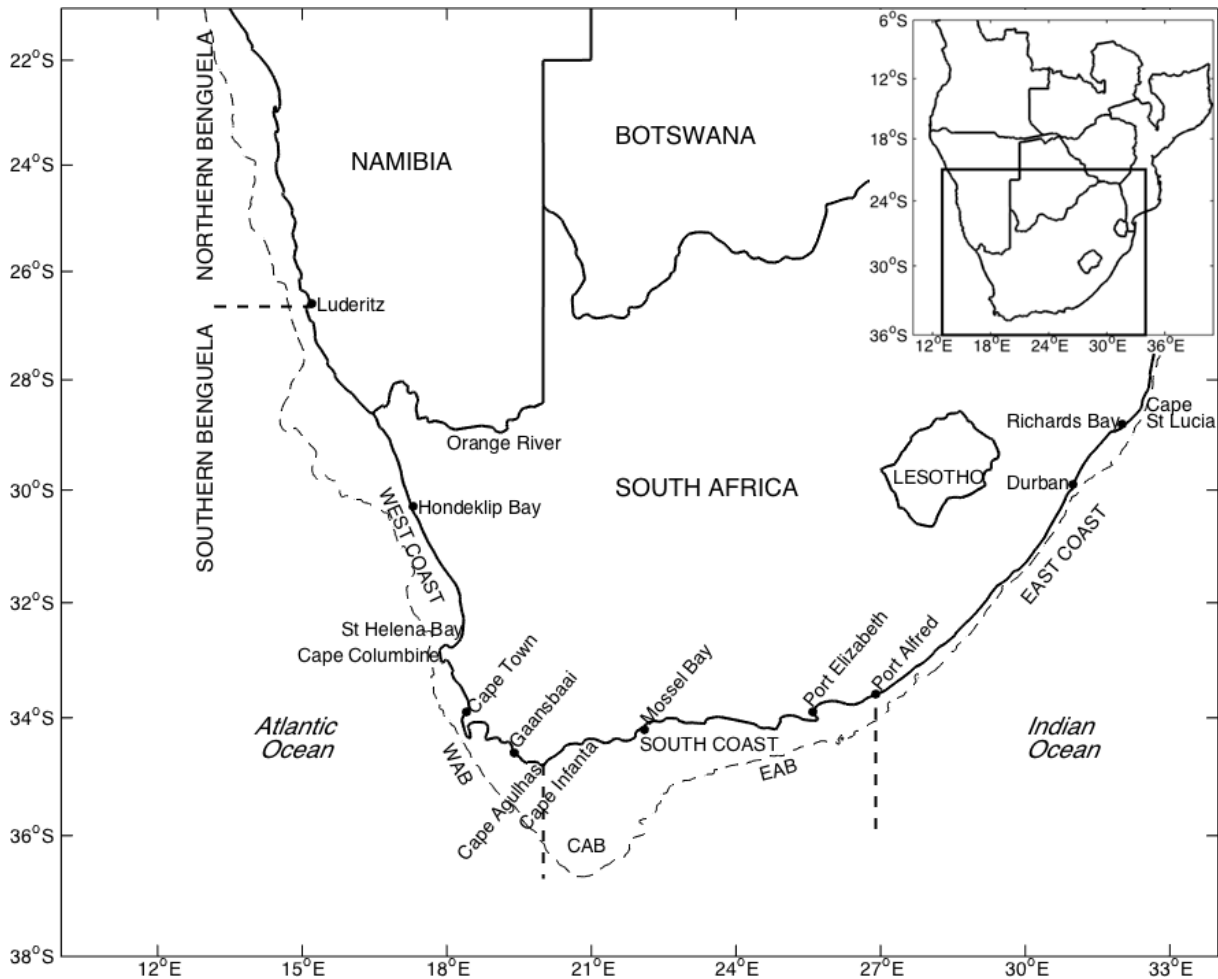


Figure 1.1: Map of southern Africa showing cities and features mentioned in the text. The thick dashed lines display how the coastline is divided into west, south and east coasts. The thin dashed line displays the 200m isobath. WAB = western Agulhas Bank, CAB = central Agulhas Bank and EAB = eastern Agulhas Bank.

The abundance and distribution of sardine off South Africa is assessed by two hydro-acoustic surveys per year that have been undertaken off South Africa by the Department of Agriculture, Forestry and Fisheries (DAFF) since 1984. The first of these, the biomass survey, happens in November and estimates total adult spawner biomass, whilst the second, the recruitment survey, happens in May/June and estimates juvenile (0-year-old) abundance. The biomass surveys range from Hondeklip Bay on the west coast to Port Alfred on the south coast, and the recruitment surveys range from the Orange River mouth to Cape Infanta, however the recruitment surveys have gone east of this, sometimes to Port Alfred, in recent years. These surveys are conducted along a series of pre-stratified,

randomly spaced, parallel transects. During a large portion of the period for which there are acoustic-survey results, most of the adult sardine biomass has been confined to the south-west coast and the Agulhas Bank region, but expanded east and west during the mid 2000s (Coetzee et al., 2008b). A gradual increase in the proportion of sardine biomass to the east of Cape Agulhas has been noted since 1995, and in 1999 the proportion of total sardine biomass to the east of Cape Agulhas exceeded that to the west; this distribution has since persisted (Coetzee et al., 2008b). During the major spawning seasons in spring and late summer, spawners have been concentrated mainly on the western Agulhas Bank (WAB) and lower west coast (Hampton, 1992; van der Lingen and Huggett, 2003; Coetzee et al., 2008b). However there have been frequent shifts between predominantly west coast spawning and predominantly south coast spawning in the past (van der Lingen et al., 2001).

Sardine are relatively unspecific in their selection of spawning conditions as they are less restricted by temperature than other small pelagic fishes, and therefore are able to spawn on both the west and south coasts (van der Lingen et al., 2001; Twatwa et al., 2005; Mhlongo et al., 2015). Ichthyoplankton spawned on the western Agulhas Bank and lower west coast are transported west and north to the west coast recruitment area by a shelf-edge jet flowing equatorward along the coast (Boyd et al., 1992; Fowler and Boyd, 1998). West coast recruitment is the predominant pattern, however during the recruitment surveys in winter, a large number of sardine recruits has been observed at times on the south coast (Barange et al., 1999; Beckley and van der Lingen, 1999). A south coast recruitment system for sardine has been hypothesised, which relies on retention of eggs and larvae in this region (Lett et al., 2006; Miller et al., 2006). It has also been proposed that Algoa Bay on the south coast is a suitable area for sardine to spawn and be recruited (Pattrick et al., 2016). This implies that sardine could enhance their reproductive strategy and success by spawning in either area, or sometimes both (van der Lingen et al., 2001; Miller et al., 2006).

During austral winter there is a natural phenomenon, popularly known as the 'sardine run', in which large schools of sardine migrate from the Agulhas Bank up the KwaZulu-Natal coast to Durban. This is hypothesised to be a seasonal reproductive migration of a small portion of the South African sardine population, which is genetically distinct (Fréon et al., 2010). During the run schools of sardine rapidly move northwards along the Transkei coast, arriving in southern KwaZulu-Natal coastal waters in late May to early June, and then disappearing north of Durban into waters of the KwaZulu-Natal Bight (van der Lingen et al., 2010a). During the run, sardine are targeted by a beach-seine

fishery, and fishers and members of the public also catch the fish using throw nets and various make-shift equipment. The beach-seine catches are negligible compared to the purse-seine catches of the country (van der Lingen et al., 2010b). Owing to the fact that the sardine run has been recorded as far back as 1853 (Shelton, 1976 cited in van der Lingen et al. 2010a), and is unique to South Africa, it has become part of the cultural heritage of South Africans. It also acts as a tourist attraction, having considerable impacts on the local economy (Myeza et al., 2010).

The sudden increase in abundance and almost concurrent eastward shift in the distribution of sardine in the early 2000s provoked research into the population structure. A suite of multi-disciplinary studies, described below, have hypothesised that the sardine population consists of multiple, spatially-structured stocks off the South African coast, with putative western, southern and eastern stocks (Figure 1.2). It is hypothesised that the western stock spawns offshore on the west coast and western Agulhas Bank in spring to summer. The eggs are transported northwards to recruitment areas inshore on the west coast. The southern stock spawns in autumn to spring offshore on the Agulhas Bank and eggs are retained in the inshore recruitment area. The eastern stock spawns inshore in winter to spring during the sardine run, and there is local retention with a likely southwards transport of eggs to inshore recruitment areas on the south coast (van der Lingen et al., 2015).

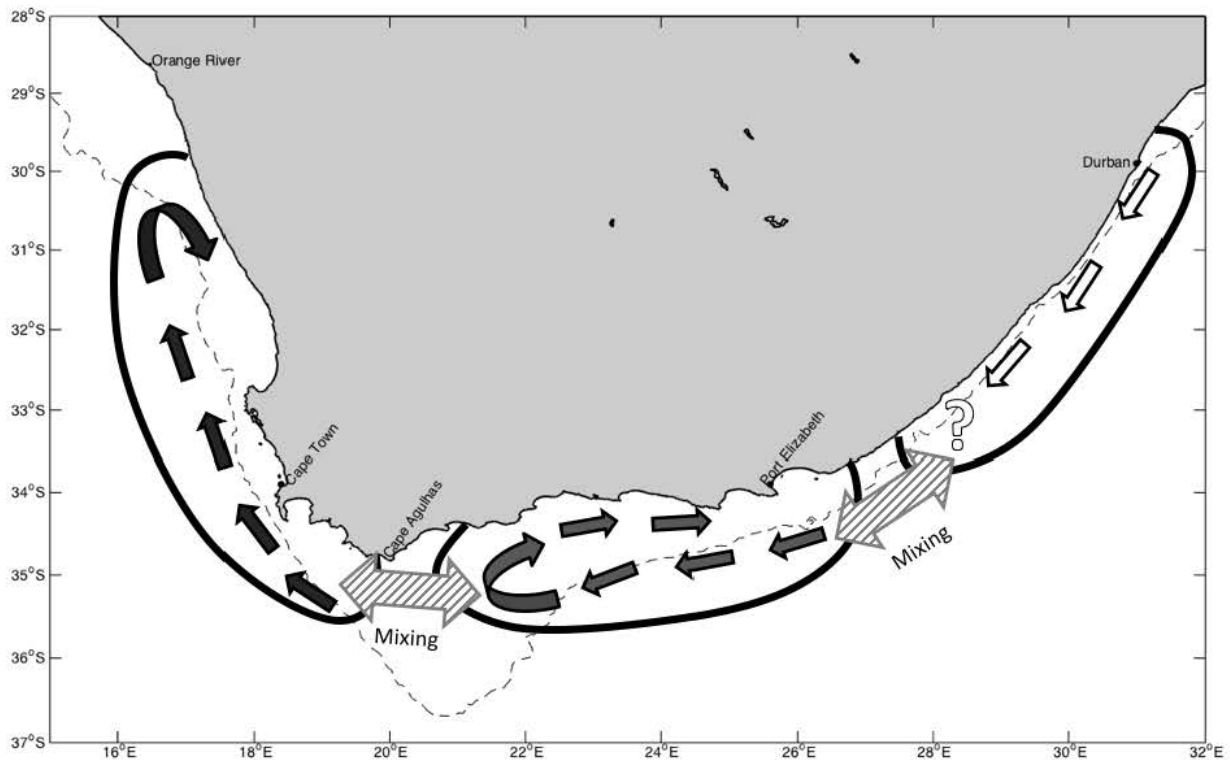


Figure 1.2: Conceptual model showing the spawning grounds (ellipses) and passive (for early life history stages) movement from and between the hypothesised western, southern and eastern stocks of the South African sardine population (adapted from van der Lingen et al. (2015)).

Coetzee et al. (2008b) described sardine distribution patterns around South Africa using results from the November acoustic surveys, and reported a distinct separation between Cape Agulhas and Mossel Bay at low and medium biomass levels (Figure 1.3). Sardine to the west of Cape Agulhas occupied the western Agulhas Bank (WAB) at all biomass levels, extending northwards up the west coast and eastwards onto the inner shelf of the central Agulhas Bank (CAB, 20-22°E) with increasing biomass levels. Sardine to the east of Cape Agulhas mainly occupied the eastern Agulhas Bank (EAB, >22°E) at low biomass levels, extending westward on to the outer shelf of the CAB at medium to high biomass levels. This spatial separation supports the hypothesis of distinct spawning units, one on either side of Cape Agulhas, corresponding to the western and southern stocks.

Sardine eggs have been collected between Hondeklip Bay on the west coast and Durban on the east coast using net tows during research surveys at different times of the year (Connell, 2010; van der Lingen and Huggett, 2003). On the west and south coasts two discrete spawning areas, separated by the CAB, are also seen in sardine egg distribution maps (Figure 1.4). The environmental conditions of each spawning area differ, with eggs off the west coast being found in the cool Benguela waters of 14-17°C, compared to warm

Agulhas waters of 19-22°C for eggs off the eastern Agulhas Bank (van der Lingen, 2011; Mhlongo et al., 2015).

Variability in meristic and morphometric characteristics that may be indicative of multiple stocks of the South African sardine population has been assessed by comparing fish collected from around South Africa. Vertebral counts from fish collected off KwaZulu-Natal showed a significant difference to those from fish collected on the west and south coasts. However, there was no significant difference in vertebral counts between fish from the west and south coasts (Wessels, 2009; van der Lingen et al., 2010b; Ukomadu, 2017). Significant differences in branchial basket characteristics of fish from each coast were shown by Idris et al. (2016), although this was not consistent across fish size classes. Similarly, morphological analyses to date indicate that there is significant variation in sardine body shape among the three coasts (Wessels, 2009; van der Lingen et al., 2010b; Ukomadu, 2017). Ukomadu (2017) applied multiple stock identification methods (meristic, morphometric and parasite markers) on individual sardine from the west and south coasts, and reported on evidence of two mixing stocks. Although these changes may be caused by environmental conditions throughout life, it is not uncommon for population structure to be indicated by these factors (Sharp et al., 1978; Turan, 2004).

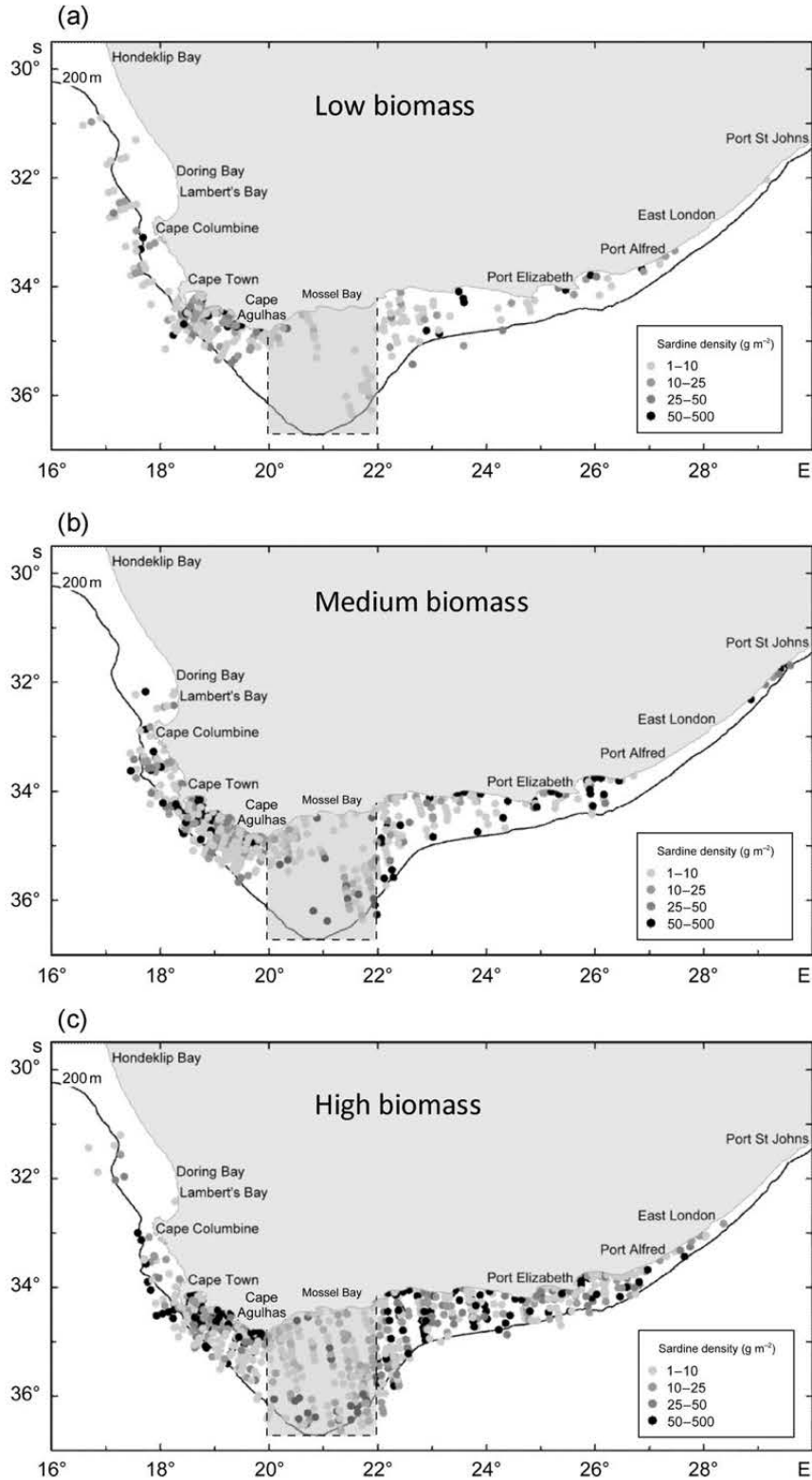


Figure 1.3: Composite density maps from November survey data for periods of a) low, b) medium, and c) high sardine biomass. The grey block indicates the transition zone between the west coast system and the Agulhas Bank system (from Coetzee et al., 2008b).

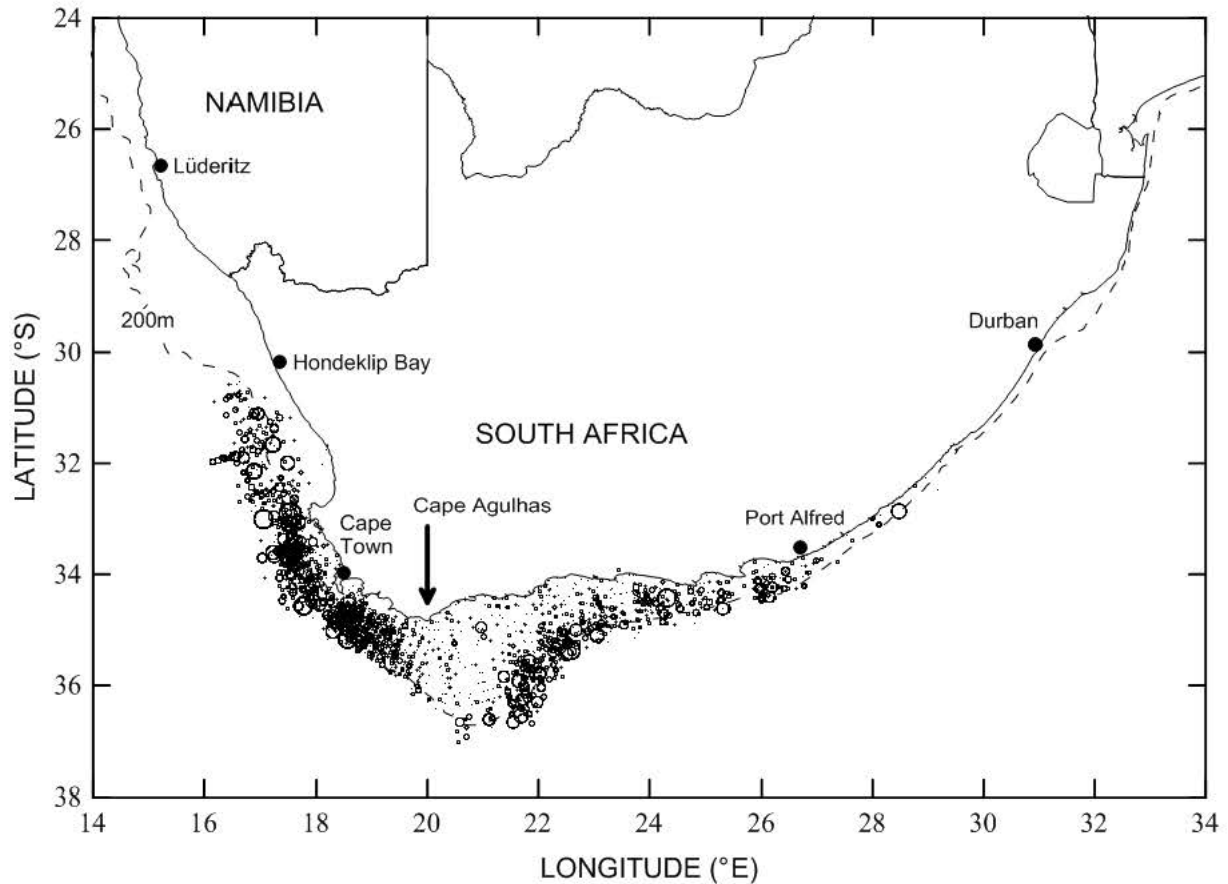


Figure 1.4: Map showing the composite egg density (eggs per square metre; circles with diameter proportional to abundance, maximum size = 9193 eggs/m²), derived from Cal-VET net samples collected during annual hydroacoustic surveys of small pelagic biomass, conducted between Hondeklip Bay and Port Alfred from 1986 to 2010. The 200m isobath is indicated by the dashed line. Adapted from de Moor et al., 2017).

Reed et al. (2012) suggested that a Tetracotyle-type metacercarian parasite (TTMP) of the genus *Cardiocephaloides*, found in the humour of sardine eyes, had the greatest potential as a biological tag for South African sardine stock identification. This parasite was nominated because of its observed discontinuous distribution in infection, site-specificity in the host and long life span, all of which are criteria for a good parasite biotag (MacKenzie and Abuanza, 2005). Weston (2013) and Weston et al. (2015) investigated the spatial and temporal variation in infection of South African sardine by analysing commercial catch samples from 2011 and 2012. West coast fish had higher levels of infection compared to south coast fish. This significant difference in the distribution of infection by the parasite supports the hypothesis of western and southern components of the sardine population off the coast of South Africa. The presence of the parasite biotag in fish caught on the south coast indicates a degree of mixing between the two components as the parasite is assumed to be endemic to the west coast area (Weston, 2013; van der Lingen et al.,

2015).

1.1.3 The South African sardine fishery

Sardine, along with anchovy and round herring (*Etrumeus whiteheadi*), account for 90% of the total South African purse-seine catch (Department of Agriculture, Forestry and Fisheries, 2014). The commercial, pelagic purse-seine fishery is South Africa's largest fishery in terms of landed mass, with a long term average annual catch of 350 000t and with an average annual sardine catch of 130 000t (Figure 1.5a). This fishery employs approximately 10 000 people, and is the second most valuable fishery after the hake fishery (Department of Agriculture, Forestry and Fisheries, 2014). Sardine have been commercially exploited off the west coast since the 1940s, initiated by a demand for canned products during World War II. Sardine dominated the purse-seine catches in the early years and catches increased rapidly from less than 200 000t per year in the 1950s to more than 400 000t per year in the 1960s (Department of Agriculture, Forestry and Fisheries, 2014). These high catches could not be sustained and in the late 1960s the sardine fishery collapsed. Catches of sardine remained low for the next thirty years with anchovy dominating the catch. In 1983 a fishery-independent, stock-rebuilding programme of acoustic surveys to estimate pelagic fish abundance was initiated (Barange et al., 1999). Results from these surveys enabled fishery managers to implement and enforce an annual total allowable catch (TAC) from the mid-1980s. A conservative management strategy and good recruitment allowed sardine stocks to recover, with high estimated recruitment and biomass between 2001 and 2003 (Figure 1.5). Catches of over 300 000t were landed during this time. The relative contribution of south coast catches rapidly increased from 5% in 2000 to 64% in 2005; this was followed by a decline to 35% in 2009, which has since persisted (Department of Agriculture, Forestry and Fisheries, 2016). However, several successive years of poor sardine recruitment since then, except in 2010, have resulted in a present low sardine biomass (Figure 1.5b) and reduced annual sardine catches since 2005 (Coetzee et al., 2008a; Department of Agriculture, Forestry and Fisheries, 2014). In 2015 the sardine-directed TAC was reduced below 90 000t, the first time since 1997 (Department of Agriculture, Forestry and Fisheries, 2016). Following the November biomass surveys the adult sardine biomass was estimated to be only 363 230t in 2015, and 258 575t in 2016, representing a depleted population (Figure 1.5) (Department of Agriculture, Forestry and Fisheries, 2016; de Moor et al., 2017). The initial 2017 sardine-directed TAC was therefore drastically lowered and set to 29 955t.

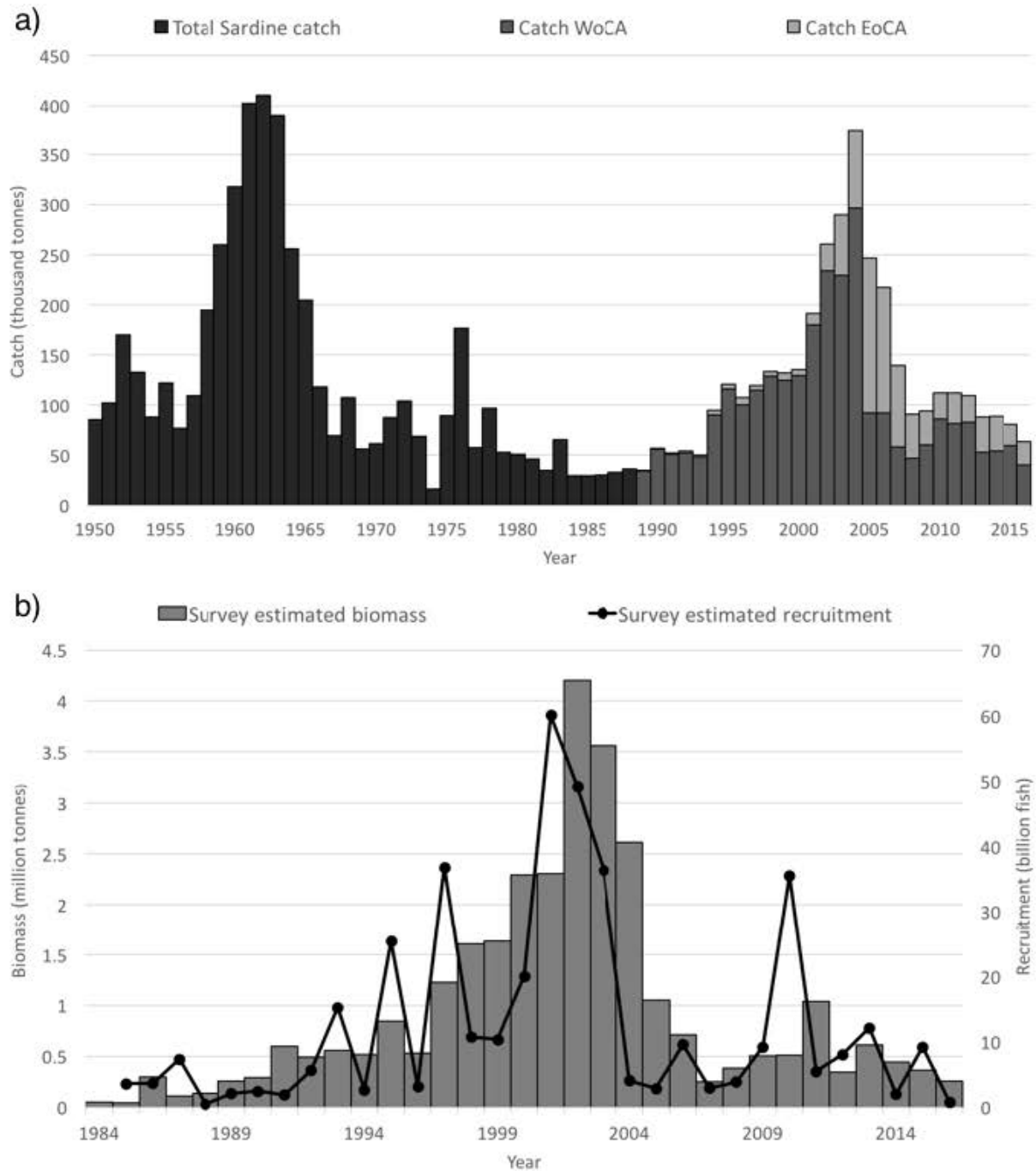


Figure 1.5: a) Annual total sardine landings taken by the small pelagic fishery (adult and juvenile sardine combined) from 1950 to 2016, with catches to the west of Cape Agulhas (WoCA) and east of Cape Agulhas (EoCA), as indicated from 1987 onwards (updated from van der Lingen et al. (2015)) b) Annual acoustic estimates of total sardine biomass, measured in November, and sardine recruitment, measured in the preceding May, since 1984 during acoustic surveys (Department of Agriculture, Forestry and Fisheries, 2016).

Since 1994 the anchovy and sardine fisheries in South Africa have been regulated using an operational management procedure (OMP), which is an adaptive management strategy that is able to respond quickly, without increasing risk, to changes in resource abundance. Sardine and anchovy school together as juveniles and therefore the anchovy fishery, which targets juveniles, has a juvenile sardine bycatch. This results in a trade-off between catches of juvenile anchovy (and therefore juvenile sardine as bycatch) and future catches of adult sardine. Therefore, the OMP ensures the sustainable utilisation of both resources, by setting separate TACs for anchovy, bycatch sardine and sardine (Department of Agriculture, Forestry and Fisheries, 2014).

The purse-seine fishery targets sardine off the western and southern coasts and therefore these stocks are important with regards to management, and will be the focus of this dissertation. The present agreed-upon hypothesis regarding the two stocks suggests that the west coast stock contributes to west coast recruitment, whereas the south coast stock contributes to south coast recruitment and a variable portion to west coast recruitment (Butterworth et al., 2016). Parasite data show that there is active movement of fish, at all ages, from the west coast to the south coast (Weston et al., 2015; de Moor et al., 2017). If the current hypothesis is valid, management strategies need to be readdressed to spatially manage the stocks, as they are currently managed as a single population using the OMP. The implications of the sardine resource consisting of multiple stocks is being investigated in the development of a new OMP, which may include spatial management strategies to avoid overfishing one or both stocks.

1.2 Oceanographic features and circulation patterns affecting the South African sardine population

The southern African coastline has been divided into the west coast, the south coast and the east coast (Kirkman et al., 2016) (Figure 1.1). The west coast ranges from Luderitz in Namibia to the important ecological boundary, Cape Agulhas, and includes the western Agulhas Bank (WAB) region (Lett et al., 2007; Hutchings et al., 2009). The south coast stretches across the rest of the Agulhas Bank, from Cape Agulhas to Port Alfred. The east coast ranges from Port Alfred to the border of Mozambique. This dissertation focuses on the west and south coasts of South Africa and the sardine stocks that reside there.

1.2.1 West Coast

The west coast of southern Africa is influenced by the cold Benguela Current and associated wind-driven Benguela Upwelling System, one of the world's four major eastern boundary upwelling systems (Figure 1.6). The south-east winds originating from the South Atlantic high pressure cell drive the main upwelling zone, which spans the coastline from northern Namibia to Cape Agulhas in the south (Figure 1.6). This system is uniquely bordered by two warm water masses at each end, the southward flowing Angolan Current (and Angola/Benguela front) to the north (17°S) and the Agulhas Current and associated rings and filaments to the south (34°S). The system at large is divided into the northern and Southern Benguela by an intense upwelling cell at Luderitz (27°S), resulting in two mostly separate ecosystems (Lett et al., 2007).

