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DRIFT PATTERNS OF ANCHOVY *ENGRAULIS CAPENSIS* LARVAE IN THE SOUTHERN BENGUELA, AND THEIR POSSIBLE IMPORTANCE FOR RECRUITMENT

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In the southern Benguela, successful recruitment of Cape anchovy *Engraulis capensis* is highly variable and seems to be dependent on the spawning biomass only to a small extent. This paper investigates how the variations in the drift patterns of larvae from the spawning areas on the Agulhas Bank to the upwelling-dominated regions on the west and south-west coasts of South Africa can explain these observed variations. Through the coupling of a three-dimensional circulation model, a Lagrangian particle-tracking model and spawning data, the number of particles ending up in different areas are used to investigate observed variability in recruitment. The model was able to explain 95% of the observed variability in recruitment for the period 1987–1993 (excluding 1989) using a simple linear regression formula. The model also suggests that, of the interannual variability in currents and egg distribution, the latter is the most important cause of the changes observed in the recruitment of anchovy.

Key words: anchovy, Benguela, Lagrangian model, recruitment, transport

Cape anchovy *Engraulis capensis* spawn mainly east of Cape Point, predominantly over the western Agulhas Bank (Fig. 1) from October to January (Crawford 1980). Being pelagic spawners, their eggs and larvae are transported by currents. Of importance is the shelf-edge jet current flowing north to regions of strong upwelling on the South African west coast (Bang and Andrews 1974, Nelson 1985). Recruits migrate in-shore to nursery areas along the West Coast between Cape Columbine and the Orange River. There, they continue to grow before migrating back to the spawning areas, where they recruit to the fishery in their first year and are targeted by purse-seiners for the production of fishmeal. By spawning upstream of the recruitment areas (Hutchings 1992), anchovy eggs and larvae are separated from spawners, reducing cannibalism (Valdés Szeinfeld and Cochrane 1992) while taking advantage of currents transporting spawning products to the nursery grounds.

The biomass of adult anchovy has fluctuated by an order of magnitude during the period 1984–1997 (Barange *et al*. 1999). Understanding this variability is of particular importance to the anchovy fishery, because 70% of the catch consists of 0-year-old recruits (Cochrane and Hutchings 1995). There is a positive relationship between spawner biomass and the recruitment six months earlier derived from back-calculated surveys (Barange *et al*. 1999), although there seems to be no clear relationship between spawner stock size and subsequent recruitment (Cochrane and Hutchings 1995). Therefore, it is likely that environmental and ecological factors affect the recruitment of anchovy, such as condition and feeding of spawning adults on the spawning grounds, retention in and transport from the spawning grounds, and larval feeding conditions in the recruitment and nursery areas (Hutchings 1992). Also, the abundance and distribution of anchovy predators are likely to be important factors contributing to anchovy recruitment success in the southern Benguela (Shannon *et al*. 1996). In particular, cannibalism of anchovy eggs and larvae (Valdés Szeinfeld and Cochrane 1992) will vary according to the distribution and density of spawning anchovy. In 1988, a multidisciplinary programme was initiated to investigate these linkages, with the long-term objective of developing a method to forecast anchovy recruitment using environmental and biological data obtained during the spawning season (Cochrane and Hutchings 1995). To date, the forecasting of anchovy recruitment has been based on two different approaches: empirical relationships between environmental and biological variables and recruitment, and expert systems (see Painting *et al*. 1998 and Hutchings *et al*. 1998 for an overview of the approaches).

Boyd *et al*. (1997) found a negative correlation between acoustic estimates of recruitment and south-easterly winds between 1985 and 1994. Using a transport model based on ADCP-derived currents (Boyd and Oberholster 1994), Shannon *et al*. (1996) showed that passive transport of young anchovy may

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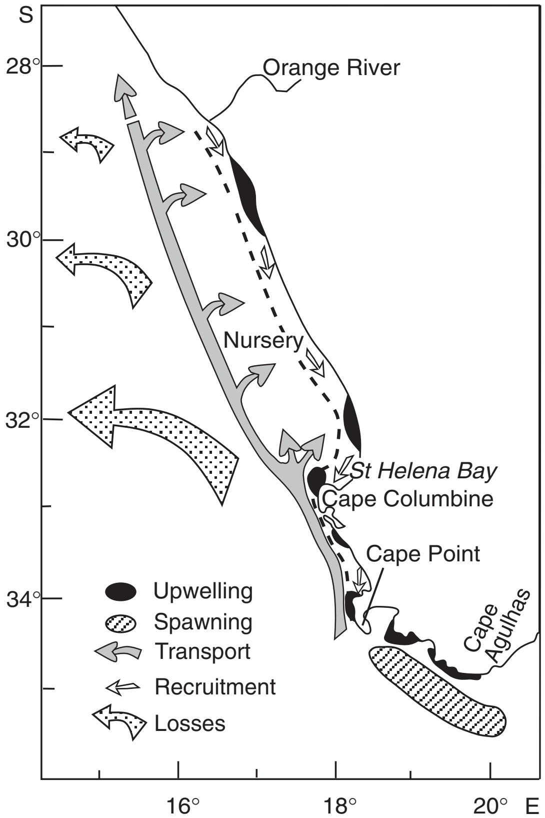

