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TRANSPORT OF ANCHOVY AND SARDINE EGGS AND LARVAE FROM THE WESTERN AGULHAS BANK TO THE WEST COAST DURING THE 1993/94 AND 1994/95 SPAWNING SEASONS

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The transport of eggs and larvae of anchovy *Engraulus capensis* and sardine *Sardinops sagax* from the western Agulhas Bank to the nursery grounds on the Cape west coast was investigated. Samples were taken monthly between August 1993 and March 1994 and September 1994 and March 1995. A comparison of eggs and larval distributions with current features from selected months supports previous studies, indicating that the frontal jet plays an important role in the transport of the early life history stages of anchovy and sardine, but that the position of such transport can vary between the 200 and 500-m isobaths. During October 1994, November 1994 and February 1995, the greatest concentrations of eggs corresponded with areas of strong north-north-westerly flow just beyond the 200 m isobath off the Cape Peninsula, whereas in November 1993 and January 1994 eggs were concentrated farther offshore, increasing the vulnerability of developing larvae to further dispersion offshore. Offshore concentrations, intensified by strong south-easterly winds, occurred during January 1994. Areas of probable egg loss include the western Agulhas Bank, where currents flowing south-south-west can remove eggs before they are transported to the West Coast. Offshore currents also can develop west of the Cape Peninsula, but onshore currents are able to return eggs to the region of the jet, from where they are transported northwards. Other losses may result from offshore transport in the outer branch of the frontal jet off Cape Columbine. Variations in the ability of the jet current flowing north-north-west to transport eggs and larvae to areas favourable for growth and survival may influence recruitment success.

Many small pelagic fish species spawn in areas where their eggs and larvae will be retained in, or transported to, areas of high productivity in order to maximize growth and survival. From these observations, Bakun (1993) formulated a triad of requirements for successful recruitment, namely retention, production, and concentration processes. Several authors have shown that variations in entrainment of spawned products by currents can be a major factor affecting recruitment (see Norcross and Shaw 1984 for a review, Fletcher *et al*. 1994). Consequently, the relationship between hydrographic features and the distribution of pelagic eggs and larvae has received considerable attention over the past two decades.

In the southern Benguela, eggs of anchovy *Engraulis capensis* and sardine *Sardinops sagax* are transported from the Agulhas Bank to the food-rich nursery grounds on the west coast of South Africa (Shelton and Hutchings 1982, Armstrong *et al.* 1987, Boyd *et al*. 1992). Shelton and Hutchings (1982) showed the first clear evidence that the shelf-edge frontal jet plays an important role in the transport of ichthyoplankton from the Agulhas Bank to the West Coast. The frontal jet is a regular spring/summer feature off the Cape Peninsula, and its significance to the transport of eggs and larvae in the region off Cape Columbine was discussed by Armstrong *et al*. (1987). Boyd *et al.* (1992) corroborated those findings using more extensive anchovy egg data collected over many years, together with Acoustic Doppler Current Profiler (ADCP) data. Whereas previous authors have focused attention on specific features of the West and Southern Cape coasts, Boyd *et al.* (1992) studied the area from Port Elizabeth on the eastern Agulhas Bank to Lambert's Bay on the West Coast. From this comprehensive dataset, those authors were able to show that, despite a clear funnelling of anchovy eggs from the western Agulhas Bank to the nursery grounds, there was substantial egg loss at various localities along the "funnel". Recent biophysical modelling studies, using ADCP and spawner biomass data collected over several years, have demonstrated that anchovy year-class strength could be influenced by variations in advective processes which transport anchovy eggs and larvae in the southern Benguela (Shannon *et al*. 1996, Boyd *et al*. 1998).

A study of within-season variations in the processes most likely to influence pelagic fish recruitment has been the central focus of the South African Sardine and Anchovy Recruitment Programme (SARP). This study has afforded the opportunity to validate and elaborate on the above-mentioned conceptual model of transport of pelagic eggs and larvae in the southern

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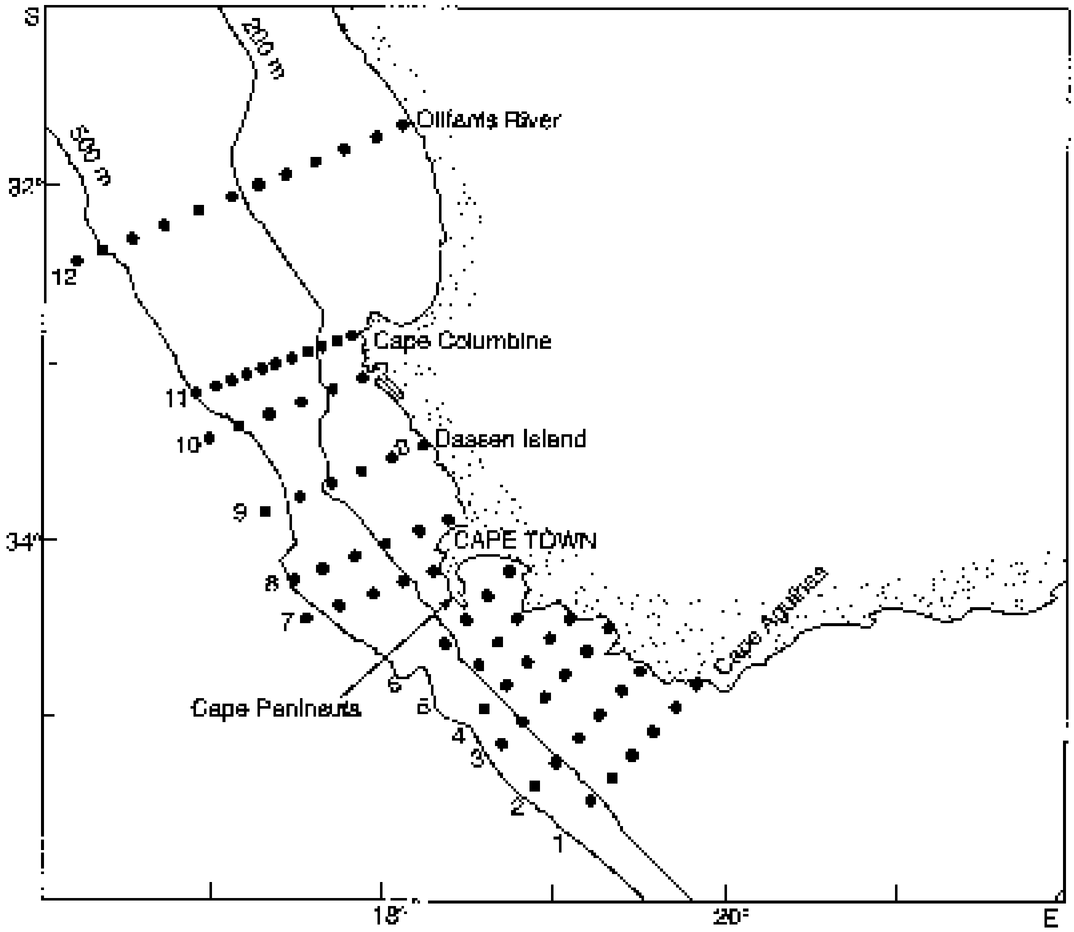

Fig. 1: Map showing the area sampled during the SARP cruises. Each transect is numbered and the dots indicate the positions of each station

Benguela. Intra-annual variations in current features between Cape Agulhas and the Olifants River (Fig. 1) were examined in relation to the distribution of spawned products. The work expands on previous studies by including data for anchovy larvae in addition to those for anchovy eggs and sardine eggs and larvae.

