Modelling the effect of buoyancy on the transport of anchovy (*Engraulis capensis*) eggs from spawning to nursery grounds in the southern Benguela: an IBM approach

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ABSTRACT

An individual-based model (IBM) was used to investigate the effects of physical and biological variables on the transport via a jet current of anchovy (*Engraulis capensis*) eggs from spawning to the nursery grounds in the southern Benguela ecosystem. As transport of eggs and early larvae is considered to be one of the major factors impacting on anchovy recruitment success, this approach may be useful to understand further the recruitment variability in this economically and ecologically important species. By coupling the IBM to a 3D hydrodynamic model of the region called Plume, and by varying parameters such as the spatial and temporal location of spawning, particle buoyancy, and the depth range over which particles were released, we could assess the influences of these parameters on transport success. A sensitivity analysis using a General Linear Model identified the primary determinants of transport success in the various experimental simulations, and model outputs were examined and compared with patterns observed in field studies. Model outputs compared well with observed patterns of vertical and horizontal egg distribution. Particle buoyancy and area of particle release were the major single determinants of transport success, with an egg density of 1.025 g cm^{-3} maximizing average particle transport success and the western Agulhas Bank being the most successful spawning area. This IBM may be useful as a generic prototype for other upwelling ecosystems.

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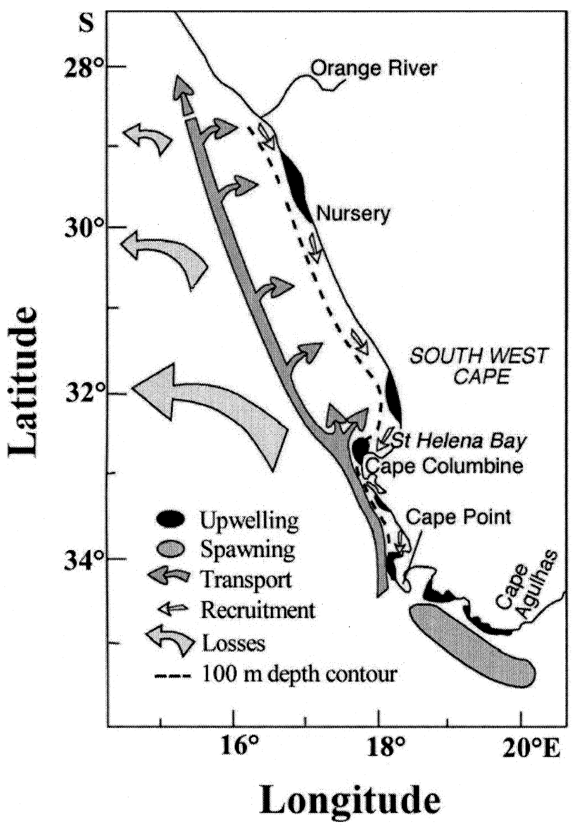
INTRODUCTION

Cape anchovy *Engraulis capensis* is an important component of the pelagic fishery off South Africa, and has shown large interannual fluctuations in population size. These population fluctuations arise from highly variable recruitment and are compounded by the short lifespan of this species; anchovy mature after their first year and seldom live beyond 3 years. As a large proportion (70% on average) of anchovy caught by the pelagic fishery are recruits (6+ months; Cochrane and Hutchings, 1995), large fluctuations in recruitment strength have serious implications for effective management of this important resource.

The life history of anchovy in the southern Benguela has been relatively well studied, with particular emphasis placed on examining the factors causing variability in recruitment success (Hutchings *et al.*, 1998). Anchovy spawn over the Agulhas Bank in austral summer between September and February with a mid-season peak in November (Shelton, 1986). Eggs which require 1–4 days to hatch, depending on temperature (King *et al.*, 1978), and early larvae are transported via a shelf-edge jet current to the nursery grounds between Cape Columbine and the Orange River (Shelton and Hutchings, 1982; Fig. 1). Variability in the transport of eggs from spawning to nursery grounds is considered to be among the primary determinants of anchovy recruitment success (Hutchings, 1992; Hutchings *et al.*, 1998). Once anchovy have grown into juveniles (approximately 3–6 months), they migrate southwards back to the Agulhas Bank and spawn there at an age of around 1 year.

Variability in the horizontal and vertical distribution patterns of recently spawned eggs could result in differential transport to the nursery grounds and hence impact on recruitment success. Horizontal egg

Figure 1. Conceptual model of the anchovy's life history (from Hutchings *et al.*, 1998; reproduced with permission).



distributions are characterized by interannual variability in the location of peak concentrations (van der Lingen *et al.*, 2001), whilst the pattern of vertical distribution is likely to be strongly affected by both the depth of spawning and by the buoyancy properties of the eggs themselves, as indicated in previous studies (Sundby, 1983, 1991, 1997).

In this paper we present an individual-based model (IBM) which aims to identify the importance of various factors on the successful transport and hence subsequent recruitment success of anchovy in the southern Benguela. Biological parameters such as spawning area, date of spawning, depth of spawning and egg buoyancy, and physical parameters including salinity, temperature and velocity fields, were incorporated into the IBM. A sensitivity analysis using a General Linear Model (GLM), with transport success as the dependent variable, was carried out to establish the relative importance of the above parameters and their contribution to explaining the variance of the model outputs. Finally, model outputs were compared with observed vertical and horizontal distribution patterns of anchovy eggs in the southern Benguela.