Fig. 1: Present hypothesis on the life history of Cape anchovy (after Hutchings *et al.* 1998)

account for a substantial proportion of year-class variability. This model showed that the distribution of spawners influenced the distribution of young-of-the-year, as well as the number and the location of advective losses across offshore boundaries. Based on the total area of 16–19°C water on the western Agulhas Bank, Richardson *et al.* (1998) found a significant relationship with the total abundance of anchovy eggs, and thereby derived a possible method for predicting spawning success. Waldron *et al.* (1997) presented a relationship between the end-of-year anchovy spawner biomass and the potential annual production on the West Coast by the use of an "optimal environmental window". Bloomer *et al.* (1994) used a rule-based model with environmental parameters (wind frequency and velocity and sea surface temperature) and spawner biomass in the spawning, transport and nursery areas. An expert system (Korrûbel 1995) gives predictions based on four different environmental and biological parameters in November: instantaneous egg production of anchovy, distance offshore of the 16°C isotherm at 33°S on the West Coast, the percentage of gonad atresia in female anchovy, and *El Niño* Southern Oscillation events.

The present work presents a new approach to investigating the contribution of environmental factors to variability in recruitment success of Cape anchovy. By use of a wind- and density-driven three-dimensional circulation model (Skogen 1999), post-spawning processes that may explain recruitment variability are investigated. The focus is on the retention and transport of eggs and larvae from the spawning grounds on the Agulhas Bank to the productive nursery areas on the West Coast by the shelf-edge jet current. Such an approach integrates many environmental factors that may not be easy to measure, and therefore has the potential to include factors for which it is not possible to establish quantitative relationships with recruitment.

MATERIAL AND METHODS

Model design

The NORWegian ECOlogical Model system (NORWECOM) is a coupled physical, chemical and biological model system applied to study primary production and dispersion of particles (e.g. fish larvae and pollution). The model is fully described by Skogen (1993) – see also Aksnes *et al.* (1995) and Skogen *et al.* (1995). The model was validated by comparison with field data in the North Sea/Skagerrak and Norwegian Sea (North-East Atlantic) in Svendsen *et al.* (1995, 1996), Berntsen *et al.* (1996) and Skogen *et al.* (1997). The Benguela implementation has been validated in Skogen (1999). In the present study, the physical part of NORWECOM is coupled to a Lagrangian particle-tracking model.

The circulation model is based on the three-dimensional, primitive equation, time-dependent, wind- and density-driven Princeton Ocean Model (POM, Blumberg and Mellor 1987). Prognostic variables of this model are: three components of the velocity field, temperature, salinity, turbulent kinetic energy, a turbulent macroscale and the water level. The governing equations of the model are the horizontal momentum equations, the hydrostatic approximation, the continuity equation, conservation equations for temperature and salinity and a turbulence closure model for calculating the two turbulence variables (Mellor and Yamada 1982). The equations and boundary conditions are approximated by finite difference techniques in an Arakawa C-grid (Mesinger and Arakawa 1976).

For the present study, the model is used with a horizontal resolution of 20 × 20 km on a grid covering the African coast and the open ocean in the area 12–46°S, 4–30°E (Fig. 2). The bottom topography is inter- and extrapolated from data from the South African Naval Hydrographic Office, and from the General Bathymetric Chart of the Oceans (GEBCO) digital atlas (IOC, IHO and BODC 1994). In the vertical, 18 bottom-following σ layers are used.

Forcing variables are 12-hourly hindcast atmospheric pressure fields and wind-stress fields, interpolated from the NCEP/NCAR Reanalysis Project (Kalnay *et al*. 1996). Initial values (monthly fields) for salinity and temperature are interpolated from the 1 × 1 degree NOAA Atlas (Levitus and Boyer 1994, Levitus *et al.* 1994), whereas initial fields for velocities and water elevation are derived from the density fields using the thermal wind equation and assuming zero net flux in each water column. Interpolation between these monthly fields is also used at all open boundaries. To absorb inconsistencies between the forced boundary conditions and the model results, a 7-grid cell "Flow Relaxation Scheme" (FRS) zone (Martinsen and Engedahl 1987) is used around these open boundaries. In this zone, each prognostic variable (ϕ) is simply updated by the translation $\phi = (1-\beta)\phi_{int} + \beta\phi_{ext}$, where ϕ_{int} contains the time-integrated, unrelaxed values calculated in the entire model domain, i.e. also in the areas covered by the FRS-zone, ϕ_{ext} is the specified external solution in the zone, ϕ the new value, and β is a relaxation parameter, which varies from 0, at the end of the zone facing the interior model domain, to 1 at the outer end of the zone.