MATERIAL AND METHODS

Sampling during the SARP was conducted monthly between August 1993 and March 1994 (except January 1995) and between September 1994 and March 1995 aboard the Sea Fisheries (SF) vessels F.R.S. *Algoa* and F.R.S. *Africana* and the Norwegian research vessel *Dr Fridtjof Nansen* (Painting *et al.* in press a). During each of the 14 cruises, biological, hydrographic and physical properties of the water column were sampled. Stations were generally 10 miles apart, occasionally 5 miles apart on transects perpendicular to the coastline between Cape Agulhas and the Olifants River mouth (Fig. 1). All transects were approximately 50 miles long, with the exception of the northernmost one (Line 12), which extended 110 miles offshore. During November of 1993 and 1994, the SARP cruises formed part of the annual spawner biomass survey conducted by the SF, when a more detailed dataset, with better spatial coverage, was obtained than for the other cruises.

Collection of eggs and larvae

Sardine and anchovy eggs were collected at each station by means of a CalVET net of 0.05 m^2 mouth area and 300-μm mesh size (Smith *et al*. 1985). The net was hauled vertically at a speed of 1 $m \cdot s^{-1}$ from a maximum depth of 70 m or to within 5 m of the bottom where shallower. Samples were preserved in 5% buffered formalin. All anchovy and sardine eggs were identified (King 1977, King *et al.* 1978, Brownell 1979), and counts were standardized to numbers·m^2 from knowledge of the volume of water filtered by the net.

Larvae were collected at each station by means of a paired Bongo net (0.255 m^2 mouth area) of 300-μm mesh, obliquely towed from a maximum depth of 70 m or to within 5 m of the bottom where shallower. Of the paired samples collected at each station, one sample was preserved in 95% ethanol. Samples were sorted in the laboratory and all sardine and anchovy larvae were identified (King 1977, King *et al*. 1978, Brownell 1979). Counts were again standardized to numbers·m^2. Assuming an average handling time of 10 minutes per sample, lengths of preserved larvae were adjusted to live lengths using the shrinkage factors reported by Theilacker (1980) for northern anchovy *Engraulis mordax*. When Bongo samples were taken during daylight, larval abundances were corrected for net avoidance using size-specific day:night ratios (Hewitson 1987) and by applying correction factors given by Hewitt and Methot (1982).

Current-data recordings

Currents were measured 30 m deep (the depth approximating the base of the upper mixed layer where the bulk of the reproductive products are found) by means of 150 kHz RDI narrow band ADCPs mounted in the hulls of F.R.S. *Africana* and F.R.S. *Algoa*. Methods of ADCP data collection and analysis are described by Boyd *et al*. (1992). In October 1994, data were collected on *Dr Fridtjof Nansen* using a similar broadband profiler. Measurements were made on station and augmented on certain lines by underway measurements between stations.

The quality of the current data varied substantially throughout the programme. The two November surveys on F.R.S. *Africana* yielded the best data, because the performance of the profiler enabled bottom-referenced currents to be measured from the coast to the shelf edge (500 m deep) with an accuracy better than 5 $cm \cdot s^{-1}$ (Boyd *et al*. 1992). The performance of the profiler on F.R.S. *Algoa* was poor in 1993/94. Improved results were achieved in 1994/95 following the use of the new "Transect" software which allowed bottom-tracking solutions to be obtained if only three of the four beams tracked the bottom. Bottom-referenced currents could be obtained, in most instances, to depths close to 300 m on F.R.S. *Algoa* in 1994/95. Because of the exclusion of poor data, current vectors were not available for all stations, particularly offshore.

RESULTS AND DISCUSSION

Although both current and ichthyoplankton data were collected from 14 monthly cruises, only data from selected months will be described individually. These data will be used to highlight certain features in the southern Benguela that influence the transport of eggs and larvae from spawning to recruitment grounds. In particular, the data from October 1994 and February 1995, depict early summer and late summer features respectively, whereas data from the two November cruises were chosen because of good spatial coverage during those months. Prolonged south-easterly winds prior to sampling in January 1994 resulted in unusual conditions during that cruise, therefore, these data are shown. Data from all 14 cruises have been integrated to illustrate transport of spawned products over the whole spawning season.

Transport of eggs and larvae from the western Agulhas Bank past the Cape Peninsula

A comparison between egg and larval distributions and current data for October 1994 provides evidence for current features which promote the rapid movement of spawned products to the West Coast (Fig. 2). Convergent flow just south of Cape Point (Fig. 2e) coincided with the greatest densities of both anchovy and sardine eggs on the western Agulhas Bank (Fig. 2a, b). Eggs were entrained in the jet current, which was typified by very strong north-north-westerly flow (80 $cm \cdot s^{-1}$) inshore off the Peninsula in the region of the 200-m isobath. Similar flow patterns were measured repeatedly in the spring of 1995 by Boyd and Nelson (1998). Relative to anchovy eggs, the larvae were found farther offshore off the Cape Peninsula (Fig. 2c), suggesting either that currents were directed more offshore prior to sampling, or that spawning had taken place farther offshore. The presence of adult spawners (Painting *et al.* in press b) as well as young larvae (5–6 mm) on the outer western Bank supports the latter theory. However, a substantial proportion of larvae on the outer Bank were between 8 and 13 mm long, with some as large as 23 mm (Fig. 3), suggesting that currents were directed more offshore prior to sampling, or possibly

