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MULTIPLE FACTORS AFFECTING SOUTH AFRICAN ANCHOVY RECRUITMENT IN THE SPAWNING, TRANSPORT AND NURSERY AREAS

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Despite high primary productivity, the yield of pelagic fish in the southern Benguela is relatively low compared to that in the Humboldt system. Part of the constraint may be the ability of pelagic fish to reproduce successfully in a strongly pulsed upwelling environment, where enrichment, retention and concentration mechanisms are less compatible than in Peru-Chile. Anchovy *Engraulis capensis* spawn upstream of the main upwelling centres on the food-poor, thermally stratified western Agulhas Bank, over a protracted summer season (October–February) when high wind speeds of 7–8 $m \cdot s^{-1}$ are prevalent. Eggs spawned farther east, on the central or eastern Agulhas Bank, may be subject to increased cannibalism and advective losses, whereas those spawned farther west could be susceptible to heavy advective losses offshore during periods of strong southerly winds. Copepod concentrations are negatively correlated with spawner biomass on the western Bank and are inversely linked to high rates of gonad atresia in anchovy and reduced subsequent recruitment. There is a restricted area of suitable spawning temperatures (16–19°C) on the western Bank, and fish outside that range appear to have less successful spawning, affecting recruitment; a reduction of the duration of spawning appears to decrease the chances of good recruitment. Oil content of pelagic catches on the west coast of South Africa suggests that good feeding conditions for adult fish are also favourable for growth of young fish in the nursery area. An inverse correlation between the numbers of recruits estimated in June and the strength of upwelling-favourable winds over the previous summer indicates the importance of advective loss of eggs and larvae in the transport and nursery areas. The presence of Agulhas Rings close to the shelf-edge, predators on juvenile anchovy, and the strength of upwelling on the West Coast could also be important factors affecting recruitment success. There seem to have been changes in the inshore-offshore distributions of spawning anchovy and/or their eggs over the past three decades, resulting in different recruitment responses to south-easterly winds.

The Benguela Ecology Programme (BEP) was credited by Rothschild and Wooster (1992) with "being on the brink of a recruitment prediction breakthrough". However, after a series of predictions given each January on the prospects for the following years recruitment, several papers and theses on recruitment prediction, three intraseasonal Sardine and Anchovy Recruitment Programme (SARP) studies and much birthdate distribution analysis, the breakthrough has not been achieved. Recruitment prediction is a vigorous, if inexact, science, and a number of promising indicators and relationships have been described. The successes and failures of these predictors have given improved insights into the complexity of mechanisms affecting recruitment of anchovy *Engraulis capensis* in the southern Benguela, and intensive holistic monitoring has taken place as the relative dominance of anchovy has declined and that of sardine *Sardinops sagax* has increased (Fig.1); a reversal of the process that occurred in the early 1960s. This contribution synthesizes the findings of the past 13 years of monitoring. For the past nine years, intensive environmental and biological sampling has been carried out, both during and between hydroacoustic surveys, and it has provided indices of spawner and recruitment strength of pelagic fish for the period 1983–1996.

The current hypotheses on the life history of anchovy are shown in Figure 2. Despite the oceanographic complexity of the southern Benguela, anchovy life history is unusually clear-cut, with distinct spawning, transport and nursery regions. It is assumed that most of the recruits to the West Coast fishery originate from the stratified western Agulhas Bank, which contains the bulk of the spawner population in November, at

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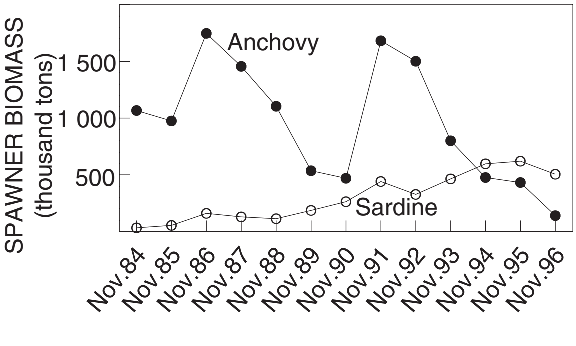

Fig. 1: Annual trends in acoustic estimates of anchovy and sardine spawner biomass, November 1985–1996 (Sea Fisheries, unpublished data)

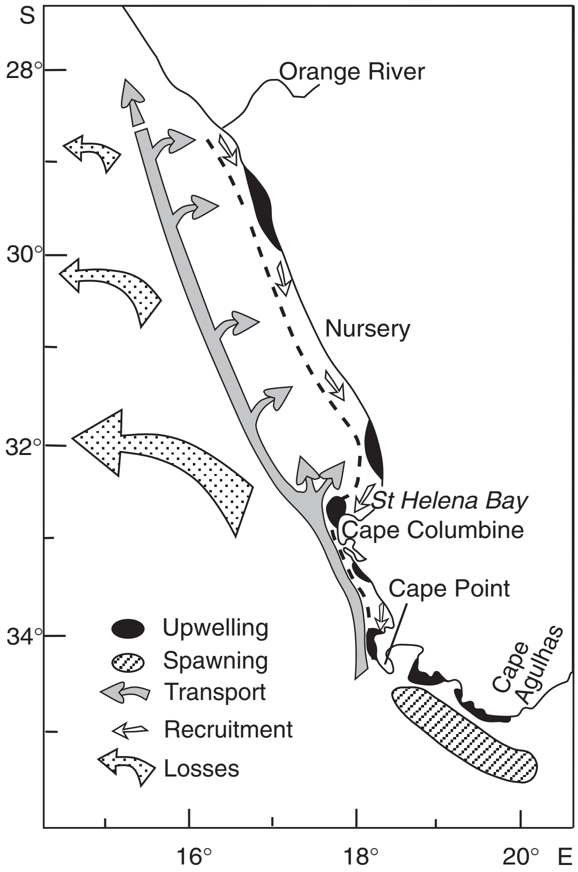

Fig. 2: Present hypothesis on anchovy life history (after Hutchings 1992)

the peak of the spawning season. Transport from the spawning ground to the nursery area on the West Coast is facilitated by frontal jet currents on the boundaries of the upwelling centres. These strong currents rapidly move eggs and larvae from the western Agulhas Bank to the productive West Coast, downstream from the active upwelling cells, possibly reducing cannibalism considerably. In this manner, the triad of enrichment, retention and concentration factors, as suggested by Bakun (1996), are at least partially satisfied.