MATERIALS AND METHODS

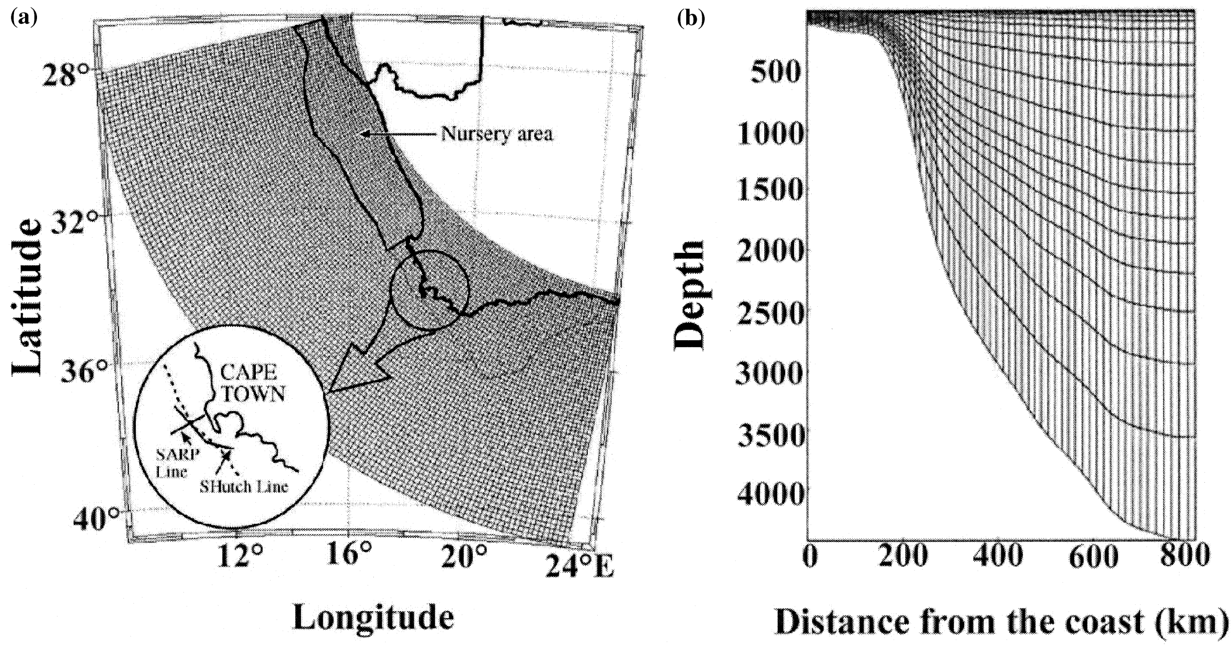
An IBM approach was used to investigate the effects of a series of physical and biological variables on the transport of anchovy eggs from the Agulhas Bank spawning grounds to the west coast nursery area. Outputs from a 3D hydrodynamic model of the southern Benguela subregion (Penven *et al.*, 2001), including velocity, salinity and temperature fields, were used to implement the IBM, and particles representing individual anchovy eggs were tracked through time and space.

Overview of the Plume 3D hydrodynamic model

The ocean model of the southern Benguela upwelling subregion, known as Plume (Penven, 2000), uses the Regional Ocean Modeling System (ROMS) (see Haidvogel *et al.*, 2000) that solves the free surface, hydrostatic, primitive equations of the ocean dynamics over a variable topography using orthogonal curvilinear coordinates in the horizontal and stretched terrain-following coordinates in the vertical (Song and Haidvogel, 1994). The curvilinear grid is pie-shaped (Fig. 2a) to follow the southwestern corner of the African continent from 28 to 40°S and from 10 to 24°E. Horizontal resolution ranges from 9 km at the coast to 16 km offshore and 20 vertical levels preserve a high vertical resolution near the surface (Fig. 2b). At the three lateral boundaries facing the open ocean, an implicit active radiative boundary scheme (Marchesiello *et al.*, 2001), forced by seasonal time-averaged outputs of a basin scale ocean model (Biastoch and Krauß, 1999), connects all model variables to the surroundings (Penven *et al.*, 2001). The model was forced using monthly average fluxes of wind, heat and salinity from the Comprehensive Ocean-Atmosphere Data Set (COADS) ocean surface climatology, which has a spatial resolution of 0.5° (Da Silva *et al.*, 1994). The model was started from rest and summer values were used for initial conditions. As the model domain is relatively small, Plume reaches an equilibrium after a spin-up period of about 2 years (Penven *et al.*, 2001).

The model was run for 10 years and forced by a repeated climatology (i.e. no interannual variability in the forcing fields). Although the forcing was identical each year and the model was considered to be in a state of equilibrium, the highly turbulent dynamics found in this region would lead one to expect slight differences in model solutions from 1 year to the next. Such differences were found and were attributed to intrinsic mesoscale activity resulting from oceanic instability processes in the absence of added forced variability (Penven *et al.*, 2001), and this is similar to

Figure 2. (a) The pie-shaped horizontal grid of the Plume model. The thick line represents the coastline, the thin line the 500-m isobath, and the grid resolution is approximately 10 km at the coast. The location of the west coast nursery grounds and the SARP and SHutch Lines are shown. (b) Vertical S-coordinate levels of the Plume model following topography. The resolution is 9 m for the first surface level, and approximately 1000 m for the deepest level on the oceanic plain.



prior studies developed in the California upwelling system (Marchesiello *et al.*, 2001). A snapshot of the surface structure of temperature (SST) and surface currents output by Plume (Fig. 3) shows a high level of realistic, mesoscale activity and some of the main features of the southern Benguela, including the jet current, the generation of Agulhas rings and the shedding of cyclonic eddies from the southern tips of the Agulhas Bank, Cape Peninsula and Cape Columbine. The average behaviour of the model and its variability has been checked against observed data and the close comparison between model output and field observations provides confidence in the reliability of the model output to reproduce typical oceanic states for the southern Benguela (see Penven *et al.*, 2001 for details).

The configuration of Plume used for our analysis stored output data every two simulation days and was not intended to reproduce any true year in particular but, rather to provide a virtual environment that had a high level of spatial and temporal realism for use in the biological model. From the 8 years of post-equilibrium Plume output, we selected only 5 years (years 4–8) for coupling to the IBM, this limitation being the result of the computational constraints imposed by this type of modelling approach that involve solving the equations for every particular 'individual'. These 5 years provide sufficiently different scenarios to test the hypothesis that egg buoyancy has a significant impact on transport success.

Overview of IBM, experiments and simulations

The IBM was used to track the movement of particles representing anchovy eggs spawned over the Agulhas Bank and transported northwards to the west coast nursery grounds. Both the horizontal and vertical movements of particles were modelled: horizontal movements resulted from outputs of the 3D hydrodynamic model whilst vertical movement was the result of model outputs and particle buoyancy properties, which included parameters such as density and diameter, water density and viscosity, and gravitational force. By incorporating a buoyancy property and varying the parameters used to generate this, the IBM provided a variety of vertical and horizontal particle distribution patterns that gave rise to differential transport success.