The Southern Benguela is characterised by seasonal, wind-driven upwelling in spring and summer and is extremely productive during these times, with an estimated $3.7 \text{ kg.C.m}^{-2}.\text{yr}^{-1}$ of primary production (Andrews and Hutchings, 1980; Hutchings et al., 2009). Mesoscale cyclonic eddies often occur along the Southern Benguela upwelling front, making the front strongly irregular (Rubio et al., 2009). These eddies can export significant volumes of nutrient-rich waters out of the coastal upwelling region as they have a lifetime of several months (Rubio et al., 2009). The persistent cyclonic wind stress curl and upwelling along the coast are crucial in driving short-term variability in plankton development and fish recruitment (Hutchings et al., 2009; Rykaczewski and Checkley, 2008; Junker et al., 2015). This region provides important inshore nursery grounds for small pelagic fish species such as sardine, anchovy and round herring. The WAB is strongly influenced by the Agulhas Retroflection and rings and shows a general north-westerly drift of surface waters (Lutjeharms, 2006). The upwelling inshore on the WAB is driven by seasonal winds, creating strong vertical stratification in austral summer. This upwelling, as well as the input of warm, salty Agulhas Current water in this region, drives a coastal jet current (Benguela Jet) that accelerates from the bank along the west coast and aids in the transport of eggs and larvae to the nursery grounds on the west coast (Boyd et al., 1992; Hutchings et al., 2002; Veitch and Penven, 2017).

1.2.2 South Coast

The south coast encompasses all of the central and eastern regions of the Agulhas Bank (Figure 1.6). This triangular bank is a broad extension of the coastal shelf, spanning approximately $116,000\text{km}^2$, influenced by the warm Agulhas Current to the east and the cold Benguela Current to the west. The whole bank is relatively productive, with complex,

gyre-like circulation patterns (Boyd and Shillington, 1994). By convention, the bank east of Cape Agulhas is sub-divided into the central Agulhas Bank (CAB) and the eastern Agulhas bank (EAB).

The oceanography on the central and eastern bank is largely forced by the Agulhas Current and its retroflection, mesoscale and accompanying inshore features, the prevailing winds, and seasonal conditions (Boyd and Shillington, 1994). In contrast to the wider-scale upwelling in the west, the coastal upwelling on the CAB and EAB is generally confined to capes and headlands. In austral summer there is an introduction of subtropical water, separated by strong thermoclines from cool waters drawn onto the central bank as the Agulhas Current moves off the coast (Hutchings et al., 2002). The cool water upwelled at headlands is shifted westward to form a broad, quasi-permanent, subsurface cold-water ridge (Swart and Largier, 1987; Roberts, 2005). This system is important and can aid in retention of eggs and larvae of sardine and chokka squid (*Loligo vulgaris reynaudii*) on the bank. However, its dynamics are not well understood (Roberts, 2005; Miller et al., 2006; Hutchings et al., 2009).

The widening of the continental shelf, at the origin of the Agulhas Bank around Port Elizabeth, causes increased meandering of the Agulhas Current and prevalence of variable mesoscale and sub-mesoscale features, such as plumes and eddies (Lutjeharms, 2006; Krug et al., 2017). The sub-mesoscale eddies formed at the origin of the Agulhas Bank are likely generated by horizontal shear instability, and they extract their energy from the mean current (Krug et al., 2017). These plumes and eddies can extend shoreward and north-eastward over considerable areas of the Agulhas Bank (Lutjeharms, 2006; Krug et al., 2017).

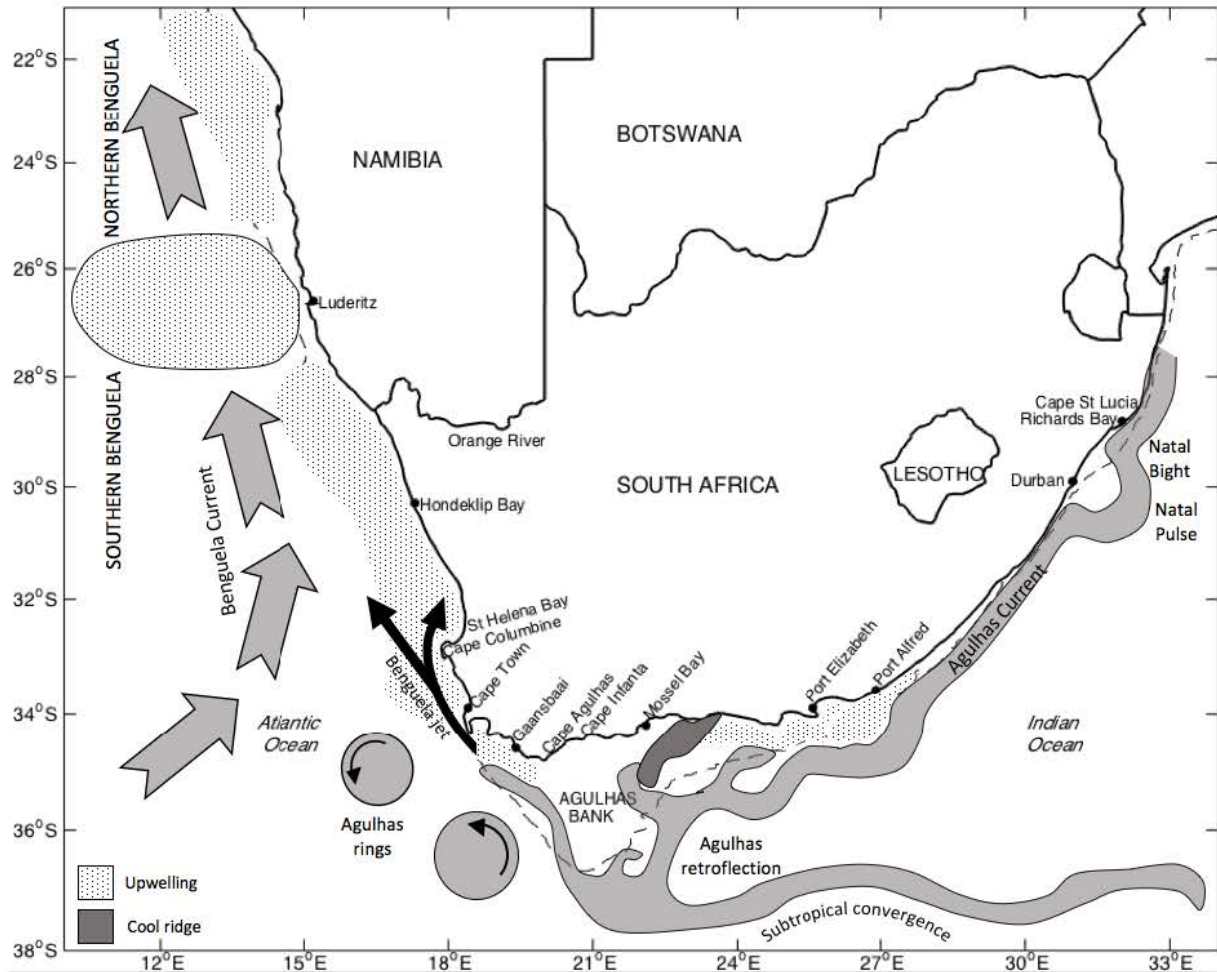


Figure 1.6: Map showing the key oceanographic features around southern Africa mentioned in the text. Dotted areas represent upwelling regions, and the dark grey area represents the cool ridge. Based on information from Roberts (2005) and Lutjeharms (2006).

1.3 Hydrodynamic ocean models

Numerical models have become useful tools to investigate conditions and processes in the ocean, and to address the spatial and temporal gaps not filled by *in-situ* observations and remote sensing. There are many different types of ocean models, varying in numerics and schemes used to solve the fundamental geophysical fluid equations governing ocean dynamics. These models can be coupled with atmospheric, biogeochemical or biological models to enhance the research. The focus here is on the Regional Ocean Modelling System (ROMS), individual-based models (IBMs) and the Lagrangian particle tracking tool, Ichthyop.

1.3.1 The Regional Ocean Modelling System (ROMS)

ROMS (Shchepetkin and McWilliams, 2003; Shchepetkin and McWilliams, 2005) has been widely used by the scientific community for a range of applications relevant to South Africa (for example: Penven et al., 2001; Lett et al., 2007; Veitch et al., 2009; Veitch and Penven, 2017). ROMS solves the incompressible primitive equations in an Earth-centred rotating environment, using the Boussinesq approximation and hydrostatic vertical momentum balance. The model domain is discretized in coastline-following and terrain-following curvilinear coordinates using high-order numerical methods. It is a split-explicit ocean model with a free surface, where short time steps are used to advance the surface elevation and barotropic momentum, and a much longer time step is used for temperature, salinity, and baroclinic momentum (Shchepetkin and McWilliams, 2005). ROMS includes an accurate pressure gradient algorithm (Shchepetkin and McWilliams, 2003) and other features, including turbulent closure schemes for sub-grid scale processes, wetting and drying for mud flat and beach simulations (Warner et al., 2013), and sediment and biological models.

ROMSAGRIF (Penven et al., 2006; Debreu et al., 2012) is a version of ROMS that is maintained by the French institutes, Institut de recherche pour le développement (IRD) and French Institute for Research in Computer Science and Automation (Inria). This version includes 2-way nesting, which allows for more than one fixed grid and embedding levels, therefore the physics in the nested grid can input the physics on the mother grid. More information and details regarding ROMS and ROMSAGRIF can be found in the ROMSAGRIF User Guide (<https://www.croco-ocean.org/documentation/>).

The first ROMS model used to depict the oceans around South Africa was developed by Penven et al. (2001) and was used in a variety of individual-based model studies of fish eggs and larvae.

1.3.2 Individual-based models

Modelling has contributed to research and management of pelagic fish populations for a long time, largely due to their big stock sizes, extensive distributions and inaccessibility, limiting scientists' ability to sample these populations. However, large inter-annual variability of small pelagic fish populations makes their recruitment particularly hard to model. Traditional stock management models examine whole-stock population dynamics based on a compensatory model of the stock-recruitment relationship (Heath and Gallego, 1997). Incorrect assumptions regarding the spawning stock or failure to account for the spatio-temporal scales of the factors governing the relationship sometimes cause inaccura-

cies in stock-recruit models (Hutchinson, 2008). It has become clear that environmental factors affect the recruitment success of small pelagic fish (Sharp, 1987; Armstrong and Shelton, 1990; Hinckley et al., 1996; Checkley et al., 2009). This led to the development and implementation of individual-based models (IBMs), which can be used in conjunction with traditional stock models (Grimm, 1999).

IBMs integrate environmental, ecological and biological data, and can effectively deal with ecosystems in which spatial distribution is important. DeAngelis and Coutant (1979) developed the first fish IBM, using largemouth bass (*Micropterus salmoides*) individuals as the basic units and explicitly investigating processes affecting individuals. Heath and Gallego (1997) synthesised the progress and use of IBMs in studies of early life history stages of fish, and identified gaps in knowledge. Grimm (1999) also provided a comprehensive review of IBMs used in ecology studies during the 1990s.

Fish early life history stages are commonly represented in IBMs as passive particles placed in virtual environments created by 3-D hydrodynamic models. A number of IBM studies that have investigated anchovy (Mullon et al., 2002; Huggett et al., 2003; Parada et al., 2003) and sardine (Miller et al., 2006) in the Southern Benguela and Agulhas Bank region used variations of the ROMS model, PLUME (Penven et al., 2001; Blanke et al., 2002). These results were synthesized by Mullon et al. (2003) and more recently by Lett et al. (2015).

Mullon et al. (2002) developed an evolutionary IBM for the recruitment of anchovy in the Southern Benguela, in which an evolutionarily-based reproductive strategy for adult fish and passive transport for early life stages were modelled. Anchovy egg and larval transport success in the Southern Benguela was modelled using an IBM by Huggett et al. (2003). Results suggested that the anchovy spawning strategy, in which eggs and larvae are passively transported from the Agulhas Bank to their nursery grounds on the west coast, is mainly the result of adaption to the circulation patterns in the region. The effect of buoyancy on the transport of anchovy eggs and larvae to nursery grounds in the Southern Benguela was modelled by Parada et al. (2003). Buoyancy was a significant determinant of transport success, with assumed particle density of 1.025 g.cm^{-3} maximising average particle transport success.

Miller et al. (2006) modelled the effects of physical-biological interactions and spatial variability in spawning and nursery areas on transport and retention of sardine eggs and larvae in the Southern Benguela ecosystem. A series of simulations was run in which input parameters, such as spawning area, month, depth of release and year, were varied. Nine

spawning areas covering the west and south coasts were defined, as well as two recruitment areas on each coast. Three viable recruitment systems were identified, two of which were dependent on retention of eggs in the area they were spawned (west coast or south coast), and the other depended on the transport of eggs from the south coast spawning area to the west coast recruitment area. Depth of release and spawning area respectively proved to be important determinants of recruitment in the west coast and south coast retention-based systems. Spawning area also influenced successful recruitment in the transport-based system; the further east on the Agulhas Bank that eggs were spawned, the less likely they were to successfully recruit on the west coast. In the simulations, a small average percentage ($\approx 15\%$) of particles spawned on the entire Agulhas Bank were transported to the west coast. This average decreased to $\approx 9\%$ when the WAB was excluded from the south coast to west coast analyses. This small percentage of mixing between coasts supports the hypothesis of the South African sardine population consisting of multiple spatially-structured stocks and two main systems were identified: the west coast system (spawning on the western Agulhas Bank and west coast and recruiting on the west coast), and the Agulhas Bank system (spawning on the central and eastern Agulhas Bank and recruiting on the south coast). Similar IBM approaches have also been implemented for sardine in the northern Benguela (Stenevik et al., 2003), western Iberia (Santos et al., 2004) and the Canary Current System (Brochier et al., 2008b).

1.3.3 Ichthyop

Ichthyop is a freely available Java tool designed to study the effects of physical and biological factors on ichthyoplankton dynamics (Lett et al., 2008). The Lagrangian programme incorporates spawning, movement, growth, mortality and recruitment, which are important processes involved in early life history stages of fish. Oceanic models are used to provide velocity, temperature and salinity time series fields, and simulate the physical environment experienced by ichthyoplankton. The tool allows for experiments to be run offline in simulations, using a user-friendly interface, varying certain properties, and recording the results in manageable netCDF files.

1.4 Objectives of this study

This work aims to contribute to the understanding of stock structure and spawning strategies of sardine in the Southern Benguela. This chapter has introduced and explained topics that are important in this study, covering South African sardine population dynamics and the fishery, oceanographic features around South Africa, ocean modelling and individual-based modelling. Chapter 2 describes the methods and modelling approach of this study, including ocean model configurations, and experiments to determine the optimum number of particles. In Chapter 3, a purely Lagrangian approach is taken and the same individual-based model (IBM) configuration is coupled to two different underlying hydrodynamic models, a historic low resolution model used in a previous sardine IBM in the Southern Benguela (Miller, 2006; Miller et al., 2006), and a more recent, higher resolution model. Results testing the differences brought about by increased resolution and other hydrodynamic modelling advances are compared and discussed. Chapter 4 describes an updated Southern Benguela and Agulhas Bank sardine IBM coupled to a high resolution model, with a configuration that more accurately matches the hypothesised and observed sardine spawning pattern. The final chapter synthesises the results of this study and addresses the implications and the direction of future studies. This dissertation

has two main objectives:

1. To examine how advances in hydrodynamic models, such as increased spatial and temporal resolution, affect the modelled transport and retention success of sardine eggs and larvae in the Southern Benguela and Agulhas Bank region. To achieve this, a particle-tracking individual-based model configured in Ichthyop, similar to Miller et al. (2006), is coupled with two configurations of the Regional Ocean Modelling System, ROMS. The first is the historic ROMS configuration, PLUME (Penven et al., 2001; Blanke et al., 2002), used by Miller et al. (2006), and the second is BENGSAFE (Ragoasha, 2017), which has higher spatial and temporal resolution with higher frequency forcings.
2. To configure an updated particle-tracking individual-based model in Ichthyop that accurately represents the hypothesised west coast and south coast spawning stocks of South African sardine by expanding the model domain eastwards to Port Alfred. This IBM is coupled with the high resolution BENGSAFE model (Ragoasha, 2017), to investigate how spatial and temporal variability in spawning influence the transport and retention of sardine eggs and larvae in the Southern Benguela and Agulhas Bank region. Results can act as a base with which to compare future IBMs with added extra layers of complexity.

Chapter 2

Modelling Approach and Methods

2.1 Modelling Overview

The methodological approach has three components: a hydrodynamic model (either an old configuration called PLUME or a more recent configuration called BENGSAFE), a particle tracking Individual Based Model (IBM), and statistical analyses of the results (Figure 2.1). The hydrodynamic models were run independently of this dissertation (Blanke et al., 2002; Ragoasha, 2017) and their outputs were used to provide inputs to the IBM simulations via the offline particle-tracking tool, Ichthyop. The modelling approach was kept the same as Miller (2006) and Miller et al. (2006) to allow for comparison of results.

2.1.1 PLUME configuration

PLUME is a Regional Ocean Modelling System (ROMS) configuration of the Southern Benguela (Penven et al., 2001; Blanke et al., 2002). It consists of a pie-shaped, curvilinear grid which follows the southwestern coast of Africa from 40°S to 28°S and from 10°E to 24°E (Figure 2.2). The horizontal resolution ranges from 9 km at the coast and increases linearly to 16 km offshore. There are 20 terrain-following vertical levels which decrease in resolution with depth to preserve high resolution near the surface. Realistic topographic features are slightly smoothed to enable stable and accurate simulations (Haidvogel et al., 2000). The first-baroclinic Rossby radius of deformation for the region is approximately 20-30 km, therefore PLUME can resolve the dominant scale of the most unstable waves, and baroclinic instabilities are properly represented (Blanke et al., 2002). An implicit active radiative boundary scheme (Marchesiello et al., 2001) estimates the horizontal velocities at PLUME's three open, seaward boundaries. Conditions from the surrounding ocean are given by seasonal, time-averaged outputs of the Agulhas As Primitive Equations (AGAPE) basin-scale ocean model (Bjostoch and Krauss, 1999). PLUME is forced by

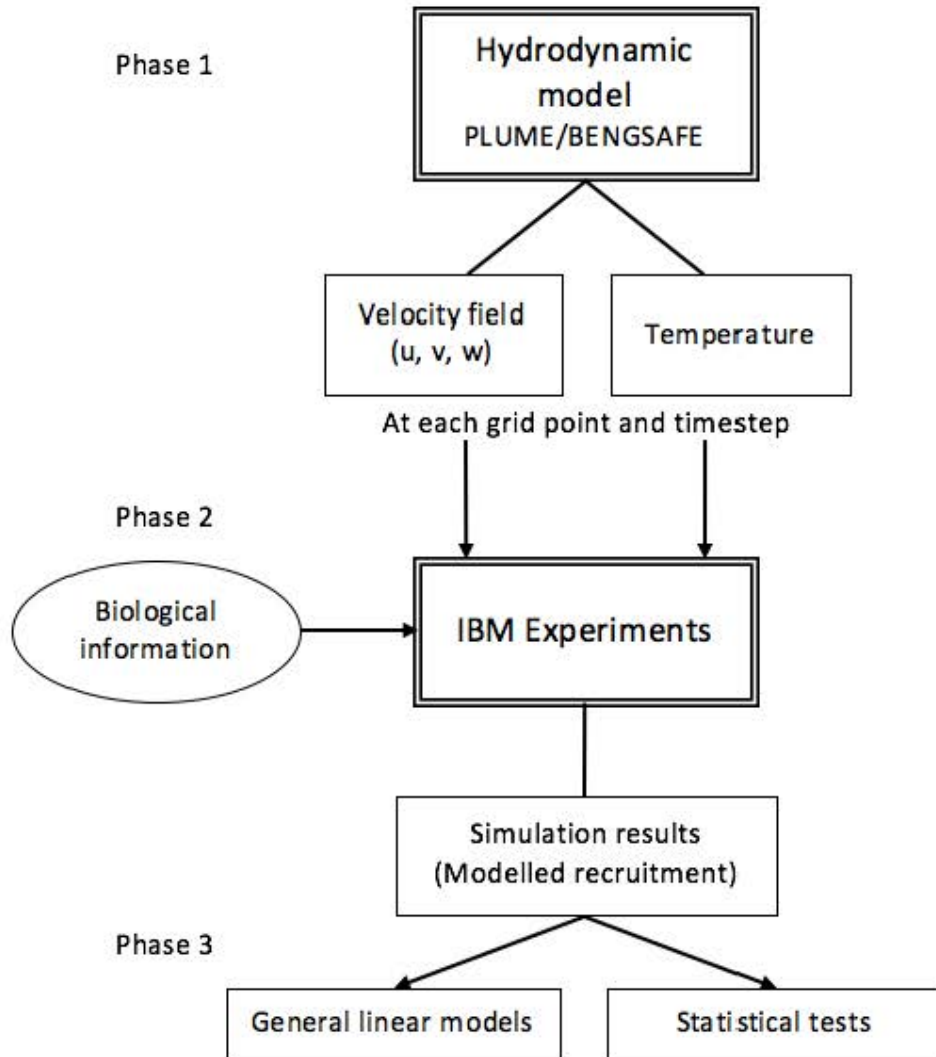


Figure 2.1: Methodological approach of the modelling process. Adapted from Miller (2006).

heat and salinity fluxes derived from the COADS ocean surface monthly climatology (da Silva et al., 1994) and the run used in this dissertation was forced by the ERS1/2 satellite wind stress data, a weekly wind product with $1^\circ \times 1^\circ$ horizontal resolution (Bentamy et al., 1996). The model is not able to address the impact of anomalous events or sub-weekly events, such as storms and tides (Blanke et al., 2002). Output from the PLUME model was saved every two days from July 1991 to June 1999. PLUME forced by climatological wind stress (Penven et al., 2001) has been used in previous ichthyoplankton studies in the Southern Benguela (Mullon et al., 2002; Huggett et al., 2003; Parada et al., 2003). The PLUME configuration used in this study was first used by Miller et al. (2006) in a sardine ichthyoplankton study in the Southern Benguela. It was included in this study to allow comparison with a higher resolution, more recent hydrodynamic model configuration,

BENGSAFE (described below).

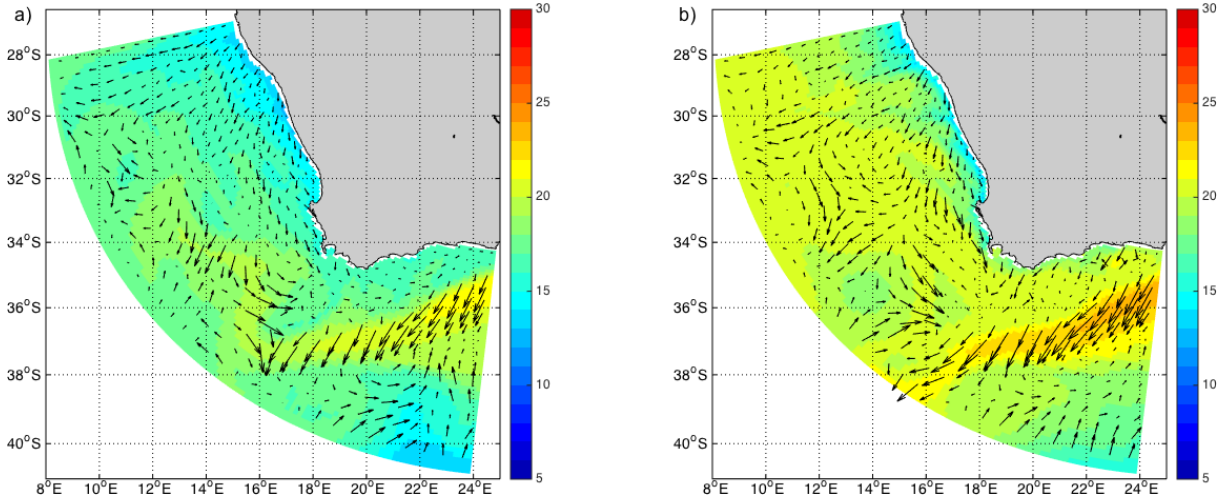


Figure 2.2: Snapshot of the average sea surface temperature (SST °C) during a) July, Year 11 (representing 1994) and b) January, Year 12 (representing 1995) from the PLUME model.

2.1.2 BENGSAFE configuration

BENGSAFE is a ROMS coded hydrodynamic model configuration representing southern Africa (Ragoasha, 2017). The model grid, forcing and initial conditions are built using the ROMSTOOLS package (Penven et al., 2008). The rectangular domain covers 4.8°S to 54.5°S in latitude and 2.4°W to 55.2°E in longitude, with three lateral open boundaries to the east, south and west (Figure 2.3). The horizontal resolution is approximately 7km. The model has 100 vertical terrain-following levels (σ coordinates) that are stretched to obtain a higher resolution at the surface and at the bottom. The σ coordinates are transformed to study shelf dynamics (Shchepetkin and McWilliams, 2009; Lemarié et al., 2012). A K-profile parameterisation (KPP) boundary layer scheme (Large et al., 1994) is used for vertical turbulence closure in the surface layer and at the bottom layer to introduce subgrid-scale vertical mixing. Bottom topography (h) is extracted from the NASA Shuttle Radar Topography Mission (SRTM) elevation database, which is sampled at 1 arc-second (approximately 30m) (Farr et al., 2007). SRTM is interpolated on the model grid and smoothed to satisfy an r target of less than 0.2 ($r = \frac{\delta h}{h} < 0.2$) and therefore reduce pressure gradient errors.

Wind stress, heat flux and freshwater flux are computed using bulk formulae (Fairall et al., 1996) and forced by the NCEP Climate Forecast System Reanalysis (CFSR), which has 6-hourly sampling and a spatial resolution of 0.34° (Saha et al., 2010). Surrounding conditions of temperature, salinity, horizontal velocity and sea level at the lateral boundaries

are provided by a monthly climatology derived from SODA 2.3.4 reanalysis (Carton and Giese, 2008). This product ranges from 1958 to 2005 and has a horizontal resolution of 0.25° in longitude and 0.4° in latitude, with 40 vertical levels. It assimilates observational data in a general circulation model based on Parallel Ocean Program numerics (Smith et al., 1992).

Output from this model was saved every three days from July 1989 to June 2010. For the purpose of this dissertation, an extraction of the BENGSAFE domain is used, spanning 22°S to 45°S and 5°E to 35°E ; this is referred to as BENGSAFE for the remainder of this dissertation.

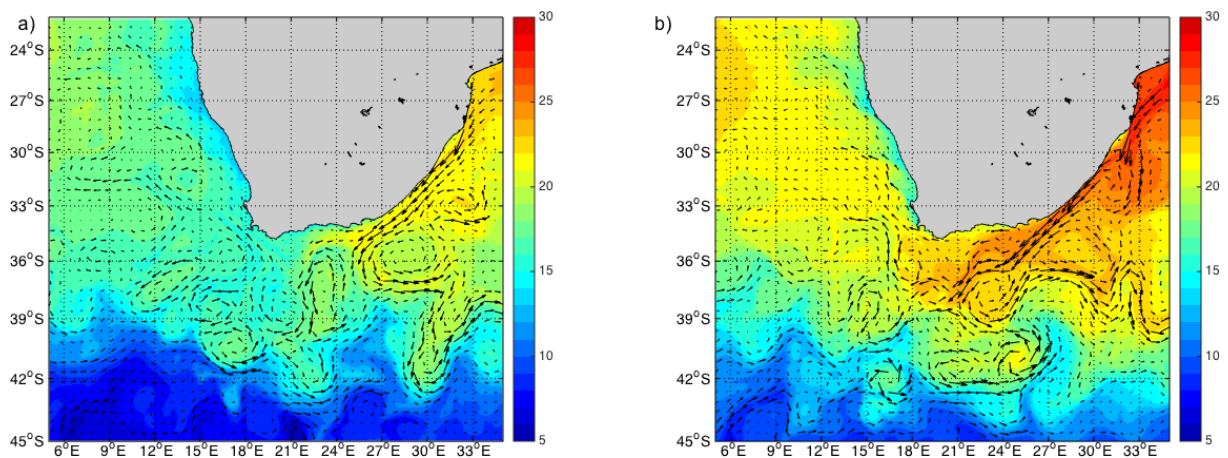


Figure 2.3: Snapshot of the average sea surface temperature (SST $^\circ\text{C}$) during a) July, 1994 and b) January, 1995 from the BENGSAFE model

2.1.3 Model comparisons and evaluation

It is important to explore how hydrodynamic model outputs compare to observations. Because of the limited spatial and temporal coverage, and lack of homogeneity of *in situ* measurements in the region, satellite products are used. Although it would be ideal to compare outputs over the same time period, PLUME outputs are only available up to 2000 and computation for the AVISO and BENGSAFE data was done prior to this dissertation (Ragoasha, 2017). It is unlikely that the different time periods affected the outcomes. PLUME's spatial extent is also much smaller than that of BENGSAFE.

Sea surface temperature

A comparison of sea surface temperature (SST) between the Climate Change Initiative (CCI) global satellite product (<http://www.esa-sst-cci.org/>) and modelled SST (PLUME and BENGSAFE) is shown in Figure 2.4 (a, b, c). The CCI SST product is daily analysis

with a horizontal resolution of 0.05° . SST inputs from Along Track Scanning Radiometer (ATSR) and Advanced Very High Resolution Radiometer (AVHRR) are optimally interpolated to form a spatially and temporally complete dataset, which extends from 1991 to 2010 (Merchant et al., 2014).

A cool coastal band on the west coast, representing west coast upwelling, is present in all three SST plots (Figure 2.4a, b, c), and the Agulhas Current can be identified in all three by its warm SST. The BENGSAFE SST (Figure 2.4c) shows warmer water over the Agulhas Bank and less obvious separation of the Agulhas Current from the coast at the widening of the Agulhas Bank, compared to CCI SST and PLUME SST. Realistic climatological SST values are apparent in both ocean models.

The snapshots shown in Figures 2.2 and 2.3 display seasonality in the modelled SSTs. The SSTs are higher in the figures representing summer (Figure 2.2b and Figure 2.3b) than in the figures representing winter (Figure 2.2a and Figure 2.3a) for both PLUME and BENGSAFE.

Sea surface height

Root mean squared (RMS) sea level anomaly fields (SLA) were computed from a satellite-derived sea surface height product, AVISO, and outputs of PLUME and BENGSAFE (Figure 2.4d, e, f) to compare deviations in sea level. The SLA gridded satellite dataset is a DUACS (Data Unification and Altimeter Combination System) product supplied by AVISO (Archiving, Validation, and Interpretation of Satellite Oceanographic data) (Ducet et al., 2000). It provides weekly data from 1992 to 2010, with a $1/3^\circ$ resolution. The gridded product is a merge of observations from satellites TOPEX/POSEIDON, ERS and JASON. RMS SLA values are low on the west coast, consistent with the prevailing equatorward, alongshore Benguela Current in the region. The Agulhas Current and retroreflection are clearly visible by high RMS SLA values in the AVISO and BENGSAFE data (Figure 2.4d, f). The leakage of mesoscale eddies from the retroreflection into the south-eastern Atlantic is also shown. The PLUME RMS SLA values underestimate the expected high RMS SLA to the south of the Agulhas Bank, that are present in the AVISO and BENGSAFE data. The PLUME RMS SLA data show low values in the retroreflection region and the Agulhas Current is not visible. This could be due to the domain only extending to 24°E and therefore not adequately resolving the Agulhas Current. However, increased RMS SLA values are seen offshore on the south-west coast.

