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INFLUENCE OF BUOYANCY AND VERTICAL DISTRIBUTION OF SARDINE *SARDINOPS SAGAX* EGGS AND LARVAE ON THEIR TRANSPORT IN THE NORTHERN BENGUELA ECOSYSTEM

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In recent years, sardine *Sardinops sagax* spawning has been recorded inshore off central Namibia. Field observations on eggs and laboratory measurements show that spawning, demonstrated by the distribution of newly spawned eggs, takes place just below the upper mixed layer. The high positive buoyancy of the eggs causes them to ascend rapidly to the surface layer, where they are moved offshore by upwelling-induced offshore transport. However, increased wind-induced mixing also influences the vertical distribution of eggs, causing them to be partly mixed down below the layer moving offshore and into the layer moving inshore. This mechanism acts to retard the transport and offshore loss of eggs from the spawning areas. The vertical distribution of sardine larvae, with highest concentrations deeper than 20 m, indicates active movement out of the layer moving offshore, and this tendency seems to be more pronounced for older larvae. Hence, vertical migration of larvae is an additional factor mitigating their loss from nearshore. Taken together, these features seem to minimize the offshore loss of offspring, particularly in periods of low stock biomass when spawning close to the shore seems to be common.

Key words: buoyancy, northern Benguela, sardine, vertical distribution

Transport and dispersal of fish eggs and larvae are important components affecting recruitment of fish populations. Successful recruitment depends on the planktonic stages being retained in, or transported to, nursery areas favourable for growth and survival. Advective loss of larvae into less favourable areas would clearly have a negative impact on recruitment (Iles and Sinclair 1982), particularly in upwelling systems where offshore loss of larvae may be considerable (Bakun and Parrish 1982). In his triad theory, Bakun (1996) identified three major groups of environmental processes of importance to fish recruitment in upwelling areas: enrichment of the food chain, retention of the offspring in suitable habitats, and concentration of the food organisms suitable for larvae within these habitats.

Based on Bakun's triad, it seems reasonable to assume that fish with pelagic eggs and larvae will spawn in upwelling areas at certain times of the year and in specific regions that provide optimal conditions for growth and survival of the larvae. Such conditions might be found in coastal indentations where wind-induced offshore transport and turbulence are reduced and the width of the continental shelf tends to be greater (Parrish *et al*. 1983).

In the northern Benguela upwelling system, transport within the upper layer will fluctuate with the intensity of upwelling as a result of variation in offshore surface Ekman transport caused by variations in the wind/pressure field (Shannon 1985). Modelling studies in the northern Benguela (Sundby *et al*. 1999, Stenevik *et al*. in prep.) have shown that the thickness of the offshore-moving upper layer is about 20 m and depends on distance offshore and wind force. The same depth was mentioned by Parrish *et al*. (1981) as a reasonable one for the Ekman layer. Below this depth the water moves inshore.

Historically, sardine have been one of the major commercial fish species in the northern Benguela and are typical of upwelling systems in general. The sardine stock in the northern Benguela declined drastically between the 1960s and the 1980s, and has remained low ever since (Beckley and van der Lingen 1999, Schwartzlose *et al*. 1999). At present the fishable biomass is estimated at around 250 000 tons (Boyer and Boyer 2000). Sardine eggs and larvae are considered to be pelagic, which generally means that they accumulate in the upper mixed layer and are found in increasing concentrations towards the surface, depending on the degree of wind-induced mixing (Sundby 1991). In upwelling systems this means that eggs would have a tendency to be transported offshore within the upper layer and potentially be lost. On the other hand, increased upwelling also favours plankton production and consequently the production of food for larvae (Bakun 1973, 1990). Based on these two opposing processes, Cury and Roy (1989) suggested that optimal recruitment is a trade-off between strong winds, that

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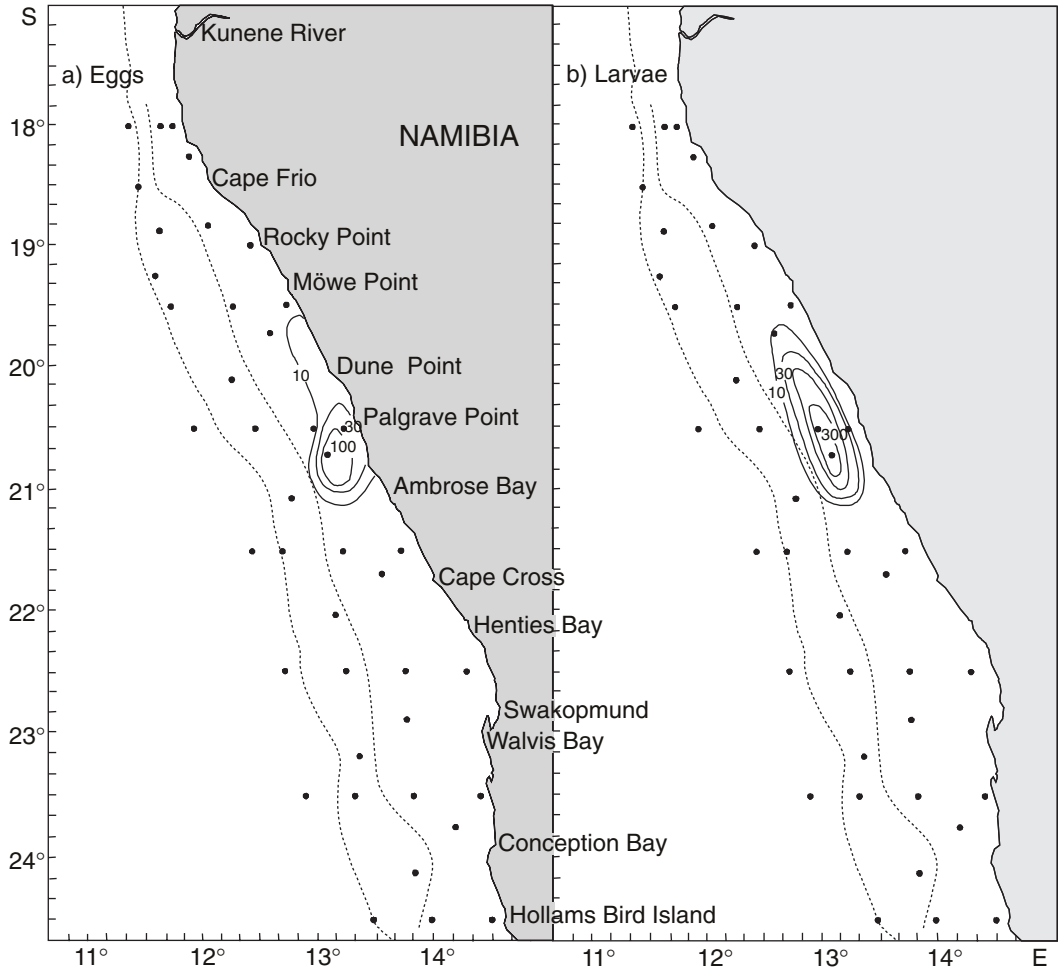