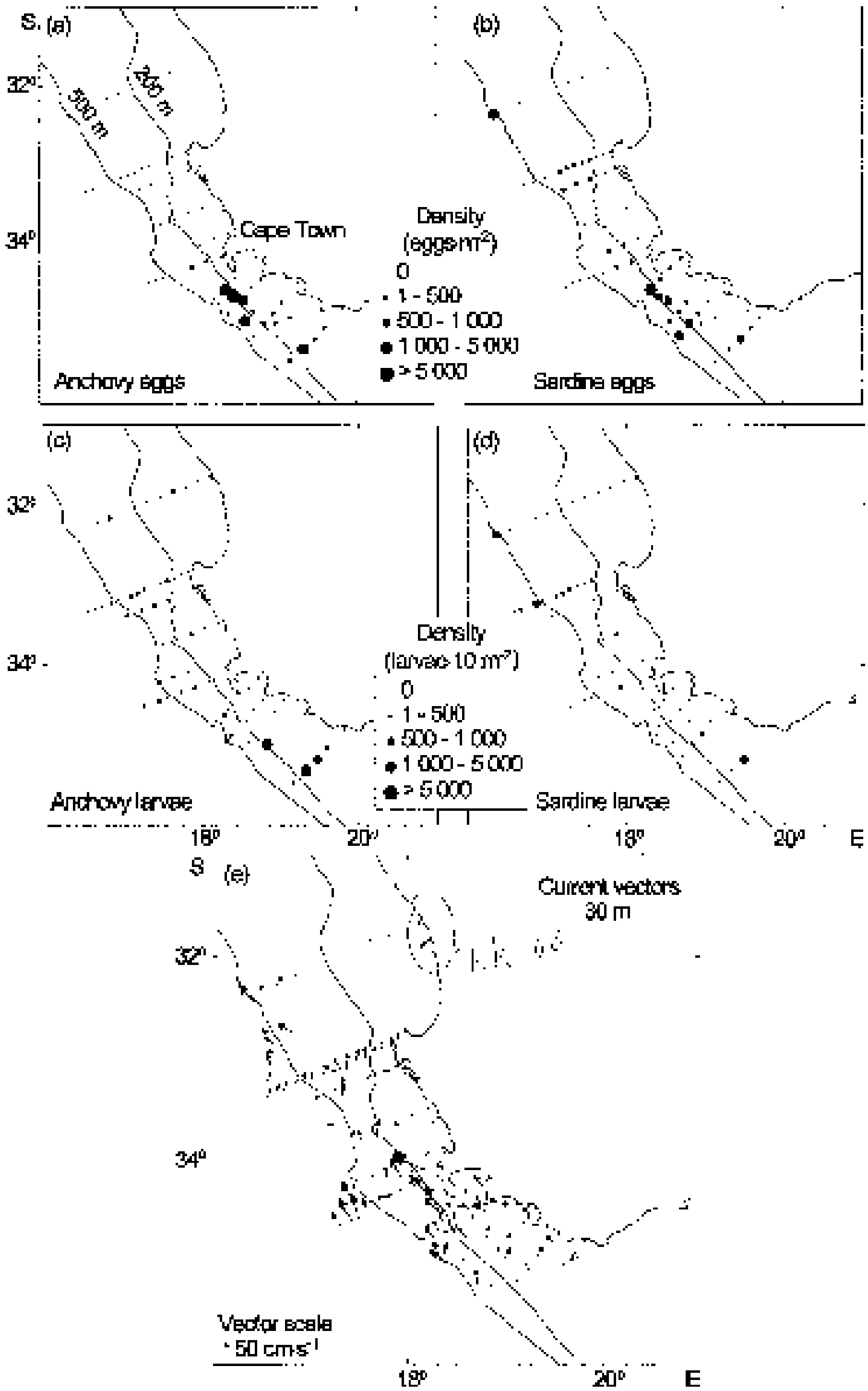

Fig. 2: The west coast of South Africa showing (a–d) relative density of anchovy and sardine eggs and larvae and (e) current vectors 30 m deep during October 1994

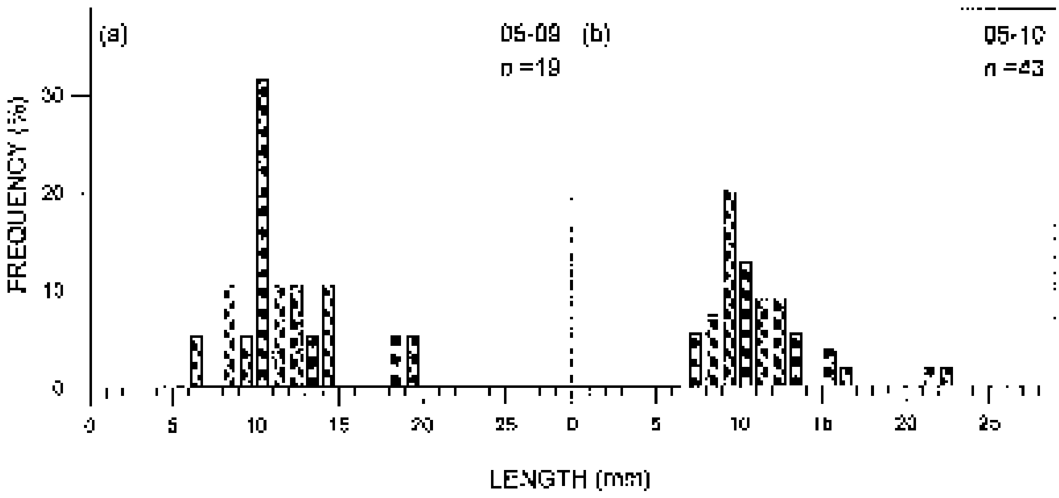

Fig. 3: Size frequency distributions of anchovy larvae observed at (a) Station 9 and (b) Station 10 on the outer western Agulhas Bank (Line 5) during October 1994

that larvae were spawned farther east and had grown after they moved long- and offshore with the currents.

Convergent flow on the western Bank was also noted during November 1993 (Fig. 4e), although it was farther offshore between the 200 and 500-m isobaths. The jet current off the Cape Peninsula was also comparatively far offshore during that period. Anchovy and sardine eggs were in the vicinity of the jet, suggesting rapid transport to the West Coast (Fig. 4a, b). Eggs and larvae of the two species were not recorded in the strong currents at the outer stations offshore of the 500 m isobath, both south and west of the Cape Peninsula, indicating no losses in those regions at that time.

The thermal front on the western Bank was clearly discernible over the midshelf during January 1994 (Fig. 5e). Off the Cape Peninsula, the front moved far offshore before bending sharply back towards the coast. The currents shown in Figure 5e correspond closely with the changing orientation of the front. Most adult sardine and some adult anchovy were also found in frontal regions in January 1994 (Painting *et al.* in press b). The presence of high concentrations of eggs over the midshelf on the western Bank suggests that adult fish were spawning in an area which coincided with the inner margin of the current flowing north-west (Fig. 5a, b, e). These data suggest that the position of adult spawners in relation to certain current features is important in ensuring efficient entrainment of spawned products by the jet current. A similar result has been obtained from biophysical modelling of the region (Shannon *et al.* 1996).

Biological and hydrographic features observed during November 1994 (Fig. 6) show that prevailing conditions during the anchovy spawning season do not always favour speedy transport of spawned products from the western Bank to the West Coast. In contrast to the October 1994 survey, the western Bank and waters of the Cape Peninsula during November 1994 were characterized by weak currents resulting from successive weak cold fronts and north-westerly winds (Richardson *et al.* 1998). Despite these conditions, currents were still predominantly to the north-west, indicating that offshore transport was reduced or absent. Whereas the prevailing current features on the western Bank favoured the transport of spawned products to the West Coast, such transport would have been slower than during October 1994. This could have resulted in increased cannibalism and predation (Valdés *et al.* 1987), particularly by adult spawners (Painting *et al.* in press b). Indeed, very few larvae were found on the western Bank in November 1994 and only a few anchovy larvae were encountered on the eastern margin of the grid (Fig. 6c). The absence of larvae was also noted in November 1993 (Fig. 4c, d). Although transport was reduced during November 1994, there could also have been a sustained break in spawning prior to both those cruises. Given the high density of sardine spawners on the West Coast during November 1994 (Painting *et al.* in press b) and the large number of sardine eggs found north of the Cape Peninsula, it is likely that sardine spawning had shifted northwards, reducing the importance of the contribution from the western Bank.