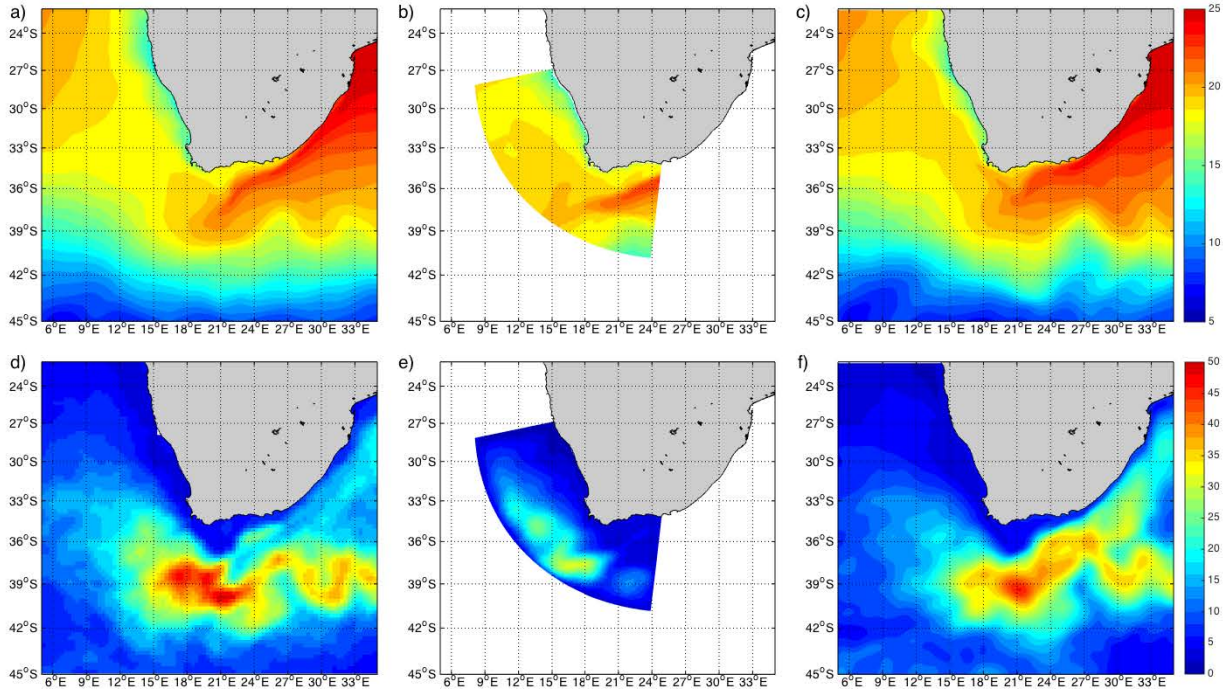


Figure 2.4: The top panel shows mean SST ($^{\circ}\text{C}$) from a) Climate Change Initiative (CCI) satellite product for 1992 - 2010, b) PLUME for 1992 - 2000, and c) BENGSAFE for 1992-2010. The bottom panel shows root mean squared sea level anomalies (m) calculated using d) AVISO satellite altimetry for 1992 - 2010, e) PLUME for 1992 - 2000, and f) BENGSAFE for 1992 - 2010.

2.1.4 Ichthyop configurations

Ichthyop is used to study the effects of physical and biological factors on ichthyoplankton dynamics, by tracking particles in a virtual environment provided by hydrodynamic ocean models (Lett et al., 2008). It is a freely available open source Java tool. Ichthyop incorporates important early life history processes such as spawning, movement, growth, mortality and recruitment. Hydrodynamic ocean models provide 3-D fields of velocity, temperature and salinity over time, and simulate the physical environment experienced by ichthyoplankton. Ichthyop creates a population of individuals that are released within the 4-D advective environment of the hydrodynamic model outputs, and that increase in age at each IBM timestep. Each particle is exposed to its own environmental conditions, determined by its position, and follows its own path, determined by the hydrodynamics. Each particle has a memory of where and when it was spawned (location, date, depth), its age and its recruitment area should it be successfully recruited. In each simulation, the number of particles released, date of release, depth of release, lethal temperature, tracking period, recording frequency, time step, and recruitment and spawning areas are defined by the user. In this study Ichthyop Version 3.2 is used (downloadable from

2.2 Modelling protocol

2.2.1 Assumptions

Models are not exact reproductions of the real world, which is complex, and therefore certain assumptions need to be made to simplify them. Results from models need to be interpreted within the limits of these assumptions so it is important that they are clearly defined. The following assumptions were made about the hydrodynamic models and the IBMs:

1. The output of both 3-D hydrodynamic models provide realistic fields of temperature, salinity and velocity, as well as sufficient seasonal and inter-annual variations that represent the dynamics of the ecosystem. Validation of PLUME output was conducted by Penven et al. (2001) and Blanke et al. (2002), and validation of BENGSAFE was conducted by Ragoasha (2017).
2. Eggs and larvae are passive drifters in this virtual environment. The effect of density, diffusion, active movement and biological processes (including predation and food availability) are assumed to be negligible for recruitment success (Huggett et al., 2003; Parada et al., 2003; Miller, 2006; Miller et al., 2006).
3. Recruitment occurs between the coast and the 500m isobath on the west coast from Cape Columbine to Oranjemond, and on the south coast from Cape Infanta to Plettenberg Bay (Chapter 3; Figure 3.3; Miller, 2006; Miller et al., 2006). In Chapter 4 the west coast recruitment area remains the same, but the south coast recruitment area changes to between the coast and the 500m isobath from Cape Infanta to Port Alfred.
4. Successful retention in or transport to a particular recruitment area (south or west coast) is achieved when particles reach the recruitment areas within a time period of 14 to 60 days after release, and stay in the recruitment area for 2 days with PLUME and 3 days with BENGSAFE, which are the output frequencies of the respective models (Huggett et al., 2003; Parada et al., 2003; Miller, 2006). The term recruitment refers to successful retention/transport in or to the recruitment areas in the IBM and does not refer to recruitment in reality.
5. The extensive subdivided spawning areas are sufficient to explore the influence of spatial variability in spawning on recruitment success (Miller, 2006; Miller et al.,

2006).

6. Frequency and patchiness of spawning is considered to have no significant effect on the level of recruitment success (Huggett et al., 2003; Miller, 2006, Miller et al., 2006).

2.2.2 Parameters

Fixed parameters and the majority of the variables were unchanged throughout the series of experiments to allow for direct comparison between models (Table 2.1). The difference in parameters between Chapter 3 and 4 is in the number of spawning areas (*Spawning Area*), the time period (*Year*), and the number of particles. Chapter 3 is limited by the spatial and temporal extent of PLUME and includes nine spawning areas and eight spawning seasons (July 1991 - June 1999), identical to those used in the previous Southern Benguela sardine IBM (Miller, 2006; Miller et al., 2006). BENGSAFE's extended domain and time period in Chapter 4 allows for one extra spawning area on the south coast, which better represents the hypothesised sardine spawning strategy and better matches observations (Figure 1.4; Pattrick et al., 2016). A more recent, longer time period (July 1989 - June 2010) is also used in Chapter 4. As the spatial coverage of the spawning areas increases by approximately 10% in Chapter 4, 10% more particles were released compared to Chapter 3. These variables are described in the relevant chapters.

Table 2.1: The fixed parameters and variables used in the IBM experiments.

	Chapter 3	<i>n</i>	Chapter 4	<i>n</i>
Fixed Parameters				
Number of particles	10 000	-	11 000	-
Duration of release of particles	30 days	-	30 days	-
Tracking period	60 days	-	60 days	-
Lethal minimum temperature	13°C	-	13°C	-
Variables				
<i>Spawning Area</i>	See Figure 3.2	9	See Figure 4.2	10
<i>Year</i>	91/92-98/99	8	89/90-09/10	21
<i>Month</i>	July-June	12	July-June	12
<i>Depth</i>	0-25m, 25-50m, 50-75m	3	0-25m, 25-50m, 50-75m	3
<i>Trial</i>	-	3	-	-
Total number of simulations		864		756

Particles were released randomly across all spawning areas, with the number of particles released in each area dependent on the size of that area. Following Miller (2006) and Miller

et al. (2006), particles were released in batches every two or three days (depending on the hydrodynamic model) during each month of the hydrodynamic ocean model's output (*Month*). The release depth ranges (*Depth*), 0-25, 25-50 and 50-75m, were identical to previous IBMs in the region (Huggett et al., 2003; Parada et al., 2003; Miller, 2006; Miller et al., 2006). These depth ranges were assumed to adequately capture the vertical extent of sardine spawning as Dopolo et al. (2005) found that most of the sardine eggs on the western Agulhas Bank were widely distributed down to 60m. This is in agreement with other sardine ichthyoplankton studies in waters off Namibia (Stenevik et al., 2001), southern Australia (Fletcher and Sumner, 1999) and Japan (Matsuoka et al., 2002). Osman et al. (2010) found that the majority of sardine eggs on the eastern Agulhas Bank were close to the surface, within the top 10m. Once particles were released they were not constrained to their initial depth range and were allowed to be moved by vertical advection within the hydrodynamic model domain.

2.2.3 Dependent variables

The dependent variable for all simulations is successful transport to, or retention in, one of the designated recruitment areas. This is termed either 'Modelled transport' or 'Modelled retention' for the remainder of this dissertation, depending on the nature of the system in question. Modelled retention/transport was calculated as the percentage of particles from each spawning area that meet the criteria for recruitment at the end of the tracking period. Once successfully recruited, particles were removed from the simulation. There is a lack of data on sardine larval development and behaviour in the Southern Benguela. As a result, a minimum age at which larvae could be considered successfully retained or transported was set at 14 days, as in Huggett et al. (2003), Parada et al. (2003) and Miller (2006). It is thought that larvae older than 14 days have swimming capabilities, and can maintain themselves in recruitment areas, hence they cannot be considered as passive particles (Parada et al., 2003). Additionally, particles had to remain in the recruitment area for a period of 2 or 3 days, depending on the model in question for successful recruitment. A lethal temperature of 13°C was set for all simulations. Temperature-induced mortality was calculated as the percentage of particles from each spawning area that was subjected to temperatures below the lethal temperature and thus removed from the simulation. Particles that were not recruited at the end of the tracking period or removed due to lethal temperature were considered to have been advected offshore away from recruitment areas and out of the domain, or to shallow waters, resulting in beaching. Mortality was calculated as an emergent variable but was not used as a dependent variable for linear models.

2.3 Comparability of results

2.3.1 Number of particles

Tests were run for each hydrodynamic model to determine whether the total number of particles released per run affects the variation in the modelled retention/transport and temperature-induced mortality, and to determine the optimal number of particles to release for stable outputs. Three trials were run for each number of particles released (100, 500, 1000, 2500, 5000, 7500, 10000 and 15000 particles). The tests were conducted for the three depth categories (0-25m, 25-50m, and 50-75m) to determine whether depth affected the number of particles required for stable outputs. Particles were released in batches every 2 days (for PLUME) and 3 days (for BENGSAFE) over four months (March, June, September and December), each month representative of a season, for the year representing 1994.

Mean modelled retention/transport is considered stable when the simulations, both across particle number and inter-trial, yield similar means and standard deviations. For all simulations, standard deviations decreased then stabilised as the number of particles used increased (Figure 2.5). For retention/transport on the west coast, stable outputs were obtained if more than 2500 particles were used in simulations coupled with PLUME, and 5000 particles in simulations coupled with BENGSAFE. For retention/transport on the south coast, 2500 particles also were needed for stable outputs with PLUME, and the same for simulations in BENGSAFE. The standard deviations calculated for simulations coupled with BENGSAFE were larger than the standard deviations when coupled with PLUME. Temperature-induced mortality stabilised if more than 5000 particles were used in simulations coupled with either PLUME or BENGSAFE.

Results from these experiments show that a minimum of 5000 particles are needed for stability in modelled retention/transport and modelled temperature-induced mortality when coupling with hydrodynamic models PLUME or BENGSAFE. To be extra cautious, and to be analogous to previous IBMs in the southern Benguela, 10 000 particles were released each month in the simulations described in Chapter 3, and 11 000 particles were released each month in Chapter 4 due to the increased spawning extent.

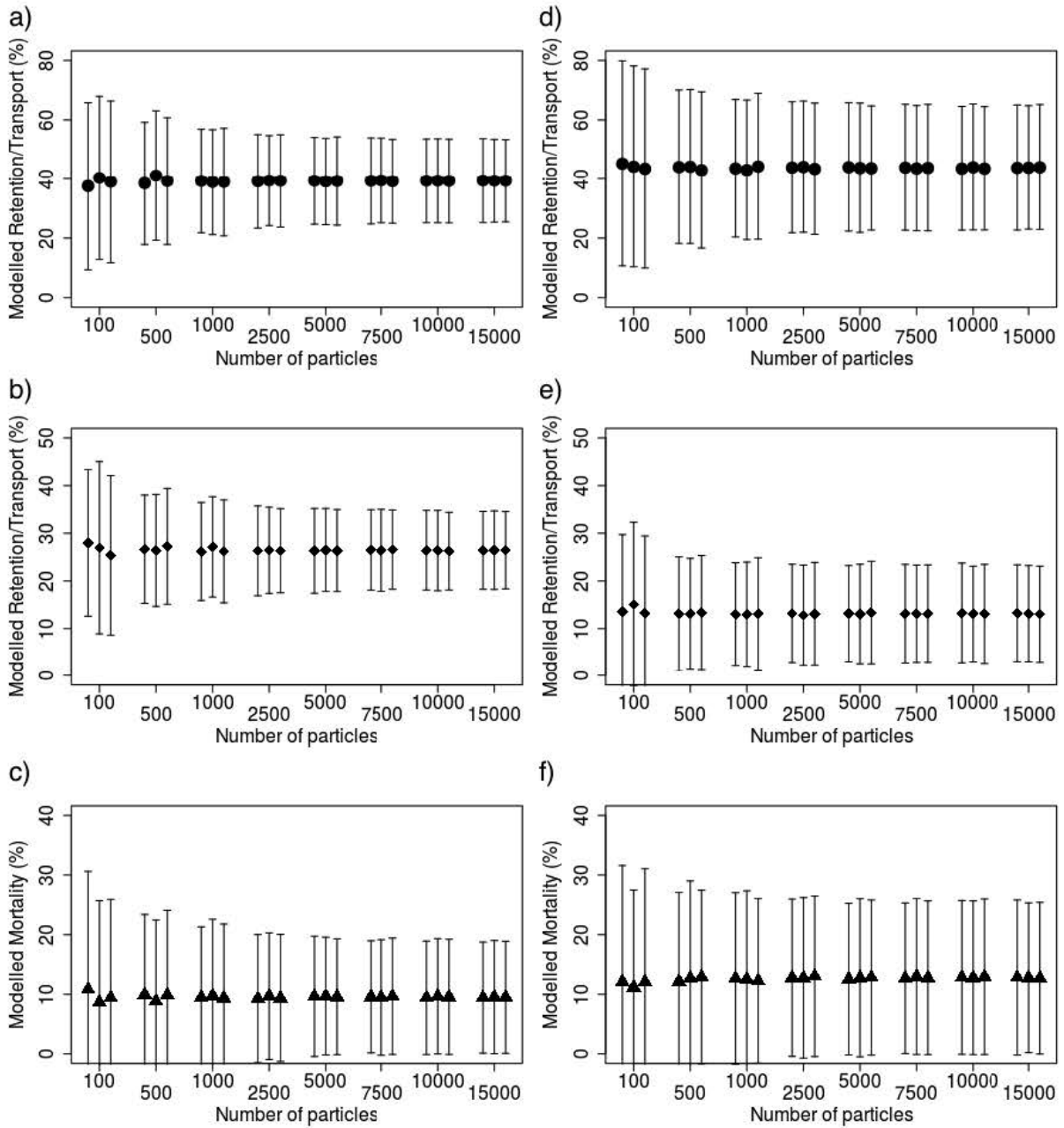


Figure 2.5: The effect of the number of particles used in the experiments on mean modelled retention/transport (\pm one standard deviation) to the west coast (circles) and to the south coast (diamonds), and mean modelled temperature-induced mortality (\pm one standard deviation) (triangles) from IBMs coupled with PLUME (left panel, a-c) and BENGSAFE (right panel, d-f), irrespective of *Spawning Area*, *Month*, *Year* and *Depth*. For each number of particles the three trials are shown.

2.4 Sensitivity and statistical analyses

Sensitivity analyses highlight the relative importance of a model's parameters in causing changes in the output. Sensitivity analyses are an essential part of the modelling process, and provide foundations for recommendations based on the model (Beres and Hawkins, 2001). Sensitivity analyses allow the examination of "main" effects, as well as the likelihood of interactions between variables. A complete factorial design allows interactions of interest to be identified and analysed, as all possible combinations of variables are assessed.

The results of the simulations were analysed using linear models and balanced multifactor analysis of variance (ANOVA) in RStudio (version 1.0.136). A visual residual analysis was performed to check for normality in the distribution of residuals, and to ensure there was no trend in the residuals in relation to the output.

Modelled retention/transport was the dependent variable and the model variables (*Spawning area, Year, Month, Depth, Trial*) were the explanatory factors in the linear models and ANOVA. A full crossed model with all possible interactions up to the 2nd degree (2-way interactions) was applied to the output. The adjusted R^2 and p-values were noted, as well as all main and interaction effects. The R^2 values indicate the proportion of the total variance in the dependent variable that is explained by each model. The relative variance explained by each factor was calculated as the proportion of the total sum of squares (SS) explained by the sum of squares of each factor (equation 2.1).

$$\% \text{Variance explained} = \frac{\text{SS}_{\text{factor}}}{\text{SS}_{\text{total}}} \times 100 \quad (2.1)$$

Chi-squared (χ^2) tests were used to test whether noticeable seasonal peaks and troughs in retention/transport success were significant ($p < 0.05$). The simulated seasonal pattern of retention/transport success was compared to a mean distribution of the simulated success rates. If significant departure from the mean distribution was observed, a *post-hoc* test was conducted to identify the months that caused the deviation. Data from the identified months were then removed and the χ^2 test was repeated. In the case that the repeated test was non significant, it was assumed that the removed months were responsible for the deviation, and the seasonal peaks and troughs were significant.

Chapter 3

Comparing modelled transport and retention of sardine (*Sardinops sagax*) eggs and larvae off South Africa using two configurations of the Regional Ocean Modelling System

Abstract

The South African sardine population is hypothesised to consist of western, southern and eastern stocks, each of which has distinct spawning grounds, and management of the sardine fishery needs to take account of this structure and likely mixing between stocks. The western stock spawns and recruits off the west coast, and whereas the southern stock spawns and mostly recruits off the south coast, this stock also makes an annually varying contribution to west coast recruitment. A particle-tracking individual-based model (IBM), coupled with either an older 3-D hydrodynamic model configuration or a more recent, higher resolution configuration, was used to investigate how ocean dynamics affect the transport and retention of sardine eggs and larvae around South Africa. Estimating the proportion of eggs spawned off the south coast that recruit off the west coast, and how this may vary, was a focus. The effects of spawning area, and month, year, and depth of particle release, were investigated for each coupled 3D-IBM simulation using linear models. Qualitatively-similar results are obtained when using the two 3-D hydrodynamic model configurations but some quantitative differences are observed, with a higher contribution to west coast recruitment from south coast spawning in the higher resolution model (20.9% transport success) compared to the lower resolution model (7.6% transport success).

3.1 Introduction

Although upwelling systems all over the world provide productive habitats that small pelagic fishes thrive in, they are fiercely dynamic and constantly changing. Eggs and larvae of sardine are planktonic in their early stages and therefore the circulation of the region is a primary determinant of where they will end up (Nelson and Hutchings, 1987). The South African sardine (*Sardinops sagax*) population is hypothesised to consist of western, southern and eastern stocks, each of which has distinct spawning grounds, with a likely degree of mixing between stocks (van der Lingen et al., 2015; Butterworth et al., 2016). The South African purse seine fishery targets sardines off the west and south coasts, and therefore these two stocks are the focus of this dissertation. The western stock spawns and recruits off the west coast, whereas the southern stock spawns and mostly recruits off the south coast. This stock also makes an annually-varying contribution to west coast recruitment via some eggs and larvae being transported from the south coast to the west coast recruitment area (Figure 1.2). This stock structure and the extent to which the south coast spawning biomass contributes to recruitment to the west coast stock needs to be taken into account in the sardine fishery management procedure.

Estimating and quantifying the mixing has been the focus of many recent discussions, including the Annual International Stock Assessment Review Workshop (de Moor and Butterworth, 2015; Butterworth, 2016a,b; Coetzee, 2016; de Moor, 2016a,b; de Moor et al., 2016; van der Lingen et al., 2016). The proportion of early life history stages spawned on the south coast and transported to the west coast, termed P_0 , has been a particular focus. A high P_0 value, as suggested by some investigations cited above, indicates mixing one stock, whilst a low P_0 indicates two largely separate stocks.

In an effort to understand the life history strategies of small pelagic fishes in the Southern Benguela, a suite of studies using bio-physical individual-based models (IBMs) was conducted in the early to mid 2000s (Mullon et al., 2002; Huggett et al., 2003; Parada et al., 2003; Miller, 2006 and Miller et al., 2006). Except for Miller (2006) and Miller et al. (2006), these studies were largely focused on anchovy and made use of a hydrodynamic model forced by climatological winds (Penven et al., 2001). Miller et al. (2006) modelled the effects of physical-biological interactions and spatial variability in spawning and nursery areas on the transport and retention of sardine eggs and larvae. A temperature-dependent development model was incorporated into a particle-tracking IBM and coupled with the hydrodynamic model, PLUME, forced by interannual winds. Miller et al. (2006) showed that recruitment could occur in two distinct nursery areas on the west and south coasts of South Africa, with an average south coast to west coast transport success rate

(P_0) of $\sim 9\%$ was suggested.

The 2016 International Stock Assessment Review Panel Report (Dunn et al., 2016) recommended revisiting Miller et al. (2006)'s method using a more recent and higher resolution 3D hydrodynamic model configuration with the aim of eventually adding more biological realism. Advances and developments in hydrodynamic modelling and computing power in the last decade, since Miller et al. (2006), have enabled models of higher temporal and spatial resolution, as well as improved forcings and numerical schemes. It is important to understand if results obtained by Miller (2006) and Miller et al. (2006) will change with the improvements in 3D hydrodynamic model configurations. The simulations presented in this chapter examine the transport and retention of sardine eggs and larvae within physical environments provided by two model configurations of different generations. The first is PLUME, previously used for a sardine IBM for the Southern Benguela by Miller (2006) and Miller et al. (2006), and the second is BENGSAFE, a more recent, better resolved configuration. As recommended by the International Stock Assessment Review Panel Report, keeping the IBM the same and only varying the hydrodynamic model configuration it is coupled with will allow comparisons to be made and the effect of different resolutions on transport and retention success to be analysed, and provide more confidence in estimates of P_0 .

3.2 Methods

3.2.1 Experimental design

Modelling process

The modelling process in this chapter has three stages (experimental design, IBM simulations and statistical analyses), following Miller et al. (2006) and which are displayed in detail in Figure 3.1. For each simulation a total of 10 000 particles was released randomly over all nine spawning areas (Figure 3.2), every month from June 1991 to July 1999, at three different depth ranges. The distribution of particles tends to a uniform distribution due to the large number of particles, and the number of particles released in each spawning area was dependent on the size of the area. The 10 000 particles were released in batches for the 30 days, and each particle was tracked for 60 days. Particles were released every 2 days in the PLUME IBM and every 3 days in the BENGSAFE IBM. At every IBM timestep, the hydrodynamic velocities (u , v , and w) were used to estimate the horizontal and vertical trajectories of particles and then move the particles accordingly. A brief summary of the two hydrodynamic models is shown in Table 3.1. Comparisons of model

SST and RMS SLA were conducted and are detailed in Section 2.1.3. The IBM timestep when coupled with PLUME was 34560s (9.6 hours), and when coupled with BENGSAFE was 2160s (36 minutes). Temperature was also estimated every IBM timestep using the hydrodynamic model outputs. Because of the lethal temperature criterion, if a particle was exposed to water colder than 13°C, the particle was considered to be dead and was removed from the simulation. Each particle increased in age with each IBM time step until it satisfied the criteria for recruitment or reached the maximum age without successfully recruiting. In both cases the particle was then removed from the simulation. The recruitment criteria were: reaching a recruitment area and remaining there for the length of the hydrodynamic model output, and being aged between 14 days and a maximum age of 60 days. Each particle’s spawning area, year, month and depth of release were recorded, as well as the recruitment area, if the particle successfully recruited.

Each simulation was run three times (*Trial*) to determine whether the initial random position of particles within release areas affected the model results. It is important that *Trial* has a negligible effect so that the effects of the different variables can be analysed with confidence.

Table 3.1: The configuration details for the hydrodynamic models used in this study, PLUME and BENGSAFE

	PLUME	BENGSAFE
Domain	40°- 28°S, 10°- 24°E	22°- 45°S, 5°- 35°E
Horizontal resolution	1/12°decreasing offshore	1/15°
Vertical levels	20	100
Wind forcing	Weekly ERS 1/2	6 hourly CSFR
Heat and salinity forcing	COADS	SODA
Frequency	2 day outputs	3 day outputs

Fixed parameters and variables

Table 3.2 displays the fixed parameters and variables used in the simulations and their values or ranges, for each hydrodynamic model.

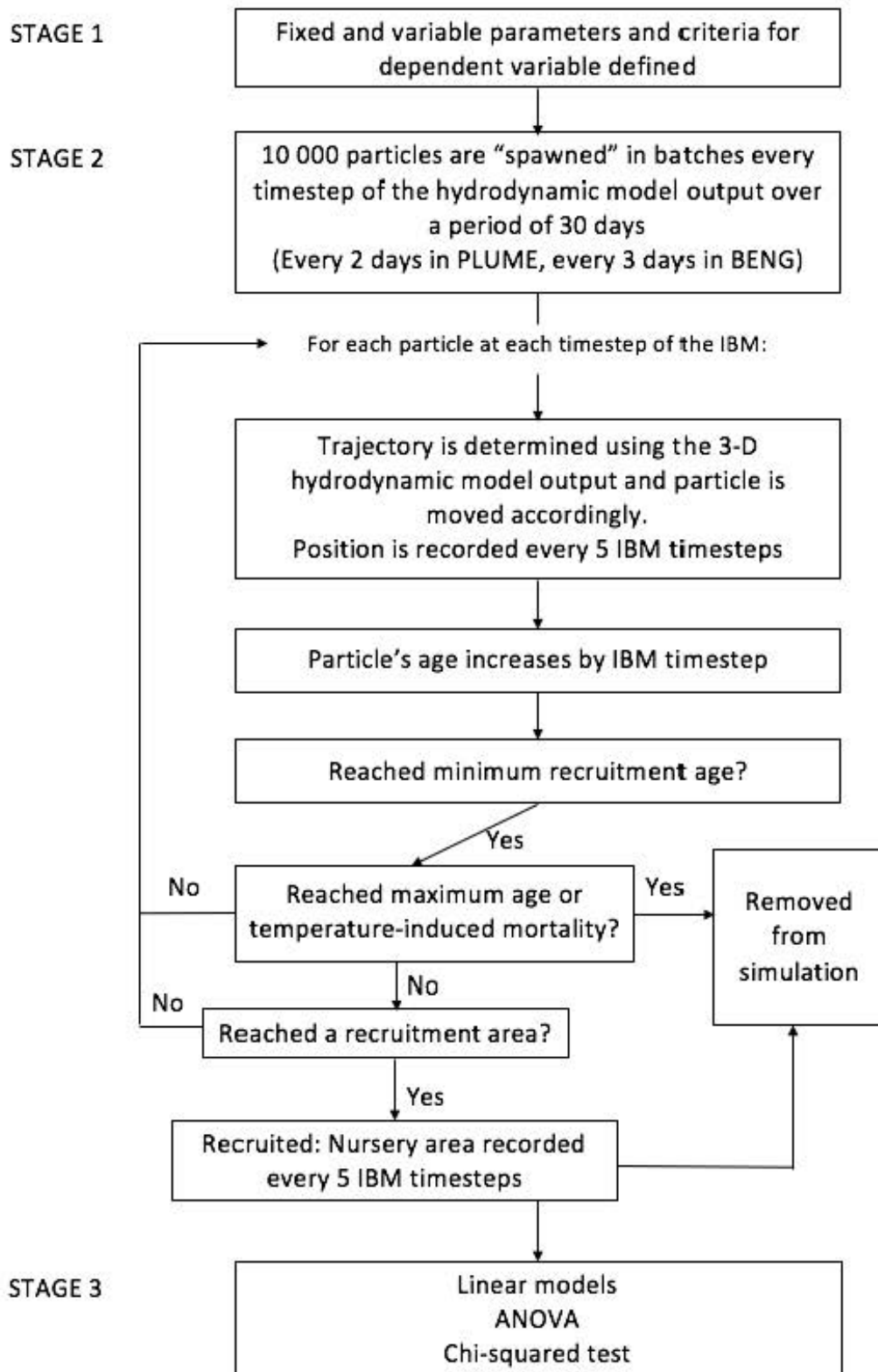


Figure 3.1: Methodological approach of the modelling process. Adapted from Miller (2006).

Table 3.2: The fixed parameters and variables used in the IBM simulations of sardine spawning and recruitment in the Southern Benguela.

	PLUME	BENGSAFE	<i>n</i>
Fixed Parameters			
Number of particles	10 000	10 000	-
Duration of release of particles	30 days	30 days	-
Particles released every	2 days	3 days	-
Tracking period	60 days	60 days	-
Lethal minimum temperature	13°C	13°C	-
IBM timestep	34560s (9.6hr)	2160s (36min)	-
Position recorded every	2 days	3 hours	-
Variables			
<i>Spawning Area</i>	See Figure 3.2	See Figure 3.2	9
<i>Year</i>	91/92-98/99	91/92-98/99	8
<i>Month</i>	July-June	July-June	12
<i>Depth</i>	0-25m, 25-50m, 50-75m	0-25m, 25-50m, 50-75m	3
<i>Trial</i>	3	3	3
Total number of simulations			864

Spawning Areas

The nine defined spawning areas (*Spawning Area*, Figure 3.2) are identical to those in Miller (2006) and Miller et al. (2006). They were chosen to encompass as much of the widespread spawning area of sardine as the PLUME model domain would allow. Sardine spawn off the west coast and over the entire Agulhas Bank and into Algoa Bay, and sometimes even as far east as Durban (van der Lingen et al., 2015). However, the PLUME domain does not allow spawning areas to be defined east of Cape St Francis. The BENGSAFE model domain extends further up the east coast but the spawning areas were kept the same as in the PLUME simulations to allow for accurate comparisons. The five Agulhas Bank areas (western Agulhas Bank (WAB), central Agulhas Bank inshore and offshore (CABin and CABoff), and eastern Agulhas Bank inshore and offshore (EABin and EABoff) were originally set according to previous IBM experiments in the region (Huggett et al., 2003; Parada et al., 2003) and are retained by convention. In reality, inshore areas have low spawning intensity compared to the high intensity offshore spawning areas (Coetzee et al., 2008b; Figure 1.4), particularly east of Cape Agulhas. The 125m isobath from the model bathymetry, which more accurately represents the 100m isobath due to topographical smoothing, separates these inshore and offshore spawning areas. The remaining four spawning areas are on the narrower west coast shelf (upper west coast inshore and offshore (UWCin and UWCoff), and lower west coast inshore and offshore (LWCin and LWCoff). The inshore areas are confined between the coast and the

200m isobath from the model bathymetry, while the offshore areas are confined between the 200m and 500m isobaths. It is thought that the position of the frontal jet, which acts to transport small pelagic fish eggs and larvae to the west coast recruitment area, varies between the 200m and 500m isobaths (Boyd et al., 1992; Hutchings et al., 2002).