After spawning, some of the adult anchovy move to the West Coast, where they are caught during the first three months of the fishing season (January– April). Other adult fish move eastwards to the central and eastern Bank, where there is no purse-seining (Hampton 1992). Young fish begin to appear in the fishery in April each year, peaking in the period May-July when they are 8–10 cm long (caudal length) and 6–9 months old. "Recruitment" can be interpreted in a number of ways for South African anchovy. Recruitment to the fishery takes place on the West Coast in autumn (April–July), whereas recruitment to the spawning population takes place later in the year. Spawners are >10 cm long. An acoustic survey is conducted during May/June to estimate the numbers and biomass of new recruits to the fishery and, in November, to estimate the spawner biomass (Fig. 3a). Recruitment strength has varied considerably during the past 13 years, with lows in biomass in 1989, 1993/4 and 1996 (Fig. 3b). Recruitment in terms of numbers (Fig. 3c) generally follows the trends in recruitment biomass (Fig. 3b), except in 1993 when there were high numbers of small recruits. Recruitment is also back-calculated after the spawner biomass survey and takes into account the catches and natural mortality during the year (Butterworth *et al.* 1993). This is considered the most accurate estimate of recruitment strength (Fig. 3d). Low recruitment levels resulted in a rapid decline of the adult spawner biomass (Fig. 3a) and severe economic dislocations for the purse-seine industry, which is generally dependent on recruits of the year for approximately 70% of the total catch. Years of good recruitment were in 1986–88, 1991–92 and 1995. Good recruitment, while being a less serious risk to the population, may represent lost opportunities to the fishery if unexpectedly high recruitment is constrained by low catch limits set by the management procedure.

Comprehensive environmental and biological monitoring has been conducted during and between acoustic surveys, covering the factors considered most likely to affect recruitment success. However, there are a large number of factors that are not measured routinely because of manpower, feasibility and logistic constraints. A number of different approaches have been

Table I: Summary of the models that have been developed to predict anchovy recruitment in the southern Benguela

Source	Approach	Factors	Results
Bloomer *et al.* (1994) (Fig. 5)	Rule-based model using environmental parameters and spawner biomass in the spawning, transport and nursery areas	Wind frequency, wind velocity, SST and spawner biomass	Good agreement for 1984–1991, except for 1989
Cochrane and Hutchings (1995) (Fig. 4)	Preliminary correlation analyses, 1984–1992	Wind, copepod biomass and production, spawner biomass, spawning area, oocyte atresia, SST, fish condition and predation	Most promising factors: copepod biomass and production, atresia, winds and distance offshore of the 16°C isotherm
Korrûbel (1995), Korrûbel *et al.* (1998) (Fig. 6a, b)	Expert system, deterministic and probabilistic approaches, 1984–1993. Hindcasting against back-calculated recruitment	As for Cochrane and Hutchings (1995)	Good agreement using egg production, distance offshore of the 16°C isotherm, gonad atresia, ENSO events, in deterministic system in all years
Boyd *et al.* (1998) (Figs 8, 9)	Linear correlations of wind and oil : meal ratios with recruitment survey results	Wind (October–March), oil : meal ratio of pelagic fishery from January to March	Negative correlation with south-easterly winds, positive correlation with oil : meal ratio. Wrong for 1986 (wind), 1990 and 1992 (oil : meal)
Waldron *et al.* (1997) (Fig. 7)	Optimal environmental window	New production v. fish spawner biomass	Incorrect for 1989
Richardson *et al.* (1998)	Correlation of area of 16–19°C water on the spawning area with egg density on a monthly basis	Monthly SST on western Agulhas Bank, copepod biomass and production and chlorophyll *a*	16–19°C water optimal for food availability for fish from October to December
Painting and Korrûbel (1998)	Expert system, deterministic approach. Monthly SARP data 1993–1995	Distance offshore of the 16°C isotherm; southerly wind stress, anchovy egg abundance, oocyte atresia, fish starvation index and oil : meal ratio	Good agreement between back-calculated recruitment and cumulative monthly indices

attempted to try to predict anchovy recruitment (Table I). The measured factors were structured into an expert system (Fig. 4) in an attempt to predict recruitment prospects in January, at the start of the fishing season. Bloomer *et al.* (1994) used wind frequency, wind velocity, temperature and spawner biomass in a rule-based model to predict recruitment (Fig. 5). Cochrane and Hutchings (1995), with a limited time-series of data, identified a reduced number of important factors from those then being monitored. These included spawner biomass, copepod biomass and production on the western Agulhas Bank, gonad atresia in November, the incidence of southerly winds at Cape Point, and the distance offshore of the 16°C isotherm off the West Coast. Korrûbel (1995) developed this approach further, utilizing both deterministic and probabilistic approaches to recruitment prediction. By manipulation of the information likely to be available at the end of January each year (e.g. by varying the combination of factors, utilizing "fuzzy" thresholds and by differential weighting), Korrûbel (1995) produced reasonable predictions of recruitment using the deterministic system (Fig. 6a) and less well-fitted predictions using the theoretically superior probabilistic system (Fig. 6b). The most successful factors used in the deterministic model included egg production by spawning anchovy, distance offshore of the 16°C isotherm on the West Coast, percentage female gonad atresia in November, and *El Niño* Southern Oscillation (ENSO) events.

Richardson *et al.* (1998) proposed that the extent of 16–19°C water on the western Agulhas Bank was