Fig. 1: Horizontal distribution (number 10 m^{-2}) of sardine (a) eggs and (b) larvae caught in a Multinet sampler during the northward leg of the survey, 5–14 October 1999. Multinet stations are indicated

favour the production of food for larvae, and weak winds, that favour retention of larvae. This "optimal environmental window" theory has subsequently been supported by data from the Californian upwelling system (Cury *et al*. 1995).

Historically, when the Namibian sardine stock was larger than it is at present, sardine spawned in the northern Benguela throughout most of the year (O'Toole 1977, Shannon and Pillar 1986, Le Clus 1990), with two distinct spawning maxima, one in late winter-spring (August/September) and the other in late summer-autumn (January/February). Then, there were two principal spawning areas, one offshore between 19 and 22°S and one near Walvis Bay (O'Toole 1977, Shannon and Pillar 1986, Le Clus 1990). During the recent period of low stock biomass, sardine eggs have been observed around Palgrave Point (20–21°S) in September/October (Sundby *et al*. 1998). This spawning area is located between the two main upwelling cells off Namibia, the Lüderitz cell in the south and the Cape Frio cell in the north. Hence, although the wind is generally strong along the Namibian coast at that time of the year, there is a local minimum in upwelling at Palgrave Point.

Sardine nursery grounds are often nearshore (Fowler and Boyd 1998). Such a distribution pattern might be explained by the fact that only the (small) fraction of larvae retained inshore would experience

Table I: Material used in the analyses. Weighted mean depth is calculated according to the formula given in text, and $\overline{W}_5$ is the average wind for the five hours before the station was sampled

Station	Date (1999)	Position	Number of larvae	Mean depth of larvae (m)	Number of eggs	Weighted mean depth of eggs (m)	$\overline{W}_5$ (knots)
58	15 October	19°45´S, 12°34´E	22	40.4	1	50.0	14.4
60	16 October	19°59´S, 12°24´E	14	55.2			22.6
61	16 October	20°00´S, 12°40´E	13	24.8			20.4
62	16 October	19°59´S, 12°56´E	2	10.0	1	10.0	18.5
63	16 October	20°14´S, 12°48´E	37	34.0			17.4
64	16 October	20°29´S, 12°40´E	16	51.2			18.0
65	16 October	20°30´S, 12°56´E	36	37.6	162	23.4	17.8
66	16 October	20°29´S, 13°11´S	2	22.8			16.0
67	16 October	20°44´S, 13°03´E			14	12.4	16.8
68	16 October	20°59´S, 12°39´E	3	10.0			25.5
69	17 October	20°59´S, 12°54´E	33	31.3			25.4
72	17 October	21°15´S, 13°19´E			1	10.0	21.8
73	17 October	21°21´S, 12°59´E	49	26.4			19.4
74	17 October	21°34´S, 12°43´E	1	90.0			19.5
75	17 October	21°34´S, 13°04´E	3	90.0	272	23.6	20.0

favourable conditions for survival, whereas most larvae would be lost offshore. An alternative explanation could be that most larvae are advected inshore, as shown for hake *Merluccius* spp. in the northern Benguela (Sundby and O'Toole 1995, Sundby *et al.* 1998, 2001). It will be shown here that, with the proper combination of (a) spawning site and depth, (b) vertical distribution of eggs and larvae, and (c) cross-shelf circulation, offshore loss of sardine larvae can be substantially reduced, so increasing the probability of larvae being retained near the shore. The physical mechanisms here are similar to those described for nearshore concentrations of hake larvae in the northern Benguela (Sundby *et al.* 2001); hake are demersal, but they have mesopelagic eggs and larvae.

Sundby (1991) stressed the importance of buoyancy in the horizontal transport of eggs and other early life history stages from spawning areas to the nursery grounds. The purpose of this paper is to examine whether this principle applies to sardine in the northern Benguela. To do this, recent data on the vertical distribution of sardine eggs and larvae are used. Further, an independent approach of calculating the vertical egg distribution on the basis of shipboard measurements of the specific gravity of sardine eggs and subsequent modelling of the vertical distribution of the eggs is employed.

MATERIAL AND METHODS

Sampling was carried out aboard the R.V. *Dr Fridtjof Nansen* from 29 September to 18 October 1999; it covered most of the Namibian coast. The cruise had several purposes, including hydrographic research, examination of hake sexual maturity and studies of the vertical and horizontal distribution of sardine eggs and larvae. The Namibian coast was covered between 1 and 14 October to collect hydrographic data and information on hake sexual maturity (Fig. 1). Thereafter, five days were dedicated to studies on the vertical distribution of sardine eggs and larvae in the area where sardine eggs and larvae had been observed during the first part of the survey (Fig. 2, Table I). The grid followed a zig-zag pattern with transects running southwestwards and eastwards.