To account for a lack of appropriate data on surface heat flux, a "relaxation towards climatology" method is used for the surface layer (Cox and Bryan 1984). For this purpose, monthly climatological fine-scale satellite derived SST fields from the Cloud and Ocean Remote Sensing around Africa Project at the Joint Research Centre in Ispra, Italy (http://me-www.jrc.it/CORSA/index.html) are used. During calm wind conditions, the surface temperature field adjusts to the climatological values after about 10 days (Oey and Chen 1992). For deep water (below 500 m), a weak relaxation to climatological salinity and temperature fields is performed (Sarmiento and Bryan 1982), so that the model does not drift too far from known values. The time factor in this relaxation increases with depth. The net evaporation precipitation flux is set to zero. Freshwater runoff from rivers and tidal forcing are not included.

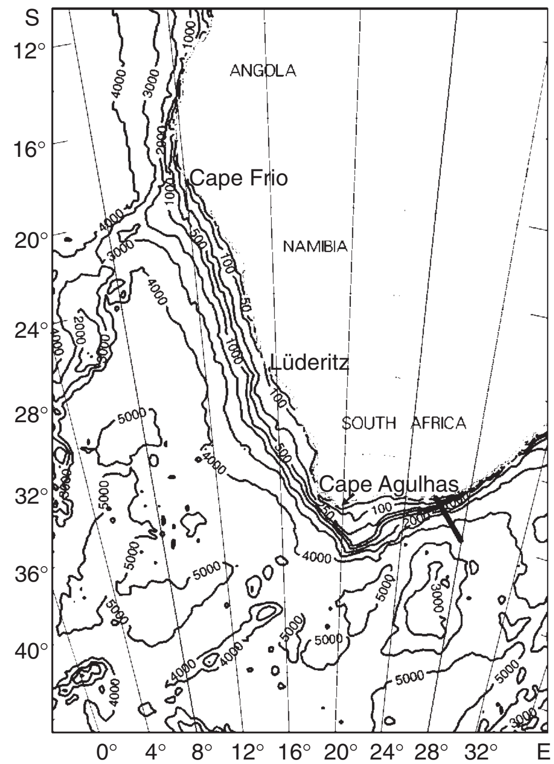

Fig. 2: Model domain showing bottom topography

Interpolation between daily mean (25 h) currents from the circulation model are fed into the Lagrangian particle-tracking model to simulate the transport of fish larvae. A 3-hour time step is used in the model. Particles are released and fixed at 30-m depth, corresponding closely with the depth of peak concentration of larvae reported by Shelton and Hutchings (1982). No particle diffusion or larval mortality is introduced in the transport model.

Simulation design

The study focused on the period 1987–1996. During this period, years of good recruitment of anchovy were 1987–1988, 1991–1992 and 1995, on the basis of recruitment estimates from the biomass of recruits on the recruitment grounds. The circulation model was run for all 10 years (1986/87–1995/96). After a 3-month spin-up starting on 1 July, daily (25 h) mean

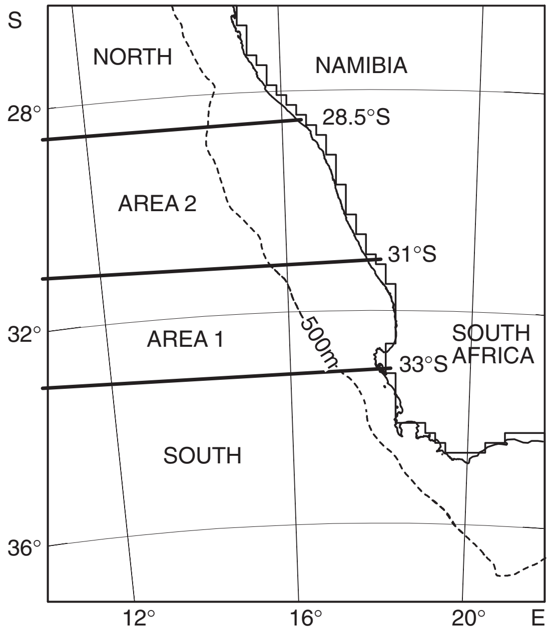

Fig. 3: The areas for which particle statistics were calculated

velocities were stored from 1 October to 30 June the following year (9 months). New, updated velocity fields were read into the transport model daily. The Lagrangian transport model started on 1 October, and egg data (see below) were read daily so that new particles were released in the model for 183 days (end of March). The particle transport then continued until day 270 (end of June). Each particle's number and position were stored daily so that all individual particles could be tracked from their release to the end of the simulation.