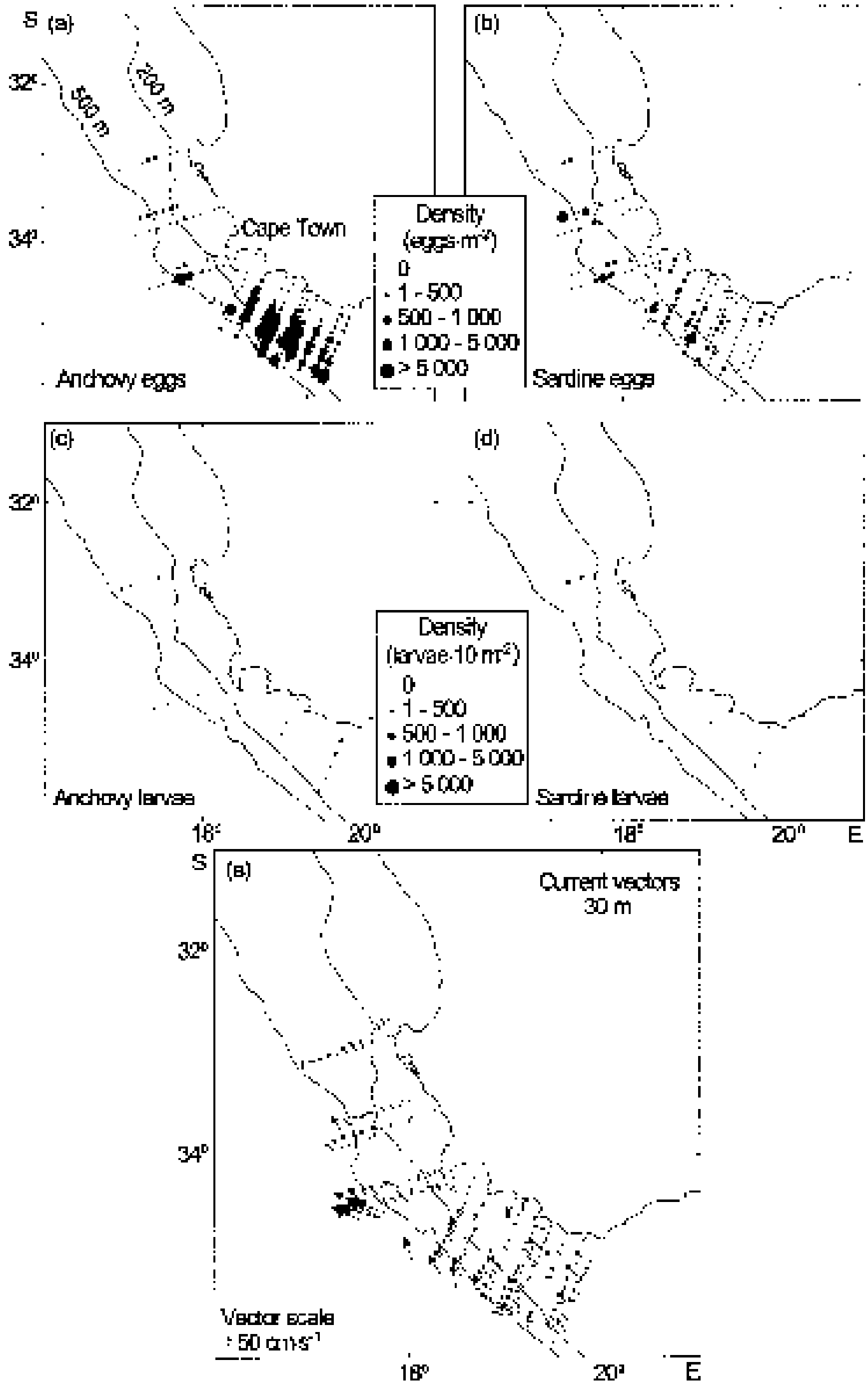

Fig. 4: The west coast of South Africa showing (a–d) relative density of anchovy and sardine eggs and larvae and (e) current vectors 30 m deep during November 1993

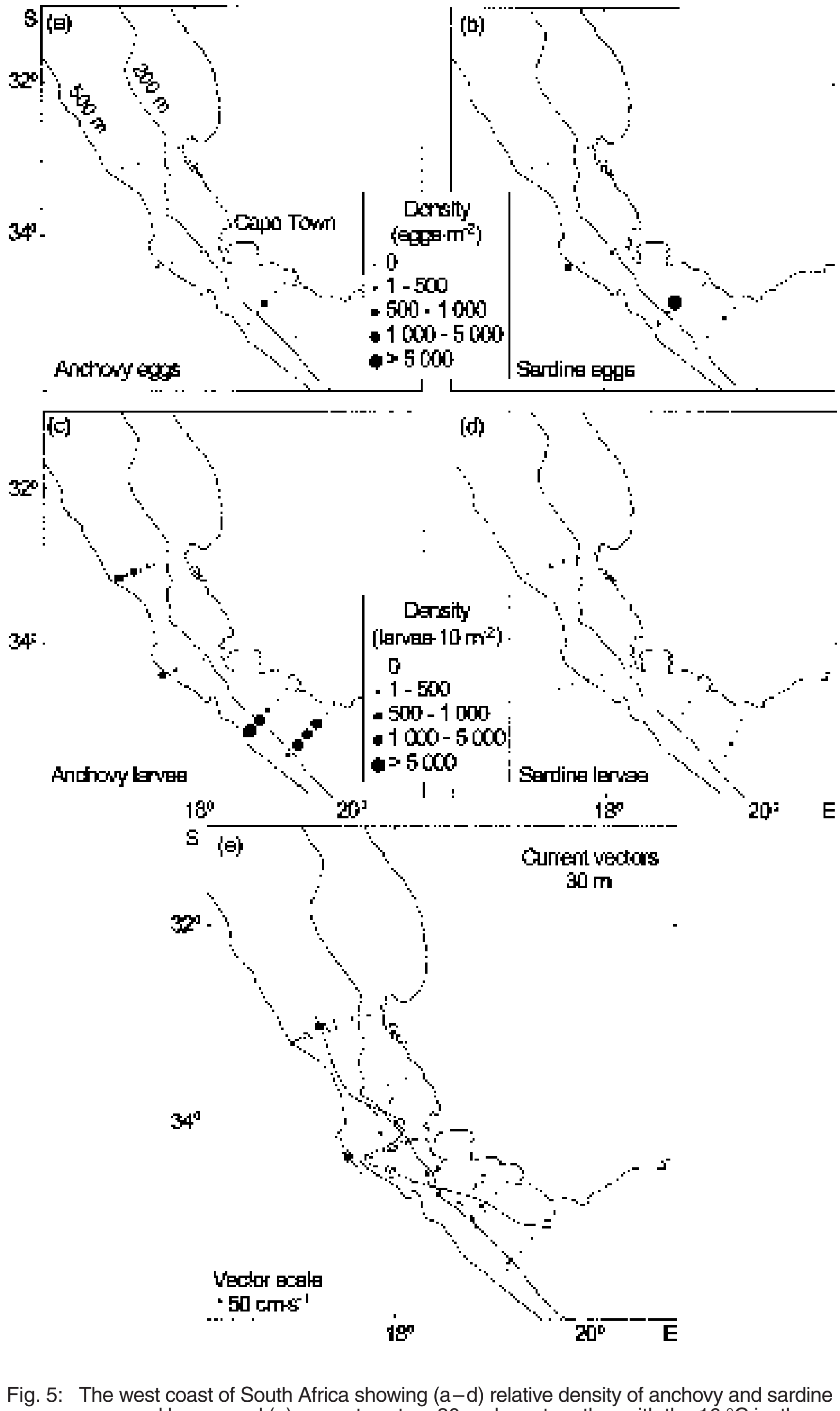

Fig. 5: The west coast of South Africa showing (a–d) relative density of anchovy and sardine eggs and larvae and (e) current vectors 30 m deep, together with the 16 °C isotherm depicting the position of the front during January 1994