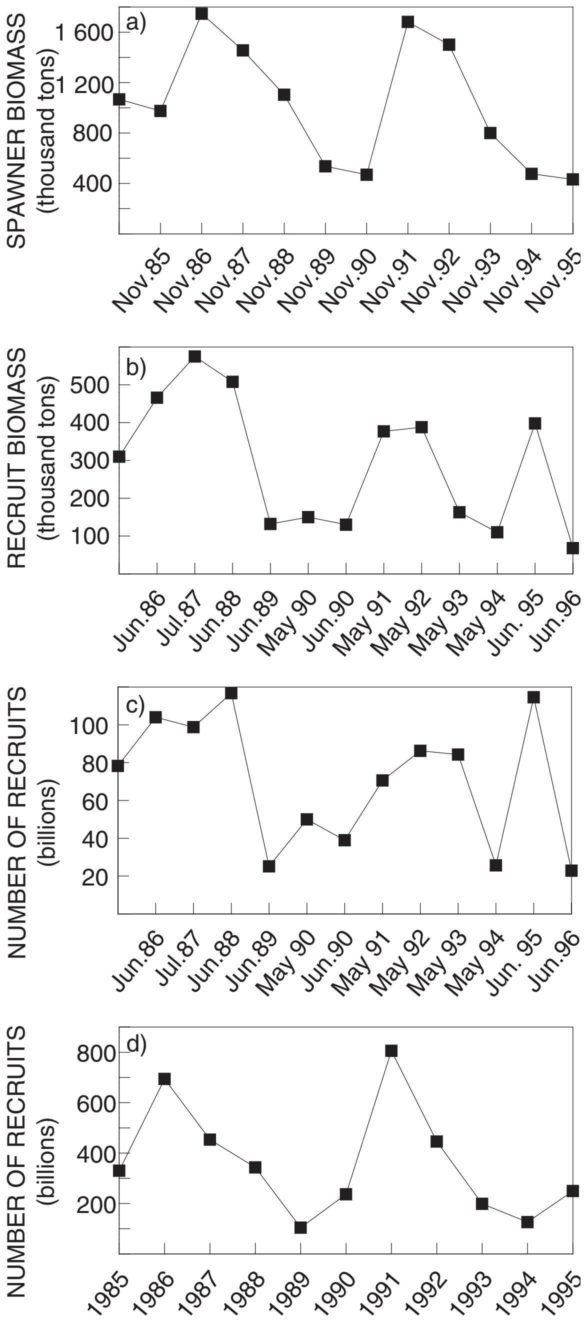

Fig. 3: Fluctuations in (a) spawner biomass, (b) recruitment biomass and (c) number of recruits from acoustic surveys (SF, unpublished data), and (d) numbers of recruits back-calculated from the estimation procedure, 1985–1996 (SF, unpublished data)

important seasonally and interannually, providing suitable food for spawning fish and optimal temperatures for egg development. Waldron *et al.* (1997) proposed that the spawner biomass of anchovy estimated in November was linked to the potential new production in the southern Benguela in the previous year (except in 1989), based on the links between temperature, nitrate, upwelling intensity and the changes in sea level, integrated over space and time. The relationship took the form of an "optimal environmental window" (Fig. 7). Boyd *et al.* (1998) developed linear relationships between south-easterly winds and numbers of anchovy recruits (Fig. 8), and oil yield and biomass of recruits (Fig. 9). All of these factors reflect conditions on the spawning, transport and nursery grounds, which are discussed below.

FACTORS ON THE SPAWNING GROUND

There are numerous links between the different factors measured each year on the western Agulhas Bank during November. For example, the number of eggs depends partially on the spawner biomass, there are inverse relationships between anchovy and copepod biomass, and atresia appears to track the percentage of starvation stations on the western Bank. Moreover, fish are in poorer condition (in terms of lipid content) on the western Bank than farther east or west, and food availability is minimum on the western Bank (Fig. 10). Clearly, there must be compelling reasons why spawning occurs at this particular location, in temperatures of 16–19°C.

The high atresia in November 1988 was reflected in the birthdate distribution the following June, few recruits being found with birthdates after December 1988 (Fig. 11). This is probably why the model of Bloomer *et al.* (1994) failed (Table I); there was no input regarding food availability or fish condition. Since then, food has never been as limiting on the western Bank, although atresia has increased in the period 1991–1994, following the proportion of starvation stations. Strong south-east winds (Boyd *et al.* 1998) and advective losses as a result of an Agulhas ring (Duncombe Rae *et al.* 1992) could also account for the reduced recruitment in 1988/9. Strong south-east winds in 1986 resulted in increased recruitment, but an intrusion of warm Agulhas water along the West Coast nursery grounds appeared to mitigate the effects of offshore winds. A similar anomaly on the Boyd *et al.* (1998) regression (Fig. 6) appears to have occurred in 1996/97, with strong south-east winds but good anchovy recruitment.

Another factor became apparent during a SARP cruise in January 1994, when very high gonad atresia

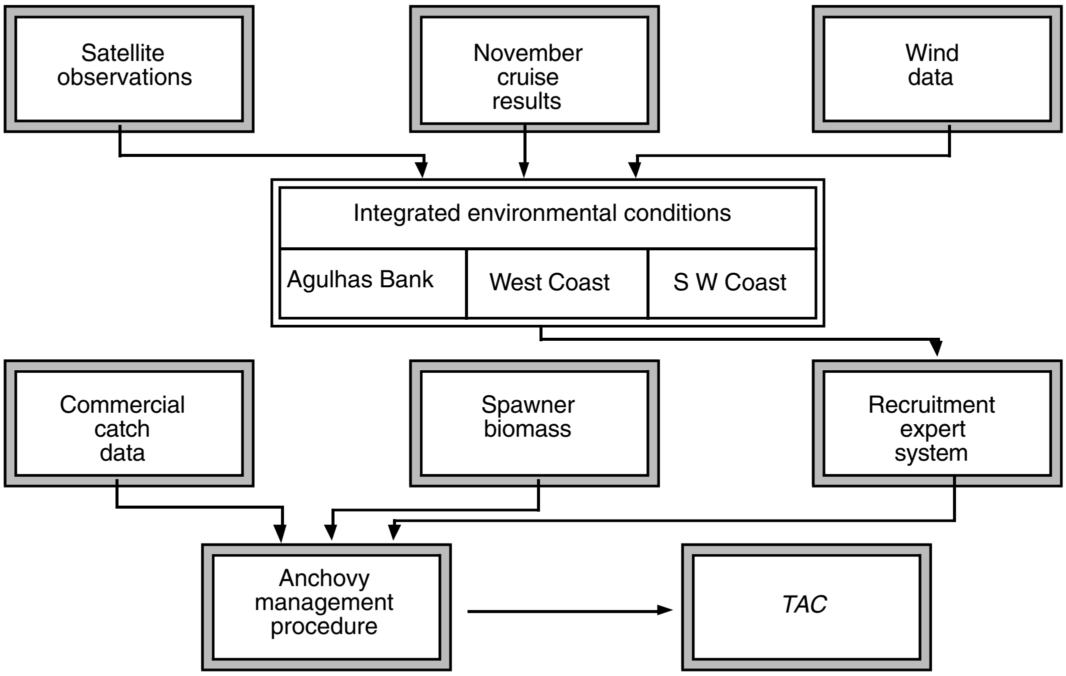

Fig. 4: A potential scheme for incorporating environmental and biological factors in an expert system into a management procedure (after Cochrane and Hutchings 1995

was observed in anchovy found in cool, inshore waters. Strong south-easterly winds blew between December 1993 and January 1994, resulting in vigorous upwelling inshore and offshore advection of warm surface water >20°C westwards from the central and eastern Agulhas Bank. The optimum temperatures for spawning of 16–19°C (Anders 1965, King 1977) were restricted to a very small volume of water (Richardson *et al.* 1998). This restricted spawning in 1994 to the early part of the season and may have contributed to the poor recruitment in 1994 (Figs 3, 11). This fact also emphasizes the point that November surveys are very restrictive in terms of their ability to predict subsequent recruitment. Richardson *et al.* (1998) showed that early summer is the most consistent period in terms of water stability and food availability on the western Bank, and that contraction of the spawning season diminishes recruitment strength (Figs 3, 11). This indicates a lack of a single critical period in defining the recruitment strength of a serially spawning population and implies that several factors are likely to play a role in regulating recruitment.