The IBM used a combination of fixed and varied parameters (Table 1). Two groups of experiments were conducted. The first group (called Lagrangian experiments) excluded buoyancy and treated particles as pure Lagrangian particles, the vertical velocities of

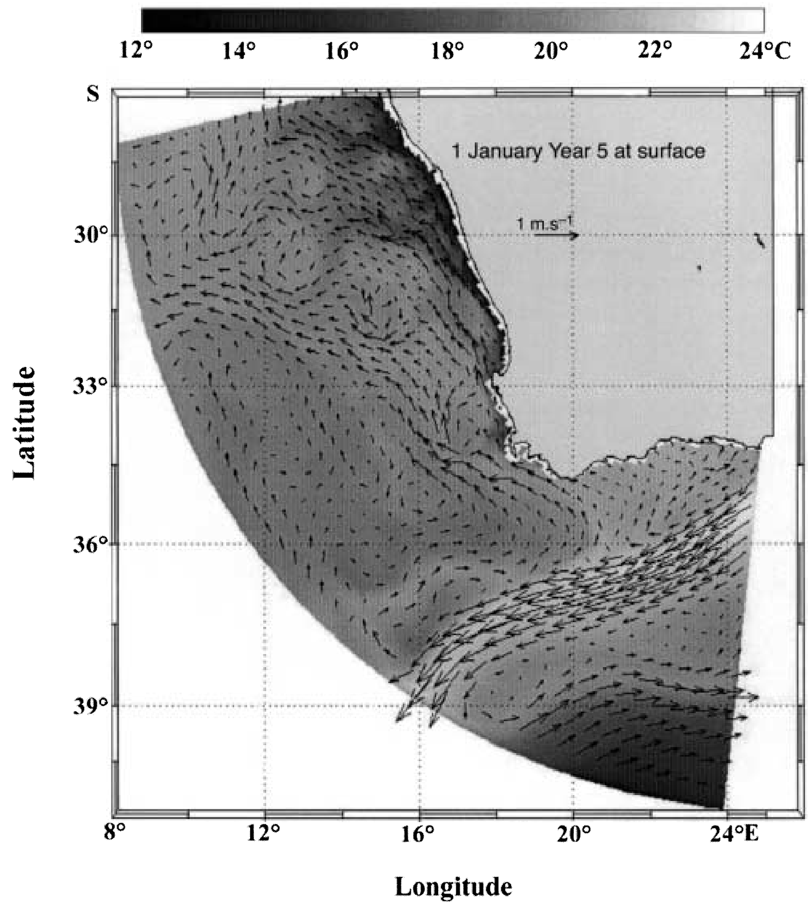


Figure 3. A snapshot (1 January of year 5) of sea surface temperature and currents (arrows, only every third vector drawn) in the southern Benguela region simulated by Plume.

which depended only on the flow-field output from Plume. The second group of experiments (called buoyancy experiments) incorporated the effect of buoyancy, and computed particle vertical velocity as a function of buoyancy and vertical flow-fields. The buoyancy properties of eggs and early larvae were assumed to be the same, hence the buoyancy scheme was applied unchanged to all particles throughout the IBM simulations.

The configuration of experiments is shown in Fig. 4. Once the model was initialized and the parameters were set for each simulation, outputs from the Plume model were used as inputs to the IBM. A population of 5000 particles was then randomly released over the Agulhas Bank spawning area, the spawning duration determining the period over which new individuals entered the population. Based on field observations of anchovy egg distributions (Fig. 5), four areas were selected for particle release: the Western Agulhas Bank (WAB), the offshore Central Agulhas Bank (CAB_{Off}), and the inshore (EAB_{In}) and offshore (EAB_{Off}) regions of the Eastern Agulhas Bank. During the 90-day simulation period, the position of each particle in the Plume 3D hydrodynamic model was monitored. For each 2-day time step, the vertical velocity of each particle was estimated according to the buoyancy scheme (see below), and particles were individually moved to their new positions. Throughout the simulation, the IBM recorded the number and age of particles meeting the criteria for successful transport (see next section). Each individual simulation was independently launched three times, each time being called a subsimulation.

Dependent variable: criteria of transport success

During IBM simulations the number of particles older than 14 days (equivalent to seven model time steps) that arrived on the west coast nursery grounds (Fig. 2a) was recorded. This value was used as the criterion for successful transport and was taken as the dependent variable in subsequent statistical analyses. Our choice of 14 days as the successful criterion for anchovy arriving in the nursery grounds was based on the findings of Badenhorst and Boyd (1980), who showed that anchovy larvae >7-mm caudal length (corresponding to an approximate age of 14 days;

Table 1. Variables and parameters used to formulate the individual-based buoyancy model.

	Description
Variable	
Water temperature and salinity	Plume (Penven, 2000) outputs with time step of 2 days in the model domain of the Benguela ecosystem
Water density	UNESCO equations for calculation of water density as a function of water temperature, salinity, and pressure
Velocity field	Hydrodynamic model output *u*, *v*, and *w* velocities with time steps of 2 days, used to estimate the Lagrangian trajectory of particles at a given time
Fixed parameters	
Spawning duration	Spawning is a constant process starting on the first day of simulation and lasting for 30 days
Death age	All particles representing eggs were set to die at age of 60 days
Duration of simulation	Every simulation was run over 90 days (spawning duration + death age)
Number of eggs	The number of particles was set to 5000 per simulation and particles were released continuously over the spawning duration
Egg shape	A prolate spheroid with a major axis of 1.4 mm and a minor axis of 0.5 mm was used
Varied parameters	
Area	Particles were released over all four spawning areas [Western Agulhas Bank (WAB), Central Agulhas Bank offshore (CAB_{Off}), Eastern Agulhas Bank inshore (EAB_{In}) and Eastern Agulhas Bank offshore (EAB_{Off})] in proportion to the relative size (in km^2) of each area
Date	The dates of spawning were set to: 1 October, 1 November, 1 December, 1 January, 1 February and 1 March
Year	Years 4–8 from Plume (Penven, 2000) were used in the IBM
Depth	Particles were released in three depth ranges: 0–25, 25–50 and 50–75 m, and randomly distributed in the water column over the specified range
Egg density	The range of density for the particles was set in the model to 1.021, 1.023, 1.025, 1.027 (g cm^{-3}) and a passive Lagrangian experiment

Brownell, 1983) could avoid a bongo net during the day compared with night and, hence, showed active swimming. We therefore assumed that anchovy ≤7 mm could be considered as passive particles that would behave in a manner indistinguishable from eggs. Larvae ≤7 mm would not be able to retain themselves in the nursery area and would be subject to offshore advective loss; hence we considered that their transport was not successful. Larvae larger than 7 mm would have sufficiently developed swimming capabilities to maintain themselves within the nursery area.

The buoyancy scheme

We used the equations of Denny (1993) in which the terminal velocity is calculated by equating the force required to propel a prolate spheroid moving parallel to its long axis with the weight of that prolate spheroid. In the buoyancy scheme, the vertical velocity of particles are confined to the Stokes' regime when the Reynolds number is <0.5, indicating that viscosity dominates over friction. It is assumed that the vertical drag of the particle is in balance with the buoyancy forces, resulting in the terminal velocity (w_{part}) that is a function of gravitational force *g*, sea water density ρw, kinematic viscosity v (0.01 m^2s^{-1}), minor (d) and major (I) axes of the prolate spheroid (Table 1), and particle density (ρ_{part}):

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

where $\Delta\rho = \rho_{part} - \rho_w$ and w_{water} is vertical velocity $\frac{dz}{dt}$ (where z is depth and t is time) from the Plume model. Field measurements of the density of anchovy eggs from the southern Benguela range from 1.021 to 1.027 g cm^{-3} (C.D. van der Lingen, unpublished data) and were used in the modelling experiments.