For this dissertation, UWCin, UWCoff, LWCin, LWCoff and WAB are considered west coast spawning areas, while CABin, CABoff, EABin and EABoff are considered south coast spawning areas. This differs from Miller et al. (2006) where the WAB was considered a south coast spawning area. However, WAB is west of Cape Agulhas, which is an important ecological boundary (Hutchings et al., 2002; Coetzee et al., 2008b,a), so by convention WAB is considered a west coast spawning area in this dissertation.

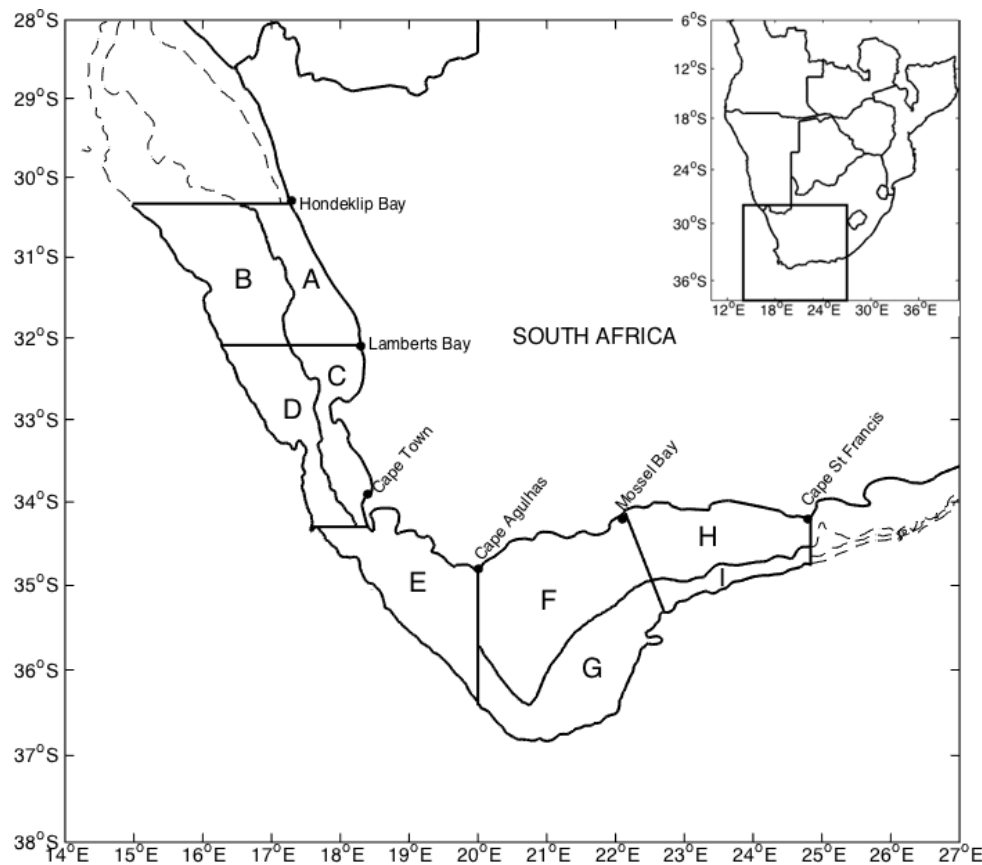


Figure 3.2: The nine spawning areas defined in the IBM simulations. A = upper west coast inshore (UWCin), B = upper west coast offshore (UWCoff), C = lower west coast inshore (LWCin), D = lower west coast offshore (LWCoff), E = western Agulhas Bank (WAB), F = central Agulhas Bank inshore (CABin), G = central Agulhas Bank offshore (CABoff), H = eastern Agulhas Bank inshore (EABin), I = eastern Agulhas Bank offshore (EABoff). The 125, 200 and 500m isobaths are displayed by dashed lines.

Dependent variables

Two recruitment areas were defined for this chapter, identical to the ones used in Miller (2006) and Miller et al. (2006) (Figure 3.3): one on the west coast, following convention in the region, and one on the south coast, encompassing the quasi-permanent cool ridge, each up to the 500m isobath. Particles were considered recruited if they were located in either recruitment area within 60 days of release and were older than 14 days. The dependent variable used in the linear models and analyses of variance (ANOVAs) was the percentage of particles released from each spawning area that was successfully recruited in either of the recruitment areas (modelled retention or modelled transport). Temperature-induced mortality, the percentage of particles from each spawning area that was removed from the simulation due to lethal temperature, was computed and investigated, but not used as a dependent variable in the linear models and ANOVAs.

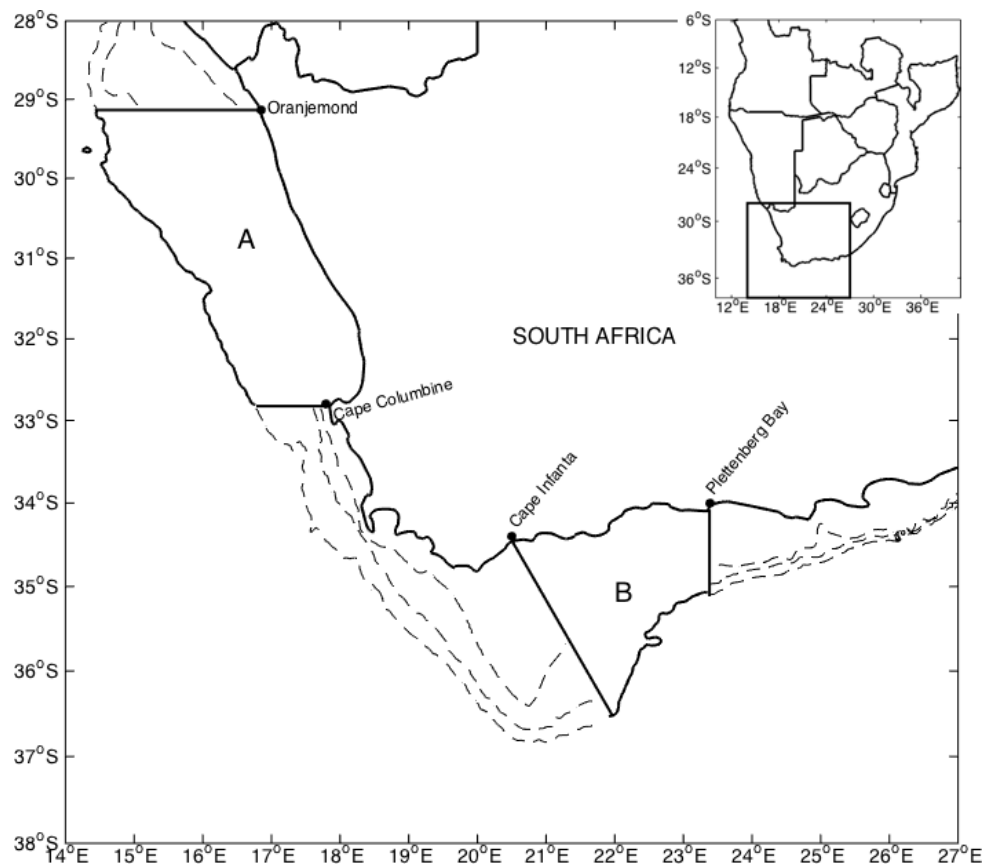


Figure 3.3: The two recruitment areas defined in the IBM simulations. A = west coast (WC), B = south coast (SC). The 125, 200 and 500m isobaths are displayed by dashed lines.

3.2.2 Statistical analyses

Based on findings by Miller et al. (2006), results from the simulations were divided into four systems depending on where the particles were spawned and recruited:

1. West coast - west coast system (WC-WC): Particles were released in the west coast spawning areas and were retained in the west coast recruitment area.
2. West coast - south coast system (WC-SC): Particles were released in the west coast spawning areas and were transported to the south coast recruitment area.
3. South coast - west coast system (SC-WC): Particles were released in the south coast spawning areas and were transported to the west coast recruitment area.
4. South coast - south coast system (SC-SC): Particles were released in the south coast spawning areas and were retained in the south coast recruitment area.

For each system, an analysis of variance, with multiple factors and one dependent variable was applied to the modelled retention/transport results. The variables in the models (*Spawning area*, *Year*, *Month*, *Depth* and *Trial*) were explanatory factors in the linear models. A full factorial design to the 2^{nd} degree was used, meaning all possible two-way interactions between factors were analysed in the ANOVAs, except for *Trial*, which was not included in the interaction terms. The R^2 and p values for each model were noted, as well as the effects of main and interaction terms on variance. Compliance with assumptions of linear models was checked by examining residuals (Section 2.4). Important main and interaction effects were plotted and visually examined. *Post-hoc* chi-squared (χ^2) tests were conducted to examine seasonal patterns and identify months with significant peaks and troughs.

3.3 Results

Figures 3.4 and 3.5 display snapshots of the Lagrangian particle movement of particles obtained from the PLUME and BENGSAFE IBMs, respectively. For both models, similar patterns of movement are seen for all depth ranges in both January and July (a and b). However, particles released shallower tend to be advected further offshore and are dispersed over a greater area than those released deeper. Offshore advection on the west coast is greater in January, in both IBMs, because of the seasonal, wind-induced upwelling in this region. This results in greater advective losses of particles released on the west coast in all depth ranges, but especially those released in the upper depth range, near the surface. Although west coast offshore advection is evident in both models, the extent is greater in the BENGSAFE IBM. West coast alongshore transport from Cape Agulhas to Cape Columbine, where particles are spread offshore (particularly in summer), is more evident in the BENGSAFE IBM throughout the year. For both the PLUME and BENGSAFE IBM there is little movement of particles released on the LWC in July, and particles released on the WAB are transported north-westwards by the jet current, slightly offshore of the LWC spawning area. There is much more movement of particles from the CAB to inshore of the west coast in the BENGSAFE IBM compared to the PLUME IBM, where a large portion of these particles are advected offshore. In both IBMs this south coast to west coast transport is greater in January than July. In the PLUME IBM there is little movement of particles released on the EAB, in both months. This is not the case in the BENGSAFE IBM, where a portion of the particles released on the Agulhas Bank are advected to the south-west, especially in July, when particles are initially advected southwards within the first 8 days after release.

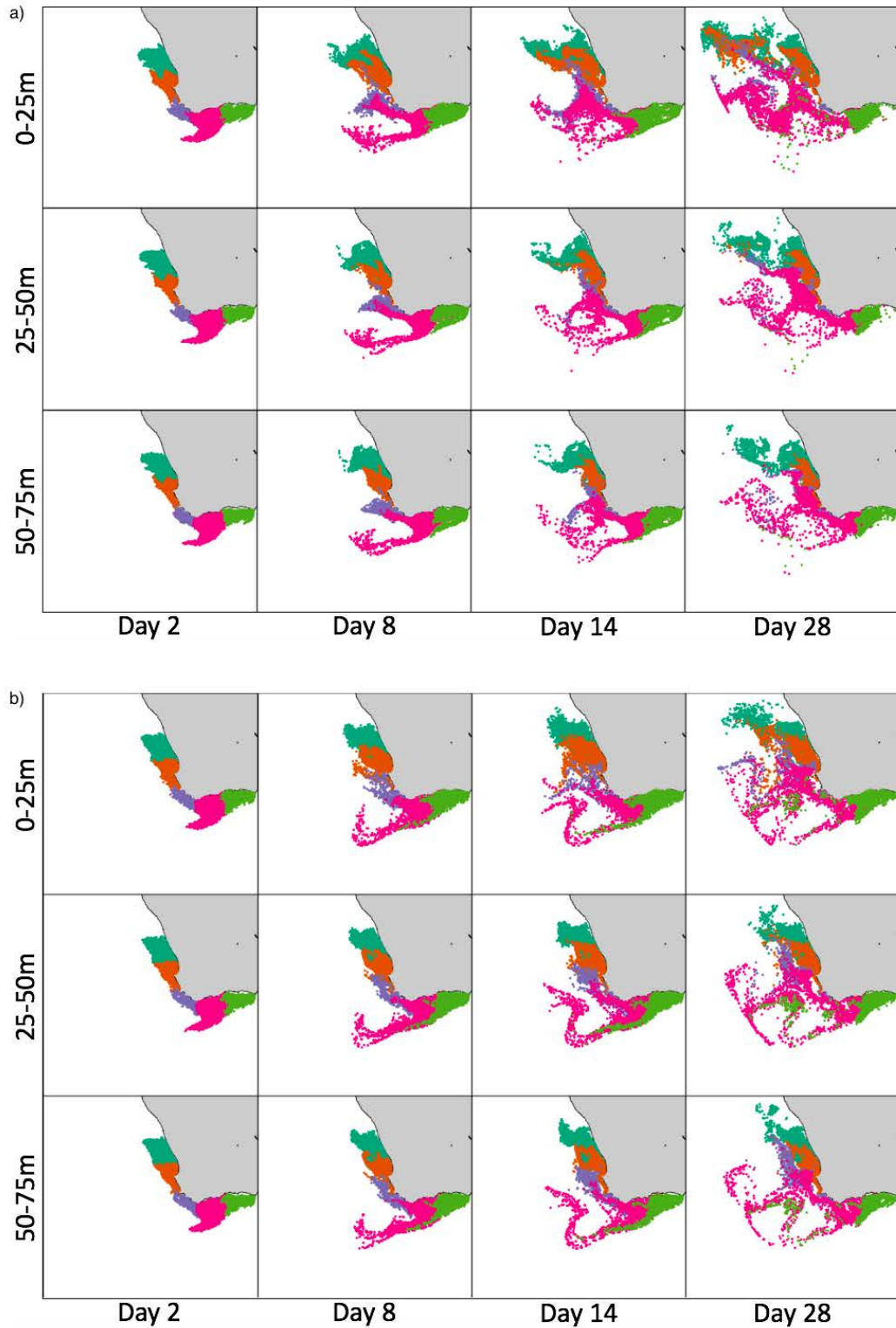


Figure 3.4: Snapshots of particles being transported within the PLUME model domain at 4 periods (2, 8, 14 and 28 days) post release and for 3 depth ranges of release. 10 000 particles were released in spawning areas during a) January and b) July in the year representing 1994. Inshore and offshore spawning areas are combined (UWC = dark green, LWC = orange, WAB = purple, CAB = pink, EAB = light green). Depth ranges indicate the initial range of depths of release.

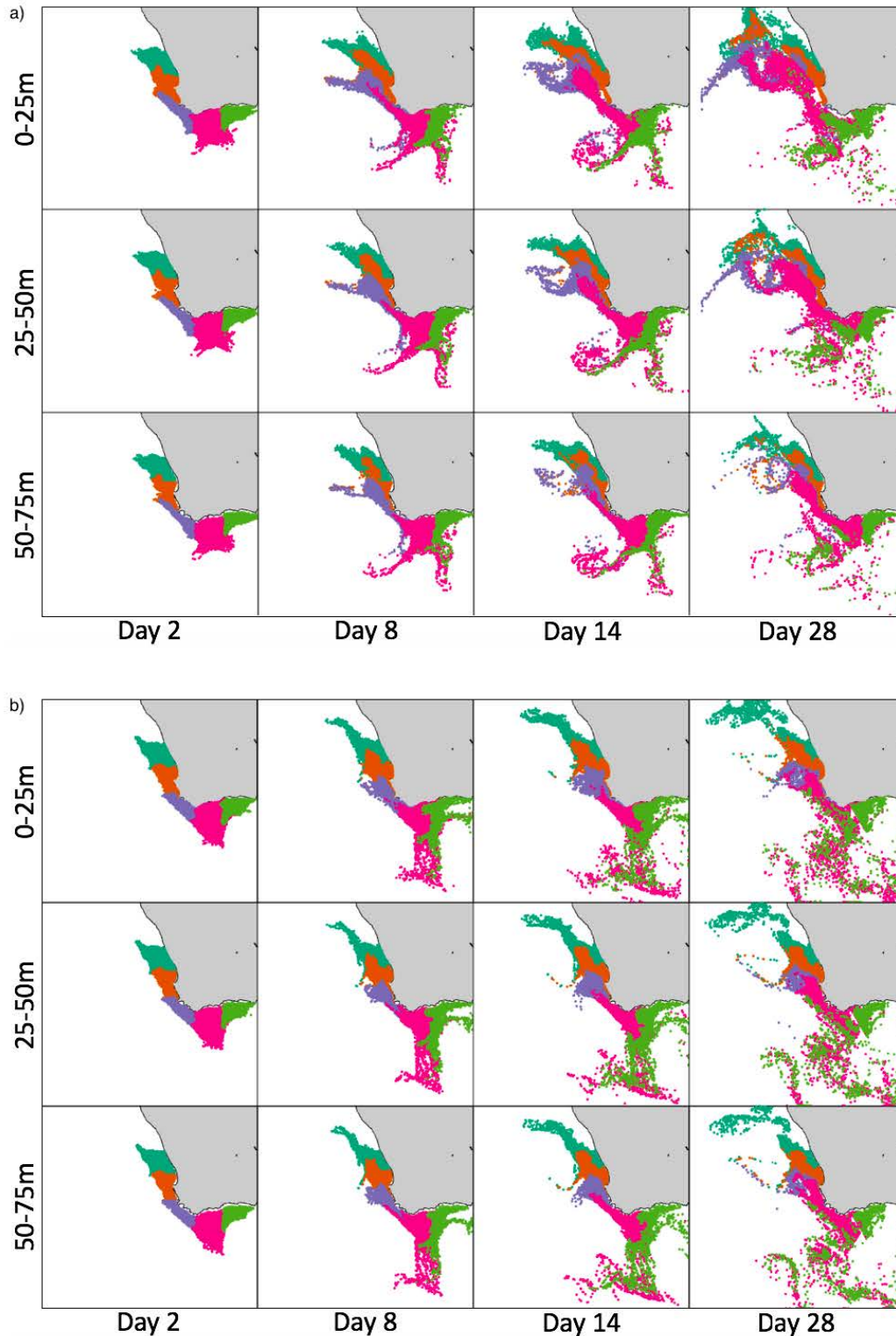


Figure 3.5: Display of particles being transported within the BENGSAFE model domain at 4 periods (2, 8, 14 and 28 days) post release and for 3 depth ranges of release. 10 000 particles were released in spawning areas during a) January and b) July in the year representing 1994. Inshore and offshore spawning areas are combined (UWC = dark green, LWC = orange, WAB = purple, CAB = pink, EAB = light green). Depth ranges indicate the initial range of depths of release.

3.3.1 Modelled retention/transport

Figure 3.6 displays modelled retention in, or transport to, the west and south coast recruitment areas from each of the nine spawning areas, irrespective of year, month, and depth of release for each hydrodynamic model. Overall, particles in PLUME showed slightly higher levels of successful retention/transport than those in BENGSAFE. For both PLUME and BENGSAFE, no particles released in the four most westerly spawning areas (UWCin, UWCoff, LWCin, LWCoff), and a small percentage ($< 5\%$ in PLUME, $< 1\%$ in BENGSAFE) released in the WAB, were transported to the south coast recruitment area. More than 50% of particles released in each west coast spawning area was retained on the west coast, with LWCoff being the most successful, in both PLUME and BENGSAFE. Few particles ($< 2\%$ in PLUME, $< 10\%$ in BENGSAFE) released on the eastern Agulhas Bank reached the west coast recruitment area, however, the portion of particles released on the south coast (CABin, CABoff, EABin, EABoff) that were transported to the west coast recruitment area was larger in BENGSAFE than in PLUME. In general, south coast retention of particles released on the south coast was higher in PLUME than in BENGSAFE, the greatest difference seen in particles released in EABoff. In PLUME, particles released on the eastern Agulhas Bank showed the highest rates of retention success in the south coast recruitment area, while in BENGSAFE similarly high rates were only achieved by particles released in EABin. Of the particles released on the central Agulhas Bank in PLUME, a higher portion was retained on the south coast than was transported to the west coast. However, the opposite was observed in BENGSAFE, with an increase in transport to the west coast recruitment area from those south coast spawning areas.

As a result of the very low values of south coast recruitment from the west coast spawning areas, this recruitment system (released on the west coast and transported to the south coast (WC-SC)) was not analysed further. The WC-WC and SC-SC retention systems and the SC-WC transport system were explored.

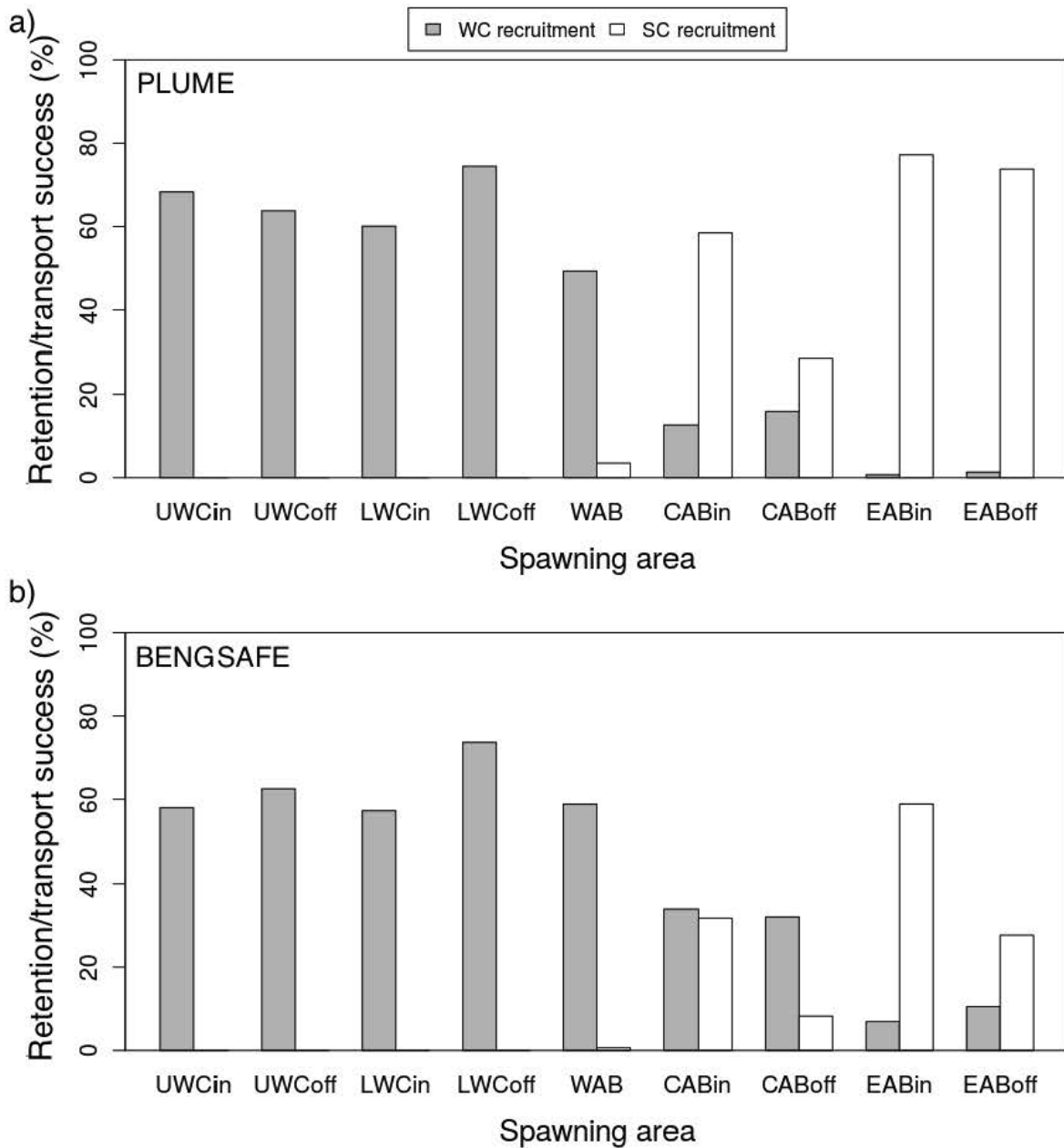


Figure 3.6: Modelled retention/transport success to the west (grey) and south (white) coast recruitment areas from the nine spawning areas, irrespective of year, month and depth of release, for a) PLUME and b) BENGSAFE.

The WC-WC system

The main effects and two-way interactions explained 61.96% and 73.38% of the variance observed in the percentage of retention success for the PLUME IBM and BENGSAFE IBM, respectively, in the WC-WC system (Table 3.3). The residuals of retention success were normally distributed and no trends were found, therefore model assumptions were satisfied. For both hydrodynamic models, the primary determinant of retention success was the interaction between *Spawning area* and *Depth*, which explained 23.92% and 29.82% of the variance in retention success for PLUME and BENGSAFE, respectively. This indicates that the impact of *Spawning area* on retention success depends on the depth of release, and vice versa (Figure 3.7). For the inshore spawning areas (UWCin and LWCin) highest retention success is achieved by particles released in the upper depth range (0-25m), and retention success decreases with depth in PLUME and even more so in BENGSAFE. The opposite pattern is observed for the offshore areas (UWCoff, LWCoff) and WAB, where retention success is lowest in the upper depth range and either increases with depth (PLUME) or remains at a similar level (BENGSAFE).

For the IBM coupled with PLUME, *Spawning area* explained the second most variance seen in retention success (12.47%) followed by *Month* (6.85%). However, when coupled with BENGSAFE, *Month* appeared to be more important than *Spawning area*, explaining 11.40% of the variance in retention success, while *Spawning area* explains 6.39%. This is displayed in Figure 3.8; the seasonality of recruitment success from the inshore spawning areas (UWCin and LWCin), as well as the western Agulhas Bank, is much more pronounced in the BENGSAFE IBM. Retention success for particles released in these areas in the BENGSAFE IBM is high (70-90%) in winter and low (30-50%) in summer. Particles released in the WAB spawning area display different seasonal patterns of retention in each of the IBMs; in the PLUME IBM moderate ($\sim 50\%$) retention is achieved throughout the year until a decrease from March to June, whereas in the BENGSAFE IBM retention is lowest in summer and highest in winter, maintaining moderately high levels of retention in spring. Particles released in the offshore spawning areas (UWCoff and LWCoff) show much less seasonality. In the BENGSAFE IBM retention success of particles released in the UWCoff area is highest in winter. In general, the retention success of particles released in the inshore areas of the two IBMs is more similar than those released in the offshore areas and WAB.

Table 3.3: Analysis of variance results for the WC-WC retention system using data from the PLUME and BENGSAFE simulations. All F values were significant at $p < 0.01$ except those for the *Trial* factor. The effect explaining the most variance is shown in bold. df = degrees of freedom.

Factor	PLUME			BENGSAFE		
	df	% Variance explained	F value	df	% Variance explained	F value
Spawning area	4	12.47	5291	4	6.39	2580
Month	11	6.85	1057	11	11.40	1673
Year	7	0.51	123	7	0.75	174
Depth	2	3.72	3159	2	11.18	9026
Spawning area x Month	44	4.69	181	44	8.33	306
Spawning area x Year	28	3.25	198	28	1.38	79
Spawning area x Depth	8	23.92	5075	8	29.82	6018
Month x Year	77	4.51	99	77	1.60	34
Month x Depth	22	1.95	151	22	2.41	177
Year x Depth	14	0.09	11	14	0.11	13
Trial	2	0.00	0	2	0.00	0
Model	219	61.96		219	73.38	
Error	64580	38.04		42980	26.62	

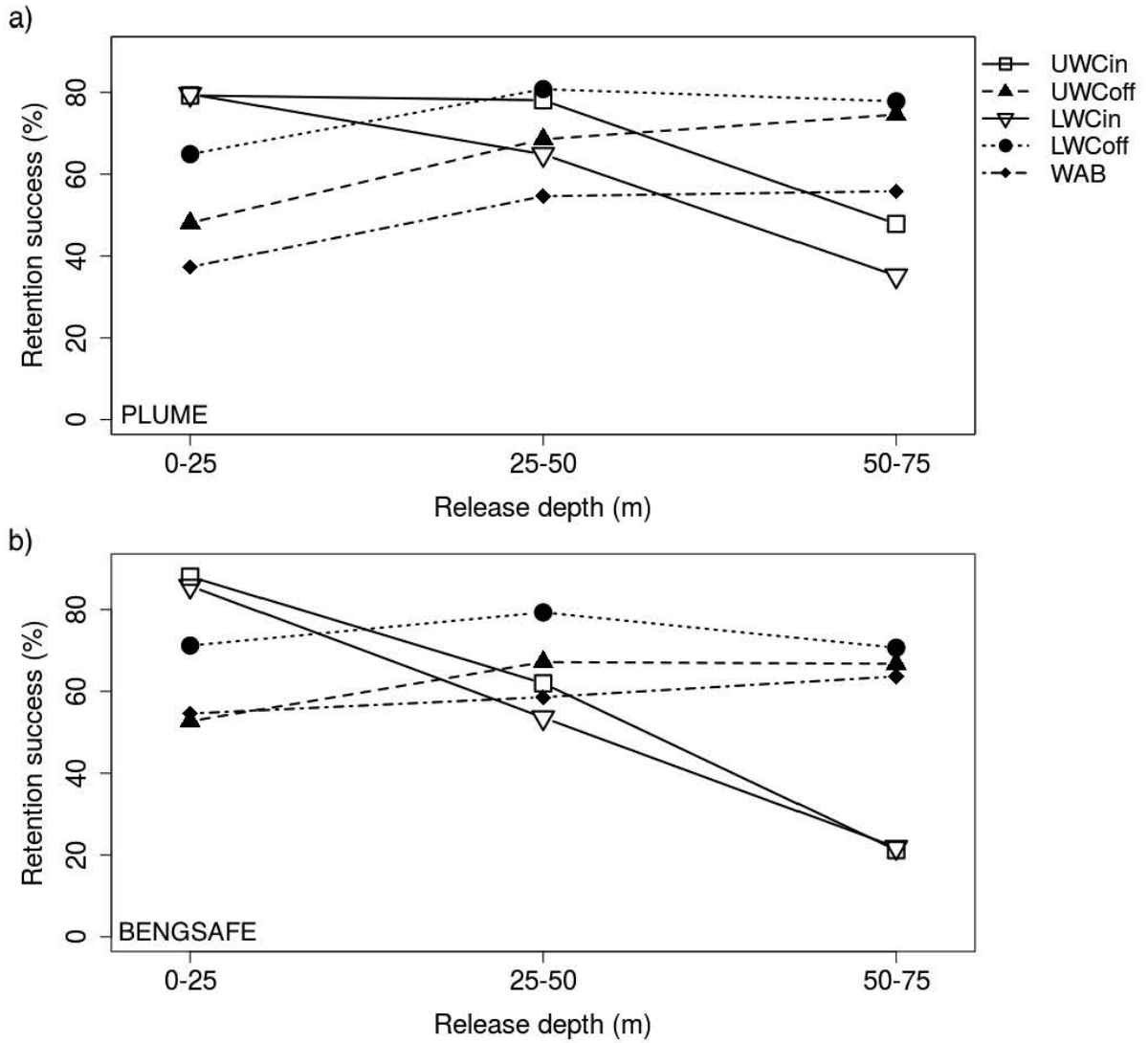


Figure 3.7: Modelled retention success for each spawning area in the WC-WC system per depth of release for a) PLUME and b) BENGSAFE.