Physical parameters (temperature, salinity, oxygen) were recorded between the surface and 10 m above the bottom at each station using a Seabird 911 CTD. Wind speed and direction were measured continuously while the vessel was underway and entered manually as the ship was on station. Sardine eggs and larvae were sampled with a Hydrobios Multinet® plankton sampler. The plankton sampler has five nets, all with a mesh size of 405 µm, that can be opened and closed from the vessel at different depths. A Scanmar depth recorder with acoustic transmission to the vessel was mounted on top of the Multinet. The sampler was towed obliquely and the nets opened and closed as the sampler was retrieved, starting with the deepest one. The depth intervals sampled were 100–80, 80–60, 60–40, 40–20 and 20–0 m. At stations where the water was shallower than 100 m, the upper depth intervals were kept the same and the lowest net was towed from 10 m above the bottom to the nearest 20 m interval. The plankton sampler was retrieved at a speed of 0.5 m s^{-1} as the vessel maintained a speed of 2 knots. A mechanical flowmeter was mounted on each net to record the volume filtered in each depth

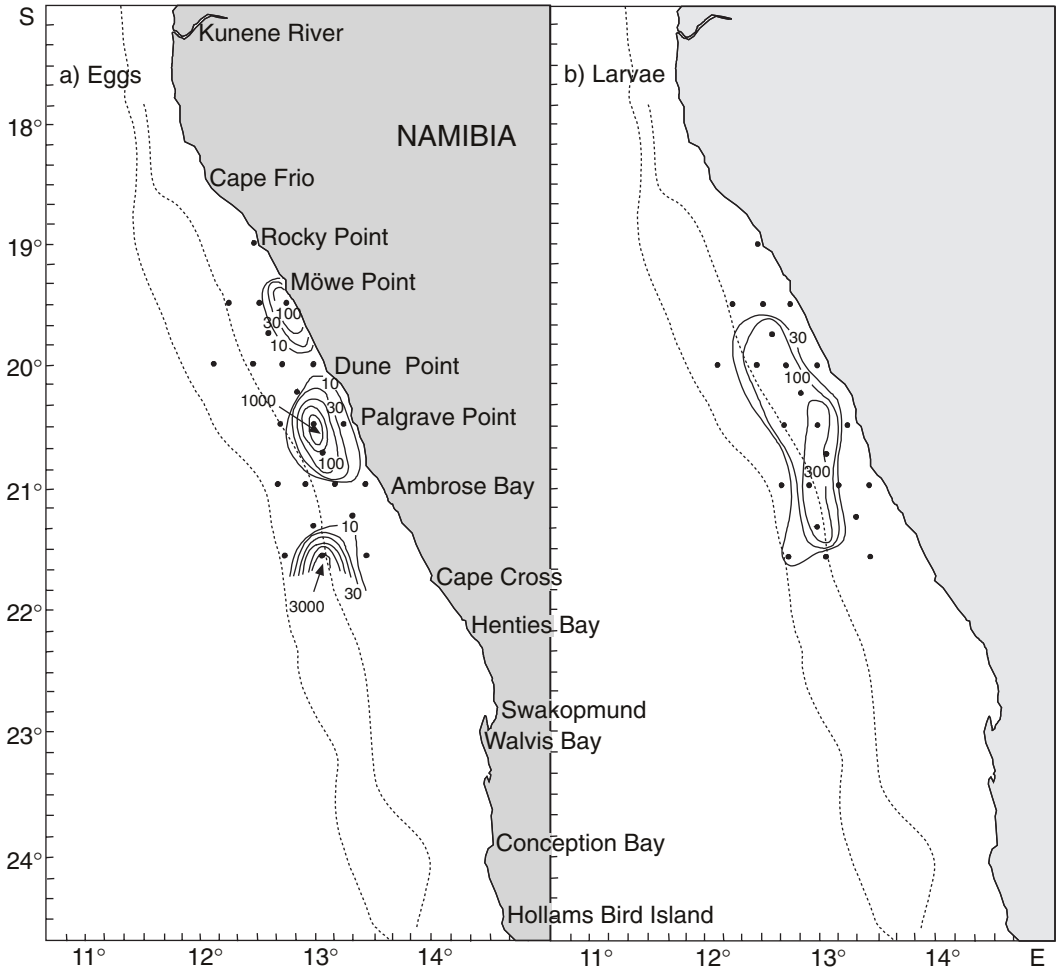

Fig. 2: Horizontal distribution (number 10 m^{-2}) of sardine (a) eggs and (b) larvae caught in a Multinet sampler during the southward leg of the survey, 14–19 October 1999. Multinet stations are indicated

interval.

Sardine eggs in the Multinet samples were identified, counted and staged according to the description of King (1977a). Eggs that appeared to be in good condition were used for buoyancy measurements and were immediately inserted in a density gradient column. Buoyancy was measured with a Martin Instruments unit installed aboard the vessel. The methods for setting up and operating the unit are described fully by Coombs (1981) and Sundby *et al*. (1998), but they are briefly summarized here. The unit contains three salinity gradient columns submersed in a water bath held in a rectangular transparent container. The water in the container was held constant at 12°C during the experiments. The salinity gradient was made by preparing two stock solutions from diluted natural seawater and salt-added natural seawater. The seawater had been passed through a 0.2 µm filter. The three columns were filled in Cape Town before the survey to prevent movement of the ship causing non-linear salinity gradients during filling. After filling, such salinity gradients are considered stable even in rough weather (Coombs 1981). The salinity gradients were calibrated with five spherical glass floats introduced in each column (accurate to ± 0.0002 g cm^{-3}).

Sardine eggs were introduced into the columns

just below the water surface with a pipette, and then allowed to settle for 3–4 h before first reading their vertical position in the water column. Neutral buoyancy of the eggs was expressed in salinity units by calculating the salinity gradient in the column from the absolute densities of the floats and the temperature in the columns. Each experiment continued until the eggs hatched or until the experiment had to be terminated before the survey ended. The positions of the eggs and the glass floats were recorded at regular intervals, normally four times a day. Thus, the changes of specific gravity through development were monitored until hatching. Precision in this method is high and differences in density may be resolved to better than 4×10^{-5} g cm^{-3} (Coombs 1981). As the eggs used for buoyancy measurements were caught in the wild, their exact age was unknown. Changes in mean neutral buoyancy among readings were relatively small and the consecutive measurements of each group of eggs were therefore pooled and are presented together.

Sardine larvae from each net were identified on the basis of the description in Olivar and Fortuño (1991), after which they were immediately counted and fixed in 96% alcohol. Standard lengths (*SL*) of the larvae were measured after the cruise using a dissecting microscope. Vertical distribution data for sardine larvae were divided into day and night stations. Stations were classified as daylight stations if the hauls were commenced between 06:00 and 18:00, and night stations the converse. The size distribution of larvae in each depth stratum was compared, and a one-way ANOVA was used to test for differences in mean *SL* among depths.

The vertical distributions of sardine eggs and larvae were expressed as the total number of individuals per cubic metre over the depth range sampled, and the fraction of individuals in each depth stratum was calculated. The weighted mean depth of eggs and larvae ($Z = \sum_{i=1}^{n} P_i Z_i$) was calculated, where Z_i is the depth of the ith sample and P_i is the proportion of larvae at depth Z_i (Fortier and Leggett 1983, Grønkjær and Wieland 1997). Regressions were established between weighted mean depth and wind speed (represented as the wind speed during the five hours preceding sampling at a station).