From acoustically estimated data on spawner biomass of anchovy in the southern Benguela (Marine & Coastal Management, unpublished data), egg distributions were modelled for seven years from 1986/87 to 1992/93 (Shannon 1995, Shannon *et al*. 1996). Total egg production was scaled to be equivalent in all years, so that the effect of distribution of spawning products could be examined (Shannon *et al*. 1996). One batch of eggs was released at the centre of each quarter-degree grid box per day of the spawning season (1 October–1 April), the size of the batch depending on the spawner biomass at that position and the fraction of female anchovy spawning during that part of the spawning period (Melo 1994, Shannon 1995). In the present work, the number of eggs were further scaled down, so that approximately 10 000 particles were released in the model.

Several different approaches were investigated. In the first (variable flow and variable distribution simulations, VFVD), which is the main focus of this study, corresponding currents and egg distributions were used. The study includes the seven years (1986/87–1992/93) for which egg distributions are available. Second, using the findings from the first approach, the relative importance of the egg distribution was compared with that of the currents. For this purpose, a reference egg distribution was constructed, by deriving an average year (with 183 daily fields) from the seven years of egg distributions available. These spawning data were fixed and used together with the currents from all 10 years (variable flow and fixed distribution simulations, VFFD). Similarly, a reference year was made for the currents by averaging the 10 daily fields (one each year) for each date from 1 October to 30 June. Together with this average year of daily current fields, all (seven) egg distributions were used to simulate the relative importance of the varying egg distributions (fixed flow and variable distribution simulation, FFVD).

The rationale for this study is that interannual variations in passive transport of anchovy eggs and larvae from the spawning grounds to the nursery areas may account for a substantial proportion of year-class variability (Shannon *et al*. 1996, Shannon 1998). Such transport is considered important in regulating recruitment of clupeoids (Parrish *et al.* 1981, Lasker 1985) such as Cape anchovy (Boyd *et al*. 1992, Hutchings 1992). In addition, by studying transport processes, periods and areas that are critical for successful recruitment can be investigated.

To account for this, an analysis tool for tracking the particles was developed. First, the coast was divided into four boxes (South, Area 1, Area 2 and North) by east-west cross-sections along 28.5, 31 and 33°S (Fig. 3). It is generally considered that, if eggs and larvae are transported too far offshore, where conditions are unfavourable for survival, they will not contribute to recruitment. In this regard, Shelton *et al.* (1985) showed that Cape anchovy tend to avoid spawning in areas with high offshore advection. To keep track of how far offshore the particles are drifting, the boxes were subdivided into a shelf and an open ocean area, by a line following a fixed depth of the bottom bathymetry. To prevent limitations by an *a priori* best guess of such a depth, depths of 50, 100, 200 and 500 m were tested as the boundary in the different simulations. This approach is more flexible and makes it easier to investigate critical depth intervals. Therefore, the line following the 500-m isobath

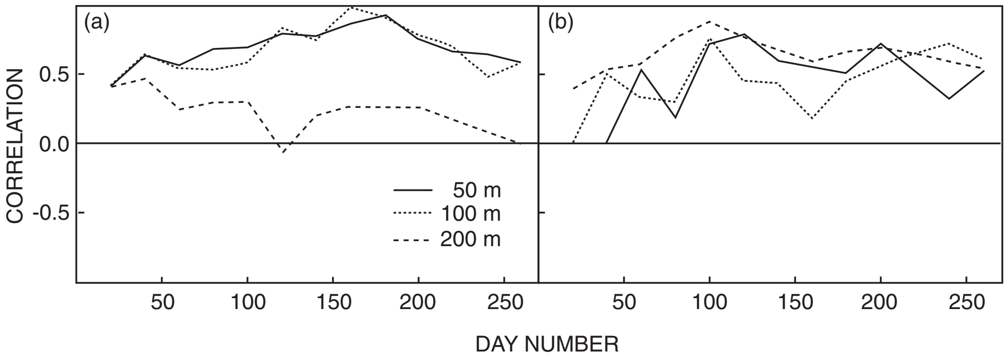

Fig. 4: Time evolution of correlations between recruitment and number of particles in areas (a) 2oo and (b) 2s for 50, 100, and 200 m depth contours (area notations are given in Table I)

in Figure 3 is only an example for such a depth.

To investigate the relative importance of the drift of eggs and larvae with respect to recruitment, the number of particles (expressed as a percentage) within each of the eight boxes were counted daily during the 270 days of passive transport. These eight time-series (for each of the seven years in this study) were then correlated with the recruitment of anchovy in the same years. In addition, to get an idea of the relative importance of different routes for the particles, through each box independent of time, accumulated numbers of particles that actually passed a certain area (and depth interval) were updated daily. These counts are referred to as HBI (Have Been Inside) in the text.