The equations solved in the IBM that determine the velocities of particles in every time step are:

$$\frac{dx_{part}}{dt} = u_{water} \quad (2)$$

$$\frac{dy_{part}}{dt} = v_{water} \quad (3)$$

$$\frac{dz_{part}}{dt} = w_{part} \quad (4)$$

where u_{water} and v_{water} are the east–west and north–south components respectively, of the velocity

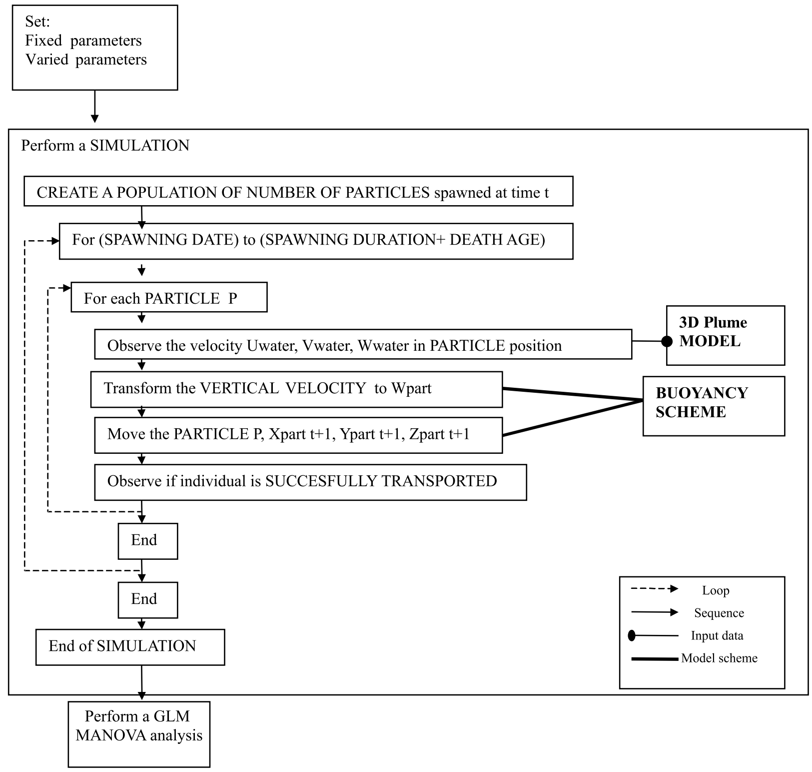


Figure 4. Flowchart of experimental simulations.

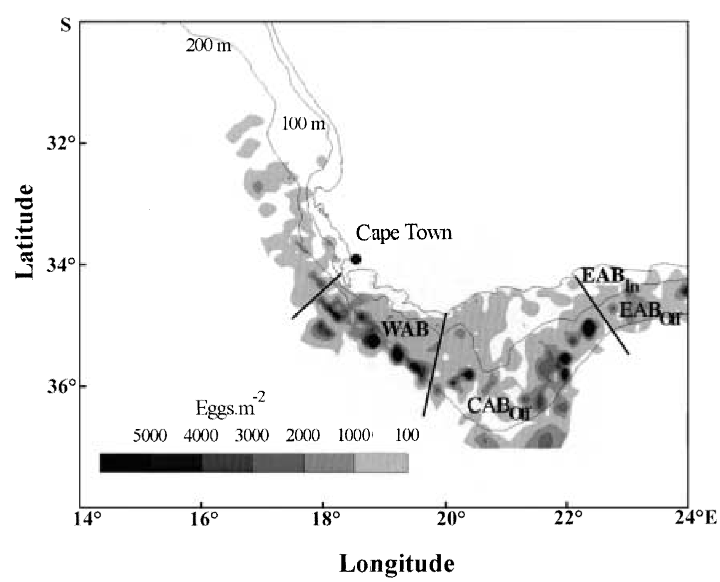


Figure 5. Composite distribution map of anchovy eggs collected using a CalVET net during annual pelagic spawner biomass surveys over the period 1983–2000. Data updated from van der Lingen *et al.* (2001). The locations of the WAB, CAB_{Off} and EAB_{In} and EAB_{Off} spawning grounds used in this IBM are shown.

output of the Plume model. The position of the particles at a given time was approximated with a Eulerian forward solution where $xpart_t$, $ypart_t$ and $zpart_t$ are the 3D positions of the particles at time t and $xpart_{t+1}$, $ypart_{t+1}$ and $zpart_{t+1}$ are positions of particles at time t+1:

$$xpart_{t+1} = xpart_t + u_{water}dt \qquad (6)$$

$$ypart_{t+1} = ypart_t + v_{water}dt \qquad (7)$$

$$zpart_{t+1} = zpart_t + w_{part}dt \qquad (8)$$

IBM outputs and analysis of results

A sensitivity analysis using a GLM (Drapper and Smith, 1966) and multiple analysis of variance (MANOVA) was applied to the outputs from both the Lagrangian and the buoyancy experiments. Transport success was the dependent variable in the GLM and the varied model parameters (Table 1) were independent variables. This analysis included a study of the frequency distribution of residuals in transport success, as well as the significance and proportion of variance explained by each of the parameters and their interactions up to the second level, and hence allowed the identification of the main parameters in the IBM that impacted on transport success. We ran a full GLM that included all parameters and their interactions up to the second level, and parameters that explained more than 5% of the variance in the model were considered important.

Effect of particle density under different jet current scenarios

Three scenarios of jet current strength and possible offshore advective loss were identified from analysis of the Plume model output, and were used to examine how particle density affected transport success within each category. The scenarios were identified using averaged transport values ($m^3\ s^{-1}$) in the jet current over a 3-month period subsequent to the date on which eggs were released. Both along-shore (north–south) and across-shelf (offshore–inshore) cumulative transport values were computed from the Plume model. Six along-shore and six across-shelf transport values, corresponding to the six different dates for the initiation of spawning (see Table 1), were computed for each model year used in this analysis (years 4–8), giving a total of 60 values. Along-shore transport values were computed for the 90-day simulation period for the upper 50 m along a line 100 km in length positioned at the location of the Sardine Anchovy Recruitment Program (SARP) line (see Fig. 2a), and across-shelf transport values were computed for the upper 50 m along a line 100 km in length and positioned 60 km from the coastline between Cape Point and Cape Columbine. These boundaries were chosen to represent the transport region and the likely vertical distribution range of anchovy eggs (Shelton and Hutchings, 1982), and the maximal offshore position of the jet current (Boyd and Nelson, 1998).