Spawning depth was estimated on the basis of the depth at which the youngest eggs (Stage *a*, King 1977a) were observed. This was done by calculating the mean depth of Stage *a* eggs from each station, and adding the estimated vertical distance the eggs had ascended from spawning, based on the buoyancy measurements. The time from spawning was estimated from data on the duration of Stage *a* eggs at different temperatures, using the following equation from King (1977a):

$$Y = 3154.192x^{-1.957} \quad , \qquad (1)$$

where Y is the duration of Stage *a* eggs and x is the temperature experienced during development. Stage *a* lasts from fertilization until the point at which the germ ring reaches the equator (King 1977a). As some eggs were early Stage *a* and others were late Stage *a*, the duration time was divided by two to arrive at a mean estimated time from spawning for the Stage *a* eggs. Mean ascent velocity was calculated (see below) and mean spawning depth could be estimated. Le Clus and Malan (1995) extended the data of King (1977a) and provided models for temperature-dependent development for nine egg stages. However, their staging system was not available during the survey and therefore the data of King (1977a) were used.

Based on the buoyancy measurements, the ascending velocities of the eggs, w, were calculated according to the equations of Sundby (1983). This means that the Stokes equation

$$w = 1/18\ g\ d^2\ \Delta\rho v^{-1} \quad , \qquad (2)$$

was used when the Reynolds number $Re = wd/v$ was <0.5 and the modified equation

$$w = 19\ (d - 0.4D)\ \Delta\rho^{2/3}\ v^{-1/3} \quad , \qquad (3)$$

was used when the Reynolds number is >0.5.

The gravity acceleration is g, d is the egg diameter, $\Delta\rho$ the difference in specific gravity between the surrounding seawater and the egg, v the molecular viscosity, and D is a diameter that is the uppermost limit of size to which the Stokes equation applies.

The equilibrium vertical distribution of the pelagic eggs, $C(z)$, with a specific gravity lower than that of the upper mixed layer, can be calculated analytically in a simplified manner after Sundby (1983):

$$C(z) = C(a)\ e^{-w/K(z-a)} \quad , \qquad (4)$$

where w is the ascent velocity of the eggs, K the mean eddy diffusivity coefficient of the upper mixed layer, and $C(a)$ is the concentration of the sardine eggs at depth a.

The mean eddy diffusivity, K, of the upper mixed layer increases with wind-induced mixing, and was estimated using the empirical relation given by Sundby (1983):

$$K = 76.1 \times 10^{-4} + 2.26 \times 10^{-4}\ W^2 \quad , \qquad (5)$$

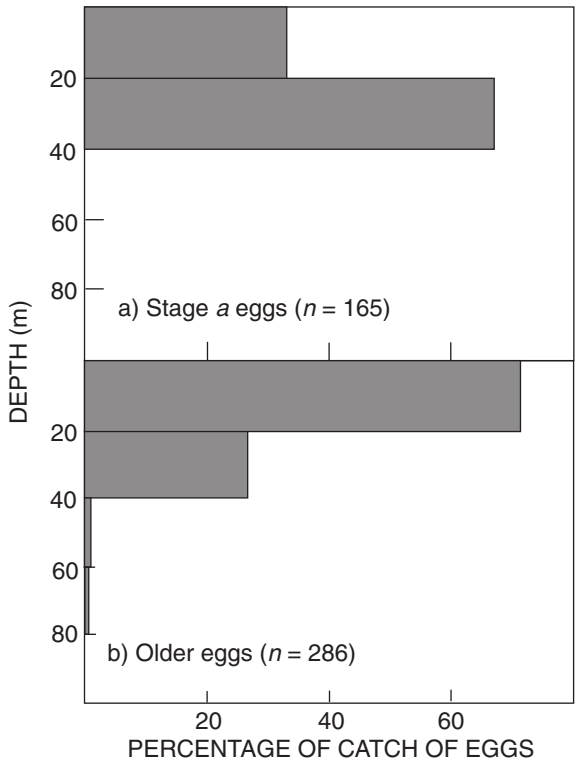

Fig. 3: Vertical distribution of sardine eggs from all stations pooled — (a) Stage *a* eggs, (b) older eggs

where W is the wind speed in m s^{-1} and K has the units m^2 s^{-1}.

RESULTS

Field observations of vertical distributions

The horizontal distributions of eggs on the northward and southward legs of the survey are shown in Figures 1 and 2 respectively. A total of 451 sardine eggs was caught with the Multinet at six stations during the southward leg. Based on egg stages, the data were split into two categories: younger eggs (Stage *a*) and older eggs (all others). Stage *a* eggs are too young to have reached an equilibrium distribution (Sundby 1983), but they may be used to give an indication of the vertical distribution of spawning. The largest fraction of Stage *a* eggs was in the 20–40 m depth interval (67%), and the rest were in the upper 20 m (Fig. 3). Spawning