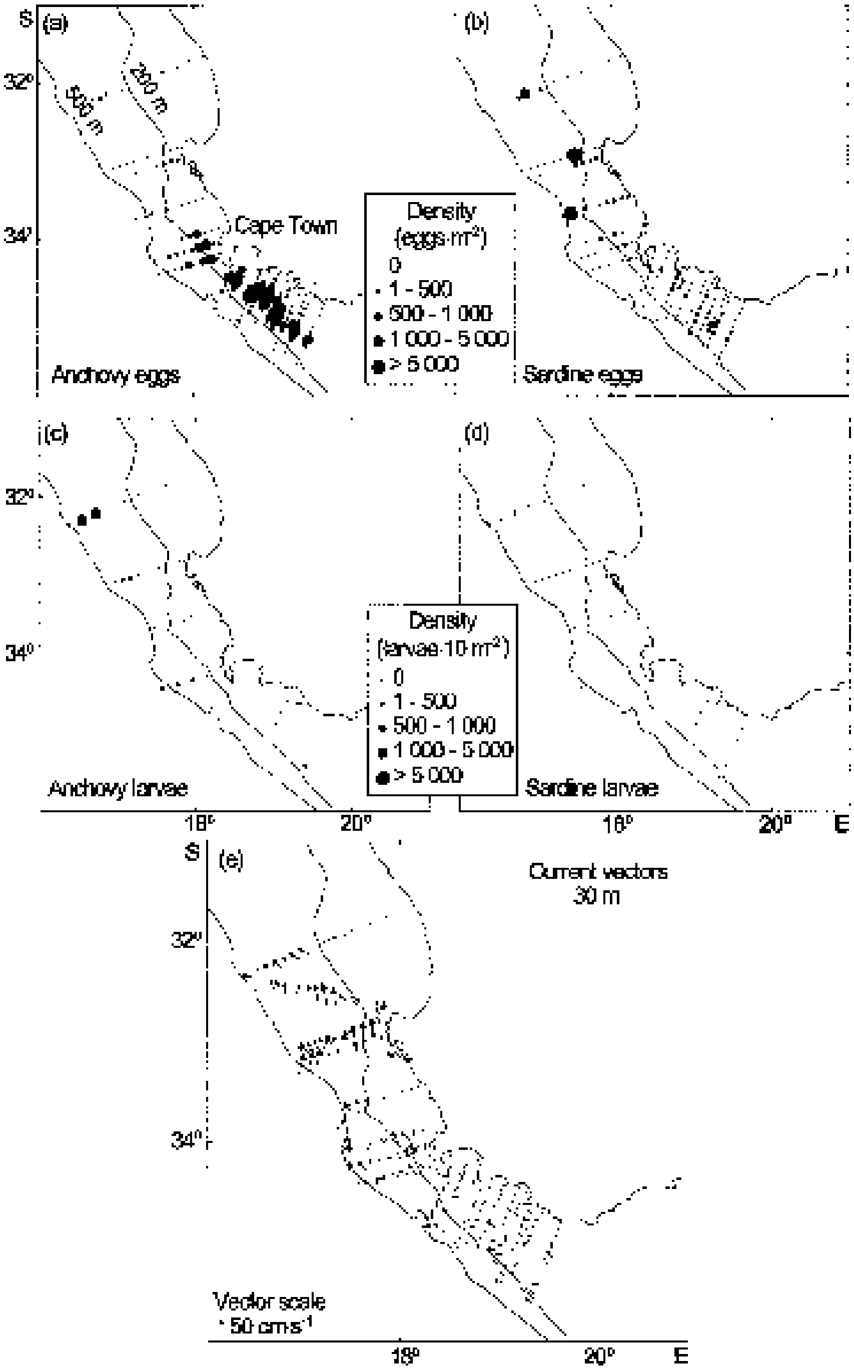

Fig. 6: The west coast of South Africa showing (a–d) relative density of anchovy and sardine eggs and larvae and (e) current vectors 30 m deep during November 1994

Transport from the Cape Peninsula to Cape Columbine and the nursery grounds

The characteristic twin jet current that occurs off Cape Columbine (and occasionally off the Cape Peninsula) was clear during some cruises. The jet has a major arm on the outer shelf (often with an offshore component of flow) and a minor northward arm farther inshore. During October 1994 (Fig. 2c–e), anchovy larvae were contained in the offshore branch of the current, off both the Cape Peninsula and Cape Columbine. Very few larvae were found on the short Dassen Island line (Line 9, Fig. 1), which suggests that larval transport may be continuous along the offshore margin of the grid. Anchovy larvae were also absent from the line during November 1994 (Fig. 6c), although they were found at the offshore stations along the Cape Peninsula, Cape Columbine and Olifants River lines (Fig. 6c). Larvae were also present along the offshore margin of the grid during January, February and March 1994 and March 1995 (data not shown), suggesting that transport along the offshore margin of the grid may be a fairly regular occurrence during summer. A biophysical model of the influence of the mean advection field on anchovy recruitment (Shannon *et al.* 1996) showed little loss of eggs and larvae in that region, despite the offshore flow at Cape Columbine. Losses were important only when additional offshore vectors were added to simulate the effect of strong south-easterly winds, as was postulated for 1993/1994 (Shannon *et al*. 1996, Boyd *et al.* 1998).

The inner branch of the Columbine jet occasionally entrained sardine eggs, and some sardine and anchovy larvae, for example during October 1994 (Fig. 2). Although densities were low at that time, the presence of anchovy and sardine larvae nearshore and over the midshelf off the Olifants River indicates that entrainment by the inshore branch of the jet would favour the retention of spawned products. Despite the potential of the inshore arm to transport larvae to the inner/midshelf region, eggs or larvae were rarely observed inshore off the Olifants River mouth. The exception to this observation was in February 1995 (Fig. 7c, d), when larvae were distributed along most of the Olifants River line (Line 12). Then, most anchovy and sardine larvae were between 8 and 17 mm long and there was no clear change in size distribution offshore (Fig. 8). Some 6–7 mm sardine larvae were found inshore (Fig. 8d), indicating that spawning may have taken place on the West Coast. Therefore, the coincidence of sardine eggs and early larvae, together with older larvae over the midshelf off Cape Columbine (Fig. 7b, d) implies local spawning as well as advection from the south.

Examples of potential losses of eggs and larvae from the shelf

Based on the current data and distributions of eggs and larvae from individual cruises, areas of potential losses of eggs and larvae could be identified. Offshore transport of eggs and larvae occasionally took place on the outer margin of the western Bank, suggesting potential loss (see Boyd *et al*. 1992). This was particularly evident during February 1995, when high densities of anchovy larvae (Fig. 7c) appeared to be entrained by relatively strong, offshore flow at 30 m over the depth contours 200 and 500 m in the region 18–19°E (Fig. 7e). However, the pattern of offshore distribution was not confined to the western Bank, but extended to the Cape Peninsula where sardine eggs and larvae (Fig. 7b, d) would have been vulnerable to offshore advection. Strong offshore currents were recorded at the outer shelf off the Cape Peninsula by Boyd and Oberholster (1994, see also Fig. 10).