Comparing model output to field observations

Outputs from the IBM experiments were compared with patterns of vertical and horizontal anchovy egg distributions observed in the field. Data on the vertical distribution of anchovy eggs in the southern Benguela are scarce, but IBM outputs were compared with vertical profiles of egg concentration along a line off the Cape Peninsula (called the SHutch Line in our model; Fig. 2a) provided by Shelton and Hutchings (1982). Modelled horizontal particle distributions were compared with egg data collected from the SARP Line, a 60-km transect of 12 evenly spaced stations running WSW of Slangkop Point off the Cape Peninsula, sampled one to two times every month (Huggett *et al.*, 1998). Model-derived patterns that compare closely with those observed in nature should enable a better understanding of the

Table 2. General Linear Model applied to Lagrangian simulation results.

General Linear Model	DF	SS	MS	*F*†	*P* value	Explained variance
Intercept	1	482369.2	482369.2	63631.1	0.00	
One-way MANOVA						
Year	4	8965.6	2241.4	295.7	0.00*	1.0
Date	5	18258.4	3651.7	481.7	0.00*	1.9
Area	3	492052.5	164017.5	21636.2	0.00*	52.1
Depth	2	159505.2	79752.6	10520.5	0.00*	16.9
Two-way MANOVA						
Area × depth	6	82097.0	13682.8	1805.0	0.00*	8.7
Three-way MANOVA						
Year × date × area	60	50220.7	837.0	110.4	0.00*	5.3
Error	2828	21438.3	7.6			2.3
Total	3239	943550.2				

*$P < 0.001$, †*F*, f-ratio.

DF, degrees of freedom; SS, Sum of squares; MS, mean square.

processes that lie behind such patterns (Grimm *et al.*, 1996).

RESULTS

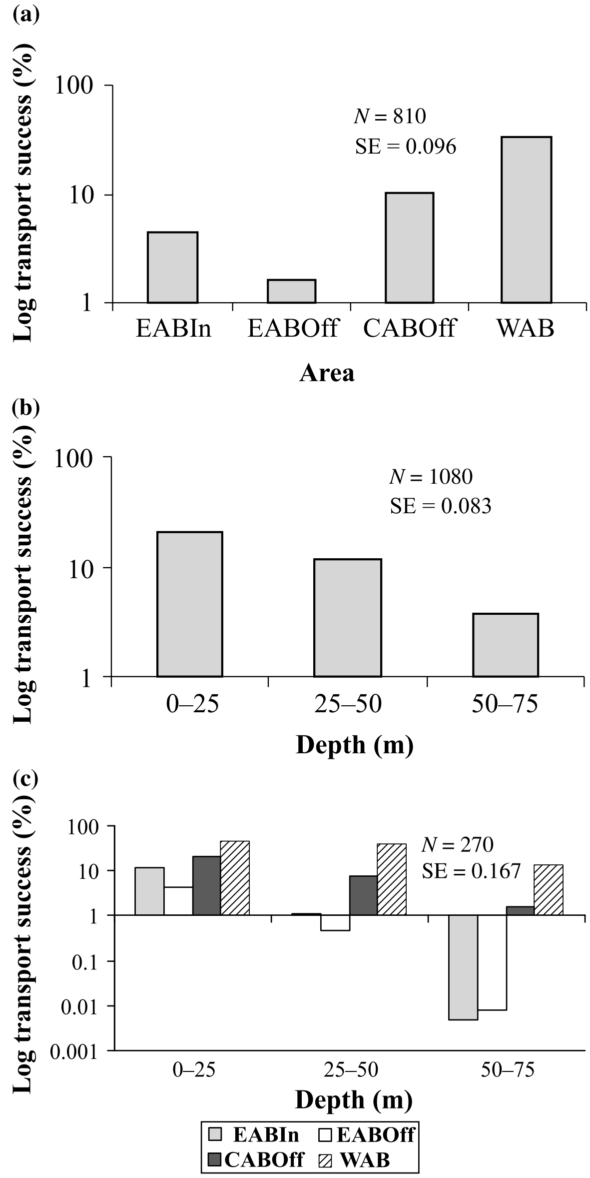
Sensitivity analyses: Lagrangian experiments

Area was the primary determinant of transport success (Table 2), with the WAB and CAB_{Off} being similarly successful spawning areas whilst the EAB_{in} and EAB_{off} were less successful (Fig. 6a). Depth of particle release had a less marked, but still significant effect on transport (Table 2), with maximum success associated with particles released nearest the surface (0–25 m) and decreasing with depth (Fig. 6b). An important first order interaction between depth and area was observed; successful transport from both the EAB_{in} and EAB_{off} only occurred for particles released near the surface, whereas those released from the CAB_{Off} showed a marked decrease in transport success with increasing depth of release and the WAB showed a slight trend of reduced transport success with increasing depth (Fig. 6c). Area, depth and the area × depth interaction, together with a second order interaction between Year, date and area, explained 83.1% of the variance of the model, with only 2.3% residual variance (Table 2). Residuals of transport success from the Lagrangian experiment appeared to be normally distributed, as required by the GLM used for the sensitivity analysis.

Sensitivity analysis: buoyancy experiments

Particle density was the most important single parameter determining transport success (Table 3), with a value of 1.025 g cm^{-3} resulting in the maximum success (Fig. 7a). Area was another important single parameter, with the WAB being the most successful spawning area and transport success decreasing as spawning moved eastward, being reduced for CAB_{Off} and close to zero for the inshore and offshore regions of the EAB (Fig. 7b). Two important interactions were observed; a first order interaction between particle density and area, and a second order interaction between date, area and particle density. The interaction between particle density and area explained over one-third of the variance in the GLM output (Table 3), indicating that the optimal particle density was different for the different spawning areas (Fig. 7c). The parameters and interaction terms listed above, together with the interaction between date and particle density, accounted for 86.5% of explained variance, with the error term being 3.7% (Table 3). Visual examination

Figure 6. Average transport success for the single parameters used in the Lagrangian experiment: (a) spawning area, (b) depth of particle release, and (c) interaction between spawning area and depth of particle release.



of the residuals of transport success from this category suggested a normal distribution.

Identification of scenarios and of particle density under different jet current scenarios

Averaged jet current transport calculated from the Plume hydrodynamic model showed a strong linear relationship between along- and across-shore components, with strong northwards flow associated with a strong offshore component and weak northwards flow

Table 3. General Linear Model applied to buoyancy simulation results.