Older anchovy are more common east of Cape Agulhas, extending to the edge of the broadest part of the Agulhas Bank (Roel *et al.* 1994). Anchovy eggs east of Cape Agulhas are most abundant along the outer edge of the cool ridge (Swart and Largier 1987) which extends over the central and eastern Bank (Fig. 12d, e). A transport model based on ADCP-derived currents (Shannon *et al.* 1996, Boyd *et al.* 1998) indicates that such eggs could also enter the West Coast nursery

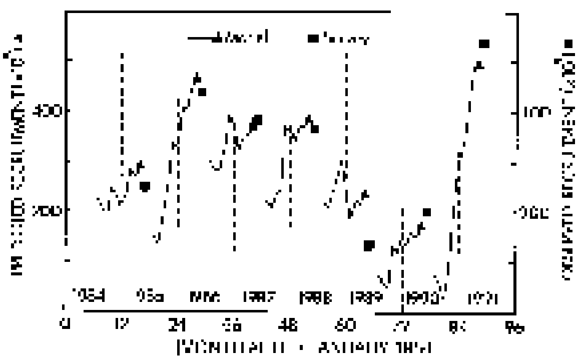

Fig. 5: Observed and predicted anchovy recruitment using the rule-based model of Bloomer *et al.* (1994)

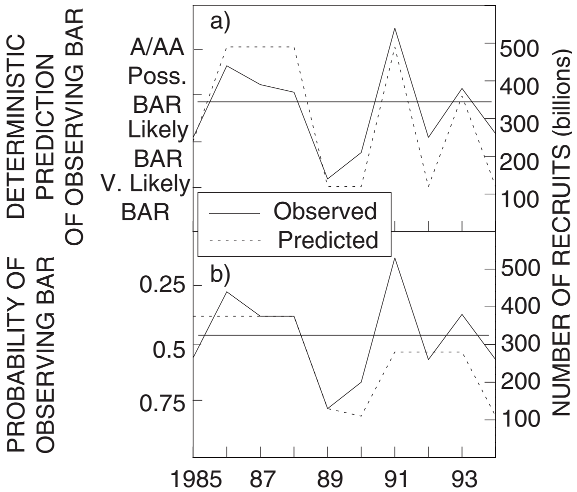

Fig. 6: Observed and predicted results using (a) the deterministic and (b) the probabilistic expert systems (after Korrûbel 1995). BAR = below average recruitment; A/AA = average/above average

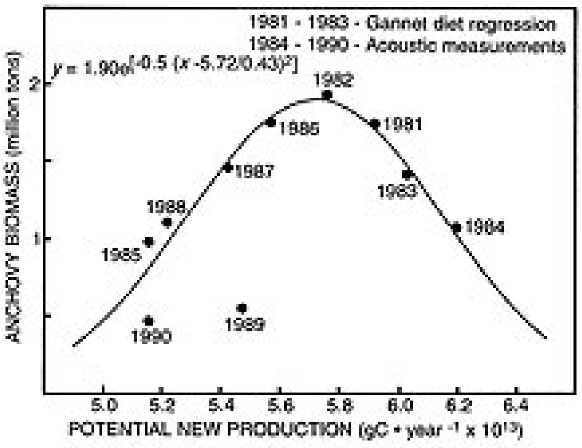

Fig. 7: The "optimal environmental window" relationship between end-of-year anchovy spawner biomass and the potential annual production on the West Coast, 1981–1990 (after Waldron *et al.* 1997)

grounds, but they are also likely to suffer losses offshore when the Agulhas Current intrudes onto the spawning grounds and eggs and larvae are swept off the Bank in the current. The eggs and larvae may also be heavily cannibalized by the bulk of the spawning population of anchovy which occupies the western Bank. The role of the spawning grounds on the eastern Bank are unclear, although it is notable that the good recruitment in 1990/91 was only partially observed on the West Coast recruitment surveys of May 1991 (Fig. 3), the biomass and numbers being average only. However, the results of the November 1991 survey and back-calculation (Fig. 3) indicated that recruitment was in fact the highest recorded. As the West Coast anchovy were not fast-growing in 1991 (Waldron 1995), it would appear that the only feasible explanation for the high adult biomass in November 1991 was good survivorship of recruits on the South Coast, east of the recruitment survey. There was an apparent shift towards a greater proportion of anchovy spawners east of Cape Agulhas in the early 1990s (Roel *et al*. 1994). This would violate the assumption that the western Agulhas Bank is the most important spawning ground for anchovy, requiring a broadening of the monitoring programmes to provide information for the expert system. In addition, there seems to have been an offshore shift in the distribution of anchovy eggs (and hence spawners) on the western Agulhas Bank in the 1990s (Fig. 12d, e), particularly when compared with the distribution in 1966/67 (Fig. 12a), 1967/68 (Fig. 12b) and 1977/78 (Fig. 12c). This would increase the risk of offshore losses of eggs during periods of south-east winds, or the close proximity of Agulhas rings or filaments to the spawning grounds.

In 1995/6, the monthly SARP cruises were replaced with weekly sampling across the frontal jet off the Cape Peninsula, in an attempt to monitor the short-term changes in spawning success on the western Agulhas Bank (Huggett *et al*. 1998). Results from those surveys indicated a very narrow window of spawning success on the western Agulhas Bank in November 1995, with few larvae being caught in late January/February. This very restricted period appears to have resulted in extremely poor recruitment, as estimated from the acoustic surveys in June and November 1996, when both numbers and biomass of recruits and spawners were the lowest of the entire time-series. However, the small size of the recruits suggests either a preliminary birthdate distribution a little later than November, at around December–January, or slow growth during the pre-recruit phase. This conclusion depends on the growth rate, which has yet to be deduced from analysis of daily age. These results suggest that the approach of Korrûbel *et al.* (1998), using results from a single cruise in November, need to be extended in time. A similar expert system was developed for the monthly SARP cruises of 1994–96 by Painting and Korrûbel (1998).