As identified by Boyd *et al*. (1998), a significant, negative relationship between recruitment and cumulative south-easterly winds during the anchovy spawning season provides evidence for advective losses of eggs and larvae. Seasonal wind patterns in 1994, 1995 and 1996 all showed an intensification of south-easterly winds at Cape Point in late summer (Boyd and Nelson 1998, Richardson *et al*. 1998), and losses on the outer western Bank may be most marked towards the end of the spawning season. Anchovy, and to a lesser extent sardine, appear to spawn primarily in early summer (Shelton 1986, Huggett *et al*. 1998, Painting *et al.* in press b), when hydrographic conditions favour effective transport to the nursery grounds.

Although the eastern Agulhas Bank was not sampled during the SARP surveys, there is evidence to suggest that spawned products were probably transported to the western Bank from farther east. For example, during January 1994, relatively high densities of anchovy larvae were found east of the egg distribution (Fig. 5c). Previous studies have indicated regular strong offshore flow from the southern tip of the Agulhas Bank that and may contribute to substantial loss of eggs and larvae. Therefore, eggs spawned on the south-east Agulhas Bank probably do not contribute significantly to recruitment (Boyd *et al.* 1992). However, it appears that, under certain circumstances, those eggs can be advected inshore where current features promote transport to the West Coast (Largier *et al*. 1992, Boyd and Shillington 1994). Although the transport of eggs from the eastern Agulhas Bank to the West Coast nursery grounds may augment recruitment (Boyd *et al.* 1992), the south-easterly winds that normally favour such transport are also likely to lead to greater advective losses on the

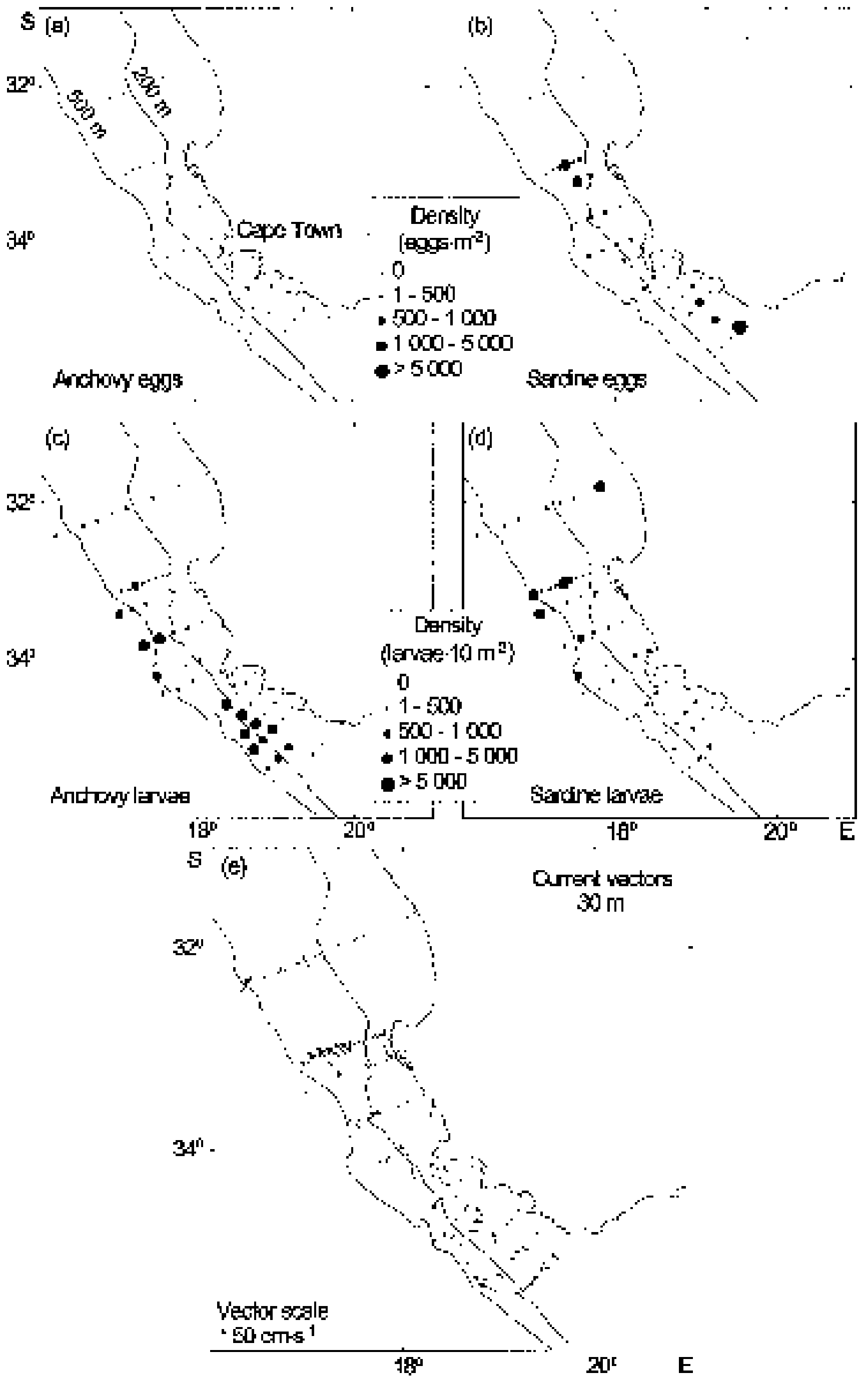

Fig. 7: The west coast of South Africa showing (a–d) relative density of anchovy and sardine eggs and larvae and (e) current vectors 30 m deep during February 1995

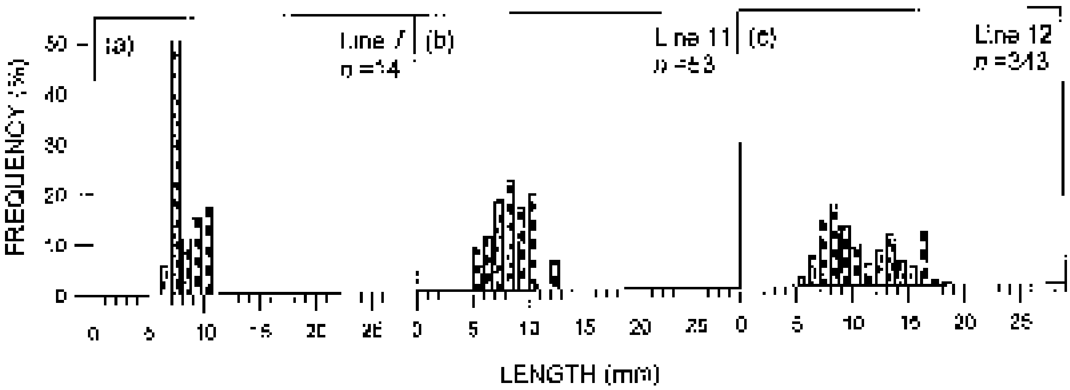

Fig. 8: Size frequency distributions of anchovy larvae averaged over (a) the Cape Peninsula line (Line 7), (b) the Cape Columbine line (Line 11) and (c) the Olifants River line (Line 12) during November 1994

West Coast (Shannon *et al.* 1996, Boyd *et al.* 1998).