General Linear Model	DF	SS	MS	*F*†	*P* value	Explained variance
Intercept	1	156220.2	156220.2	25645.7	0.00	
One-way MANOVA						
Year	4	2316.4	579.1	95.1	0.00 *	0.1
Date	5	40315.4	8063.1	1323.7	0.00 *	2.0
Area	3	231366.9	77122.3	12660.7	0.00 *	11.5
Density	3	399150.2	133050.1	21842.0	0.00 *	19.9
Depth	2	7.3	3.7	0.6	0.55	0.0
Two-way MANOVA						
Date × density	15	116460.1	7764.0	1274.6	0.00 *	5.8
Area × density	9	745782.6	82864.7	13603.4	0.00 *	37.2
Three-way MANOVA						
Date × area × density	45	241806.5	5373.5	882.1	0.00 *	12.1
Error	12200	74316.0	6.1			3.7
Total	12959	2003609.3				

$^*P < 0.001$, †*F*, f-ratio.
DF, degrees of freedom; SS, Sum of squares; MS, mean square.

associated with stronger inshore transport (Fig. 8a). Years 4, 5 and 6 were characterized by strong northwards and offshore transport, whereas inshore transport predominated in years 7 and 8 (Fig. 8b). These results allowed the selection of three jet current scenarios: scenario 1 being characterized by strong northwards and strong offshore flow (January of year 5), scenario 2 by weak northwards and weak offshore flow (December of year 6) and scenario 3 by weak northwards and strong inshore flow (March of year 8). The IBM simulations were run under each of these scenarios with varied particle density values (1.021–1.027 g cm^{-3}) but all other parameters fixed (area was the WAB and depth of spawning was 0–25 m). Maximum transport success was associated with particles having a density of 1.025 g cm^{-3} in all three scenarios (Fig. 8c) but was substantially higher for scenario 1 (80%) than for scenarios 2 and 3, which presented similar transport success values (~40%).

Comparing model output to field observations

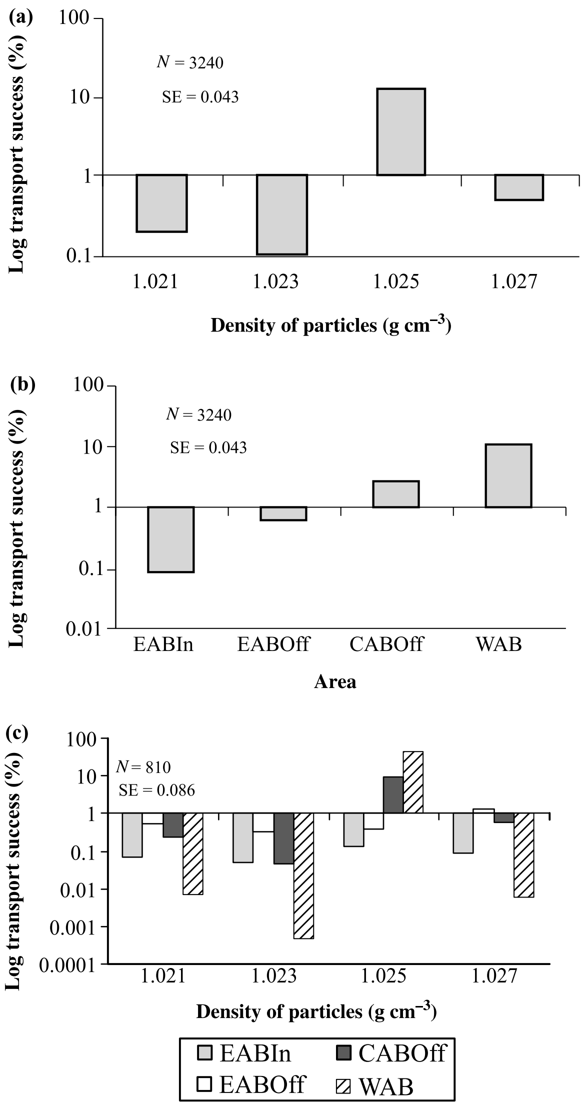
The distribution of eggs along the SARP Line during August 1995 to July 2001 is characterized by relatively few eggs at the first five (inshore) stations and higher concentrations at stations 6–12 (Fig. 9a). In general terms, the simulation outputs from the three jet current scenarios showed similar patterns to the field observations, showing low concentrations inshore and high concentrations offshore (Fig. 9b–d). Under scenario 1, a higher number of Lagrangian particles and individuals having an intermediate density (1.025 g cm^{-3}) were recorded at the SARP Line compared with particles either lighter or denser than 1.025 g cm^{-3} (Fig. 9b). Under scenario 2, the maximum number of individuals crossing the SARP Line was reduced by at least half compared with scenario 1, but more buoyant particles (1.021 and 1.023 g cm^{-3}) dominated and dense particles (1.027 g cm^{-3}) were not recorded there (Fig. 9c). The pattern of scenario 3 is similar to that of scenario 2 with lighter particles dominant, but with the difference that Lagrangian particles and those of intermediate density (1.025 g cm^{-3}) were poorly represented (Fig. 9d).

Shelton and Hutchings (1982) showed that anchovy eggs were mostly distributed in the upper 50 m of the water column, with a maximal concentration at 30 m depth (Fig. 10a). Modelled particle vertical distribution patterns along the SHutch Line differed with particle density, the particles with highest buoyancy (1.021 and 1.023 g cm^{-3}) being concentrated at the surface and the most dense ranging between 60 and 130 m depth (Fig. 10b). In the model, neutrally buoyant particles and those with a density of 1.025 g cm^{-3} showed vertical distributions that most closely resembled field observations.

DISCUSSION

The IBM approach was used to investigate the effects of various biological and physical factors on the transport success of anchovy eggs from the spawning grounds to the nursery area of the southern Benguela upwelling ecosystem. By coupling the IBM to a 3D hydrodynamic model of the region, and by varying

Figure 7. Average transport success for the single parameters used in the buoyancy experiments: (a) particle density, (b) spawning area, (c) interaction between particle density and spawning area.



parameters such as the spatial and temporal location of spawning, particle density, and the depth range over which particles were released, we were able to generate a wide range of transport success values. A sensitivity analysis using GLM was conducted to identify the primary determinants of transport success in the various experimental simulations, and model outputs were examined and compared with field observations.

In the Lagrangian experiments, area was the dominant parameter and accounted for more than 50% of the variability in anchovy egg transport success. This finding is consistent with other modelling studies of anchovy egg transport in the southern Benguela in which buoyancy was not considered (Mullon *et al.*, 2002; Huggett *et al.*, 2003). Depth of spawning was also an important parameter in the Lagrangian experiments, but not in the buoyancy simulations as the density parameter 'controls' the depth of particles at any time step during simulations.