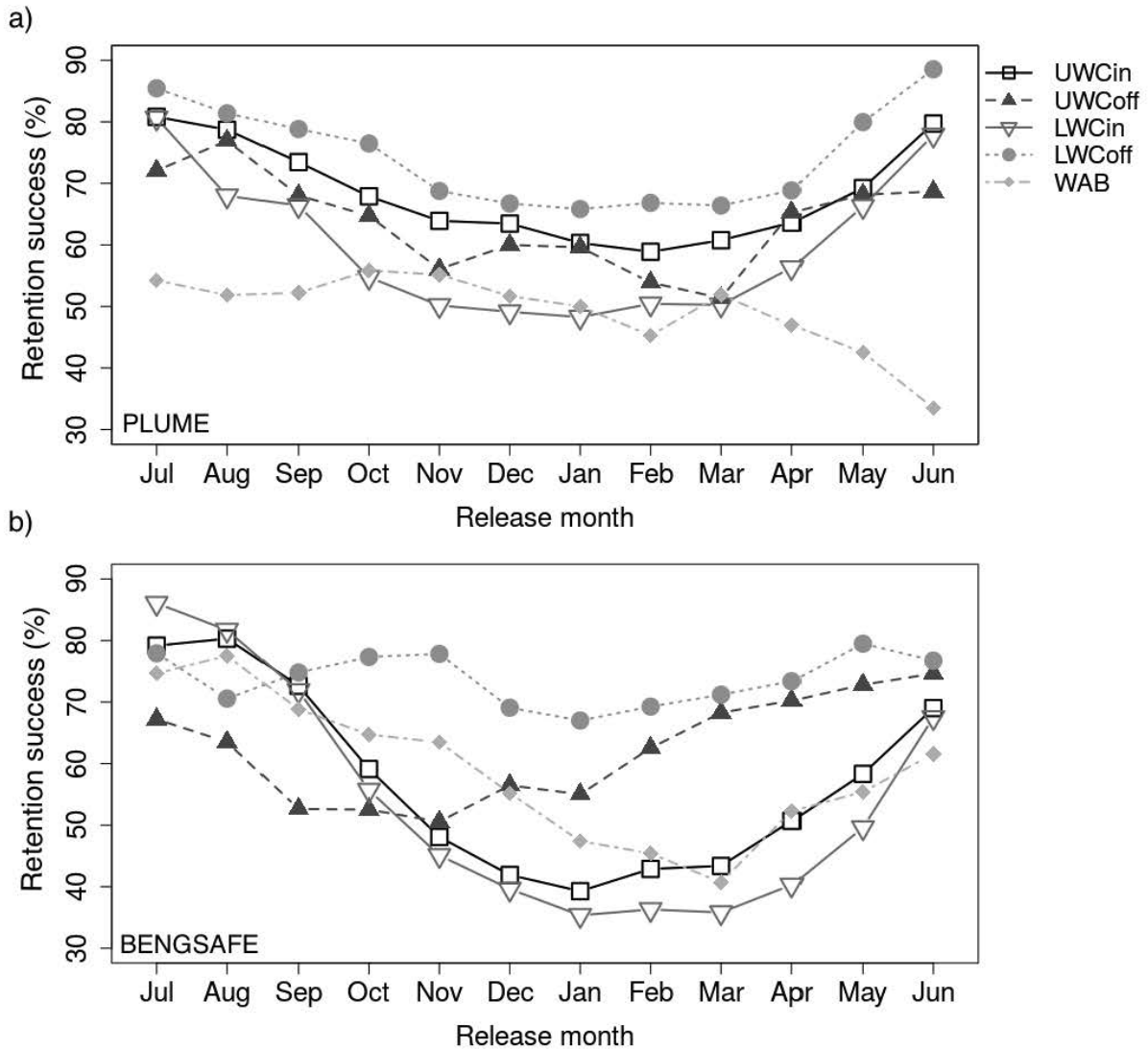


Figure 3.8: Modelled retention success for each month per spawning area in the WC-WC system for a) PLUME and b) BENGSAFE.

The SC-WC system

For the PLUME IBM, 66.26% of the variance observed in transport success was explained by the linear model, while for the BENGSAFE IBM, 70.68% was explained by the linear model (Table 3.4). Model assumptions were satisfied. The factor *Spawning area* explained the most variance in transport success for both PLUME and BENGSAFE (39.19% and 38.55% respectively). Figure 3.9 shows that particles released in the central Agulhas Bank spawning areas (CABin and CABoff) achieved a higher transport success to the west coast recruitment area than those released in the eastern Agulhas Bank areas, for both PLUME and BENGSAFE. Transport success in general was higher for all SC-WC spawning areas in the BENGSAFE IBM compared to the PLUME IBM. CABin and

CABoff had similar levels of transport success in each IBM ($\sim 15\%$ in PLUME, $\sim 35\%$ in BENGSAFE). However, in PLUME CABoff was slightly higher than CABin whereas in BENGSAFE the opposite was the case.

Month was important in both models, explaining 6.86% and 7.79% of the variance in transport success computed by the PLUME and BENGSAFE IBMs, respectively. In addition the interaction between *Spawning area* and *Month* explained 6.49% and 7.25% in PLUME and BENGSAFE respectively (Figure 3.10). Transport success by particles released in the central Agulhas Bank spawning areas (CABin and CABoff) within the PLUME model showed a bimodal pattern, with peaks in November and March (Figure 3.10a). Very low transport success ($\sim 1\%$), with no seasonality, was observed in the particles released in the eastern Agulhas Bank spawning areas (EABin and EABoff). For the PLUME IBM there was no significant monthly effect on modelled transport success from the chi-squared analysis ($\chi^2 = 17.2$, $df = 11$, $p\text{-value} = 0.10$). In the BENGSAFE simulations, CABin and CABoff showed a different seasonal pattern to that observed with PLUME (Figure 3.10b); a singular peak was present in August/September with a trough from February to May, both patterns being prominent in the CABin. Again, the eastern Agulhas Bank spawning areas showed little seasonality, although higher transport success compared to the PLUME IBM. There was a significant monthly effect on modelled transport in the BENGSAFE IBM from the chi-squared analysis ($\chi^2 = 23.1$, $df = 11$, $p\text{-value} = 0.02$), which disappeared when the months representing the peak (August-September) ($\chi^2 = 11.4$, $df = 9$, $p\text{-value} = 0.25$) or the trough (February-April) ($\chi^2 = 14.6$, $df = 8$, $p\text{-value} = 0.07$) were removed. This supports the importance of the seasonal variability for the successful transport of particles to the west coast.

The interaction between *Month* and *Year* explained 6.24% and 11.15% of the overall variance in the PLUME and BENGSAFE IBMs, respectively. For PLUME, inter-annual variation in transport success was reduced in winter and varies greatly from September to March (Figure 3.11a). The peaks observed in October and March were clear in the years 91/92 and 92/93, but not so obvious in later years. For BENGSAFE, inter-annual variation was also lower in winter than in summer (Figure 3.11b). Particles released in 91/92 have a peak in transport success in January, which isn't observed in any other year. Seasonality seems to increase with time as a pattern of higher transport success in June-October and lower transport success in January-May becomes more obvious in the later years (93/94-98/99).

Table 3.4: Analysis of variance results for the SC-WC transport system using data from the PLUME and BENGSAFE simulations. All F values were significant at $p < 0.01$ except those for the *Trial* factor. The effect explaining the most variance is shown in bold. df = degrees of freedom.

Factor	PLUME			BENGSAFE		
	df	% Variance explained	F value	df	% Variance explained	F value
Spawning area	3	39.19	19992	3	38.55	15060
Month	11	6.86	955	11	7.79	830
Year	7	1.12	244	7	1.38	231
Depth	2	1.02	783	2	0.16	94
Spawning area x Month	33	6.49	301	33	7.25	258
Spawning area x Year	21	1.70	124	21	1.34	75
Spawning area x Depth	6	2.02	516	6	1.96	382
Month x Year	77	6.24	124	77	11.15	170
Month x Depth	22	1.39	97	22	0.92	49
Year x Depth	14	0.22	25	14	0.18	15
Trial	2	0.00	0	2	0.00	1
Model	198	66.26		198	70.68	
Error	51641	33.74		34361	29.32	

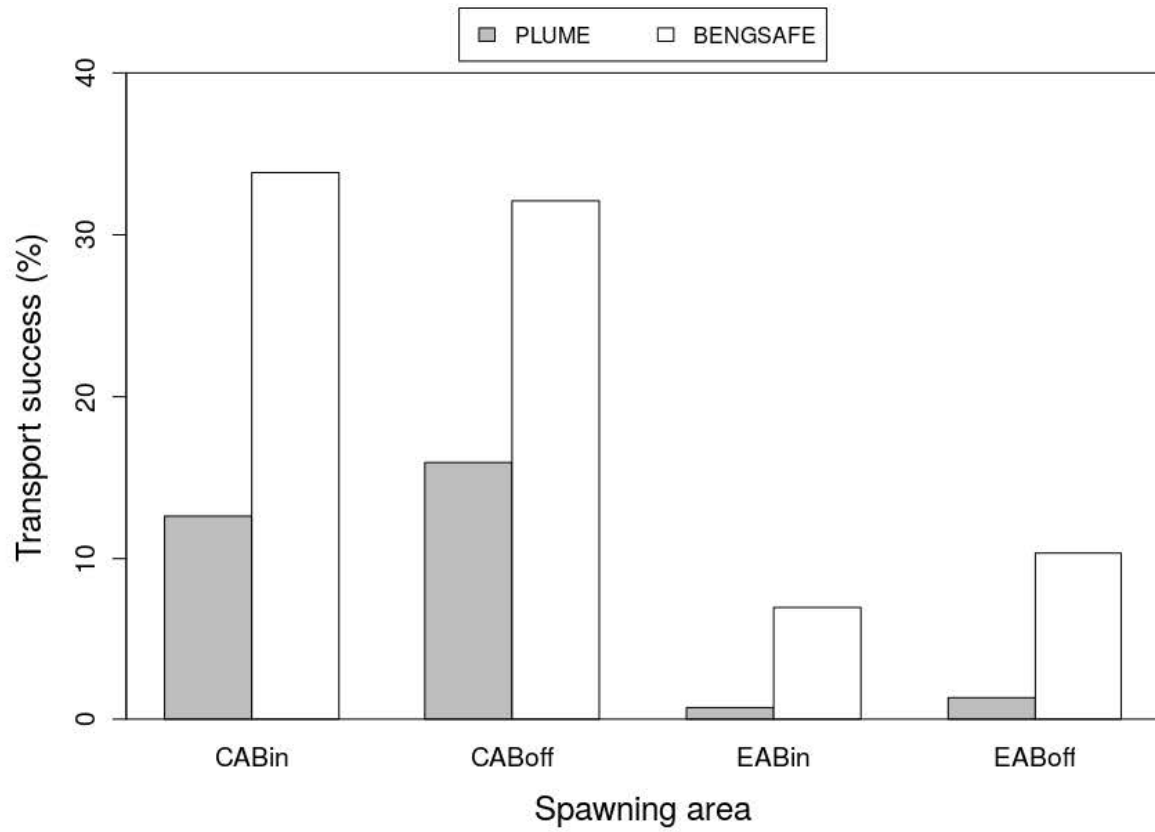


Figure 3.9: Modelled transport success for each spawning area in the SC-WC system for PLUME and BENGSAFE.

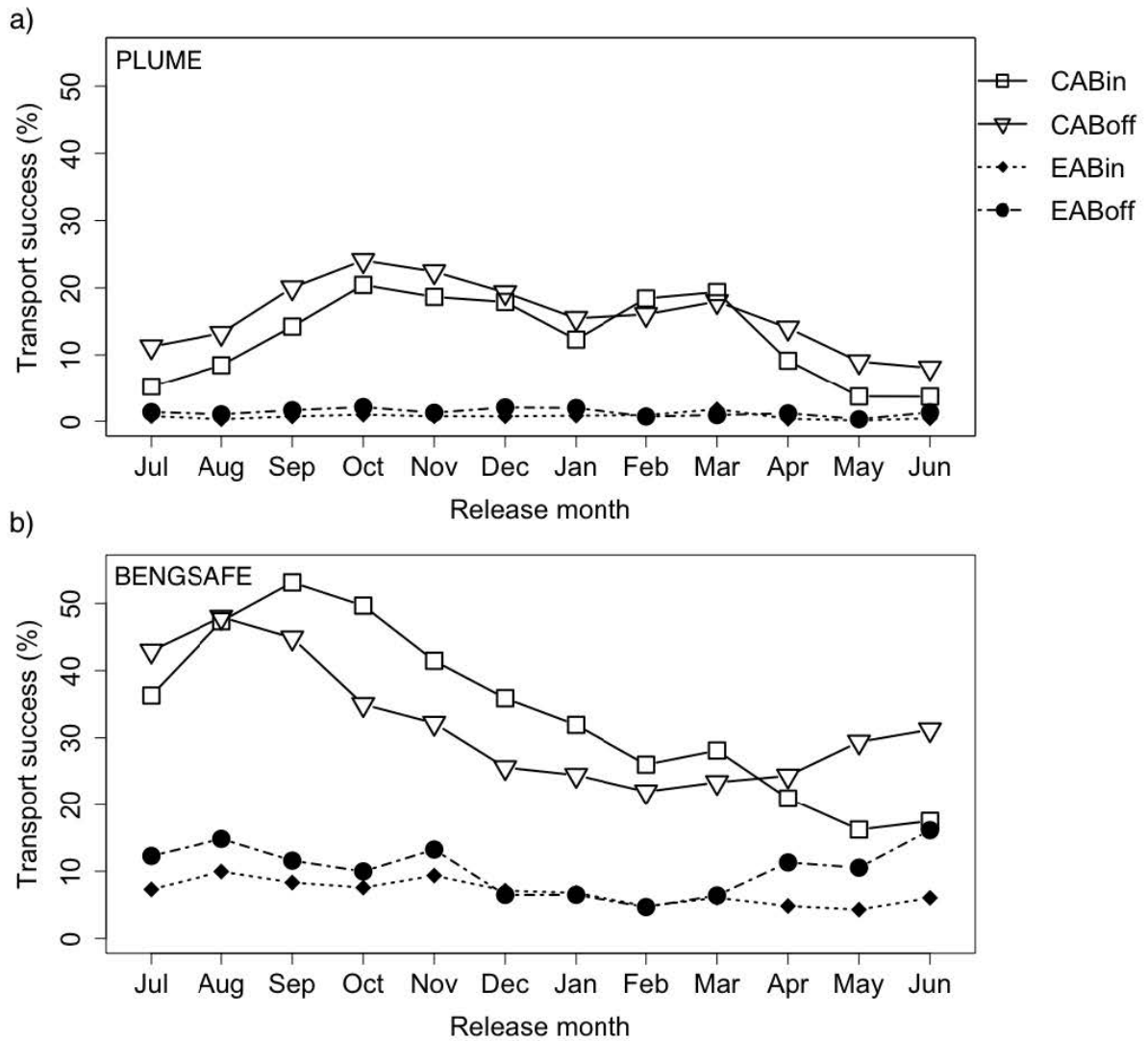


Figure 3.10: Modelled transport success for each spawning area per month in the SC-WC system for a) PLUME and b) BENGSAFE.

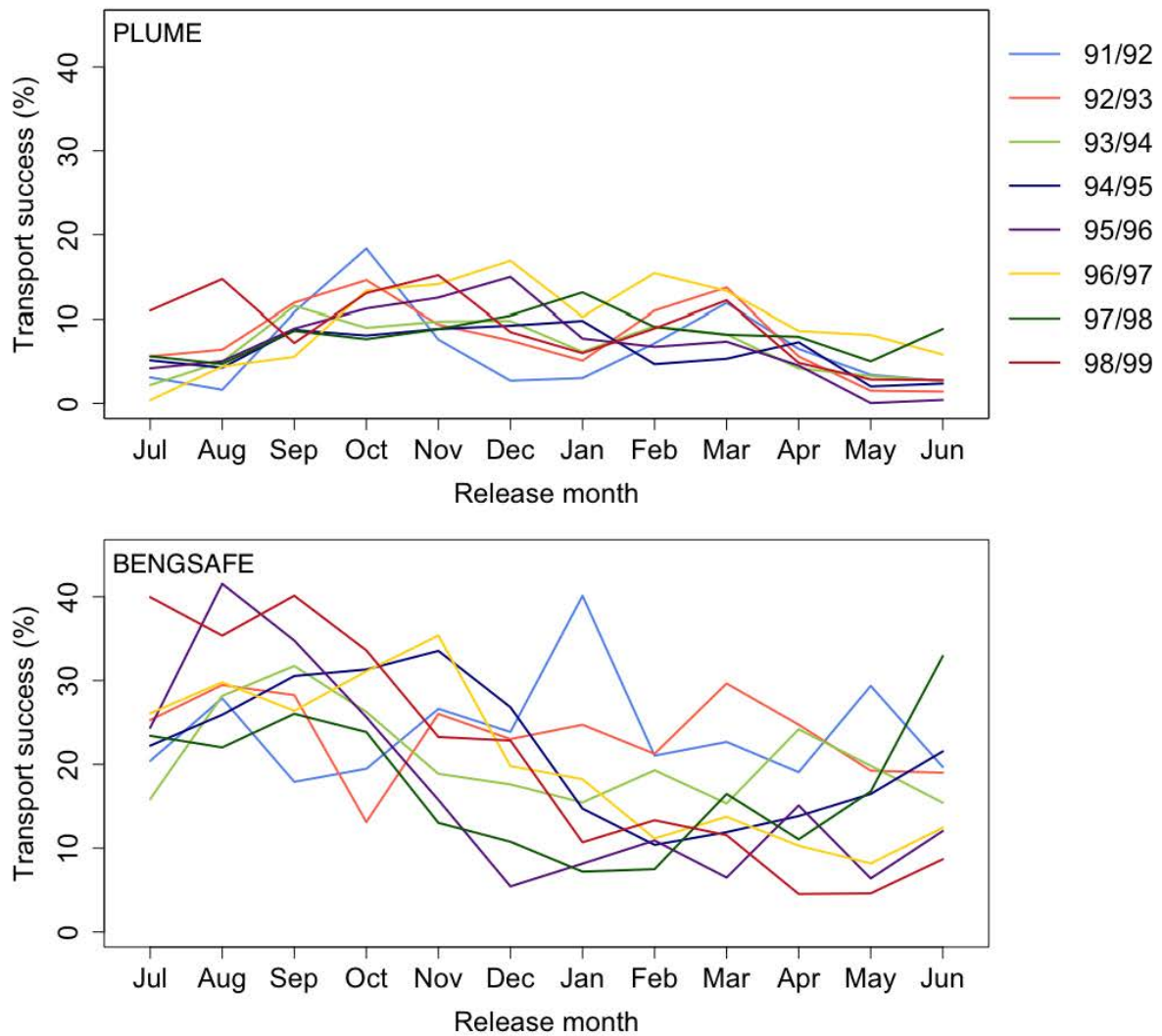


Figure 3.11: Modelled transport success for each release month per release year in the SC-WC system for a) PLUME and b) BENGSAFE.

The SC-SC system

The main effects and two-way interactions explained 70.74% and 63.97% of the total variance observed in the percentage of retention for the PLUME and BENGSAFE simulations, respectively. The residuals of retention success were normally distributed and no trends were found, therefore model assumptions were satisfied. *Spawning Area* explained the majority of the variance in both models (52.34% for PLUME, 44.87% for BENGSAFE). Figure 3.12 shows the modelled retention success for each south coast spawning area for both PLUME and BENGSAFE. For both of the hydrodynamic models, EABin was the most successful spawning area and CABoff was the least successful spawning area. Overall, retention success was lower in all spawning areas when coupled with BENGSAFE

than with PLUME, but a similar pattern was observed in both models. In particular, EABoff success rate was much lower when coupled with BENGSAFE ($\sim 25\%$) than when coupled with PLUME ($\sim 75\%$).

Figure 3.13a displays the interaction between *Spawning area* and *Month* in the PLUME IBM, which explained 10.96% of the variance in the model output. The eastern Agulhas Bank spawning areas (EABin and EABoff) and the central Agulhas Bank spawning areas (CABin and CABoff) showed opposing intra-annual patterns; particles released in CABin and CABoff achieved their highest retention success in winter, when EABin and EABoff displayed their lowest retention success.

The interaction between *Month* and *Year* explained 6.36% of the variance in the BENGSAFE IBM linear model (Figure 3.13b); in most but not all years, retention success was higher in winter. There was no significant monthly effect on modelled retention success in either the PLUME ($\chi^2 = 4.85$, $df = 11$, $p\text{-value} = 0.94$) or BENGSAFE IBMs ($\chi^2 = 4.85$, $df = 11$, $p\text{-value} = 0.94$) from the chi-squared analyses.

Table 3.5: Analysis of variance results for the SC-SC retention system using data from the PLUME and BENGSAFE simulations. All F values were significant at $p < 0.01$ except those for the *Trial* factor. The effect explaining the most variance is shown in bold. df = degrees of freedom.

Factor	PLUME			BENGSAFE		
	<i>df</i>	% Variance explained	F value	<i>df</i>	% Variance explained	F value
Spawning area	3	52.34	30796	3	44.87	13875
Month	11	1.09	175	11	2.90	245
Year	7	0.17	43	7	0.46	62
Depth	2	1.50	1325	2	0.59	274
Spawning area x Month	33	10.96	586	33	3.96	111
Spawning area x Year	21	1.02	86	21	1.33	59
Spawning area x Depth	6	1.51	443	6	0.97	149
Month x Year	77	1.70	39	77	6.36	77
Month x Depth	22	0.37	29	22	1.19	50
Year x Depth	14	0.08	11	14	0.33	22
Trial	2	0.00	0	2	0.00	0
Model	198	70.74		198	62.97	
Error	51641	29.26		34361	37.04	

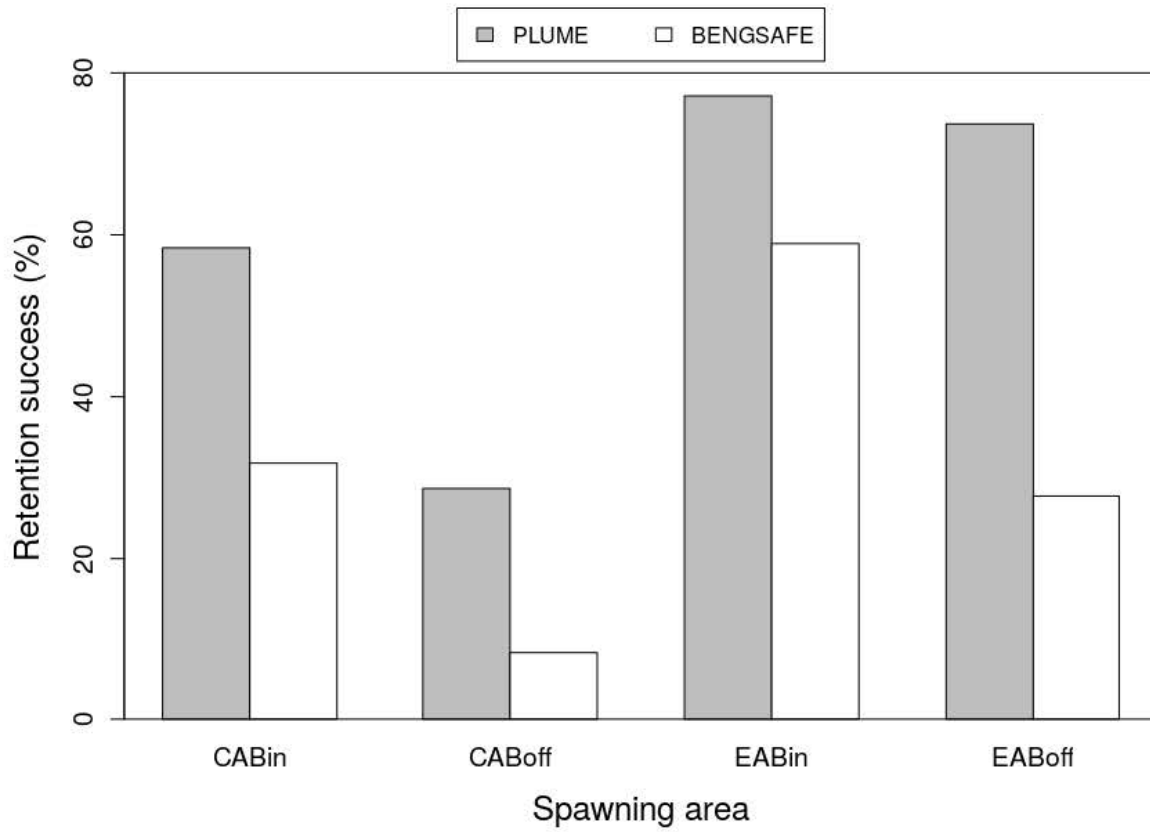


Figure 3.12: Modelled retention success for each spawning area in the SC-SC system for PLUME and BENGSAFE.

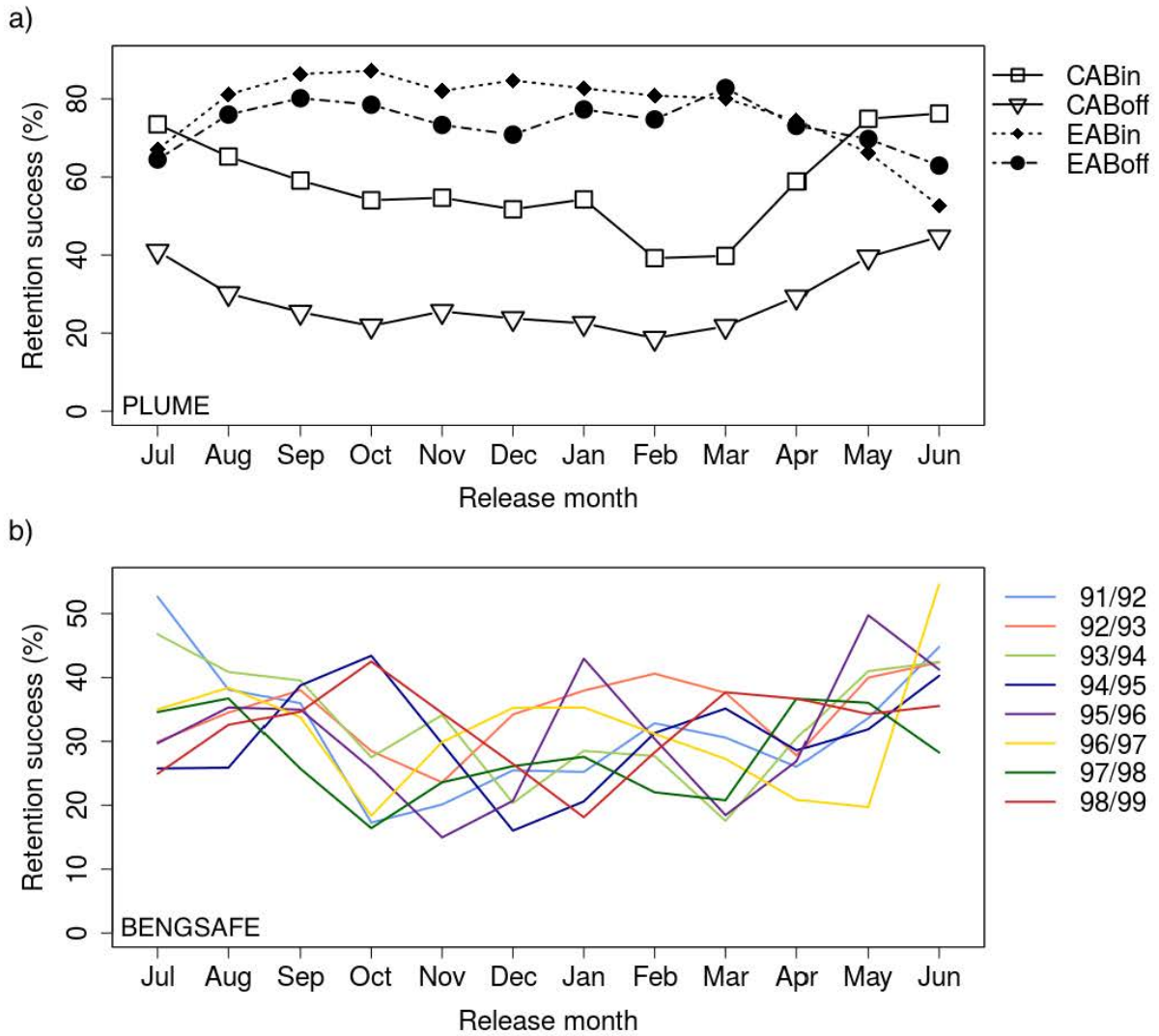


Figure 3.13: Modelled retention success for a) each spawning area in the SC-SC system per release month in PLUME and b) each release year per release month in BENGSAFE.

3.3.2 Modelled Mortality

Particles that were not successfully retained or transported to a recruitment area were either removed from the simulation, having been subjected to temperatures below 13°C, or were advected offshore to unsuitable conditions away from recruitment areas, out of the domain.

Spawning area

Temperature-induced mortality and advection losses from the PLUME and BENGSAFE IBMs display similar overall patterns with respect to spawning area (Figure 3.14). In both cases, temperature-induced mortality was highest for particles released inshore on the west coast (UWCin, LWCin). For all other spawning areas, mortality due to advection was the dominant scenario. A much larger proportion of particles ($\sim 60\%$) in the BENGSAFE IBM was advected offshore when released in the offshore EAB spawning area (EABoff) than in the PLUME IBM.

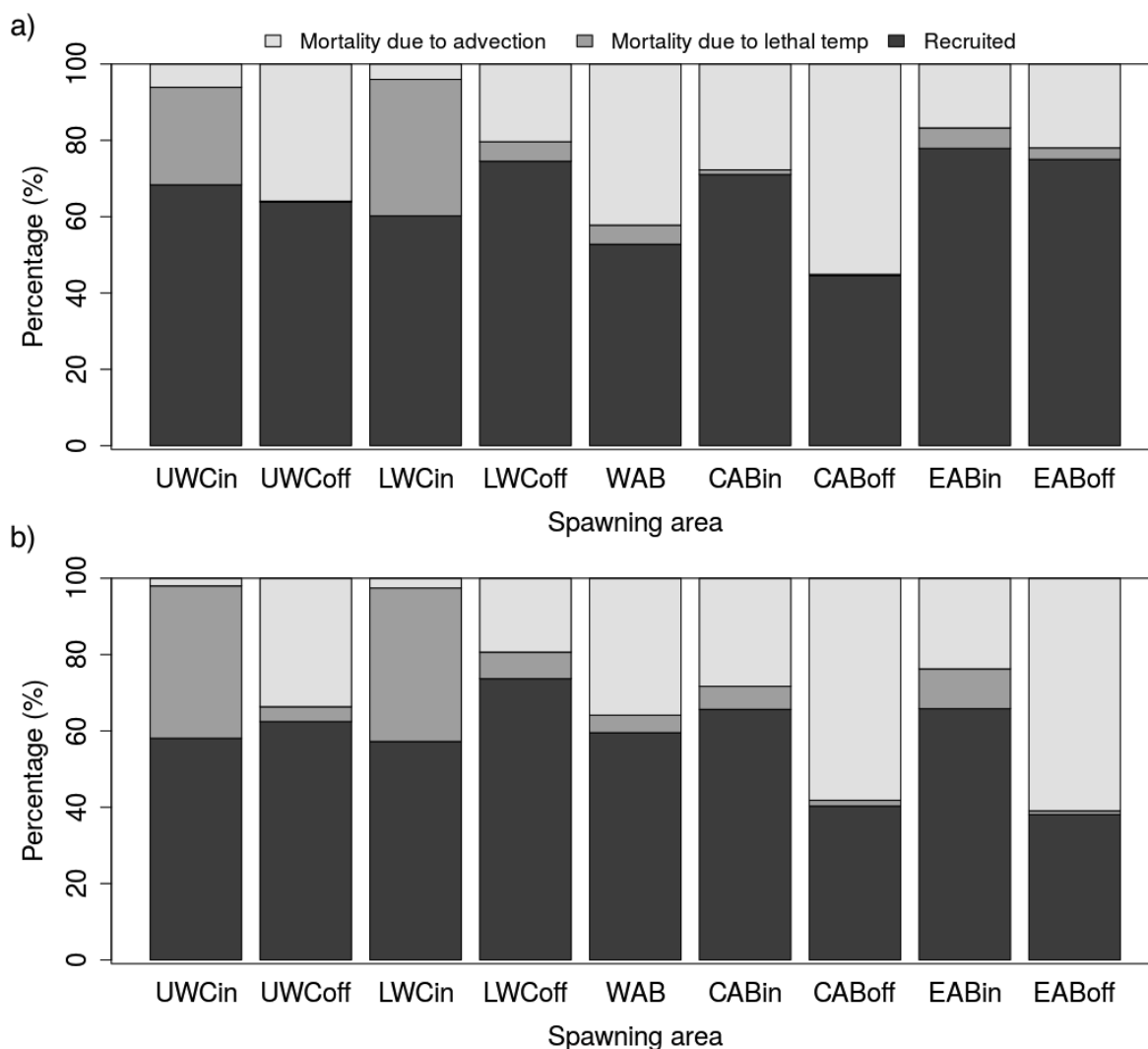


Figure 3.14: Modelled recruitment, mortality due to lethal temperature and mortality due to advection for all spawning areas, irrespective of month, year and depth, for a) PLUME and b) BENGSAFE.