The most obvious area of potential losses of eggs and larvae on the West Coast initially appeared to be the outer branch of the Columbine jet, because it had a strong offshore component during a number of the SARP cruises. The potential for loss by the offshore arm of the Columbine jet can be seen by the presence of larvae on the outer stations of the Columbine line (e.g. January 1994, Fig. 5c, d) and the Olifants River line (e.g. November 1994, Fig. 6d), where flow was directed offshore (Figs 5e and 6e).

Despite the potential for offshore losses at various localities between the spawning and nursery grounds, flow patterns observed during some surveys indicate that eggs and larvae may be returned to the system, following their offshore advection, and continue their journey northwards. Data from October, January and November 1994 (Figs 2, 5, 6) suggest that spawned products that had been swept offshore near the Cape Peninsula may have been transported back to the jet by onshore currents farther north. During October and November 1994 (Figs 2, 6), anchovy larvae were entrained in the offshore margin of the north-westerly flow, beyond the 500-m isobath off the Cape Peninsula. Although these larvae could have been advected offshore (particularly in October 1994), the presence of larvae in the coherent onshore flow in the region of the 500-m isobath off Cape Columbine suggests that a substantial portion of them might rejoin the jet. Furthermore, the size distribution of anchovy larvae along the offshore margin during November 1994 was broader off the Olifants River and Cape Columbine lines than adjacent to the Cape Peninsula (Fig. 9). Moreover, lengths of larvae at offshore stations along the Olifants River line (Fig. 9c) show small ones together with some which would have been spawned either in late October or on the eastern Agulhas Bank (12–17 mm) and transported northwards. This provides further support for the idea that, whereas some larvae may be lost by offshore flow, others may reach the nursery grounds on the West Coast via a delayed route farther offshore.

Similarly, eggs and larvae may be transported offshore at Cape Columbine but returned to the system by onshore flow farther north, off the Olifants River. For example, current features during February 1995 (Fig. 7e) indicate offshore flow on the outer margin of the Columbine line and onshore flow at 500 m on the Olifants River line. Although most sardine larvae and some anchovy larvae were found inshore off the Olifants River during that period, larvae of both species were entrained by the offshore currents at Cape Columbine and the onshore flow farther north. A similar flow pattern was evident from the average current field recorded by Boyd and Oberholster (1994). As a result of the potential for onshore flow and the sporadic sampling of the Olifants River line, the loss of reproductive products in that region was difficult to confirm. However, the potential for offshore flow near Dassen Island was examined by Nelson (1985) and Boyd *et al.* (1992), who suggested that features of short time-scale could divert eggs and larvae to the outer branch of the Cape Columbine jet, or under certain circumstances move them onshore, as described by Nelson *et al.* (1998). Such offshore and onshore transport appears to arise through the interaction of upwelling plumes and shelf waves (Nelson *et al.* 1998).

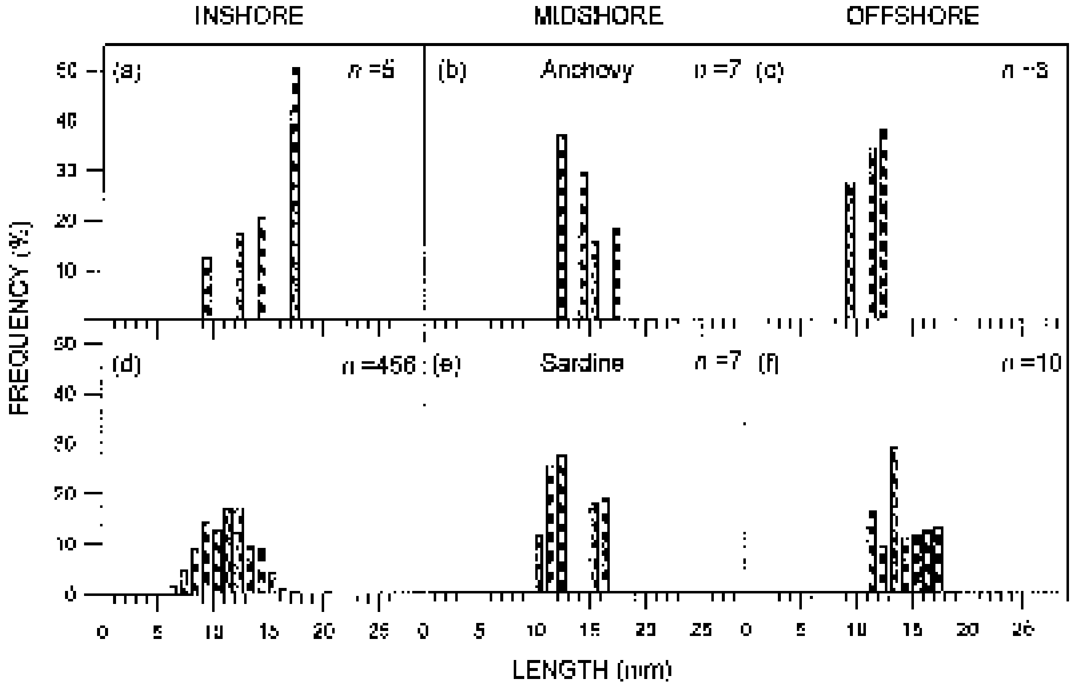

Fig. 9: Size frequency distributions of (a–c) anchovy larvae and (d–f) sardine larvae in the inshore, midshore and offshore regions along the Olifants River line (Line 12) during February 1995

Integration of the transport of spawned products during SARP over the whole spawning season

In order to complement the selected individual cruise data, mean flow patterns together with mean larval densities for all the 1993/1994 and 1994/1995 SARP cruises are presented in Figures 10. Both datasets show a similar pattern, whereby currents follow the 200 and 500 m isobaths, but flow inshore of the 200 m isobath between the Cape Peninsula and Cape Columbine was weak. During 1993/1994, vectors in the vicinity of the 500 m isobath appear to have an offshore component (Fig. 10c) in comparison with the situation during 1994/1995 (Fig. 10f). Consequently, current conditions during the 1993/1994 season may have promoted more offshore advection of eggs and larvae than during the 1994/1995 season, but too few cruises were averaged for conclusions to be drawn. Nevertheless, the increase in both anchovy and sardine recruitment from 1994 to 1995 (SF unpublished data) appears to be consistent with interannual variability in advective processes during the SARP cruises.

The distribution of the mean density of anchovy and sardine larvae (Fig. 10) was not discernibly different between years, although sardine larvae were less abundant during 1993/1994. For both species, there was a shift in the region of maximum abundance of larvae away from the 200-m isobath on the western Bank, towards the 500-m isobath off Cape Columbine. This emphasizes the importance of the "offshore transport" path as well as the need for more understanding of onshore movement in the nursery region (Hewitson 1991).