The inclusion of particle density in our buoyancy simulations showed the importance of this parameter, both by itself and in its interactions. As the density of early larvae is different to that of eggs (Coombs *et al.*, 1985; Tanaka, 1990, 1992), the assumption of unchanging particle density made by the IBM is unrealistic. To examine this more closely we performed a second set of buoyancy simulations in which eggs were accorded a density value whereas larvae were treated as Lagrangian particles; hence these simulations applied the buoyancy scheme for only three time steps. Differences between the two categories of buoyancy simulations were minimal, indicating that density impacts on transport success at a very early life history stage (i.e. primarily on eggs).

One of the patterns to emerge from the buoyancy simulations is that on average, a density of 1.025 g cm^{-3} promoted the most successful transport when particles were released over the WAB. That the WAB was the most successful spawning area in both Lagrangian and buoyancy simulations supports previous hypotheses (Shelton and Hutchings, 1982; Armstrong *et al.*, 1988; Boyd *et al.*, 1992; Roel *et al.*, 1994; Hutchings *et al.*, 1998) that anchovy spawn primarily over the WAB because of the increased probability of successful transport of eggs to the west coast nursery grounds. Similarly, other IBM studies examining anchovy egg transport in the southern Benguela also identified the WAB as the optimum site for successful transport (Mullon *et al.*, 2002; Huggett *et al.*, 2003). However, the near-zero transport success for eggs spawned over the EAB was surprising, given that field observations have shown an eastward shift in anchovy spawning in recent years (van der Lingen *et al.*, 2001) that have been followed by successful recruitment (van der Lingen *et al.*, 2002). In our simulations, only the west coast was considered as a suitable nursery ground, and the failure of successful transport of eggs spawned over the EAB was because of advective losses offshore or individual particles remaining over the EAB. As anchovy larvae and early juveniles have been found off South Africa's south and east coasts (Anders, 1975; Beckley, 1986; Beckley and Hewitson, 1994), it suggests that these areas may also act as nursery grounds. As eggs spawned over the EAB are not successfully transported to the west coast nursery grounds, successful recruitment of these eggs appears to depend on the occurrence of suitable nursery habitat on the south and/or east coasts. However, it is not possible to assess this hypothesis because the model domain is restricted in the east. Moreover, it is difficult to say how representative the output of the Plume model over the EAB is, because the eastern limit of the EAB area is too close to the boundary of the physical model domain, and boundary effects may prevail. Our results are also in contrast to those of Shannon *et al.* (1996), who used a transport model based on currents derived from Acoustic Doppler Current profiler that indicated that anchovy eggs spawned over the EAB could enter the west coast nursery grounds.

Another strong pattern observed was the change through time of jet current characteristics from the PLUME simulations. Between years 5 and 8, transport changed from having strong northwards and offshore components to having weak northwards and strong inshore components (see Fig. 8b). However, year was not a significant model parameter, indicating that this change in jet current characteristics did not result in marked changes in annual average transport success.

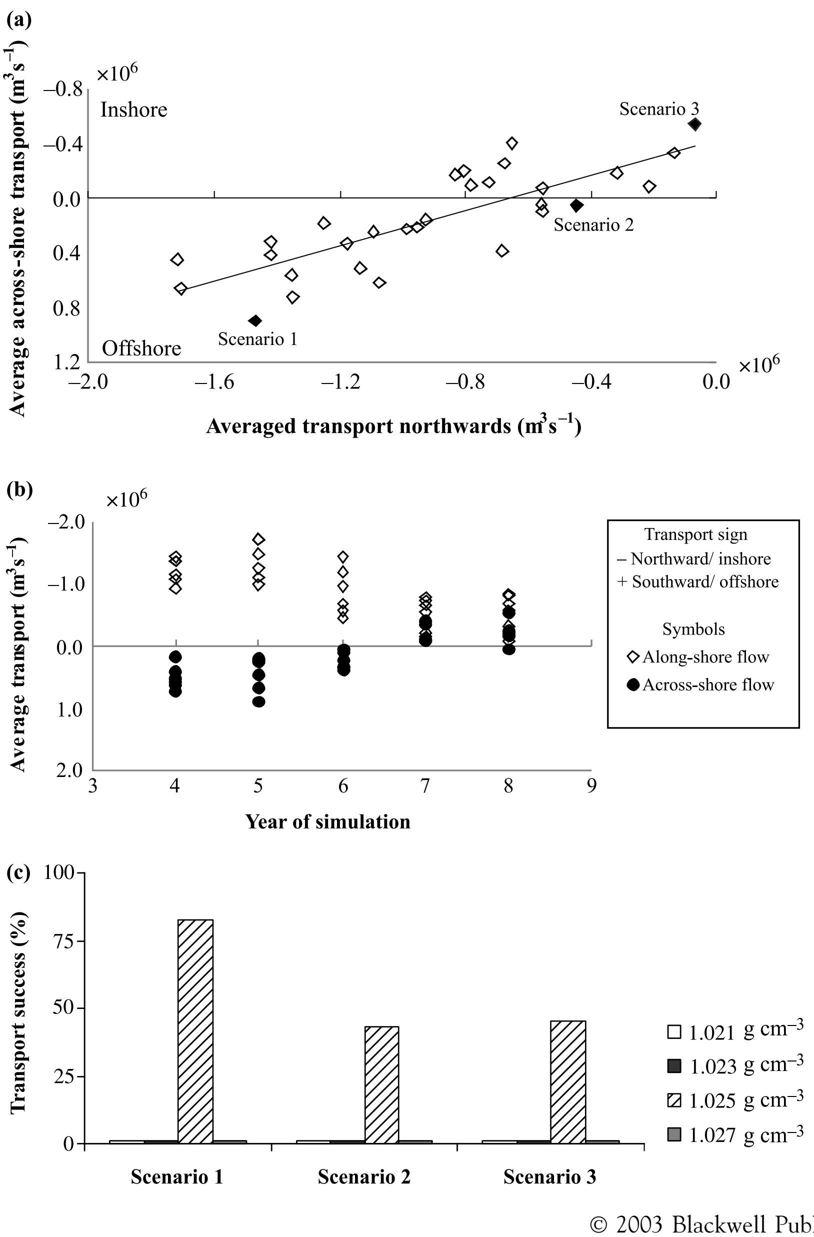
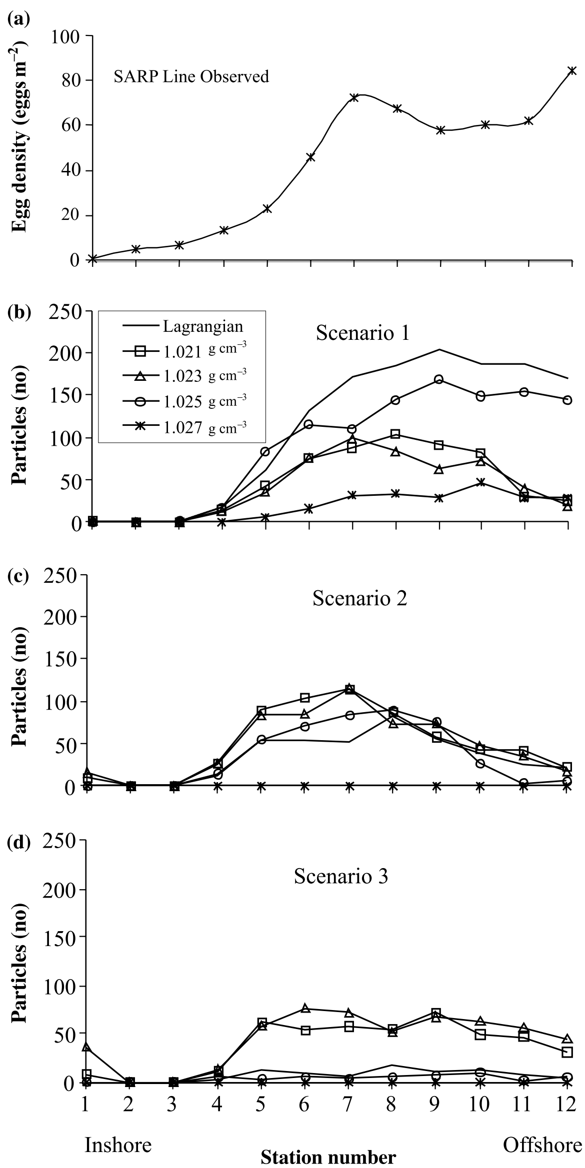