Release month

A more prominent seasonal cycle in mortality is observed in the BENGSAFE IBM compared to the PLUME IBM results (Figure 3.15), but in both models mortality due to lethal temperature is greatest in summer. Advective loss is the primary cause of mortality in all release months, in both models.

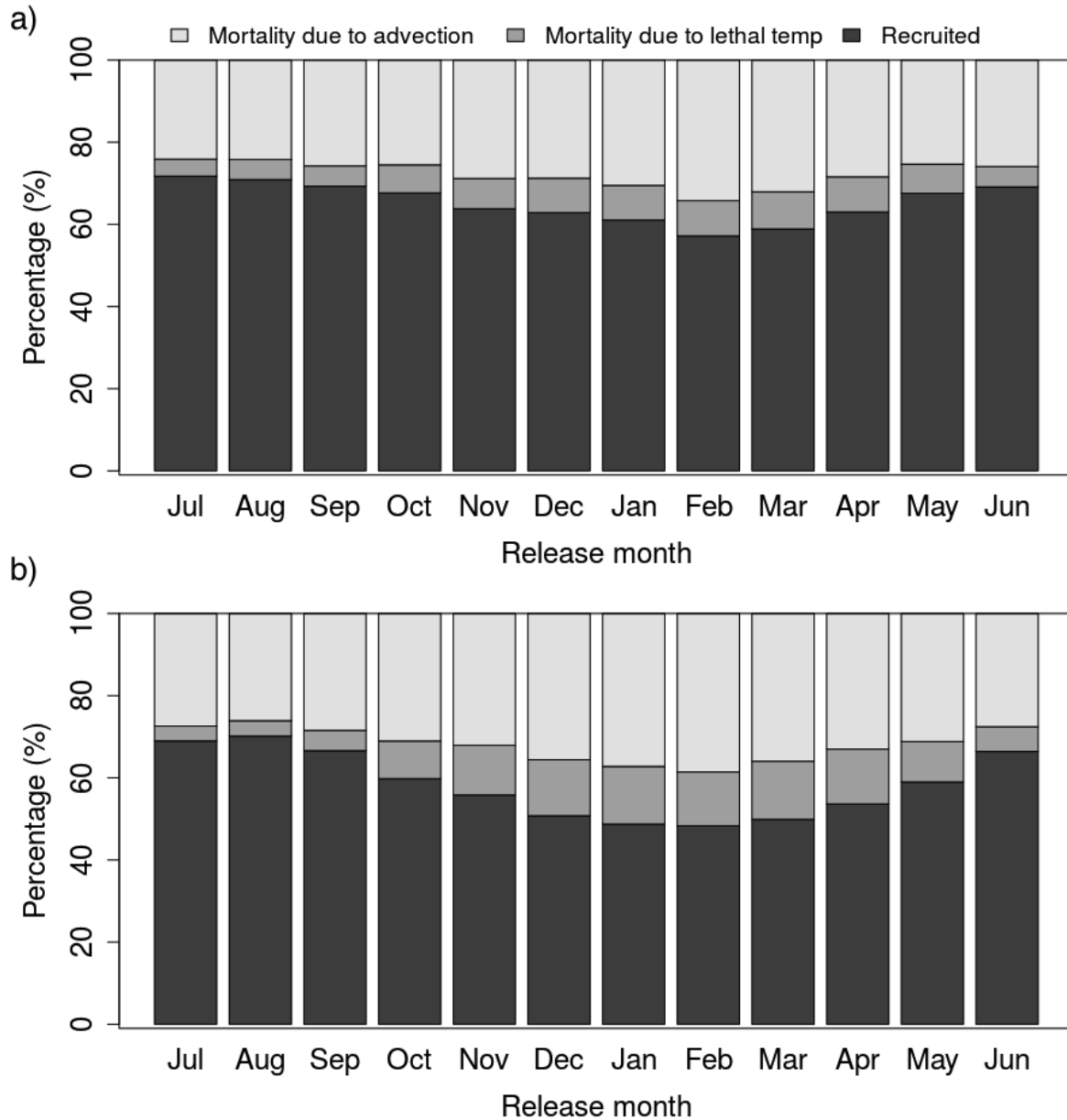


Figure 3.15: Modelled recruitment, mortality due to lethal temperature and mortality due to advection for each release month, irrespective of spawning area, year and depth, for a) PLUME and b) BENGSAFE.

Release year

Very little inter-annual variation in mortality is observed in either the PLUME or BENGSAFE IBMs (Figure 3.16). Temperature-induced mortality is slightly higher in the BENGSAFE IBM compared to the PLUME IBM, but a similar pattern is clear. There is a slight decrease in recruitment from 91/92 to 98/99 in the BENGSAFE IBM. The primary cause of mortality in all release years is advective loss.

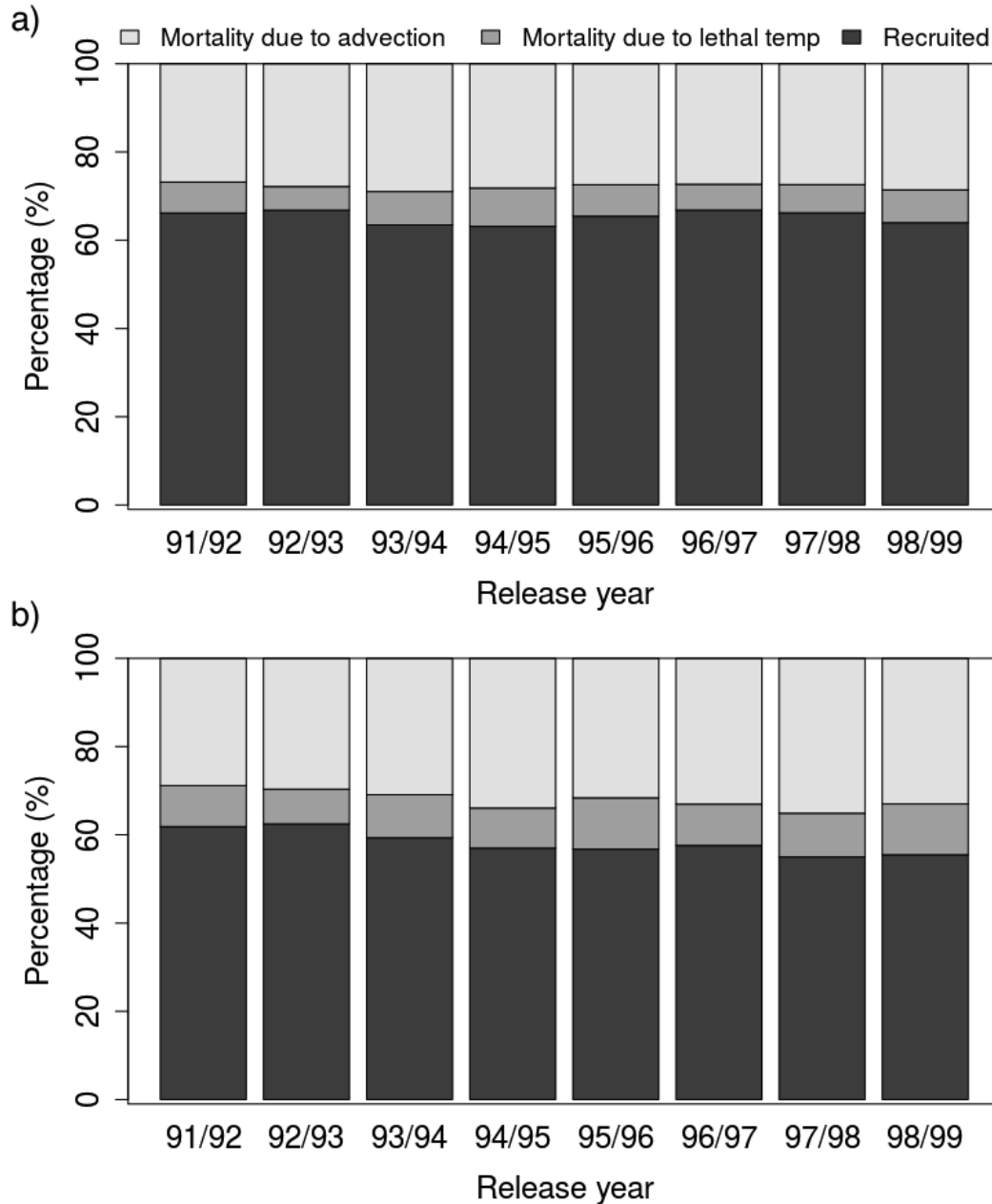


Figure 3.16: Modelled recruitment, mortality due to lethal temperature and mortality due to advection for each release year, irrespective of spawning area, month and depth, for a) PLUME and b) BENGSAFE.

Release depth

A pattern of increasing temperature-induced mortality and decreasing advection-induced mortality with depth is observed in both IBMs (Figure 3.17).

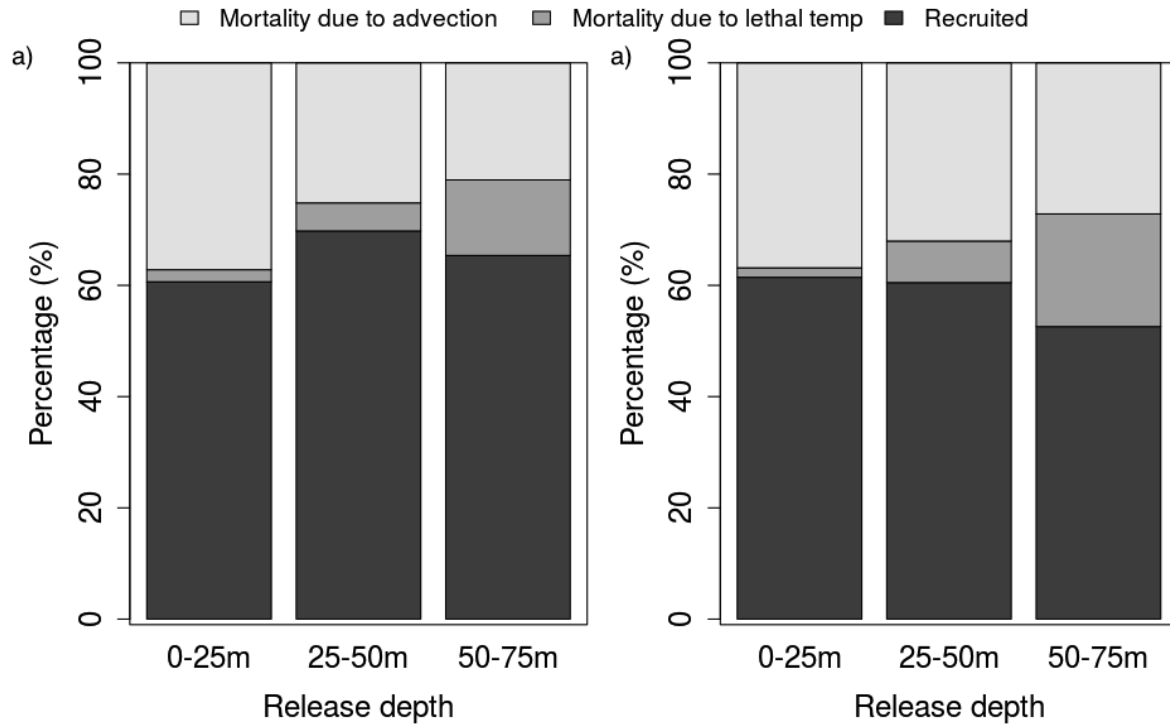


Figure 3.17: Modelled recruitment, mortality due to lethal temperature and mortality due to advection for each release depth, irrespective of spawning area, month and year, for a) PLUME and b) BENGSAFE.

3.4 Discussion

Results from the IBMs show how currents and advection in the region are likely to benefit or hinder the chances of successful recruitment of eggs spawned in different areas and at different times. The aim of this chapter was to investigate how different 3D hydrodynamic model configurations impact the results generated by the IBM.

From the initial recruitment results both the PLUME and BENGSAFE IBMs show the same general pattern, with three viable recruitment systems identified. Two of these systems were retention-based, where particles recruited in the same region they were spawned, and the other was transport-based. These identified systems match the current agreed-upon hypothesis for sardine stock structure in South Africa; western and southern substocks with discrete spawning grounds and a likely annual contribution from the south coast to west coast recruitment (van der Lingen et al., 2015; Butterworth et al., 2016). Results generated from both IBMs confirm the idea of discrete systems to the west and east of Cape Agulhas (WC-WC and SC-SC). In addition, the transport success results from the SC-WC system represent the the portion of eggs spawned east of Cape Agulhas and transported by currents into the west coast recruitment area.

It is important to address the various assumptions made about the IBMs when discussing their results (Section 2.2.1). Although hydrodynamic models provide good estimates of conditions, they are not complete replicas of reality and therefore it is possible that processes important to the retention and transport of eggs and larvae, especially extreme events or those of small spatio-temporal scales, are not represented in model outputs. It must also be highlighted that successful transport/retention does not necessarily equate to successful recruitment. There are a number of factors that could cause recruitment levels to fluctuate, for example predation and food constraints. The large populations of pelagic and mesopelagic planktivorous fish on the Agulhas Bank during summer, for example, could cause high levels of egg mortality in this area (Hutchings et al., 2002). Mortality due to temperature is only accounting for a portion of the realistic mortality rates. However, adding more complexities and imbedded mortality models in IBMs requires more computational power. One solution is the use of super-individuals to represent a number of individuals in an IBM, however this has been shown to reduce variability in results (Parry and Evans, 2008). Although spawning areas were based on recruitment and net tow survey results, the use of fixed boxes to define spawning and recruitment areas may be problematic as in reality sardine may choose to spawn and recruit in areas based on environmental, not spatial, conditions, which are likely to change over time.

The 28-day IBM dispersion plots (Figures 3.4 and 3.5) for January and June show both the seasonal differences within each model and the differences due to the respective underlying hydrodynamic model. Particles released near the surface in both IBMs were advected far offshore and dispersed over a large area, especially in January. This is likely due to wind-induced seasonal offshore Ekman transport being strongest in the surface layers at that time. The portion of particles transported offshore and the extent of the offshore drift was larger in the BENGSAFE than the PLUME IBM, which can be attributed to the model's higher spatial and temporal resolution (6 hourly and 0.34°) of wind forcing (CFSR), better resolving the degree of west coast upwelling. The higher frequency wind forcing in BENGSAFE could also be resolving downwelling events which occur between the upwelling events and are essential for successful recruitment. The BENGSAFE IBM displayed more movement of particles released on the south coast than the PLUME IBM, as well as a larger portion being transported to the west coast than in the PLUME IBM. The limited domain of PLUME only reached to 24°E , which could mean that the influence of the Agulhas Current and resulting mesoscale features were not properly simulated by the coarse climatological forcings at its boundaries, as implied by Figure 2.4.

The interaction between *Spawning area* and *Depth* was the most important determinant of retention success for the WC-WC system in both IBMs. This implies that the effect that a particle's release depth has on its retention success depends on the particle's area of release (Figure 3.7). For particles released in the inshore spawning areas (UWCin and LWCin) it was advantageous to be spawned in the shallow depth range, where particles were able to avoid cold temperatures and therefore temperature-induced mortalities at depth, and were sufficiently far inshore not to be subjected to intense offshore transport out of the recruitment area. Temperature-induced mortality was highest for particles released in these two inshore areas (Figure 3.14). However, for the offshore areas (UW-Coff, LWCin, WAB), higher retention success was achieved when particles were released deeper than 25m. The biggest contributor to mortality in these areas was advective loss, which is also greater close to the surface (Figure 3.14). Therefore particles released at intermediate depths were able to avoid being transported offshore in the upwelling region, but were not deep enough to be affected by temperature-induced mortalities. This apparent trade off between retention and temperature was identified by previous IBMs for the region (Mullon et al., 2003; Parada et al., 2003; Miller et al., 2006), and in the northern Benguela (Stenevik et al., 2003). The WC-WC system was the only system where *Depth* played an important role in determining retention success. This is due to the colder temperatures on the west coast, and the seasonal, wind-induced upwelling in this region. In the BENGSAFE model, the interaction between *Spawning area* and *Depth*

explained 5.9% more of the variance than it did in the PLUME model, and *Depth* explained three times the amount of variance observed in the BENGSAFE model compared to the PLUME model. It is likely that *Depth* was more important in the BENGSAFE IBM due to the drastically increased vertical resolution (20 vertical levels in PLUME and 100 vertical levels in BENGSAFE), which resulted in better depiction of the depth layers and therefore better resolved vertical processes.

The single factor *Month* explained the second most variance in retention success in the BENGSAFE IBM. However in the PLUME IBM, *Spawning area* was more important than *Month*. This could be due to the BENGSAFE hydrodynamic model displaying more mesoscale variability on a weekly-monthly timescale than the PLUME hydrodynamic model. The seasonality in retention success was particularly prominent for particles released in the inshore west coast spawning areas (UWCin and LWCin) in the BENGSAFE IBM, but not the PLUME IBM (Figure 3.8). Retention success for these particles was substantially lower during the upwelling season (November-February), suggesting that particles released inshore on the west coast during the upwelling months are either advected offshore by Ekman transport or are removed from the simulation due to cold temperatures. Figure 3.18 displays the monthly mortality data for particles released in the inshore west coast areas. It is clear that the cold ocean temperatures in this region were the primary cause of mortality for these particles. This effect increases, especially in the BENGSAFE IBM, during the upwelling season, when cold, nutrient-rich water is brought up from depths. This indicates that the upwelling season is more pronounced in the BENGSAFE IBM.

Spawning area proved to be the most important determinant of transport success for particles in the SC-WC system, for both the PLUME and BENGSAFE IBMs, mainly due to the higher levels of transport success to the west coast achieved by particles released on the CAB compared to the lower success levels achieved by particles released on the EAB (Figure 3.9). This spatial pattern was also identified by Miller et al. (2006). This is expected, as particles released on the EAB have a greater distance to be transported and they are also more susceptible to offshore losses caused by the fast flowing Agulhas Current and associated mesoscale features. Particles released on the CAB have a better chance of avoiding this through utilising the inshore jet currents to be transported to the west coast recruitment area. Although the spatial pattern was similar between the two models, the percentage of transport success for all south coast spawning areas was higher in the BENGSAFE IBM, with an monthly average transport success rate of 26% compared to 10% in the PLUME IBM. This implies that the physical features aiding the transport

and subsequent recruitment of particles from the south coast to the west coast (mesoscale eddies, coastal jets) are better resolved in the BENGSAFE hydrodynamic model. The seasonal and inter-annual variability was also much more pronounced in the BENGSAFE IBM, and showed a different seasonal cycle compared to the PLUME IBM.

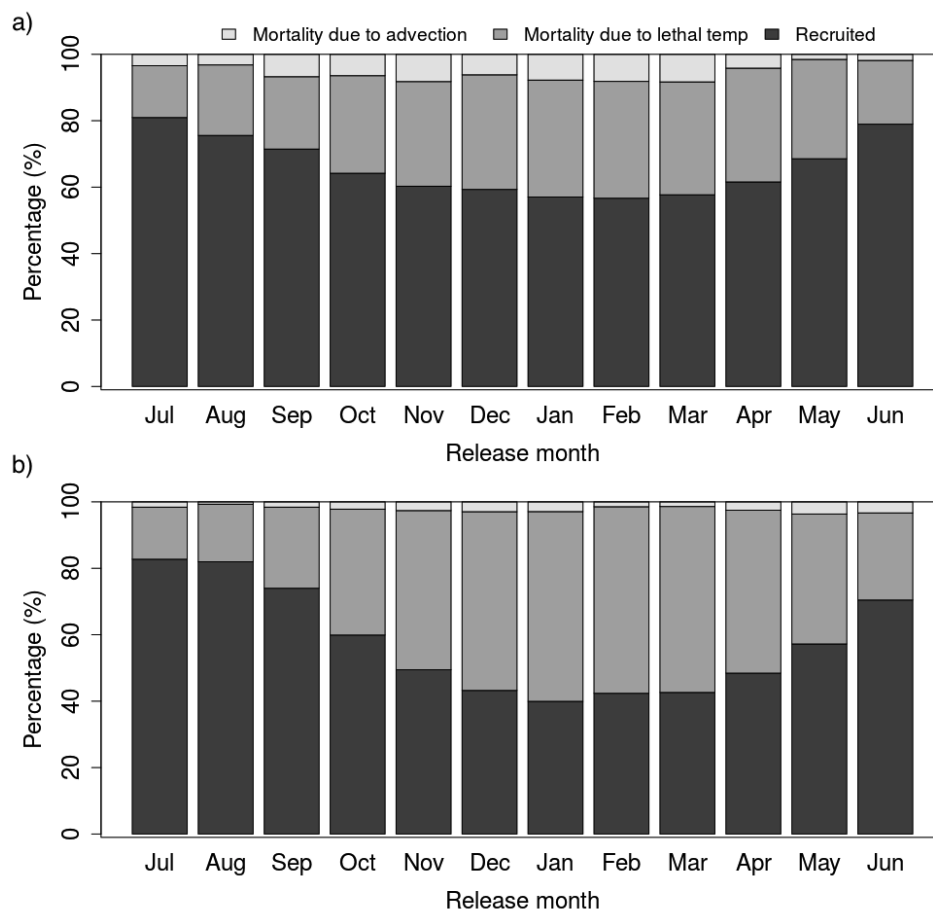


Figure 3.18: Modelled recruitment, mortality due to lethal temperature and mortality due to advection for particles released inshore on the west coast (UWCin and LWCin), for a) PLUME and b) BENGSAFE

The single factor *Month* proved relatively important in both models, as well as its relationship with *Spawning area* (Figure 3.10). A monthly effect is observed in both IBMs, although different, for particles released on the CAB. In the BENGSAFE IBM there was a significant monthly effect, and particles released on the CAB achieved the highest transport success in the second half of the year, similar to findings by Miller et al. (2006) and to the seasonal pattern that is observed in south coast spawning in reality (van der Linde and McGrath, 2017). When looking at this significant monthly effect inter-annually (Figure 3.11), it is clear that, in the initial years, relatively constant transport success was maintained, but from 1993/94 onwards the seasonality becomes increasingly more

pronounced.

In the SC-SC system the single factor *Spawning Area* explained more variance in the models than all other factors combined, for both the PLUME and BENGSAFE IBMs. In both models, particles released inshore on the EAB (EABin) achieved the highest south coast retention success (Figure 3.12), suggesting that these particles are sufficiently inshore to avoid offshore transport. Particles released in the offshore spawning area on the EAB (EABoff) in the PLUME simulation achieved similarly high south coast retention success, but this wasn't the case in the BENGSAFE simulation, where retention success for this spawning area was approximately halved. This is reiterated in the dispersion plots, which display how particles released on the EAB in the PLUME IBM show very little movement compared to the BENGSAFE IBM. This is likely due to the improved resolution of the Agulhas Current and the Retroflexion region in the BENGSAFE model. The greatest cause of mortality for particles released in this spawning area in the BENGSAFE IBM is advective loss (Figure 3.14). For particles released on the CAB, a similar spatial pattern is observed in both IBMs. However, the level of retention success is higher in the IBM coupled with PLUME. The inshore spawning area on the CAB (CABin) is more successful than the offshore area (CABoff). This is driven not only by the Agulhas Current in BENGSAFE but also by the entrainment of particles into the Retroflexion region and eastwards, as is evident in Figure 3.5. Whereas in the PLUME model the Greater Agulhas Current system and retroflexion is not resolved and the flow heads westwards.

The relationships between *Spawning area* and *Month* and between *Month* and *Year* are relatively important in the PLUME IBM and BENGSAFE IBM, respectively. However, *post-hoc* tests indicated that no significant monthly effect was present in either model for this system.

The fact that the BENGSAFE IBM simulates more transport of particles from the south to the west coast implies that there is a larger contribution from south coast spawners to west coast recruitment (P_0) than previously suggested by Miller et al. (2006). Those authors suggested an average P_0 of $\sim 9\%$, which is simply the average percentage of all particles that were released on the south coast at all depths that are transported to the west coast recruitment area. The average P_0 for the PLUME IBM was calculated to be 7.6%, whereas for the BENGSAFE IBM a much higher P_0 of 20.9% was calculated. Although P_0 increased in the BENGSAFE IBM, it is not high enough to indicate one sardine stock. Between ~ 10 -60% of all particles released on the south coast were successfully retained in the south coast recruitment area, depending where on the Agulhas Bank they were spawned. Therefore the SC-SC system is still viable, and the retention of eggs and larvae

there is possibly underestimated due to the limited domain used in this chapter, which does not encompass the whole observed spawning and recruitment grounds of the south coast. It must also be noted that the central Agulhas Bank spawning areas (CABin and CABoff) had the highest transport success rates out of the south coast spawning areas but referring back to the composite egg density figure (Figure 1.4), there are very few eggs found in this region in reality.

Overall, similar IBM results were obtained from both hydrodynamic models for the WC-WC system, especially for the inshore spawning areas. This suggests that the PLUME configuration, despite almost 15 years of advances in ocean modelling since its production, is comparable to the BENGSAFE configuration on the west coast, and represents the ocean processes and circulation on the west coast relatively well for the scale of this study. Some differences in seasonality of retention success in the IBM results arise when looking at the inshore area of the west coast, which is likely due to the increased resolution in the BENGSAFE configuration resolving inshore mesoscale processes better. For the two south coast systems (SC-WC, SC-SC) results differed between the two IBMs. The seasonality and degree of transport success from the south coast to the west coast did not match. More particles were transported to the west coast at one peak in the BENGSAFE IBM and a larger average P_0 was calculated. The advective offshore loss of particles from the south coast was also higher in the BENGSAFE IBM for the SC-SC system. These differences in south coast results from the IBMs suggest that the PLUME configuration may not have been an appropriate model to study processes on the south coast. This is due to the close proximity of the model domain's eastern boundary, and its climatological boundary forcings, to the region where we expect to see the Agulhas Current. In Chapter 4 an improved BENGSAFE IBM simulation is presented, which better represents south coast spawning and recruitment processes by extending the model domain to the east.

Another direct comparison of identical IBM models coupled with different hydrodynamic models, investigating the effect of underlying resolutions, could not be found in the literature. Brochier et al. (2011) reviewed and compared biophysical models of anchovy and sardine egg and larvae dispersals for the Northern and Southern Benguela (Stenevik et al., 2003; Miller et al., 2006), Northern Humboldt (Brochier et al., 2008a), and central Canary Current Systems (Brochier et al., 2008b). Each IBM model reviewed was coupled with a different hydrodynamic model configuration of varying horizontal and vertical resolutions. The IBM for the Northern Benguela was coupled with a hydrodynamic model configuration with the lowest horizontal resolution (20km, Stenevik et al., 2003) and obtained the highest mean retention rate ($\sim 80\%$). Mean retention rates for the higher resolved North-

ern Humboldt (12km, Brochier et al., 2008a) and central Canary Current (7km, Brochier et al., 2008b) IBMs were lower ($\sim 50\%$). However, the higher retention success in the Northern Benguela IBM could also be attributed to region specific environmental conditions. The result of decreased retention success with increased resolution matches results obtained in the PLUME and BENGSAFE IBM comparisons in this chapter, and supports the idea that retention/transport success is more accurate when IBMs are coupled with high resolution hydrodynamic models configurations.

Chapter 4

An updated and extended IBM model of transport and retention of sardine (*Sardinops sagax*) eggs and larvae around South Africa

Abstract

An updated Lagrangian sardine IBM for the southern Benguela, extended in time and space, is coupled with the BENGSAFE 3-D hydrodynamic model configuration and analysed. The IBM includes an additional spawning area and extended recruitment area on the south coast, and the extension of the IBM domain to Port Alfred on the south coast allows south coast spawning and recruitment to be fully represented. Model particles were released every month from 1989 to 2010. Despite the additional 11 years of data, similar results are observed compared with a previous model, with the same three main systems identified: WC-WC, SC-WC and SC-SC. *Spawning area* again proved to be an important determinant of modelled retention/transport success, with *Depth* playing an important role on the west coast. The average retention of particles released on the south coast increased from 31.7% to 40.7% and the average percentage of particles released on the south coast and transported to the west coast decreased from 20.9% to 17.4%, compared to the initial, spatially restricted BENGSAFE IBM. Standardised anomalies from the IBM modelled retention/transport were compared with recruitment estimates from stock assessment models but there was no correlation between the two sets anomalies.

4.1 Introduction

Estimating the extent to which spawning by the south coast sardine stock contributes to recruitment to the west coast stock is of great importance to the South African sardine fishery management, and was a major focal point of the 2016 Annual International Stock Assessment Review Workshop (Dunn et al., 2016). Concerns were raised about the capability of an older sardine IBM (Miller et al., 2006) previously used to estimate this mode of mixing between stocks, largely due to the modelling advances in the last 15 years. Therefore it was recommended in the Final Panel Report that IBM simulations should be conducted using a more recent and realistic hydrodynamic model configuration (Dunn et al., 2016).

The comparative simulations in Chapter 3 highlighted the shortcomings of PLUME in representing both the oceanography and sardine biology on the south coast, and further justifies the need for an updated sardine IBM for the greater southern Benguela region. The simulations were spatially restricted by the domain of PLUME, which only extends to 24°E and therefore does not include all potential spawning and retention areas on the south coast. Additionally, the important mesoscale variabilities and jet currents typical of the southern Agulhas Current were excluded. Therefore the purpose of this chapter is to present a sardine IBM of the southern Benguela and Agulhas Bank, which utilises a recent, high resolution hydrodynamic model configuration (BENGSAFE) spanning 21 years, and providing a more realistic representation of south coast oceanography, as well as encompassing the full extent of the south coast spawning and recruitment.

Acoustic and net tow surveys around South Africa have frequently recorded both spawners and eggs as far east as Port Alfred (27°E) on the south coast (Coetzee et al., 2008b; de Moor et al., 2017). Therefore, it is important that this region is included in the IBM. BENGSAFE's domain allows for the entire south coast to be included and therefore spawning and recruitment in this region can be properly represented.

It is important for management of the sardine fishery that the portion of south coast spawning product that is contributed to west coast recruitment is accurately estimated so that the stocks of the sardine population can be managed appropriately. If this portion (P_0) is high, as suggested by some investigations (Butterworth, 2016a; Butterworth, 2016b; de Moor et al., 2016), then the components can be managed as one mixing stock. However, if P_0 is in fact lower, indicating two spatially separated components, then this needs to be taken into account in the management procedure to ensure that one stock is not overfished to depletion.