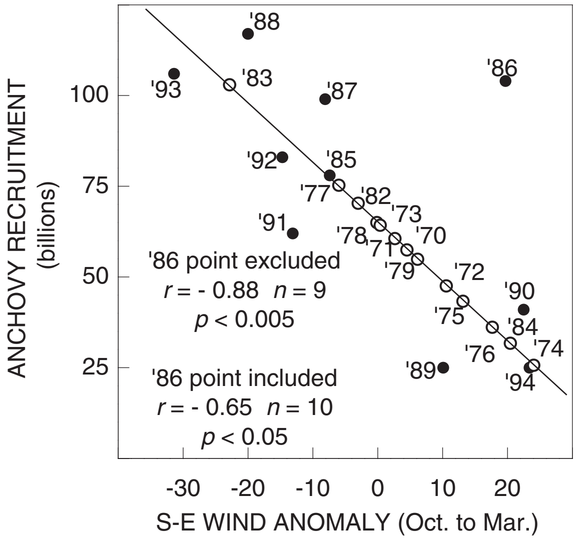

Fig. 8: Relationship between anchovy recruitment numbers and the south-east wind anomaly at Cape Point. The regression line is estimated from data for the period 1985–94 (after Boyd *et al.* 1998). The south-easterly wind anomaly data points for the period 1970–1984 are plotted on the regression line to indicate that, for most of the 1970s, those winds were much stronger than during the period 1985–1994. Closed circles denote wind and recruitment measurements and open circles denote wind only measurements

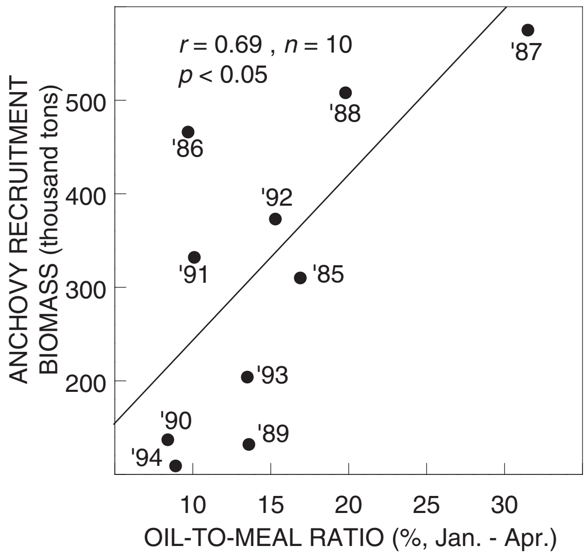

Fig. 9: Relationship between anchovy recruitment biomass (tons) and the oil-to-meal ratio (%) between January and April (after Boyd *et al.* 1998)

TRANSPORT AREA

ENSO events in the Pacific are mirrored by a decreased frequency in south-easterly winds at Cape Point during the same year, reflected in deviations from the mean (Fig. 13). Negative correlations between south-easterly winds and anchovy recruitment success, in terms of numbers of recruits on the West Coast, indicate that such winds were not conducive to good recruitment during the 1980s and 1990s (Fig. 8). Advective losses were greatest during years of strong south-easterly winds. Further, excessive turbulence may disrupt food aggregations, resulting in loss of numbers of anchovy larvae. However, if south-easterly wind anomalies for the 1970s are plotted on the same regression (see Fig. 8), it appears that anchovy recruitment should have been low throughout the 1970s. The available indicators suggest high biomass of anchovy during the 1970s. Virtual Population Analysis (VPA) estimates, based on anchovy catches on the West Coast, and the incidence of predator abundance and predator diet (Fig. 14), indicated high biomass of anchovy in the period 1973–1978, when south-easterly winds were generally stronger than in the 1980s. This suggests that anchovy response to wind has altered over the decades. It is possible that the shift offshore in the distribution of anchovy eggs on the western Agulhas Bank in the 1980s resulted in the eggs and larvae becoming more vulnerable to offshore losses when south-easterly winds are strong.

During the period 1985–88, the distribution of anchovy spawners and eggs extended well up the West Coast to latitude 32°S (Hampton 1992), short-circuiting the frontal jet transport entirely. There was good recruitment in those years, indicating that losses during the transport phase may be significant when the spawner population is restricted to the Agulhas Bank.

THE NURSERY GROUNDS

In May 1993, there were relatively high numbers of anchovy recruits (Fig. 3), but the mean mass was substantially below the mean value, indicating very late recruitment, with most fish born in December 1992 (Fig. 11). Subsequent enhancement of the spawner