Figure 8. (a) Average along-shore and across-shelf transport in the region of the jet current for all simulations, (b) average along-shore and across-shelf transport per year, and (c) transport success as a function of particle density for particles released in the upper 25 m over the WAB only for each of three scenarios. Each scenario represents a single simulation.

Figure 9. Horizontal distribution of anchovy eggs along the SARP Line (a) observed [between August 1995 and July 2001 (data from J. Huggett, Marine and Coastal Management, personnal communication)] and (b), (c), and (d) simulated results for the three jet current scenarios: scenario 1: strong northwards and strong offshore flow (January of year 5); scenario 2: weak northwards and weak offshore flow (December of year 6); and scenario 3 weak northwards and strong inshore flow (March of year 8).



This suggests that whereas strong northward transport moves substantial numbers of eggs towards the west coast, a large proportion of these are advected offshore. However, when the northwards transport is reduced, the associated increased inshore transport means that most of the particles carried to the west coast make it into the nursery area.

The vertical distributions obtained in simulations compared well with field observations from the SHutch Line for particles having a density of 1.025 g cm^{-3} and Lagrangian particles. In contrast, light particles (1.021–1.023 g cm^{-3}) tend to concentrate in the upper 5 m of the water column. Dense (1.027 g cm^{-3}) particles are distributed between 60 and 140-m, which appears to be deep compared with field observations from the southern Benguela, and for anchovy species elsewhere (Motos and Coombs, 1998; Moser and Pommeranz, 1999; Santos *et al.*, 2000).

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

The importance of particle density on transport success may have been underestimated by our analysis because of the vertical scales used in the Plume model. The minimum vertical resolution in the uppermost layer of Plume is 1 m inshore and 5 m offshore, which may be too large to capture fine-scale differences (over scales of tens to hundreds of centimetre) in egg vertical distributions that have been reported for other anchovy species (Motos and Coombs, 1998; Coombs *et al.*, 2000; Santos *et al.*, 2000 for *E. encrasicolus*; Moser and Pommeranz, 1999 for *E. mordax*). Hence it is possible that increasing the vertical resolution in the near-surface domain of the model would have resulted in egg density becoming a more important parameter than has been the case here.

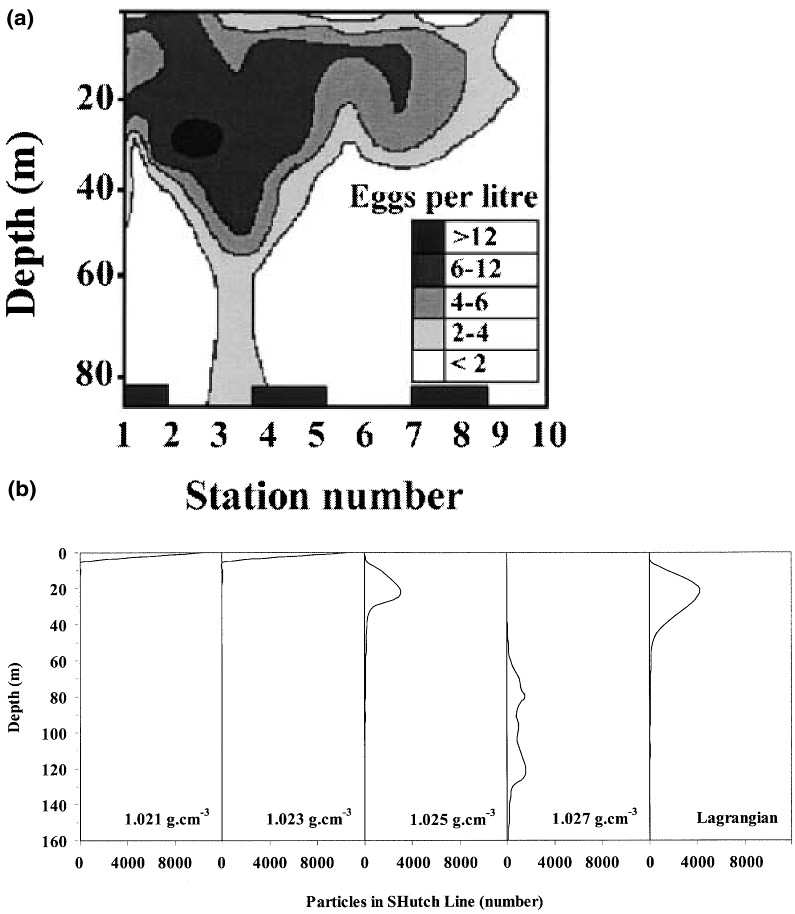


Figure 10. (a) Observed vertical distributions of anchovy eggs below the SHutch Line from Shelton and Hutchings, 1982; (the *x*-axis denotes station number, with station 1 closest to the coast), and (b) simulated vertical distributions of particles of varying densities in the SHutch Line.

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