Three different estimates of recruitment are used in the assessment of South Africa's pelagic resources: survey estimates of recruitment, back-calculated recruitment, and recruitment estimated using the assessment model. A preliminary study was performed using the estimates on biomass and numbers from surveys reported by Barange *et al*. (1999), and model assessment recruitment estimates (J. A. A. de Oliveira, CEFAS, UK, pers. comm). Most (but not all) of the findings were consistent between the assessment recruitment estimate and the biomass and numbers from surveys. Because the focus was on the distribution of particles after some months of transport, the survey estimates were preferred. From the preliminary study, the biomass of recruits on the recruitment grounds in May/June was chosen in the present study.

Table I: Example output from the analysis tool VFVD for the years 1987–1993 (excluding 1989). Correlation between recruitment and relative number of particles in each box is given every 50 days, assuming the border between the shelf and the open ocean is at 500 m depth

Day	Area notation							
	Soo	Ss	1oo	1s	2oo	2s	Noo	Ns
50	-0.09	-0.70	0.34	0.56	0.21	0.58	0.00	0.00
100	-0.20	-0.61	-0.19	0.51	0.27	0.88	0.15	0.43
150	-0.28	-0.45	-0.21	0.52	0.18	0.83	0.39	0.43
200	-0.31	-0.41	-0.27	-0.15	0.17	0.76	0.34	0.43
250	-0.42	-0.60	-0.14	0.71	0.02	0.42	0.39	0.16

Soo = Southern open ocean
Ss = Southern shelf
1oo = Area 1 open ocean
1s = Area 1 shelf
2oo = Area 2 open ocean
2s = Area 2 shelf
Noo = Northern open ocean
Ns = Northern shelf

RESULTS AND DISCUSSION

Variable flow and variable distribution (VFVD)

The first studies using the analysis tool showed weak correlation between the modelled drift and recruitment. However, because 1989 was an anomalous year (Bloomer *et al*. 1994, Waldron *et al*. 1997), a new analysis was done omitting recruitment for that year. The new analysis showed strong dependencies between the modelled drift and anchovy recruitment (hereafter the 1989 data are excluded from the analysis, unless explicitly stated).

An example of the output of the analysis tool is shown in Table I, in which the correlation for all eight boxes is given every 50 days, using the 500-m isobath as the border between the shelf and the open

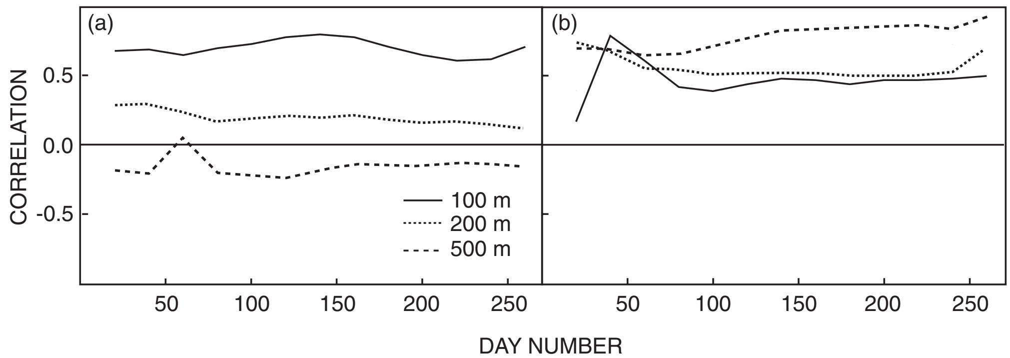

Fig. 5: Time evolution of correlations between recruitment and number of particles in areas (a) 1oo and (b) 1s for 100, 200 and 500 m depth contours (area notations are given in Table I)

ocean. There is a negative correlation between the recruitment and the number of particles that remain on the shelf in the southern area, whereas there is a positive correlation between recruitment and the number of particles inside the 500-m isobath in Area 1 and Area 2. Both the number of particles left on the southern shelf and those on the shelf in Area 2 show a reasonable consistency in time. Only in the northern areas are there weak correlations. The correlation numbers are significant to 5% for values $>r = 0.81$, and to 10% for values $>r = 0.72$.

In Figure 4, the time evolution of the correlation in the two Area 2 boxes are given for three depths (50, 100 and 200 m). For the open ocean box (Fig. 4a) there is good correlation ($r \approx 0.70$) between the number of particles found outside the 50- and 100-m isobaths and recruitment. By contrast, results for the 200-m isobath show weak correlations. Results for the shelf in Area 2 (Fig. 4b) confirm the findings for the open ocean box. This shows a good correlation ($r \approx 0.70$) with the number of particles inside 200 m, and a weaker correlation with those inside 50 and 100 m. It is concluded that there is an environmental window between 100 and 200 m in Area 2 that is beneficial for recruitment of anchovy.