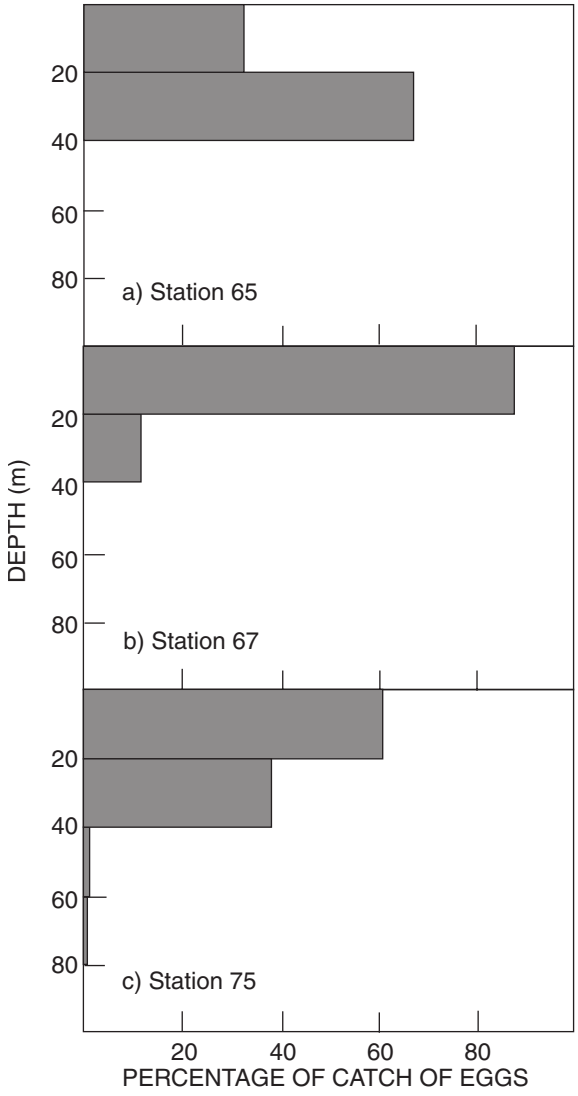

Fig. 4: Vertical distribution of sardine eggs from stations with more than 10 eggs. Eggs at Station 65 were newly spawned (Stage *a*)

depth at each station where Stage *a* eggs were found was estimated on the basis of the vertical distribution of Stage *a* eggs, the estimated age of the eggs (time from spawning) and the mean calculated ascent velocities described below. Variation in estimated spawning depth among stations was quite low (Table II) and ranged from 68 to 76 m, but for all stations except Station 65, the number of Stage *a* eggs was low. The

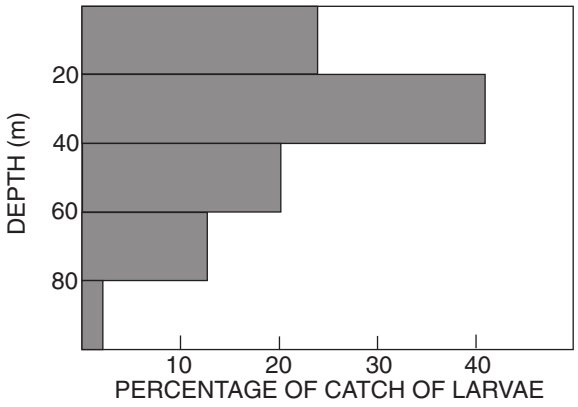

Fig. 5: Vertical distribution of sardine larvae from stations with ≥10 larvae (pooled data)

vertical distribution of older eggs, those that had reached equilibrium distribution, was different from that observed for Stage *a* eggs (Fig. 3). Older eggs were almost entirely concentrated in the upper 40 m (Fig. 3), most in the upper 20 m (71%). The weighted mean depth of those eggs was 16.2 m.

Analysing the vertical distribution of eggs station by station (Fig. 4), the two stations with most eggs show opposite trends. At Station 65, where 162 eggs were collected, the biggest fraction (67%) was in the 20–40 m depth interval, but all these eggs were newly spawned and therefore not confined to equilibrium distribution. At Station 75, 272 older eggs were collected, with the biggest fraction in the upper 20 m. At Station 67, 14 eggs were caught, 12 in the upper 20 m. These three stations provided more than 99% of all sardine eggs collected (Table I). Average wind speed for the previous five hours was higher at Station 75 than at Station 67 and, as described above, the egg distribution was deeper at Station 75, indicating increased wind-induced vertical mixing. As only two stations with older eggs were compared, no regression was established for those data.

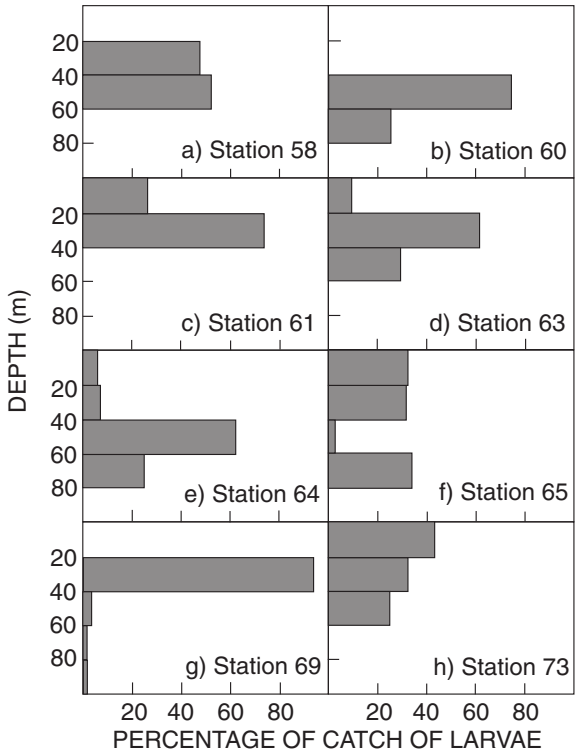

Fig. 6: Vertical distribution of sardine larvae at all stations with ≥10 larvae

Horizontal distributions of larvae are shown in Figures 1 and 2. In all, 231 sardine larvae were found at 13 stations on the southward leg. The vertical distribution of the larvae (Fig. 5) was different from that of the eggs. When all stations with 10 or more larvae were pooled, the highest concentration of larvae (41%) was in the 20–40 m depth interval. In addition, larvae were found in greater proportions in deeper intervals than were eggs, and larvae were also found at all

Table II: Calculated mean spawning depth and the observations on the youngest eggs (Stage *a*) at Stations 62, 65, 67 and 75 on which the calculation was based

Station	Number of Stage *a* eggs	Mean observed egg depth (m)	Mean estimated ascent velocity (m h^{-1})	Mean temperature (°C)	Mean development time (h)	Mean estimated spawning depth (m)
62	1	10.0	5.8	13.2	10	68
65	162	23.2	5.8	14.5	8	70
67	3	16.7	5.8	14.2	9	69
75	1	30.0	5.8	15.0	8	76

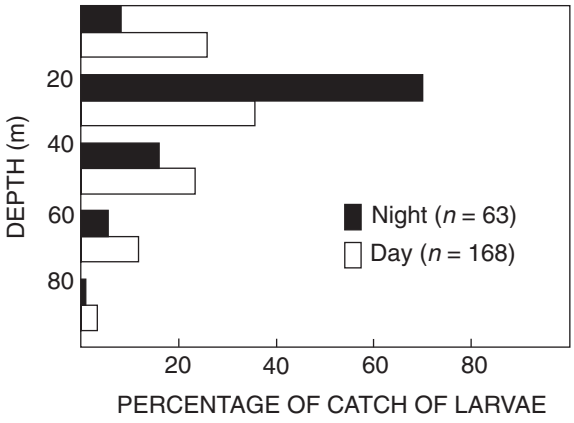

Fig. 7: Vertical distribution of sardine larvae during day and night stations (pooled data)

depth intervals. Only 24% of larvae were in the upper 20 m, whereas 20% were in the 40–60 m depth interval. The weighted mean depth of the larvae was 34.9 m, twice that observed for the equilibrium distribution of older eggs.