4.2 Methods

4.2.1 Experimental design

Modelling process

The same modelling process (experimental design, IBM simulations and statistical analyses) used in Chapter 3 is utilised in this chapter (Figure 4.1). For each simulation 11 000 particles were released randomly over ten spawning areas, every month from June 1989 to July 2010 (therefore covering 21 years). These particles were released at three depth ranges (0-25, 25-50, 50-75m). The 11 000 particles were released in batches at each time step (3 days) of the BENGSAFE model for the 30 days, of each month. The IBM used the daily 3-D hydrodynamic output (u , v , and w velocities), to estimate the horizontal and vertical trajectory of each particle and then moved the particle accordingly. Temperature values were also read from the hydrodynamic model output every day. Due to the lethal temperature criterion, if a particle was in water colder than 13°C the particle was considered to be dead and was removed from the simulation. Each particle increased in age with each time step until it satisfied the criteria for recruitment or reached the maximum age without successfully recruiting; in both cases the particle was then removed from the simulation. The recruitment criteria included reaching a recruitment area and being retained for a timestep, as well as being a minimum age of 14 days. The maximum age was 60 days. Each particle's spawning area, and year, month and depth of release were recorded, as well as the recruitment area, if the particle successfully recruited.

Only one trial was conducted in this chapter as *Trial* had no significant effect in any of the simulations in Chapter 3; this also allowed computational time to be manageable.

Fixed parameters and variables

Table 4.1 displays the fixed parameters and variables used in the simulations and their values or ranges. To keep in line with the optimum number of particle tests, 11 000 particles were released each month in the simulations described in this chapter due to the added spawning area increasing the spawning extent by approximately 10%.

Table 4.1: The fixed parameters and variables used in the IBM simulations of sardine spawning and recruitment in the Southern Benguela.

	BENGSAFE	<i>n</i>
Fixed Parameters		
Number of particles	11 000	-
Duration of release of particles	30 days	-
Particles released every	3 days	-
Tracking period	60 days	-
Lethal minimum temperature	13°C	-
Position recorded	daily	-
Variables		
<i>Spawning Area</i>	See Figure 4.2	10
<i>Year</i>	89/90-09/10	21
<i>Month</i>	July-June	12
<i>Depth</i>	0-25m, 25-50m, 50-75m	3
Total number of simulations		756

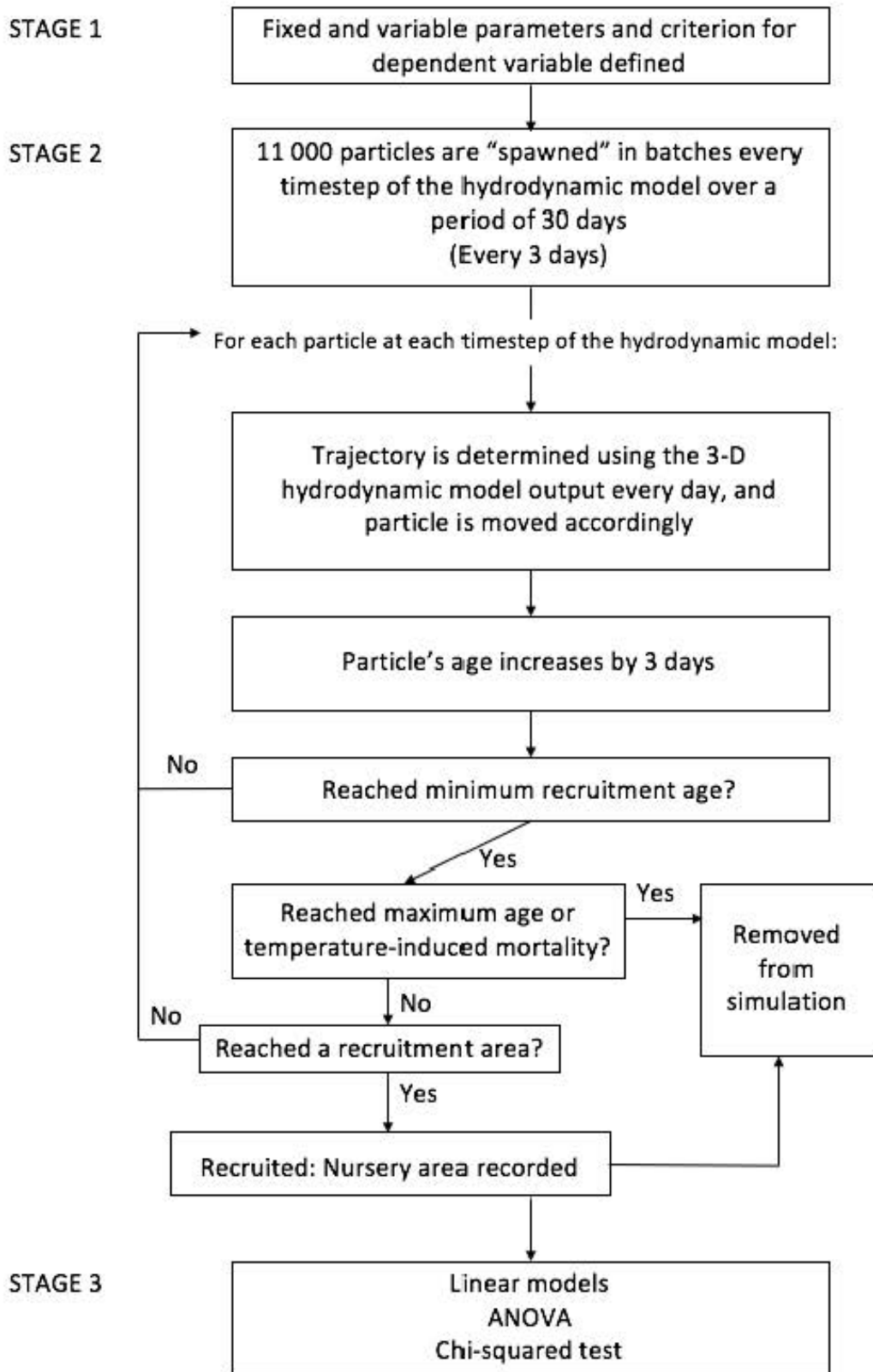


Figure 4.1: Methodological approach of the modelling process. Adapted from Miller (2006) and Chapter 3.

Spawning Areas

In this chapter, one extra spawning area is added (Figure 4.2) to those defined in the previous chapter, to better represent the extent of the spawning on the south coast (See Figure 1.4). This new spawning area (ALG) extends from Cape St Francis to Port Alfred, encompassing Algoa Bay. Having separate inshore and offshore areas in this region was not viable due to the steep continental slope at the eastern end of the Agulhas Bank, making the offshore area very narrow. Therefore, the Algoa Bay spawning area is bound by the 0 and 500m isobaths. ALG is considered a south coast spawning area, along with CABin, CABoff, EABin and EABoff.

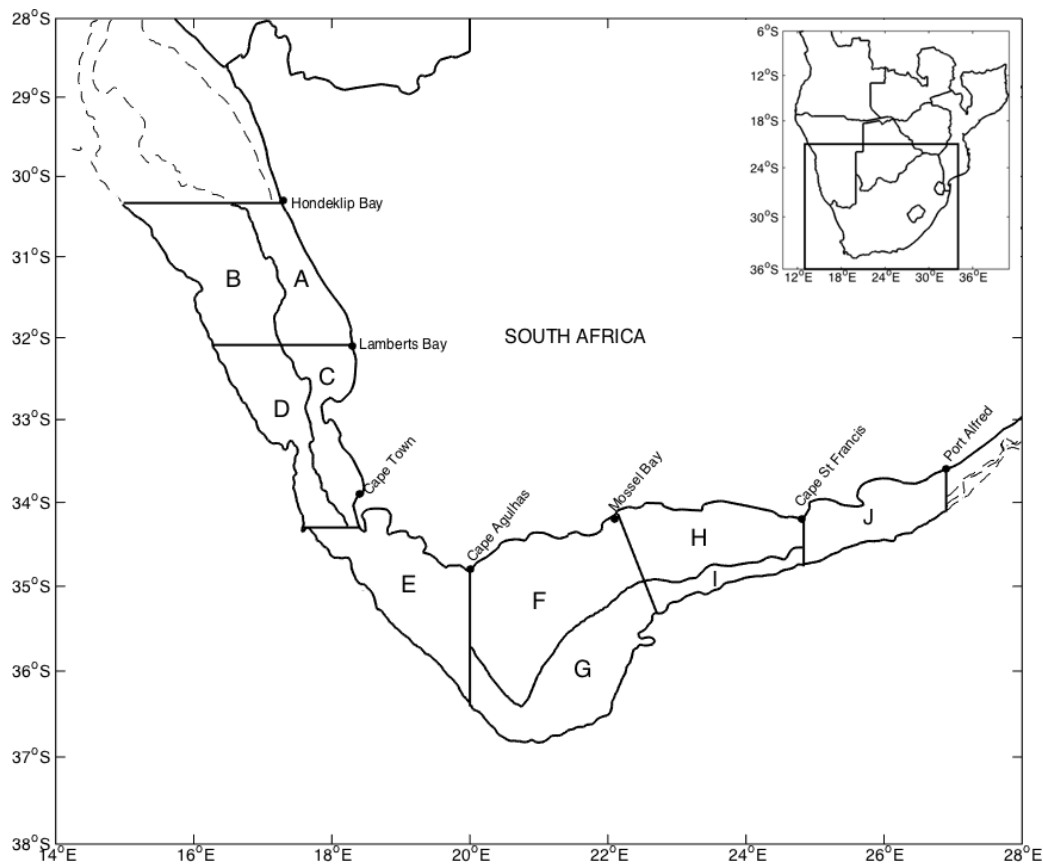


Figure 4.2: The ten spawning areas defined in the IBM simulations. A = upper west coast inshore (UWCin), B = upper west coast offshore (UWCoff), C = lower west coast inshore (LWCin), D = lower west coast offshore (LWCoff), E = western Agulhas Bank (WAB), F = central Agulhas Bank inshore (CABin), G = central Agulhas Bank offshore (CABoff), H = eastern Agulhas Bank inshore (EABin), I = eastern Agulhas Bank offshore (EABoff), J = Algoa Bay (ALG). The 125, 200 and 500m isobaths are displayed by dashed lines.

Dependent variables

Three recruitment areas were defined for this chapter (Figure 4.3), two of which are identical to those used in the previous chapter. The additional recruitment area spans from Plettenberg Bay to Port Alfred on the south coast. For analyses, the two south coast recruitment areas are grouped together to represent south coast recruitment. As in Chapter 3, the dependent variable of the linear models and analyses of variance (ANOVAs) was the percentage of particles released from each spawning area that was successfully recruited in either the west coast recruitment area or the two south coast recruitment areas (modelled retention or modelled transport). The percentage of particles from each spawning area that was removed from the simulation due to lethal temperature (temperature induced mortality) was computed and explored, but not used as a dependent variable in the linear models and ANOVAs.

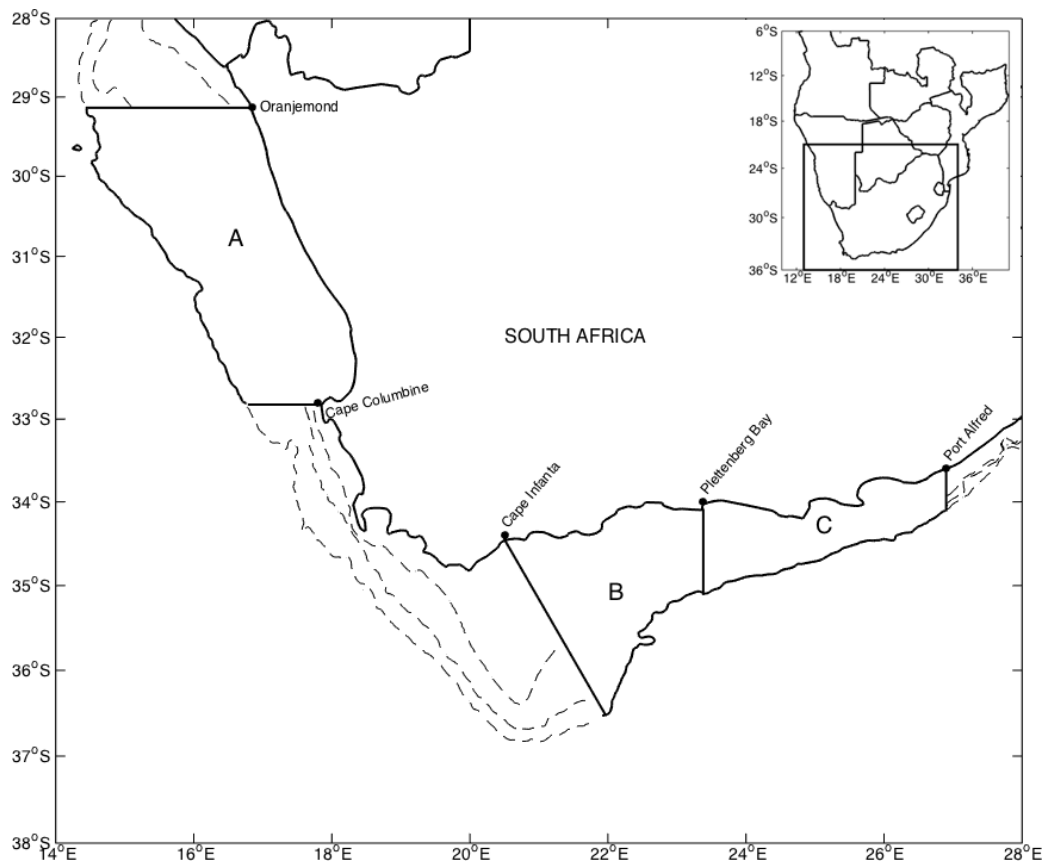


Figure 4.3: The three recruitment areas defined in the IBM simulations. A = west coast (WC), B = south-west coast (SCa), C = south-east coast (SCb). The 125, 200 and 500m isobaths are displayed by dashed lines.

4.2.2 Statistical analyses

Results from the simulations were divided into systems depending on where the particles were spawned and recruited. For each identified system, a multiple factor analysis of variance using linear models was performed on the modelled retention/transport results. The variables in the IBM models (*Spawning area, Year, Month, and Depth*) were factors in the linear models. A full factorial design to the 2nd degree was used. For each linear model, the R², p values and percentage of variance explained by each term were noted and the model assumptions were checked (Section 2.4). Important main and interaction effects were explored further. *Post-hoc* chi-squared (χ^2) tests were conducted to explore seasonal patterns and test the significance of peaks and troughs.

Standardised anomalies of IBM modelled retention/transport success and sardine assessment modelled recruitment (de Moor et al., 2017) for the west and south coasts were calculated and compared. The sardine assessment model is a sex-aggregated model with Bayesian estimation, and which uses an age-structured production model framework but is fitted directly to length-structured survey and commercial catch data. The model is stock-disaggregated and allows one-way movement of recruit and adult sardine from the west to the south stock. The model is described in detail in de Moor et al. (2017). Standardised anomalies were calculated as the difference between the individual year values and the mean over the 21 years (1989-2010), divided by the standard deviation over the 21 years. Correlations between the two modelled recruitment anomalies for the south and west components were calculated, and r and p-values were noted.

4.3 Results

Figure 4.4 shows snapshots of the Lagrangian movement of particles within the IBM domain for January and July in the year representing 1994. Similar movements of particles are observed at all three depth ranges. However, especially in January (Figure 4.4a), more particles are moved offshore from the west coast and over a greater area in the upper surface layer compared to the two deeper depth ranges. Additionally, in January, particles released in the upper depth layer and in the new spawning area (ALG) are transported further west on to the Agulhas Bank compared to those released deeper. There is more movement of particles released on the central Agulhas Bank (CABin and CABoff) to the west coast via the Benguela jet in January, compared to July. More particles are moved southwards from the Agulhas Bank and carried offshore by the Agulhas Current retroflexion in July than in January, when more retention on the bank is observed.

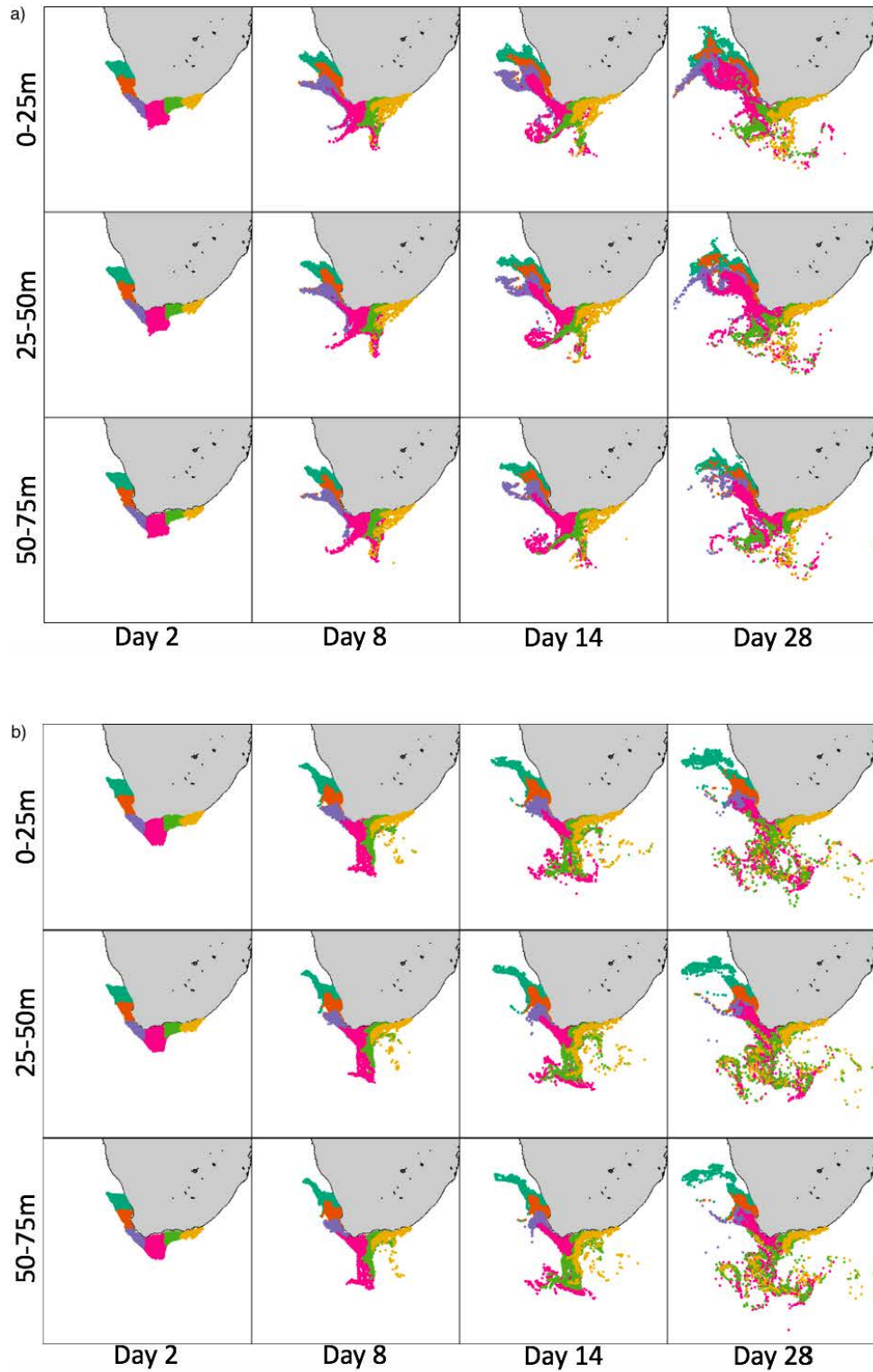


Figure 4.4: Snapshot of particles being transported within the BENGSAFE model domain at 4 periods (2, 8, 14 and 28 days) post release. 11 000 particles were released in spawning areas during a) January and b) July in the year representing 1994. Inshore and offshore spawning areas are combined (UWC = dark green, LWC = orange, WAB = purple, CAB = pink, EAB = light green, ALG = gold). Depth ranges indicate the initial range of depths of release.

4.3.1 Modelled retention/transport

Figure 4.5 shows the mean modelled retention in, or transport to the west (WC) and south coast (SCa and SCb) recruitment areas from each of the ten spawning areas for all release years, months and depths. Some particles from every spawning area were recruited on the west coast, and the level of success decreased the further east the particle was spawned. South coast recruitment however, is only viable for particles spawned east of Cape Agulhas. Over 50% of all particles released in each west coast spawning area were retained on the west coast, with particles released in the lower west coast offshore (LWCoff) area obtaining the highest west coast retention success. Approximately a third of all particles released on the central Agulhas Bank are transported to the west coast recruitment area. For particles released inshore in this region (CABin), the percentage of particles transported to the west coast area is very similar ($\sim 30\%$) to the percentage of particles that are retained on the south coast. This is not the case for particles released in the offshore area (CABoff), where a much lower percentage is retained on the south coast than is transported to the west coast. For particles released on the eastern Agulhas Bank and Algoa Bay region, south coast retention is the primary result, with less than 10% of particles from each of these areas being transported to the west coast.

The following three viable recruitment systems were identified and explored:

1. The west coast to west coast retention system (WC-WC)

This system includes particles that were released in either UWCin, UWCoff, LWCin, LWCoff or WAB and were successfully retained in the west coast recruitment area, having achieved all recruitment criteria. This system is the same as the BENGSAFE IBM WC-WC system detailed in Chapter 3, however the time period of the IBM in this chapter is longer.

2. The south coast to west coast transport system (SC-WC)

Modelled transport success in this system is the portion of particles that were released in either CABin, CABoff, EABin, EABoff or ALG and were successfully transported to the west coast recruitment area, having achieved all recruitment criteria.

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

This system includes particles that were released in either CABin, CABoff, EABin, EABoff or ALG and were successfully retained in the south coast recruitment areas (both SCa and SCb), having achieved all recruitment criteria.

The WC-WC system is the same system identified in Chapter 3. However, the SC-WC and the SC-SC systems in this chapter include the additional spawning area (ALG) and extended recruitment area (SCa + SCb) on the Agulhas Bank.

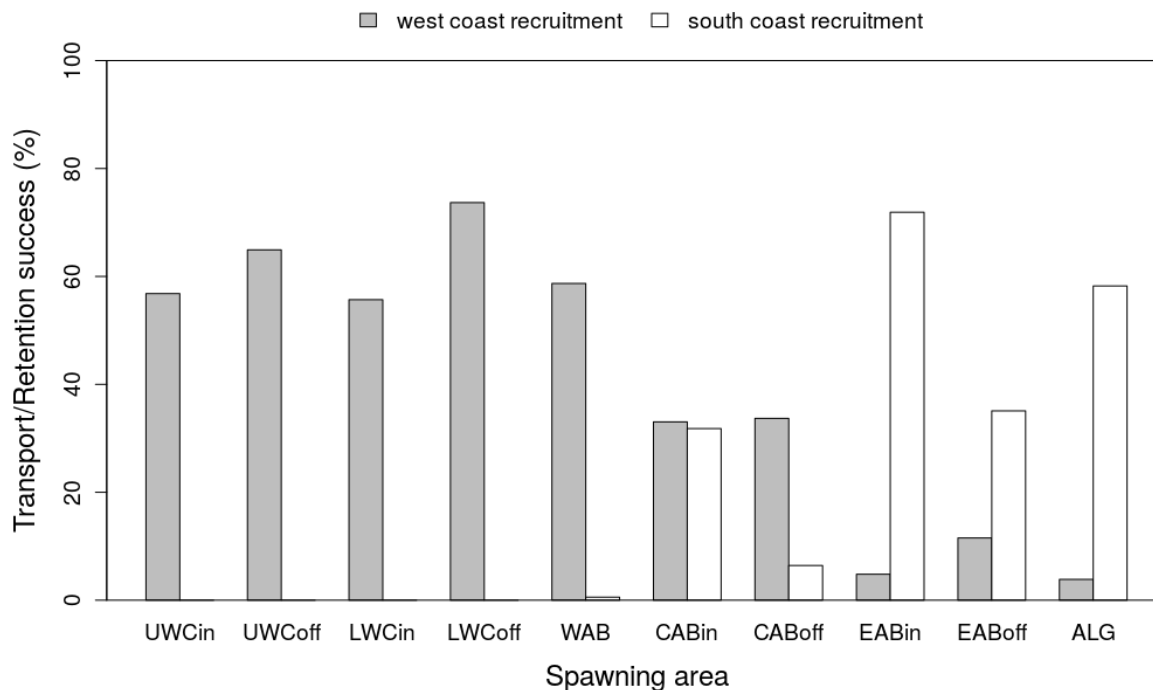


Figure 4.5: Modelled transport/retention success to the west (grey) and south (white) coast recruitment areas from the ten spawning areas, irrespective of year, month and depth of release.

WC-WC

The linear model representing the WC-WC system accounted for 73.63% of the variance present in the modelled retention. Model assumptions regarding the trend in model residuals, mean and variance were satisfied. As seen in the previous chapter, the interaction between *Spawning area* and *Depth* was the most important determinant of modelled recruitment, explaining 27.95%. This indicates that the effect of *Spawning area* differs depending on the release depth, and vice versa (Figure 4.6). The inshore areas (UWCin and LWCin) had the highest retention success when released in the upper depth layer (0-25m) and this success decreased with depth. The opposite effect was observed for particles released on the WAB, which achieved the highest retention success when released in the deepest depth range (50-75m). The offshore areas (UWCoff and LWCoff) achieved the highest retention success when released in the middle depth range (25-50m), and this success either decreased (LWCoff) or remained at a similar level (UWCoff) when particles were released deeper.

The single variables *Month* and *Depth* again prove to be important factors, explaining 12.66% and 10.69% of the modelled retention success variance, respectively. Retention success was highest in winter months and decreased in summer months (Figure 4.7). However, there was no significant monthly effect on modelled retention success for this system from the chi-squared analysis ($\chi^2 = 14.1$, $df = 11$, $p\text{-value} = 0.23$).

Table 4.2: Analysis of variance results for the WC-WC retention system. All F values were significant at $p < 0.01$. The single factor or interaction explaining the most variance is shown in bold. *df* = degrees of freedom.

Factor	<i>df</i>	% Variance explained	F value
Spawning area	4	7.07	2502
Month	11	12.66	1630
Year	20	0.77	55
Depth	2	10.69	7569
Spawning area x Month	44	7.36	237
Spawning area x Year	80	1.59	28
Spawning area x Depth	8	27.95	4949
Month x Year	220	3.31	21
Month x Depth	22	2.07	133
Year x Depth	40	0.17	6
Model	451	73.63	
Error	37348	26.37	

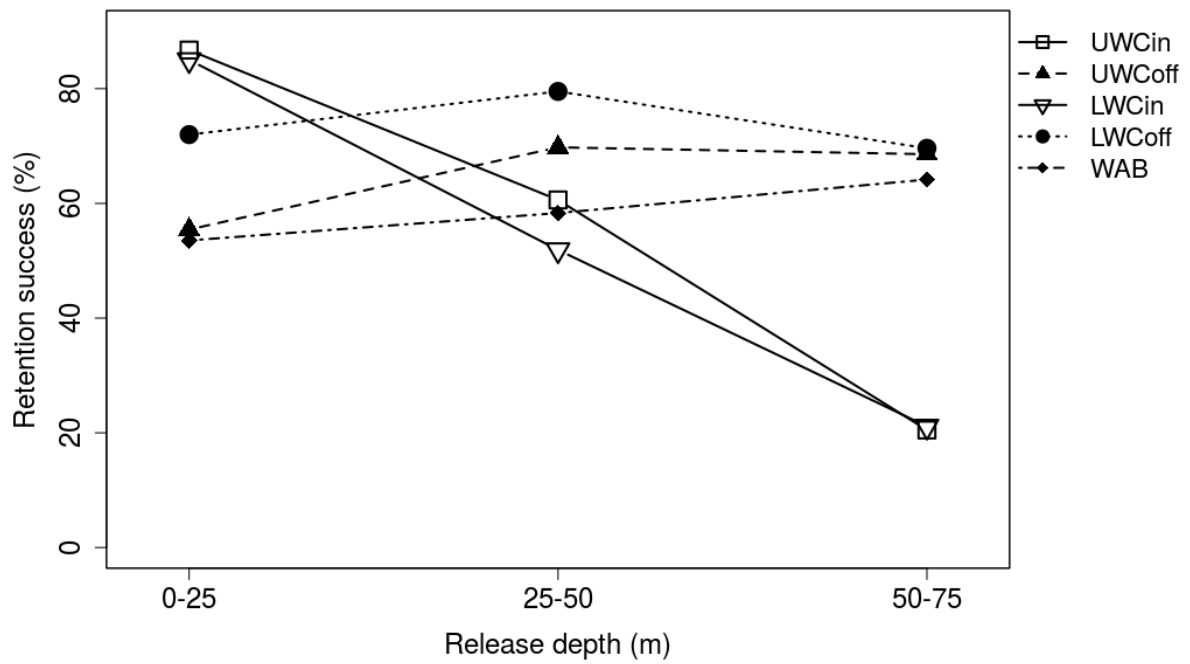


Figure 4.6: Modelled retention success for each spawning area in the WC-WC system per depth of release.

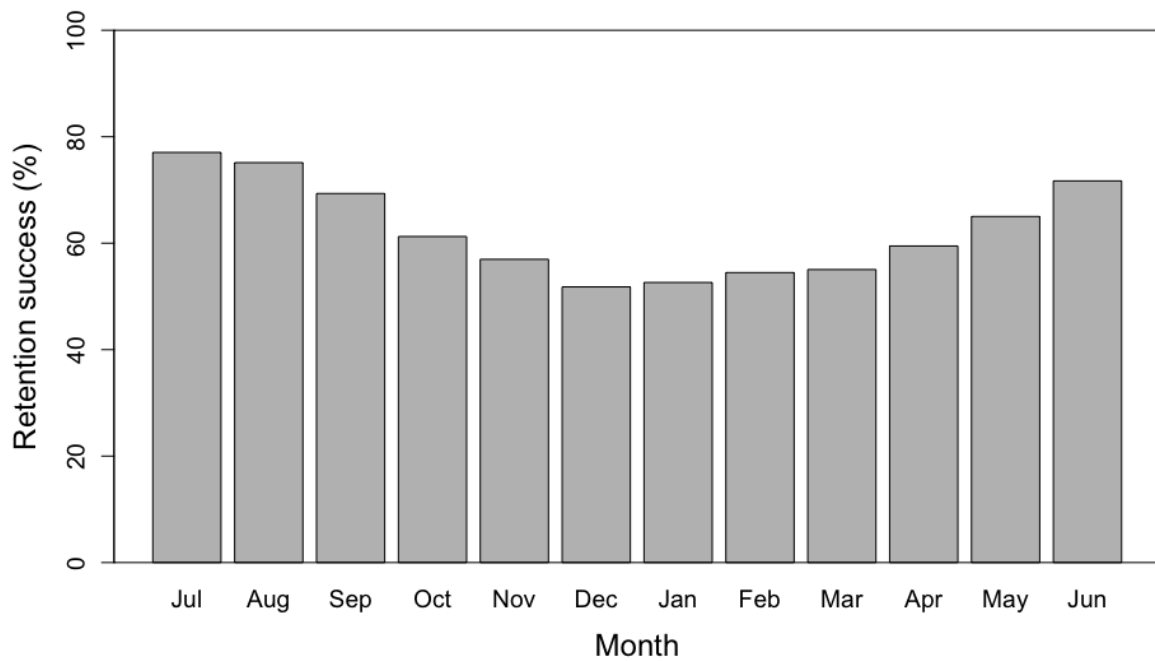


Figure 4.7: Modelled retention success for each release month in the WC-WC system.

SC-WC

The linear model representing the SC-WC system accounted for 73.13% of the variance in modelled transport success was explained by the linear model. Model assumptions were satisfied. The factor *Spawning area* was the primary determinant of transport success and explained 47.48% of the variance in transport success. Approximately 30% of all particles released on the central Agulhas Bank (CABin and CABoff) were successfully transported to the west coast recruitment area, whereas the level of transport success of particles released further east on the Agulhas Bank (EABin, EABoff and ALG) was much less (\sim 5-10%) (Figure 4.8).