A similar argument can be used for investigating the transport through Area 1. In Figure 5, the time evolution of the correlation between recruitment and the accumulated number of particles passing through the two Area 1 boxes are given for three different depths. The correlation is $0.6< = r = <0.8$ between particles passing through the area outside 100 m and recruitment (Fig. 5a), and $r \approx 0.80$ for those drifting inside 500 m (Fig. 5b). Therefore, in Area 1 there would be good recruitment if a large portion of the larvae entered between the 100- and 500-m isobaths. It is concluded that particles that pass outside the 500-m isobath in Area 1 are likely to contribute to advective losses.

The importance of the initial egg distribution (or spawning field) using the present particle transport approach will be investigated later (FFVD below). However, focusing on correlations in the southern box, where most spawning takes place, yield interesting results. The model suggests a strong negative correlation between depth and recruitment (Fig. 6a). For the 50-m isobath, there is a weak positive connection, but at 100 m, $r \approx -0.49$ through the whole simulation, and there is a decrease with increasing depths ($r \approx -0.80$ at 500 m). It is therefore concluded that spawning should take place in the shallow waters of the Agulhas Bank, in areas where the spawning products are not likely to be transported into deeper water.

There is a positive correlation of $r \approx 0.45$ for particles ending up deeper than 200 m in the northern area (Fig. 6b) It is also of note that the number of particles ending up in that region were up to an order of magnitude higher for 1987 and 1988 (the years of highest and third highest recruitment respectively) than for the other years. This suggests that larvae in deep water in the northern area may migrate inshore as they get older. No such mechanism is included in the model, so the particles will continue to be moved passively by the currents. Therefore, the positive correlation may suggest that recruitment would be good if larvae reach as far north as 28.5°S. In order to summarize the findings from the transport studies, a linear regression analysis was performed. Based on the particle statistics on day 160 (early March) the following relation for recruitment can be given:

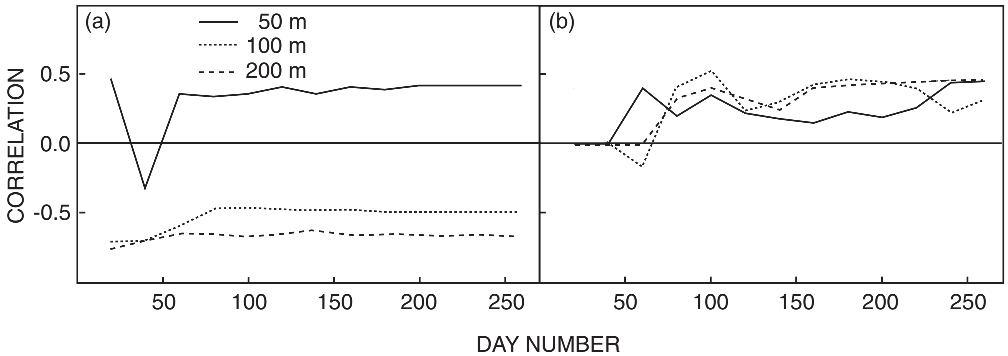

Fig. 6: Time evolution of correlation between recruitment and number of particles in areas (a) Ss and (b) Noo for 50, 100 and 200 m depth contours (area notations are given in Table I)

$$REC = -237 + 62 \times 2oo(100) \quad , \qquad (1)$$

where *REC* is the modelled recruitment biomass (in thousand tons) and 2oo(100) are the number of particles (as a percentage) outside the 100-m isobath in Area 2. This simple regression line (Fig. 7a) explains 95% ($p < 0.001$) of the total variance in the recruitment. All years are within reasonable error bounds, and the errors are <7%, except for 1992 (19%). The residuals give a maximum error in 1992 of 75 000 tons and a minimum in 1990 of 2 000 tons. Using the above regression, the recruitment in 1989 was estimated by the model to be 692 000 tons, whereas the actual recruitment for that year was only 135 000 tons.

From a management point of view, it is important to be able to predict recruitment as early as possible; the expert system used for forecasting is based on data from November (Korrûbel 1995). After an inspection of the model outputs for a simple early warning candidate, it was considered appropriate to use the accumulated number of particles that had been inside the 500-m isobath in the southern area (hSs[500]) on day 50 (November 19). The correlation based on this single number was when $r = -0.87$ (excluding 1989) and $r = -0.55$ (including 1989). Using the former relationship, the following simple formula can be used to provide an early warning candidate and explain 76% ($p < 0.05$) of the observed variation in anchovy recruitment (Fig. 7b):

$$REC = 1\,420 - 13.65 \times hSs(500) \quad . \qquad (2)$$

Fixed flow and variable distribution (FFVD)

To investigate the relative importance of the egg distribution, a reference flow-field was constructed by averaging the 10 daily fields (one each year) to create mean daily currents from 1 October to 30 June. The spawning distribution was varied in accordance with the available egg data. As in the VFVD experiment, data for 1989 were excluded from the analysis.