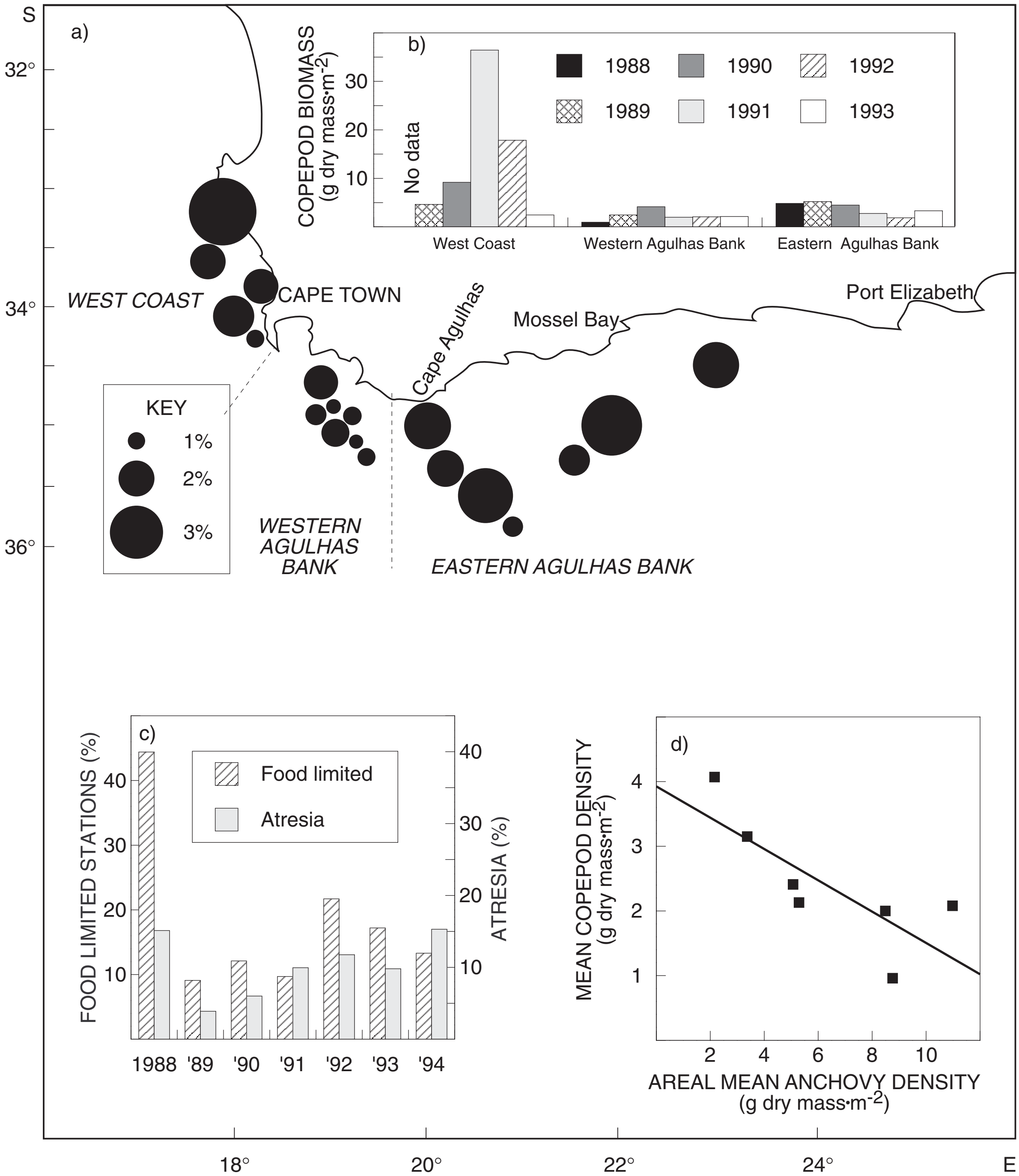

Fig. 10: (a) Spatial distribution of anchovy condition (% lipid in the whole fish) during November 1994; (b) copepod density measured during November 1988–1993 on the West Coast and Agulhas Bank, indicating lowest biomass on the western Agulhas Bank; (c) time-series of the starvation index and percentage of female anchovy sampled with oocyte atresia, 1988–1994; (d) linear regression of mean copepod density against mean anchovy density on the western Agulhas Bank (after Sea Fisheries 1995)

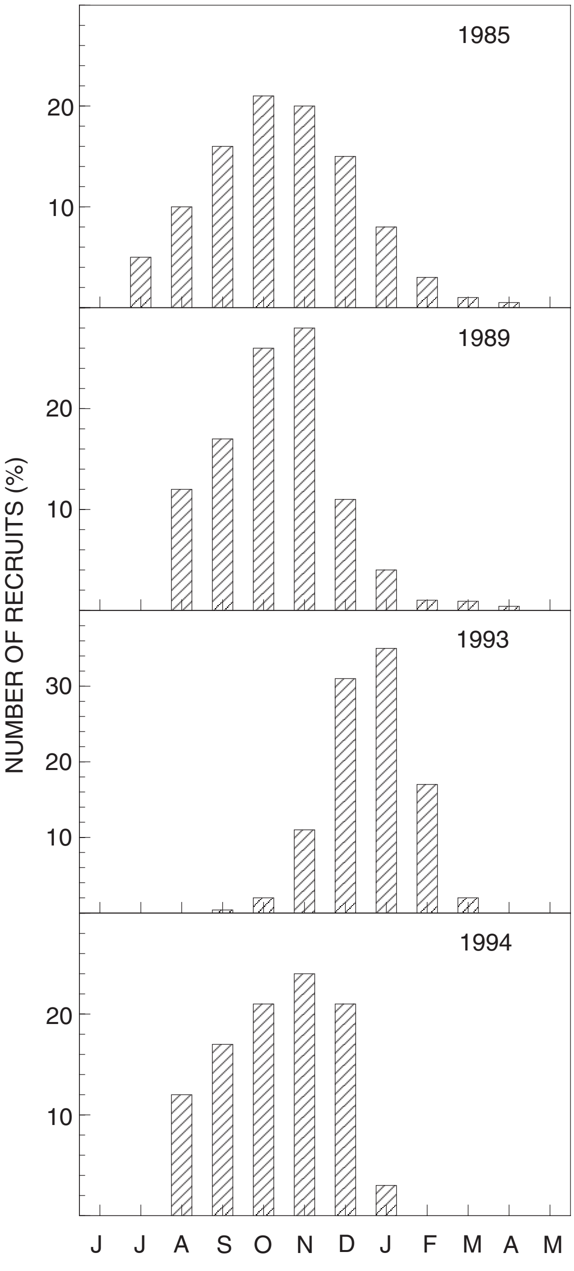

Fig. 11: Anchovy birthdate distributions for four different years, showing normal (1985), early (1989, 1994) and late (1993) recruitment (SF, unpublished data)

population in November was considerably reduced (Fig. 3), indicating higher mortality of juveniles than normal. Similarly, in June 1995, very high numbers and biomass of recruits did not yield high spawner biomass, which continued to decrease from 1993 to 1995. These events suggest that: (i) there were higher rates of predation/mortality and/or slower growth in late winter/spring than in autumn/early winter; (ii) mortality in 1995 was considerably higher than normal.

None of the approaches suggested in Table I utilize any information on predation or growth in the nursery grounds. Environmental events in the northern Benguela may provide a clue. In 1994, severe oxygen depletion was widespread in coastal waters off Namibia, resulting in the death and/or displacement of gobies *Sufflogobius bibarbatus* and hake *Merluccius capensis,* and the death of seal pups (Hamukuaya *et al.* 1998). In 1995, an intrusion of warm water from Angola resulted in catastrophic declines in the numbers of sardine and some associated predators. Snoek *Thyrsites atun* is a large predatory fish whose abundance appears to alternate in the southern and northern Benguela (Fig. 15). Poor feeding conditions in Namibia may have resulted in a shift of predators southwards, increasing snoek abundance in the southern Benguela. While it is extremely difficult to account for predation mortality quantitatively, interannual variability in natural mortality may be an important factor in determining recruitment to the spawner biomass at the end of each year. Such is the case when spawning is delayed during summer, resulting in recruits passing through the nursery grounds later in winter than normal.