CONCLUSION

The results presented here reflect the efficiency of near-surface circulation patterns within the southern Benguela ecosystem to entrain eggs and larvae. This provides further support for Shelton and Hutchings' (1982) original hypothesis that the shelf-edge frontal jet is responsible for the transport of eggs and larvae to nursery grounds on the West Coast. Convergent flow south of the Cape Peninsula, merging into the typically fast-flowing jet off the Peninsula, appeared to funnel eggs and larvae to the West Coast, particularly during early summer (e.g. October 1994 and November 1993, Figs 2, 3). Nevertheless, the probable loss of

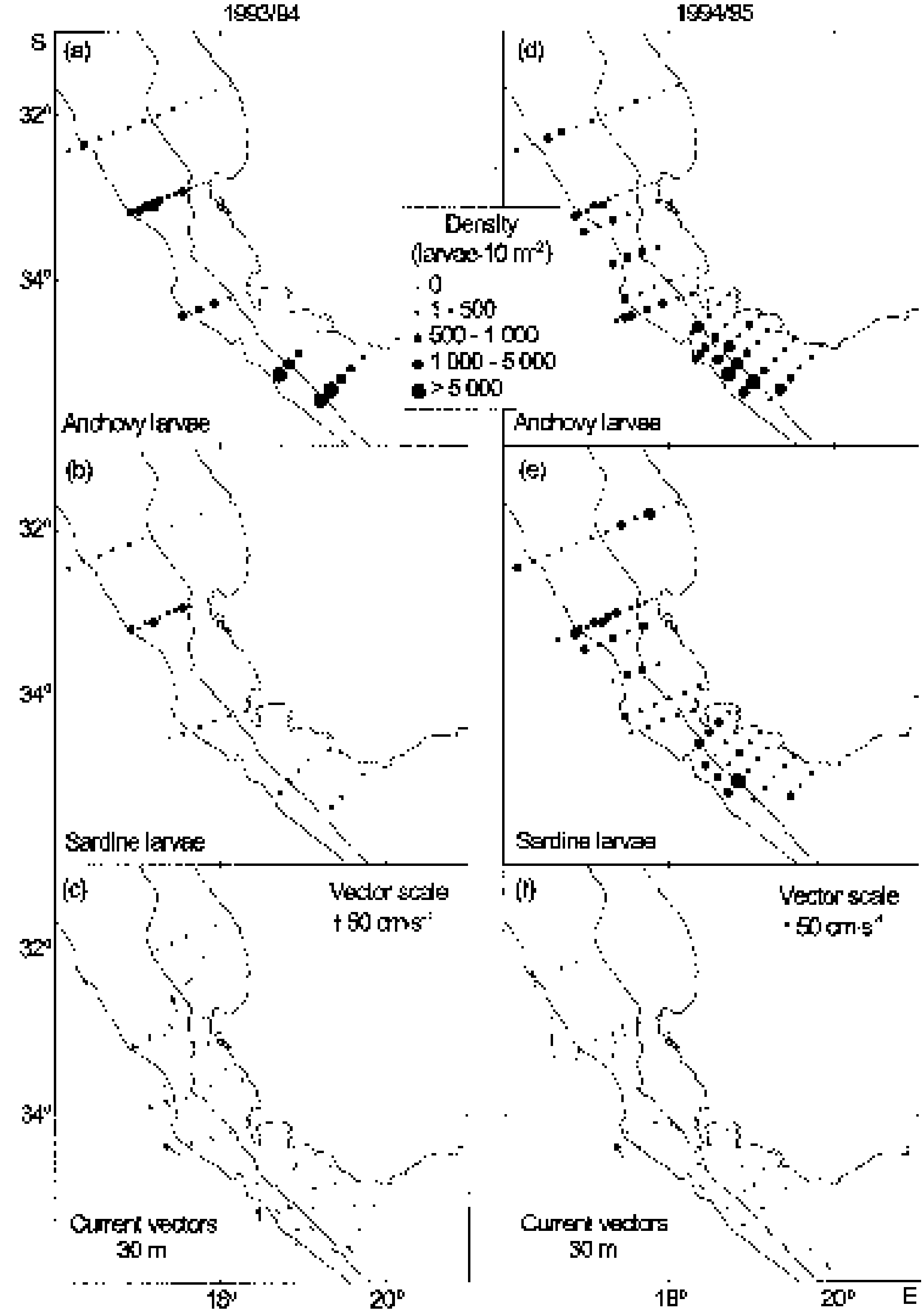

Fig. 10: Relative density of (a) anchovy larvae and (b) sardine larvae, and (c) current vectors averaged between September 1993 and March 1994, and the relative density of (d) anchovy larvae and (e) sardine larvae, and (f) current vectors averaged between September 1994 and March 1995

considerable numbers of both eggs and larvae was frequently inferred during the survey, especially when offshore distributions of spawning products coincided with strong south-easterly winds (Richardson *et al.* 1998). This generally took place later in the season (January, Fig. 5; February, Fig. 7), when offshore transport from the outer western Agulhas Bank was most marked. Advective processes early in the summer spawning season may therefore enhance reproductive success relative to later in the season. Because the spawning activity of anchovy and, to a lesser extent, sardine peaks in early summer (Shelton 1986, Fowler 1998, Huggett *et al*. 1998), advective processes could exert a particularly strong control on the spawning strategies adopted by these species. As documented by Parrish *et al*. (1981) and Bakun and Parrish (1982) for fish species in the California Current, many fish stocks in upwelling systems avoid spawning during periods of intense offshore flow.

Although conditions in the early part of the spawning season can be "ideal" for maximizing reproductive success, at the end of the season, during periods of apparent offshore loss of larvae, other factors can have a positive influence on recruitment. Observations from satellite images (Agenbag 1992) indicate situations where offshore flow rejoins the main frontal region in areas on the western Bank and the West Coast. Such onshore flow could entrain eggs and larvae from earlier offshore movement. This transport would result in fewer losses as a result of transient features than those associated with semi-permanent features, such as the offshore divergence off Cape Columbine.

By means of a biophysical advection model, Shannon *et al*. (1996) found that anchovy recruitment to be influenced by the position of adult spawners in relation to currents. During several cruises (e.g. November 1994 and February 1995), adults and spawning products of sardine were found between Cape Columbine and the Cape Peninsula. By spawning there, the journey of eggs and larvae to favourable grounds is shortened, reducing the chances of being transported offshore. In addition, being in close proximity to the highly productive feeding grounds in that region, larval survival would be enhanced. Crawford (1981) reported that, before the collapse of the sardine resource in 1962–1964, when recruitment was considerably higher than in subsequent years, sardine eggs were frequently found on the West Coast off Cape Columbine. Consequently, recruitment may be enhanced in years when the frequency of spawning on the West Coast is high. This argument may partially explain the increase in sardine recruitment from 1994 to 1995 (SF unpublished data), because average abundance of sardine eggs and larvae on the West Coast increased from the 1993/1994 season to the 1994/1995 season.

Advection is one of many factors that determine the fate of developing eggs and larvae and subsequent year-class strength. Richardson *et al*. (1998) have demonstrated that copepod production on the spawning grounds mediates recruitment of anchovy and sardine through spawning success. This study provides evidence for the influence of retention processes on recruitment, a useful adjunct to the study of Richardson *et al.* (1998).

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