From the VFVD discussion, some possible connections between recruitment and the particle distributions in the southern boxes, where most of the spawning takes place, have already been mentioned. In fact, examination of the actual numbers for hSs(500) at day 160 ($r = -0.80$) gives an average of 76%, although the year-to-year variation is large. In 1987 and 1988 (the years of good recruitment), spawning was off the West Coast as well as over the Agulhas Bank (Shannon *et al.* 1996). Such a distribution gives low values of hSs(500) for those years (66.0 and 66.8% respectively), whereas for the other years (when recruitment was lower) the numbers are between 71.1 and 92.1%. The exception is again 1989, with low recruitment and a value of only 67.2%.

The same simulations were done for the FFVD case as for the VFVD simulation. At first glance there are no major differences in the individual dependencies between the two cases, neither in magnitude nor sign. In the next step, the outputs from the FFVD simulation were used as inputs to the regression formula (Equation 1). From these calculations (excluding 1989), it was estimated that $r = 0.89$ ($p < 0.05$), suggesting that the simple equation could explain most of the observed variance in the recruitment from the variability in the spawning. Including 1989, the same calculation gave an r of 0.26.

In a similar manner, the outputs at day 50 were used as inputs to Equation 2. Keeping in mind that

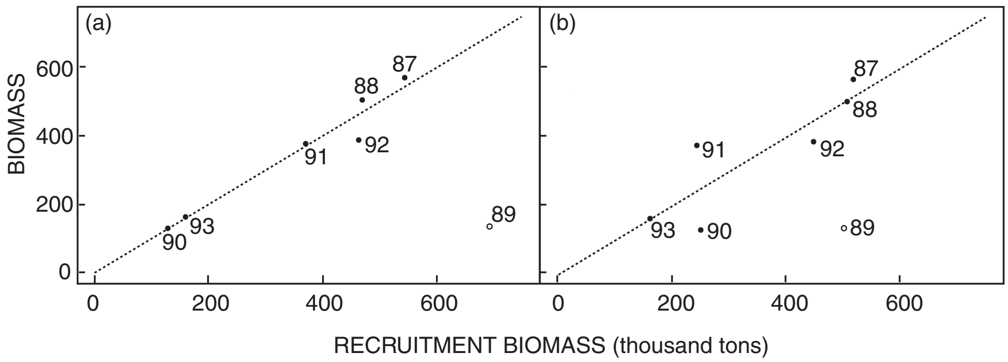

Fig. 7: Time-series of the recruitment of Cape anchovy and estimates based on the results from the numerical simulation of larval drift; (a) linear regression model (Equation 1), (b) early warning candidate (Equation 2)

these numbers are dependent on spawning, the FFVD case gives an r of 0.88 ($p < 0.05$), slightly higher than that for the VFVD simulation ($r = 0.87$).

Variable flow and fixed distribution (VFFD)

To investigate the relative importance of the flow, a mean egg distribution was created from the egg data. This distribution was fixed and used together with the different flow fields. The same exercises were performed, both for the seven years (1987–1993) used in the VFVD and FFVD exercises, and for all 10 years (1987–1996) for which the model simulated flow dynamics.

The VFFD results show a more oscillatory behaviour of the correlation curves with time. A removal of the recruitment for 1989 does not change the results. Comparing these with the VFVD results, some of the conclusions do not hold true. In the southern area and in Area 1, the respective negative and positive correlations changed signs. This is also to some extent the case in Area 2, whereas in the northern area there were some similarities between the VFVD and VFFD cases. Such a south-to-north shift is consistent with the fact that the dependence on the initial field decreases with time.

Using the outputs from the VFFD case as inputs to Equation 1 confirms the inconsistencies between this experiment and the first two experiments, independent of the number of years (7 or 10) and whether 1989 was excluded or not ($r^2 < 0.01$). From the observed variation, it is concluded that anchovy recruitment can be explained only to a small extent by a change in circulation alone. This supports the belief of Shannon (1995) and Shannon *et al*. (1996) that spawner distribution plays an important role in the recruitment process.

South Coast recruitment

The western Agulhas Bank, from Cape Point to Cape Agulhas, is believed to be the major spawning area from which anchovy recruit to the West Coast (Hutchings 1992). However, there is also evidence to suggest that some anchovy recruit on the South Coast and do not migrate up the West Coast, but remain on the Agulhas Bank during their first year (Smale 1983). Such a recruitment scenario was investigated in the present model.