The adult anchovy that migrate to the West Coast after spawning are caught by the purse-seine fishery between January and April, before the young recruits appear. The oil yield (oil-to-meal ratio) early in the fishing season is an indication of the feeding conditions that the fish are experiencing on the West Coast. It is assumed that good feeding conditions for adult fish also reflect good conditions for pre-recruit and juvenile fish. The positive regression between oil yield of adult fish caught on the West Coast early in the year and recruitment strength in terms of biomass estimated acoustically each year (Fig. 9, Schülein *et al.* 1995) indicates that good feeding conditions on the West Coast may also play a role in increasing recruitment. This suggestion is corroborated partially by the distance offshore of the 16°C isotherm off the West Coast, which is a measure of the extent of cool productive water. However, low oil yields in 1990 were followed by the highest recruitment measured (Fig. 3), reducing the value of this relationship. This discrepancy could be partially explained if the 1991 recruitment has been mostly on the central and eastern Agulhas Bank. In addition, changes in species dominance, the proportion canned, the relative size of the same species caught and the freshness of the catch have made interpretation of trends in oil yield difficult. Although the index of oil yield is derived too late in the year (April) to play a useful role in predicting recruitment, it is a useful indicator of events in hindsight. The gradual reduction

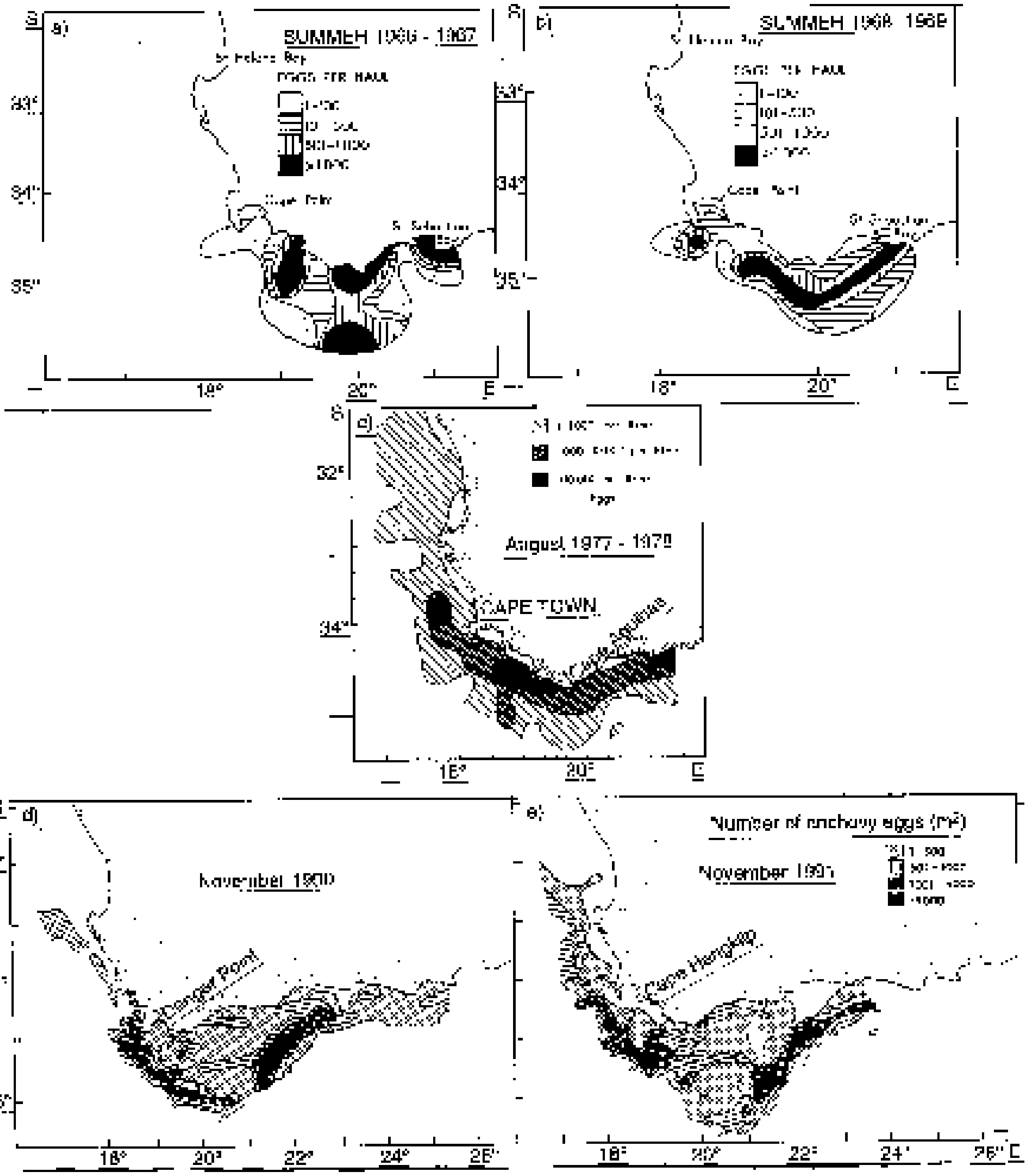

Fig. 12: Horizontal distribution of anchovy eggs; (a, b) during summer 1966–1969 (after Crawford 1981); (c) cumulative distribution during 1977/78 (after Shannon *et al.* 1984); (d, e) during November of 1990 and 1991 (after Hampton 1992)

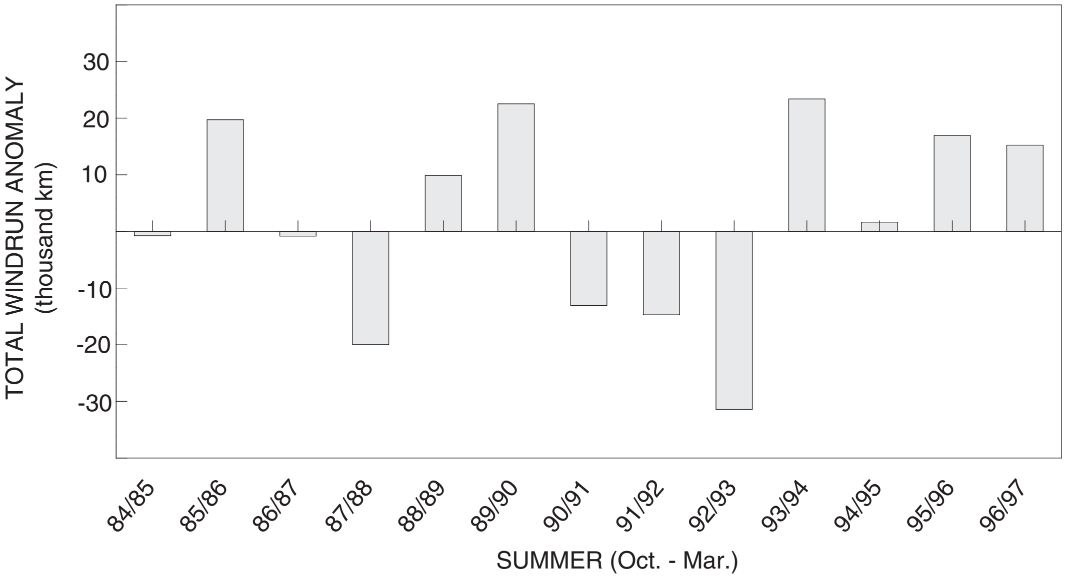

Fig. 13: Summer (October–March) south-east windrun anomalies, 1984/85–1996/97 (after Boyd *et al.* 1998)

in oil-to-meal ratios over the past three decades has been corroborated independently for both anchovy and sardine using length-mass condition factors (Van der Lingen *et al.* in prep). This suggests that feeding conditions for pelagic fish have been worsening over the period 1970–1996 in the southern Benguela. Conflicting evidence of a significant increase in copepod abundance in the St Helena Bay region over the past four decades (Verheye *et al.* 1998) requires further investigation.