Vertical distribution of larvae by station is shown in Figure 6. Mean depth at stations with 10 or more larvae varied from 24.8 to 55.2 m. There was no significant linear relationship between weighted mean depth and mean wind speed.

There were differences in vertical distribution of larvae between day and night (Fig. 7), even though the weighted mean depth was almost the same (34.7 m during the night and 36.0 m during the day). During the night, most larvae (70%) were in the 20–40 m depth interval and only a relatively small fraction (8%) in the upper 20 m. During the day the proportion of larvae in the 20–40 m interval decreased to 35%, and the larvae appeared to be more evenly distributed than during the night, 26% being caught in the upper 20 m and 23% between 40 and 60 m deep.

Comparing the size distribution of larvae between depth intervals (Fig. 8) was also revealing. In the 80–100 m depth interval, few larvae were found and only one was in such condition that reliable measurements of *SL* could be made. Therefore, this interval was omitted from the analysis of size distribution. Without this depth interval, there was a trend of increasing *SL* with depth, mean *SL* being lowest (8.10 mm) in the upper 20 m and highest (9.24 mm) in the 60–80 m interval. However, this difference was not significant when an ANOVA test was applied to the four depth intervals ($p > 0.3$).

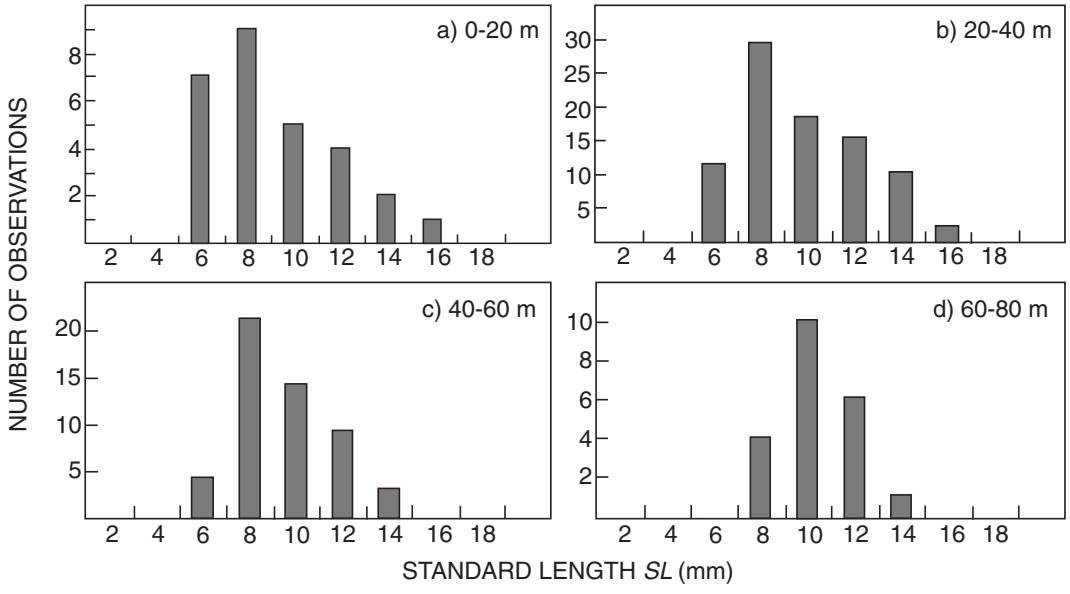

Fig. 8: Size distribution of sardine larvae by catch depth (all stations pooled)

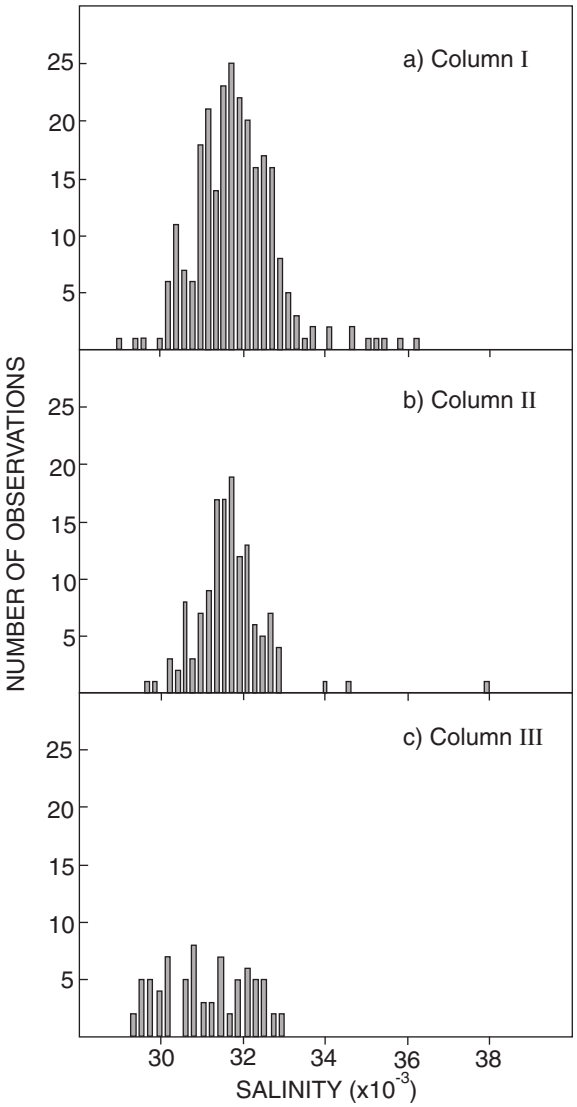

Fig. 9: Buoyancy measurements of sardine eggs from Multinet Stations 57 and 65 carried out in (a) Column I, (b) Column II and (c) Column III