Using the mean year for the modelled currents, particles were evenly spread over the Agulhas Bank inside the 500-m isobath (Fig. 8). From the egg data, about 70% of the spawning is within the area marked with these start positions. In the model, all particles were released on 1 November and transported passively at a depth of 30 m for 180 days, and their end positions were marked. For end positions east of Cape Point, spawning products from these initial position are considered likely to remain on the Bank. The start positions of those particles that did not move west of Cape Point are shown in Figure 8b. Eggs spawned in the shallow regions of the eastern Agulhas Bank did not leave the Agulhas Bank, whereas those spawned in the deeper parts of the eastern areas are in a position to enter the West Coast. This experiment supports the conclusions by Smale (1983) and Hutchings (1992) that eggs spawned on the western Agulhas Bank are likely to drift northwards and westwards, whereas spawning products originating from other parts of the

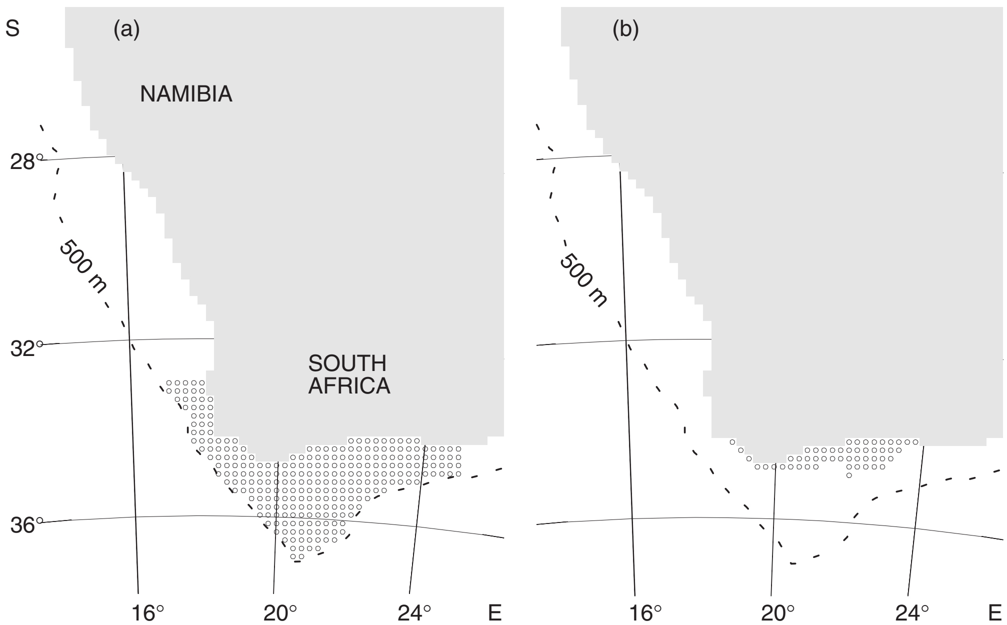

Fig. 8: Start position of (a) all particles in the South Coast recruitment experiment and (b) those particles that did not move past Cape Point to the West Coast

Bank will not be transported up the West Coast.

Although the shallow regions of the eastern and central Agulhas Bank may be favourable in terms of retention of eggs and larvae, the effect of predation needs to be considered (Shannon *et al*. 1996). In particular, cannibalism of eggs by spawning adults (Valdés Szeinfeld and Cochrane 1992) may be lower on the western Agulhas Bank, where advection separates the eggs and larvae from the spawners, than on the central and eastern Agulhas Bank where there is greater retention.

CONCLUDING REMARKS

Although some of the interannual variability in anchovy recruitment can be explained from this study, advection is only one of a number of factors determining the fate of young anchovy. Other factors such as active swimming by juveniles, cannibalism by spawning adults, predation and food availability may also influence recruitment (Shannon *et al*. 1996). Such factors are not taken into consideration in the present study. Also the vertical migratory behaviour of larvae is uncertain. The distribution of larvae through the water column is likely to have significant consequences for lateral advection. In the present model, particles were fixed at 30 m.

The present model represents a tool for gaining new insight into the complex dynamics between physics and biology in the ocean. However, limitations have to be taken into account when interpreting the results. Open boundaries are calculated from climatological seasonal fields, and the in/out flows assume geostrophy. Clearly, the horizontal resolution is a limiting factor with respect to correct simulation of, for example, nearshore and mesoscale processes. For the present application, this limitation is of special importance in the vicinity of the Cape Peninsula where the shelf is very narrow, and the shelf-edge jet is an important component of the circulation. The model does not incorporate real surface heat fluxes, only a relaxation towards monthly climatological sea surface temperature fields.

ACKNOWLEDGEMENT

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