The interaction between *Spawning area* and *Month* was the second most important factor and explained 7.49% of the variance in transport success. This indicates that the effect of *Spawning area* depends on the release month of the particles, and vice versa (Figure 4.9). As observed in the previous chapter, particles released in the central Agulhas Bank spawning areas show seasonality, with a peak in transport success in late winter and a trough in late summer. The seasonality of the CABin spawning area is approximately one month behind that of the CABoff. Very little seasonality is observed in transport success of particles released on the eastern Agulhas Bank (EABin, EABoff and ALG). There was a significant monthly effect on modelled transport success ($\chi^2 = 22.37$, $df = 11$, p -value = 0.02), which disappeared when the months representing the peak (August-September) ($\chi^2 = 11.95$, $df = 9$, p -value = 0.22) or the the trough (February-April) ($\chi^2 = 13.50$, $df = 8$, p -value = 0.09) were removed. This supports the importance of seasonal variability for the successful transport of particles to the west coast recruitment area. The interaction between *Month* and *Year* explained 6.74% of the variance in transport success, suggesting that the seasonality is not the same in all release years.

Table 4.3: Analysis of variance results for the SC-WC transport system. All F values were significant at $p < 0.01$. The single factor or interaction explaining the most variance is shown in bold. df = degrees of freedom.

Factor	df	% Variance explained	F value
Spawning area	4	47.48	16552
Month	11	6.10	773
Year	20	1.10	77
Depth	2	0.25	175
Spawning area x Month	44	7.49	237
Spawning area x Year	80	1.38	24
Spawning area x Depth	8	1.97	344
Month x Year	220	6.74	43
Month x Depth	22	0.56	36
Year x Depth	40	0.15	5
Model	451	73.13	
Error	37348	26.78	

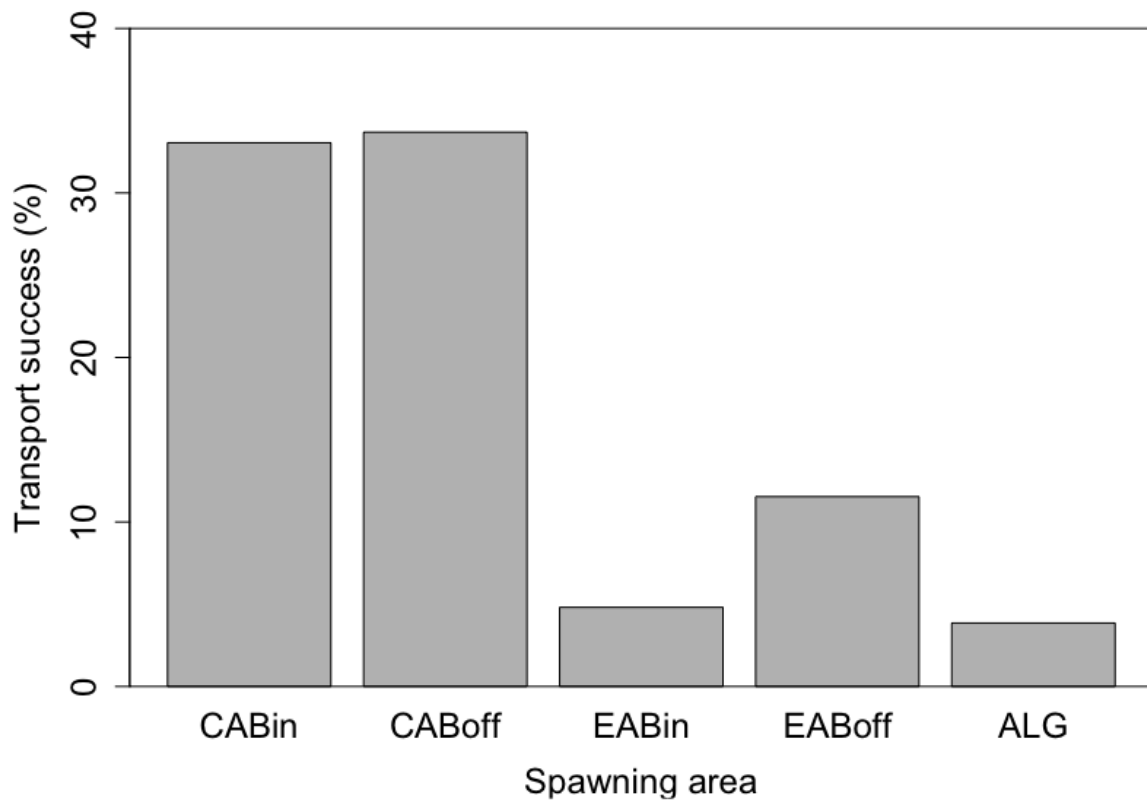


Figure 4.8: Modelled transport success for each spawning area in the SC-WC system.

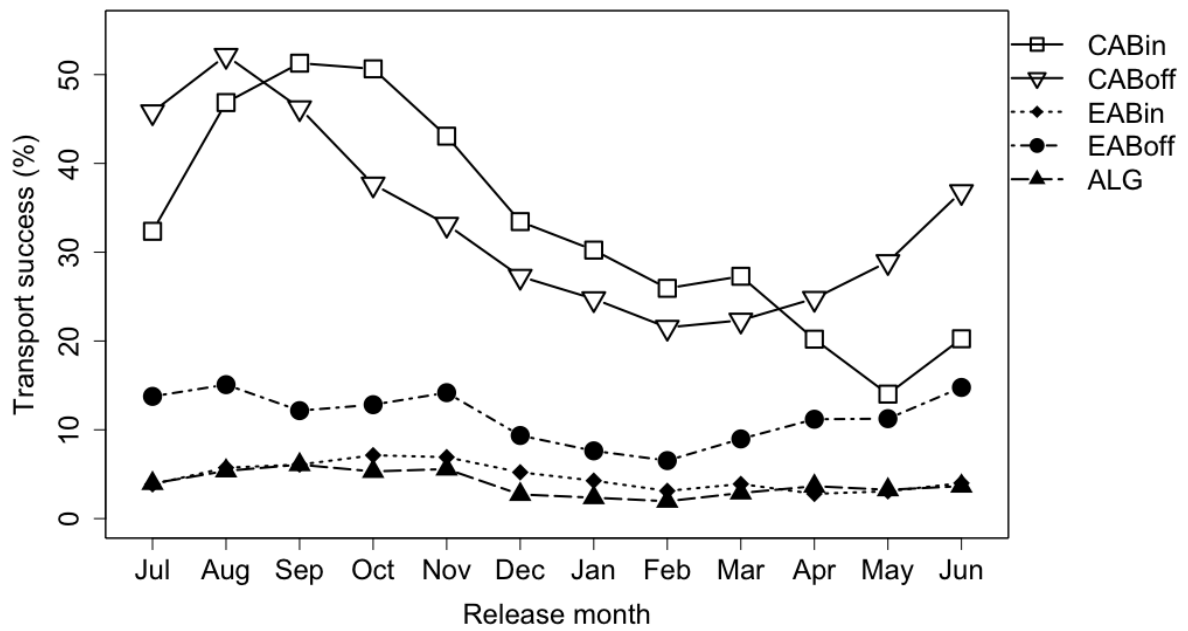


Figure 4.9: Modelled transport success for each spawning area per month in the SC-WC system.

SC-SC

The linear model representing the SC-SC system explained 69.90% of the variance in retention success. Trends in the residuals were checked and satisfied the model assumptions. Approximately half (51%) of the variance in retention success was explained by *Spawning area*. Retention success was highest for particles released inshore on the eastern Agulhas Bank (EABin) and lowest for particles released offshore on the central Agulhas Bank (CABoff) (Figure 4.10). Particles released inshore on the central Agulhas Bank (CABin) and offshore on the eastern Agulhas Bank (EABoff) achieved similar levels ($\sim 35\%$) of retention success. Approximately 60% of all particles released in the far east spawning area (ALG) were retained on the south coast. The interaction between *Month* and *Year* explained the second most variance in retention success (6.85%), which indicates that the seasonality differs from year to year.

Table 4.4: Analysis of variance results for the SC-SC retention system. All F values were significant at $p < 0.01$. The single factor or interaction explaining the most variance is shown in bold. *df* = degrees of freedom.

Factor	<i>df</i>	% Variance explained	F value
Spawning area	4	50.98	15813
Month	11	3.98	440
Year	20	0.54	34
Depth	2	1.58	983
Spawning area x Month	44	1.96	55
Spawning area x Year	80	1.61	25
Spawning area x Depth	8	1.91	296
Month x Year	220	6.85	39
Month x Depth	22	0.32	18
Year x Depth	40	0.23	7
Model	451	69.90	
Error	37348	30.10	

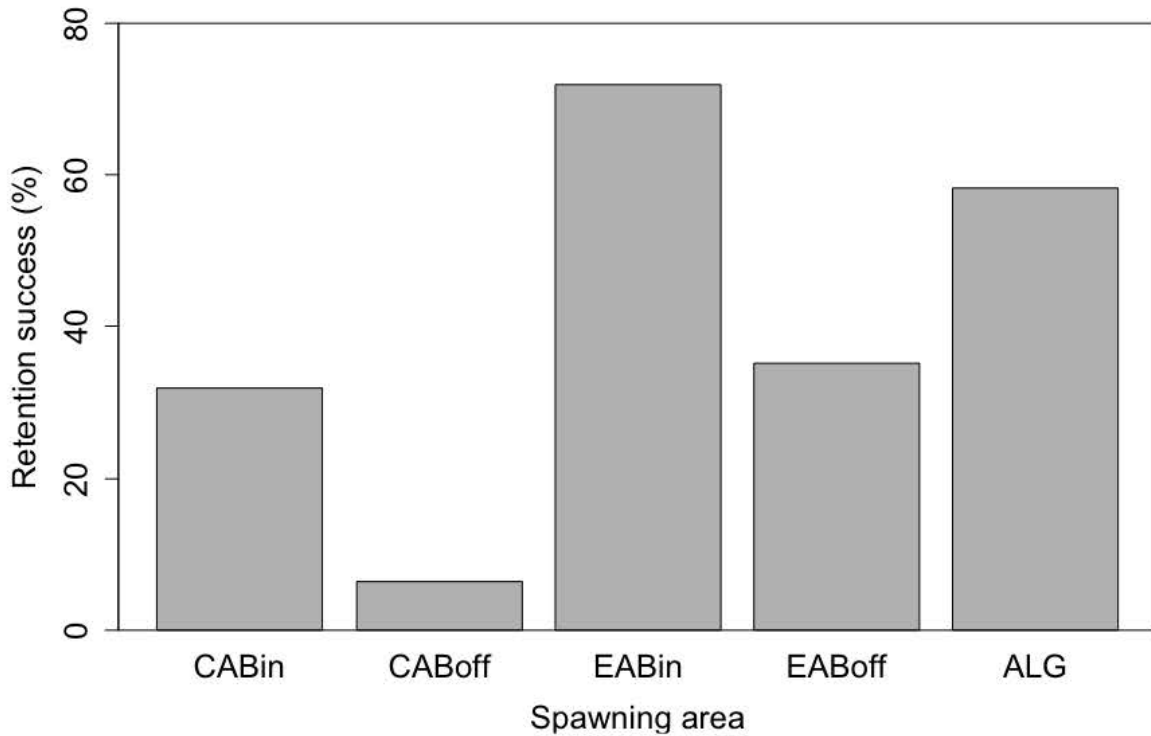


Figure 4.10: Modelled retention success for each spawning area in the SC-SC system.

4.3.2 Comparison with stock model estimates

The May model-predicted recruitment for western and southern sardine stocks from de Moor et al. (2017) was used to calculate the standardised anomalies, which are compared to the BENGSAFE IBM retention/transport success standardised anomalies in Figure 4.11. The IBM modelled retention/transport success for the west coast was calculated as the sum of the yearly retention success from the WC-WC system and the yearly transport success from the SC-WC system. The IBM modelled retention success for the south coast is the yearly retention success from the SC-SC system. The anomalies of IBM modelled retention/transport success were not significantly correlated with the model estimated recruitment for western stock recruitment or southern stock recruitment (WC: $r = 0.31$, $p\text{-value} = 0.17$; SC: $r = 0.05$, $p\text{-value} = 0.84$). Model estimated recruitment anomalies and IBM modelled retention/transport anomalies for the west coast show opposing signs until the early 2000s; thereafter the anomalies are similar (Figure 4.11a). The model estimated recruitment anomalies for south coast recruitment are positive until the late 1990s and are predominantly negative thereafter. The opposite pattern is observed for the IBM modelled retention success anomalies, which are negative for the first half of the time series and predominantly positive for the second half (Figure 4.11b). The

magnitude of the IBM retention/transport success anomalies is greater for the west coast stock than south coast stock, indicating more inter-annual variation in the west coast system.

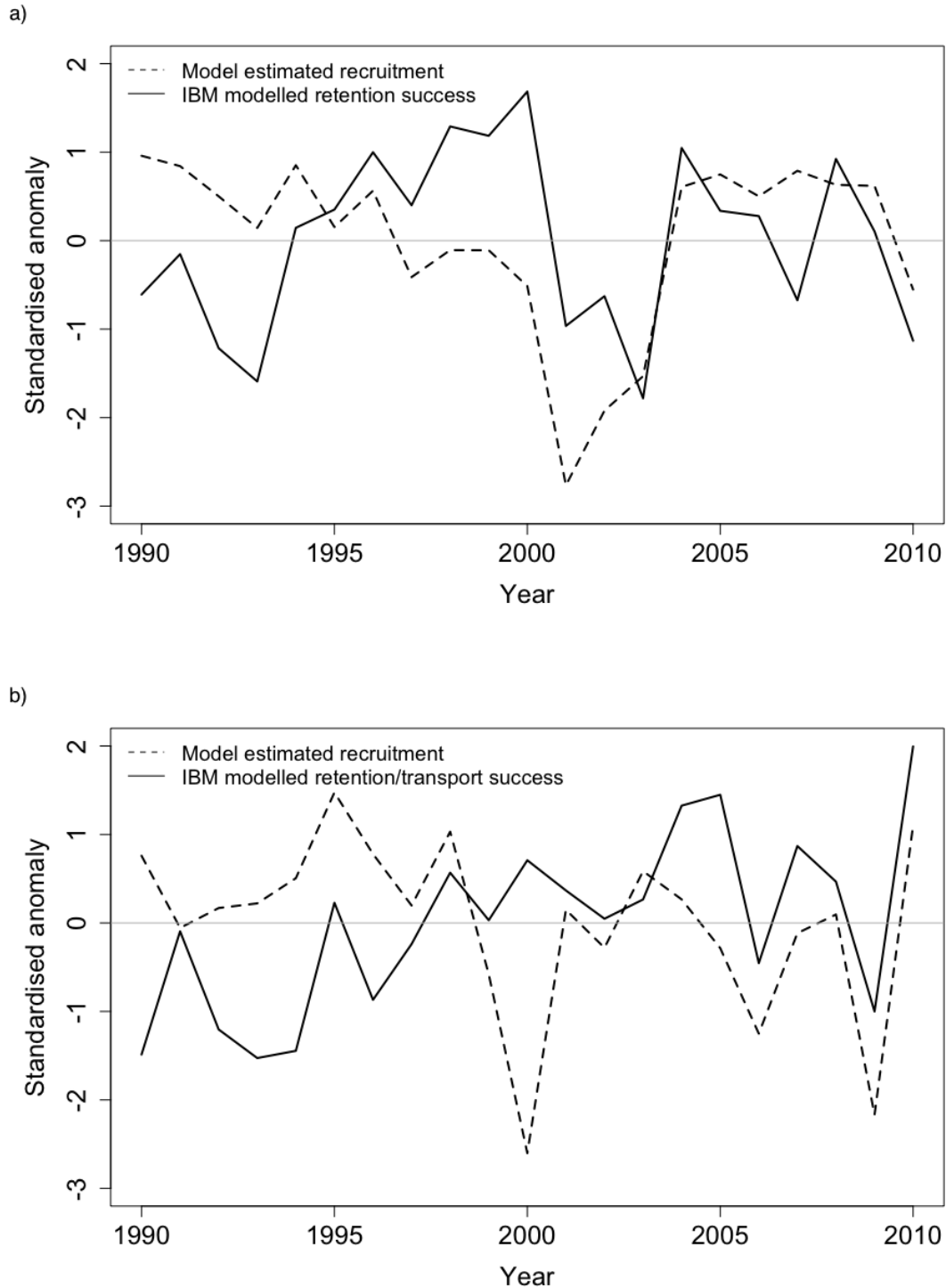


Figure 4.11: Standardised anomalies of modelled recruitment from the sardine assessment model and modelled retention/transport success from the BENGSAFE IBM from 1989 to 2010, for a) west coast recruitment and b) south coast recruitment.

4.4 Discussion

The aim of this chapter was to present a sardine IBM for the southern Benguela coupled with a suitable, recent, well resolved hydrodynamic ocean model configuration and which accurately represents the spawning and recruitment patterns of sardine along the South African coastline. Chapter 3 highlighted that the BENGSAFE configuration better represented the ocean dynamics, especially on the south coast, and does not have the spatial and temporal restrictions that PLUME had. Therefore the BENGSAFE configuration was coupled with the IBM presented in this chapter, which spans further east on the south coast and runs from 1989 to 2010.

Again, three plausible recruitment systems were identified from the initial recruitment results. These recruitment systems match the previous southern Benguela sardine IBM (Miller et al., 2006), the previous chapter's results, as well as the current agreed upon hypothesis regarding the sardine stock (van der Lingen et al., 2015; Butterworth et al., 2016); two retention based systems, one on the west coast and one on the south coast, and a transport based system from the south to the west coast.

The WC-WC system is largely influenced by the cool Benguela Current and Benguela Upwelling System, which is one of the world's four major eastern boundary upwelling systems. This region experiences high levels of offshore advection and cold temperatures due to wind-induced upwelling, especially in the summer months. Despite the additional 11 years of data, the same trade off between temperature mortalities and retention was observed in the WC-WC system as in the previous chapter and by Miller et al. (2006). The interaction between *Spawning area* and *Depth* explained 27.95% of the variation in modelled retention success. This reiterates the importance of depth in this system, and how the effect of depth differs per spawning area. Particles released in the inshore areas (UWCin and LWCin) had the highest retention success when released in the upper depth layer where they are inshore enough to avoid offshore loss and shallow enough to avoid temperature-induced mortalities. The retention success of particles released inshore decreased drastically with release depth due to the cold water temperatures and accompanying temperature-induced mortalities endured at depth. For particles released in the two offshore areas (UWCoff and LWCoff) it was advantageous to be released in the middle depth range (25-50m). At this optimum depth particles could avoid the offshore advection of the surface layer and excessive temperature-induced fatalities characteristic of the deepest layer. The success of particles released in the WAB spawning area was approximately between 50 and 60% for all three release depths, and the retention success gradually increased with depth of release. This suggests that particles released shallower

were advected offshore and lost to the system. Particles released deeper avoided this and didn't suffer from excessive temperature-induced mortalities due to the influence of the warm Agulhas Current water in this region compared to the other spawning areas further up the west coast.

Although the monthly effect was not significant, retention success was lower in summer months, during the upwelling season, when south-easterly winds push large amounts of surface water offshore and cold, nutrient-rich water is upwelled inshore.

The SC-WC system is important when discussing the portion of eggs (P_0) that are spawned on the south coast and are transported to recruit on the west coast. The most important determinant of transport success was *Spawning area*, and the further east on the Agulhas Bank that a particle was spawned the less likely it was to be transported to the west coast recruitment area. Particles released in the central Agulhas Bank spawning areas (CABin and CABoff), had the smallest distance to travel and therefore achieved the highest transport success ($\sim 35\%$). Particles released in the EABoff spawning area achieved approximately double the average transport success than particles released in its inshore counterpart, EABin. It is likely that particles released inshore were rather retained on the bank and in the south coast spawning area, whereas particles released offshore were carried in a south-westerly direction by the Agulhas Current and transported to the west coast via coastal jets. Particles released in the new spawning area, ALG, far east on the Agulhas Bank, obtained the lowest transport success. This is expected due to the substantial geographical distance a particle needed to travel to be successfully recruited on the west coast.

The interaction between *Spawning area* and *Month* explained the second most variation in transport success. This indicates that the seasonality differs depending on the spawning area a particle is released in, and that the effect of *Spawning area* depends on the release month. The transport success of particles released in the central Agulhas spawning areas (CABin and CABoff) shows a clear seasonality with a peak in success in late winter and a trough in summer. Although transport success of particles released in the other south coast spawning areas is lower than those released in the central Agulhas Bank areas, a similar trend of decreased success in summer is noticeable. The SC-WC system is the only system where there was a significant monthly effect on transport success, which highlights the importance of seasonality for this system.

The average P_0 was calculated as 17.4%, meant that 17.4% of all particles released on the south coast at all depths were transported successfully to the west coast recruitment

area.

Spawning area explained the majority of the variance in retention success for the SC-SC system. Particles released in the EABin spawning area achieved the highest retention success, whilst only a small percentage of particles released in the CABoff spawning area were retained in the south coast recruitment area. It is likely that a large portion of particles released offshore on the Agulhas Bank are caught up in the Agulhas Current and advected offshore away from the recruitment area. The majority ($\sim 60\%$) of particles that were released in the new, far east spawning area (ALG) were retained in the recruitment area. This is a significant amount of recruitment that was not present in the IBM in the previous chapter. The recruitment success of particles released in the EABin spawning area also increased by $\sim 10\%$ with the extension of the recruitment area.

It is clear that the central Agulhas Bank is a transition zone between the WC-WC and SC-SC systems, especially the inshore area. The average percentage of CABin particles that were successfully transported to the west coast was very similar to the average percentage of particles that were retained on the south coast.

The model assumptions discussed in the previous chapter still stand, and neither transport nor retention success is the only determinant of successful recruitment; other factors such as food availability, suitable spawning conditions and predators could be important.

The aim of these simulations was not to predict actual levels of recruitment but rather to investigate the impact of ocean circulation patterns and dynamics on the retention and transport of eggs and larvae. Therefore it was not surprising that the stock assessment model estimated recruitment anomalies and the IBM modelled retention/transport success anomalies were not significantly correlated. IBMs utilise theoretical conditions, therefore defining initial realistic conditions is important when comparing to indices. Standardised anomalies of retention/transport success were compared with standardised anomalies of estimated recruits by Miller et al. (2006); no correlation between the sets of anomalies was observed. The differences in the anomalies reiterates the fact that transport and retention success are not the only factors influencing successful recruitment. Both west and south coast retention/transport success anomalies were more concurrent in the second half of the time series. It is not clear why this is the case. However, the change in correlation coincides with the sudden increase in abundance and shift in distribution of sardine to east of Cape Agulhas, which occurred in the early 2000s (Coetzee et al., 2008b). Geographic shifts and changes in population distributions of a number of species in the southern Benguela in the 2000s have been noted (Blamey et al., 2015). The advantage of utilising

more than one recruitment system is shown by comparing the standardised anomalies of retention/transport success for west coast recruitment and south coast recruitment. Negative anomalies were observed for both the west coast and south coast retention/transport success for the first four years (1990-1994) however, a negative anomaly in one system was contrasted with a positive anomaly in the other system for ten of the 17 years thereafter. This indicates that if retention success is poor on the south coast then particles are more likely to be transported to the west coast, and the effects of interannual variation are buffered. This pattern is also noted by Miller et al. (2006) in the standardised anomalies of IBM modelled retention/transport success for the Southern Benguela and Agulhas systems, for five of the eight years compared (Figure 8). Allain et al. (2007) used a more complex IBM for anchovy in the Bay of Biscay to predict a recruitment index in an attempt to introduce the concept of environmental variability into fishery management. Unlike in this chapter, the recruitment variations predicted by the IBM matched the recruitment estimates made by ICES relatively well for the three years investigated (Allain et al., 2007).

Very little inter-annual variation was observed in modelled retention/transport success results and *Year* was not an important factor in any of the systems. Overall recruitment results and relative importance of factors were also relatively similar to the BENGSAFE IBM simulations in Chapter 3, despite the additional 11 years of data. In reality the sardine population has high inter-annual variation in recruitment success, which again highlights that there are processes affecting the inter-annual variation that are missing in the IBM.

Coupled 3-D IBMs have proved to have great potential for use in management of fisheries, as demonstrated by an evaluation of IBMs for four European marine ecosystems by Hinrichsen et al. (2011). Case studies of IBMs representing anchovy, cod, herring, and sprat estimated the connectivity within stocks, the transport of larval and early juvenile stages, and spatio-temporal differences in potential survival, all of which are useful in the management of the relevant fisheries (Hinrichsen et al., 2011). García-García et al. (2016) illustrated the potential connectivity between Ibero-Atlantic sardine populations from a sardine IBM for that region. However, a much more complex IBM is used than the one developed in this chapter, not focused on recruitment.

The calculated P_0 value for this IBM is slightly lower than that predicted by the spatially restricted BENGSAFE IBM in the previous chapter. It is likely that, as more biological realism is added to the IBM, the value of P_0 will decrease. For example, if particles were released according to the horizontal distribution of eggs described by the surveys (Figure

1.4) then very few particles would be released inshore on the central Agulhas Bank. P_0 would therefore decrease as the value was largely influenced by the high success of particles released on the central Agulhas Bank (CABin and CABoff).

The relatively low value of P_0 indicates two largely separate systems and therefore supports the need to manage the South African sardine stock as spatially separate components. The exploitation rate of sardine on the west coast is much higher than the south coast (Coetzee et al., 2008a) and therefore the west coast component runs the risk of being depleted if fishing pressure is not adequately managed.

For the Northern Humboldt, a Lagrangian IBM was developed to investigate the variability of anchovy egg and larval survival rates in this region (Brochier et al., 2008a). A similar sensitivity analysis approach to this chapter was conducted to determine important factors for retention. Spawning depth was the primary determinant of retention success in the IBM results. Another purely Lagrangian IBM was developed to investigate sardine and anchovy ichthyoplankton dispersion in the Canary Current system (Brochier et al., 2008b). The interaction between depth and month of release of particles was reported the most important factor affecting retention success on the continental shelf, and the interaction between release zone and month was the most important determinant of transport success from the coast to the Canary archipelago. Although the seasonal effect was not as pronounced, the factor *Depth* was also important in the extended BENGSAFE IBM WC-WC retention system, as was *Spawning area* in the SC-WC transport system. Other sardine IBMs for various regions are much more complex, and incorporate end to end models and factors such as development-dependent buoyancy, food limitation and vertical migration, and therefore cannot be compared directly to the results in this chapter (Santos et al., 2005; Itoh et al., 2009; Dias et al., 2014; García-García et al., 2016; Rose et al., 2015).

In the extended BENGSAFE IBM particles were analogous to passive drifters, and biological and behavioural traits were assumed to have negligible effects on transport and retention. This is likely not the case in reality. The simple Lagrangian IBM presented in this chapter can be used as a base level to which other layers of biological complexities can be added and compared to. Factors such as more realistic horizontal and vertical egg distributions, spawning seasonality as inferred from gonadosomatic index values, particle buoyancy, thermal effects on egg development and diurnal vertical migration of larvae should be included one by one in future sardine IBMs. An alternative, more dynamic method of defining spawning and recruitment areas would also make results more realistic.

Chapter 5

Synthesis

This dissertation tested the effect of different hydrodynamics on IBM results and investigated the factors affecting sardine egg and larval retention and transport off South Africa. This was done by developing a sardine IBM and coupling it with two hydrodynamic model configurations of varying horizontal and vertical resolutions and boundary forcings (Chapter 3). An extended and updated sardine IBM coupled with the more recent, better-suited hydrodynamic model configuration was then developed and used to investigate factors determining sardine egg and larval retention/transport success in the region (Chapter 4). From results, the hypothesis of separate west coast and south coast sardine stocks (Butterworth et al., 2016) was assessed by estimating the contribution of eggs spawned on the south coast to recruitment on the west coast (P_0), which is of great interest to the sardine fishery management (Dunn et al., 2016).

Testing the effects of different underlying hydrodynamic models on results of identical IBMs has not been done explicitly in other regions. This suggests that the importance of the hydrodynamics is not highly regarded by the scientific community conducting particle tracking IBMs. The differences in results between the PLUME and BENGSAFE IBMs were concentrated on the south coast. The increased offshore advection and transport from the south coast to the west coast were not directly linked to the resolution of the hydrodynamic model configuration but rather to the climatological forcings of the PLUME boundary close to the Agulhas Current, and the failure of PLUME in recreating the intense offshore variability in this region. This dissertation therefore highlights that the underlying hydrodynamic model configuration needs to be adequately suited to the region and properly validated prior to use, not necessarily very highly resolved.

The updated and extended BENGSAFE IBM highlighted the important factors determining successful retention/transport of sardine eggs, which were different depending on the recruitment system. 3-D coupled IBMs can be useful to fishery management by shedding

light on stock connectivity, transport of eggs and larvae and spatio-temporal variation in recruitment success (Hinrichsen et al., 2011). They also have the potential to highlight whether stock management frameworks need to be re-evaluated (Hinrichsen et al., 2011). Similar to García-García et al. (2016), results from Chapter 4 illustrated that larval connectivity between stocks can be inferred from particle tracking IBMs. Estimates of the portion of sardine eggs and larvae transported from the south coast to the west coast (P_0) will prove extremely useful for management of the sardine fishery. A low P_0 value, as suggested by this dissertation, indicates a small contribution of eggs spawned on the south coast to west coast recruitment and therefore two largely separate stocks. Management needs to take this likely separation into account and develop a new OMP, which spatially manages the fishery to ensure one or both stocks are not overfished. The IBMs in this dissertation are purely Lagrangian and only include the effect of lethal temperature on sardine eggs and larvae. Therefore results should be treated with caution as there are other factors, not included in the model, that affect transport/retention success and survival of eggs and larvae. Such factors are food availability, egg buoyancy, predators and larval behaviour. The spatial resolution of BENGSAFE (7km), although better than PLUME, does not resolve all coastal features and filaments, and therefore considerations should be made regarding whether a higher resolved model configuration would affect results.

The relative importance of accurately representing the physics of the region or the biology of the species in question in IBMs is an interesting issue. Coupling IBMs with very highly resolved hydrodynamic model configurations may give better estimations of the ocean dynamics of the region, however such outputs are computationally heavy and IBM simulations may have to be temporally and spatially restricted because of this. Most of the sardine IBMs for other regions are much more complex than the Lagrangian IBMs presented in this dissertation, including parameters such as vertical migration, development dependent buoyancy and food limitations (Santos et al., 2005; Itoh et al., 2009; Dias et al., 2014; García-García et al., 2016). Anchovy IBMs for the Southern Benguela ecosystem have included complexities such as egg buoyancy schemes (Parada et al., 2003), diurnal vertical migration of larvae (Parada et al., 2008) and food availability (Koné et al., 2013). However, it is extremely important to adopt a simple, layer-by-layer methodological approach so as to allow for changes in results to be accounted for correctly (Mullon et al., 2003), and therefore this dissertation is the first step of the modelling process and can act as a base layer to which more complex IBMs can be compared to. That being said, adding more biological complexities could increase the uncertainties related to the IBMs. There is a trade off between the accurate representation of the physics and the biology

in IBMs. This dissertation suggests that it is a combination of both suitable physics and accurate biology that is needed for optimum results.

The 2016 final panel report from the Annual International Stock Assessment Review Workshop emphasised the importance of including biological realism in IBMs (Dunn et al., 2016). Future research should be directed at trying to achieve this, in a simple, layer-by-layer approach. Incorporating more biological realism into Southern Benguela sardine IBMs would greatly enhance the model's ability to accurately demonstrate the factors affecting recruitment and potential for use in fishery management.

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