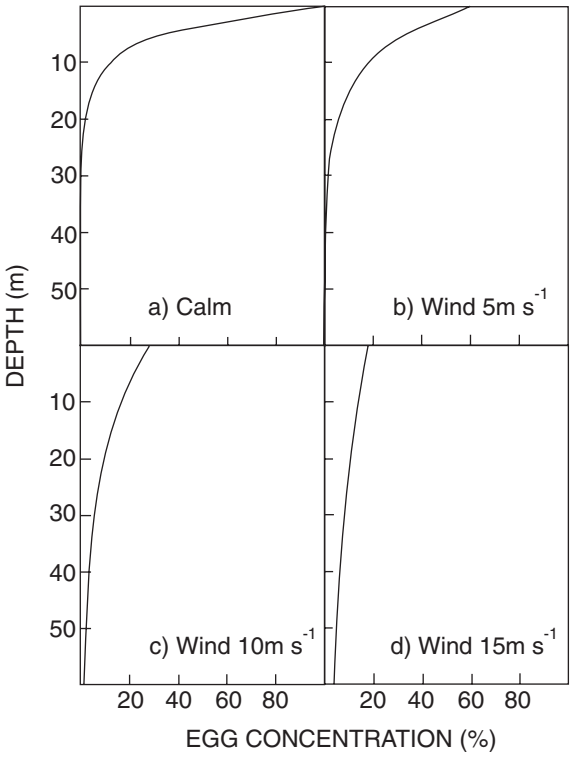

Fig. 10: Modelled vertical distribution of sardine eggs with winds ranging from 0 to 15 m s^{-1} based on the buoyancy measurements of eggs near Palgrave Point

Buoyancy measurements

The specific gravity of sardine eggs collected at Stations 57 and 65 was measured in the density gradient column. The neutral buoyancy was approximately normally distributed, with the exception of a tail of a few eggs towards higher densities (Fig. 9). These heavy eggs (neutral buoyancy at salinity $>35 \times 10^{-3}$) were, however, sinking out of the columns as a result of their poor condition, and they subsequently died. Hence, they are omitted from the calculations of mean specific gravity. The results from all columns were pooled and mean neutral buoyancy was calculated. This value was used for calculations of ascent velocity and modelling the vertical distribution of eggs.

The mean neutral buoyancy of viable sardine eggs in all columns was at a salinity of 31.7×10^{-3} and the upper and lower standard deviation at salinities of 32.8 and 30.8×10^{-3} respectively. The ambient salinity experienced by the sardine eggs varied little, between 35.15 and 35.35×10^{-3}, and there was very little vertical stratification. This implies that the calculated *in situ* mean buoyancy, expressed as the density difference between the eggs and the ambient seawater of the eggs, was 0.0028 g cm^{-3} with a standard deviation (*SD*) of ± 0.0007 g cm^{-3}. The corresponding mean as-

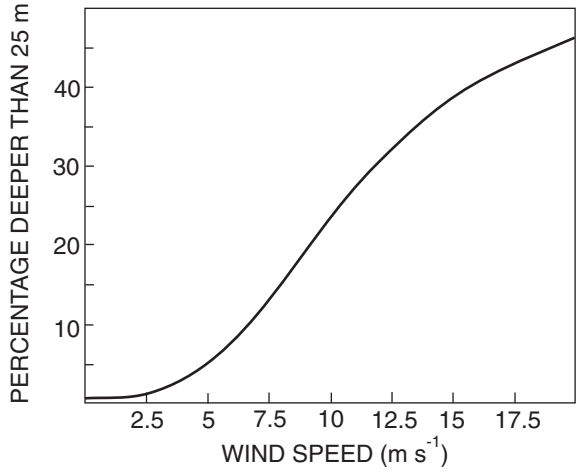

Fig. 11: Modelled fraction of sardine eggs deeper than 25 m at wind speeds from 0 to 20 m s^{-1}

cent velocity of sardine eggs was then 1.6 mm s^{-1} (5.8 m h^{-1}), with 1.3 mm s^{-1} (4.7 m h^{-1}) as the value at the lower *SD* and 1.9 mm s^{-1} (6.8 m h^{-1}) at the upper *SD*.

Model simulations of vertical distribution

Figure 10 shows the modelled vertical distribution of sardine eggs at wind speeds ranging from 0 to 15 m s^{-1}, based on the above measurements. At zero wind and low turbulent mixing, all eggs would be concentrated near the surface and no eggs would be found deeper than 20 m. As wind-induced mixing increases, eggs would be distributed deeper and deeper.

Circulation modelling (Sundby *et al*. 1999, Stenevik *et al*. in prep.) has shown that the offshore-moving upper layer in the northern Benguela is at its maximum 25 m deep. Below that a layer moves inshore. Consequently, eggs and larvae deeper than 25 m would be transported inshore. Figure 11 shows the modelled fraction of eggs deeper than 25 m as a function of the wind speed. At zero wind, practically no eggs are found deeper than 25 m. At wind speeds of 12.5 m s^{-1}, typical of the upwelling season off Namibia, one-third of the eggs are found deeper than 25 m.

DISCUSSION

The calculations of sardine spawning depth documented here, derived from the ascent of the youngest, newly spawned eggs, indicates that spawning takes place below the offshore-moving Ekman layer, at approximately 60–80 m deep. This implies that, on average, sardine eggs are transported onshore during the first hours after spawning when they are ascending towards the surface layer. After about 10 h, eggs have reached an equilibrium depth distribution, with a vertical balance between upward-directed buoyancy forces and downward-directed diffusive forces (Sundby 1983). The buoyancy forces are determined by the physical properties (specific gravity and diameter) of the eggs and by the salinity and viscosity of the ambient water. The vertical diffusive force is determined by turbulence of the water column, which off Namibia is determined mainly by wind-induced vertical mixing. As the ambient salinity varies little within the spatial distribution of the eggs, the ascent velocities, and hence the buoyancy forces, can be considered as constant with respect to environmental conditions. However, vertical mixing varies with the wind force. This means that sardine eggs are mixed variably down through the water column, depending on wind speed. Compared to the eggs of other species (e.g. hake and horse mackerel *Trachurus t. capensis*) in the northern Benguela, sardine eggs are quite buoyant, and their vertical distribution can be termed typically pelagic (Sundby 1991).

The model calculations in the current paper show that, during calm conditions (wind speed <5 m s^{-1}), more than 95% of the eggs in a vertical equilibrium distribution are confined to the upper 25 m and, consequently, are confined to the offshore-moving Ekman layer. However, when wind speed is low, upwelling is less intensive, and the speed of the offshore-moving Ekman layer is slow. As upwelling intensifies with increasing wind velocity, offshore transport of eggs in the Ekman layer increases. This transport is, however, partially compensated for by the fact that a larger fraction of the eggs is mixed down into the inshore-moving subsurface layer below. At wind speeds >15 m s^{-1}, model calculations show that >40% of the sardine eggs are deeper than 25 m. These wind-dependent vertical patterns are supported by field observations, which showed that older eggs are deeper at a station with high wind speed than at a station with low wind speed. Hence, the offshore loss of sardine eggs during strong upwelling might be reduced significantly by vertical mixing that extends below the Ekman layer into the inshore-moving flow. In such a case, vertical mixing could be a factor favouring reduction of offshore loss of eggs.

At hatching, the larva loses the chorion, the heavy fraction of the egg (Kjesbu *et al.* 1992), and the larva becomes more buoyant than the egg. However, shortly

after hatching, observations were made of larval swimming activity in the density gradient columns (EKS pers. obs.). King (1977a) made the same observation, so larvae can probably migrate out of the offshore-moving Ekman layer soon after hatching. Such a possibility is also evident from the vertical distribution. Eggs that had reached equilibrium distribution were mostly in the upper 20 m, in accord with earlier studies of the vertical distribution of sardine eggs in the northern Benguela (Olivar 1990), whereas the vertical distribution of larvae was different from that of the eggs. Most larvae were in the 20–40 m depth interval and only 24% in the upper 20 m. There was no significant relationship between the vertical distribution of larvae and the wind. Such a relationship was not expected because of the larval capability to migrate vertically, and this factor will most likely be dominant in deciding the vertical distribution of larvae as they grow and their swimming ability improves. There was a tendency for the biggest larvae to be found deepest, indicating that vertical migration to deeper water increases as larvae grow, a result reported also by Brewer and Kleppel (1986) for northern anchovy *Engraulis mordax*. However, this result for Namibian sardine was not significant, and therefore no firm conclusions should be drawn just yet. The lack of a significant relationship between size and depth distribution might be attributable to the fact that only larvae <20 mm were caught. In conclusion, the larvae, though more buoyant than the eggs, are probably distributed deeper in the water column simply as a consequence of their actively migrating out of the upper layers.

There was an overall difference in the vertical distribution of larvae by day and night, larvae being dispersed in the water column during the day and more stratified during the night. This contrasts with the results of earlier studies on related species, which revealed the opposite trend (Brewer and Kleppel 1986). The reason for this discrepancy is not clear, and further studies should be conducted with the aim of investigating the diel vertical migration of sardine larvae in the northern Benguela.

In conclusion, there are three main factors that contribute to retaining the early stages of sardine inshore and preventing them from being lost to recruitment by offshore transport from favourable nursery grounds. These are:

- inshore spawning below the offshore-moving Ekman layer that initially places the eggs in a region of relatively low offshore advection;
- wind-induced vertical mixing of the eggs that may transport significant numbers down into the inshore-moving subsurface layer;
- the vertical behaviour of larvae, with an active migration down and out of the offshore-moving Ekman layer.

Sardine in the northern Benguela spawn in areas where offshore Ekman transport caused by coastal upwelling is relatively low, i.e. between approximately 18 and 25°S (Le Clus 1990). However, the temporal and spatial distribution of sardine spawning has changed over time. Le Clus (1990) advanced several hypotheses to explain such shifts, and she concluded that changes in spawning locality were not necessarily the result of changes in biomass, age structure or the presence of genetically different stocks, but rather a result of environmental changes making certain locations unfavourable for spawning. For example, spawning peaked in the south mostly during warm years, when there was extensive thermal stratification south of 22°S (Le Clus 1990). Le Clus (1991) suggested further that spawning along the northern coast of Namibia (north of 22°S) is likely to be more intense in summer, when offshore transport and turbulence are at a local minimum. However, the data presented here for 1999 indicate a different situation.

The horizontal distribution of sardine eggs in September/October in 1998 and 1999 during a period of low stock abundance indicated that spawning had taken place in a limited region along the northern coast of Namibia. The broad distribution of sardine eggs and larvae in the 1960s and 1970s, when the stock was larger than at present, indicate that spawning took place over a much larger area (King 1977b, O'Toole 1999), although one of the peaks in abundance at that time also was near Palgrave Point. During the period of high stock biomass and strong recruitment, offshore larval loss would have been expected to be considerably greater than today, because spawning must have extended over an area where the retention mechanisms were not optimal, as observed now. Bakun (1999) introduced an interesting explanation for the changes in spawning distribution of sardine in the northern Benguela. He suggested that the observed shrinking of the spawning areas is in accord with MacCall's (1990) basin model, which postulates that a population will concentrate in the most favourable habitat as the number of individuals in the population decreases. During periods when the population is bigger, the model postulates that individual fish will spread out and occupy habitats that are less favourable, perhaps explaining the much broader distribution of sardine eggs when the stock was larger.

Cole (1997), referring to Bakun's (1996) triad theory, concluded that "there is a good reason to believe that sardine recruitment in the northern Benguela is not

so much enrichment limited, but rather is limited by levels of retention and concentration". Such a retention mechanism has also been indicated for anchovy *Engraulis capensis* in the southern Benguela, by correlating recruitment with south-easterly wind anomalies (Boyd *et al*. 1998). The data given here show that the reproductive strategy of sardine in the northern Benguela during the present period of low stock biomass seems to be adapted to the current system in a way that favours retention of larvae in favourable nursery areas restricted to a relatively narrow band near the coast. Therefore, it might be reasonable to think that current recruitment of sardine may not be limited by variability in retention, and that other factors might be more important for explaining interannual variations. As pointed out earlier, the probability of offshore loss is higher during periods of widespread spawning. However, during such periods, the probability of obtaining good conditions for recruitment might also be higher than when spawning is spatially restricted. The fact that sardine larvae in the northern Benguela in recent years seem to have been distributed in a relatively limited nursery area may make them particularly vulnerable to factors such as predation, and this could be one of the reasons why the stock size is still low. This explanation remains speculative, but it is an issue that should be investigated further to increase knowledge of recruitment mechanisms of sardine in the northern Benguela.

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