REGIME SHIFTS

Bakun (1990) has documented increased upwelling intensity worldwide as a consequence of global warming. Large-scale pressure gradient changes in the South Atlantic suggest similar events in the Benguela (Shannon *et al*. 1992), although shore-based wind measurements at Cape Point and Cape Columbine do not show the same trends. Although ENSO events result in decreased south-easterly winds south of 33°S (Cape Columbine), winds are increasingly southerly north of this region (Walker *et al.* 1984). As the distribution of adult anchovy is centred south of Cape Columbine, it is difficult to utilize trends in the northern limits of the habitat to explain events to the south. Nevertheless, both anchovy and sardine spawn principally in the restricted area of the western Agulhas Bank. Any long-term increase in offshore losses is likely to influence fish survival detrimentally.

Since the major perturbation in the environment in 1982/83, sardine appear to have gained steadily in population strength (Fig. 1), whereas anchovy have displayed two cycles of sharp increases and declines, culminating in three years of low recruitment relative to spawner biomass (Fig. 3). Sardine have occupied the inner regions of the western Agulhas Bank, where they spawn over a more protracted period than anchovy, from late winter (August) to autumn (April). Therefore, they are likely to be more resilient than anchovy to offshore advective losses caused by strong south-easterly winds in midsummer. In addition, they may predate heavily on anchovy eggs while filter-feeding (Valdes-Szeinfeld and Cochrane 1992), their dominant mode of acquiring food. They also consume large quantities of copepods eggs and nauplii, which would reduce the numbers of large copepods, the preferred prey of adult anchovy. These factors may partly explain the offshore distribution of anchovy eggs in the 1980s and 1990s compared to that in the late 1960s and 1970s, when sardine were not abundant. Years of good anchovy recruitment should theoretically lessen the fishing mortality inflicted on juvenile sardine, although the revised management procedure introduced in 1994 allows increased bycatch of juvenile sardine when anchovy recruitment is good. This was

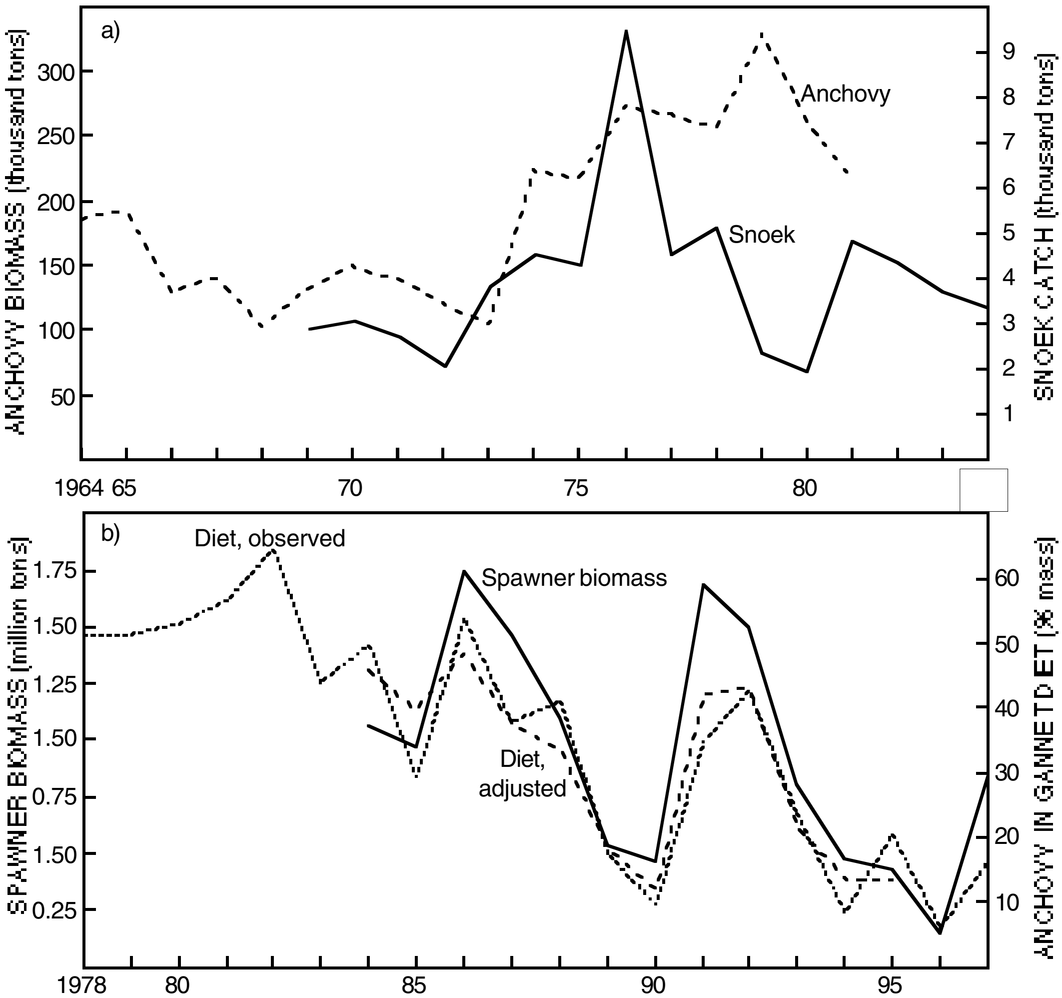

Fig. 14: (a) VPA estimates of the anchovy population, 1964–1981, and catches of handlined snoek *Thyrsites atun,*1969–1984 (after Crawford *et al.* 1987); (b) acoustic estimate of spawner biomass, 1984–1997, and the diet of Cape gannet as a percentage of anchovy by mass, 1978–1997 (after Crawford and Dyer 1995)

not the case in the mid-1980s when sardine biomass was increasing steadily. Of further interest is the pattern of fishing in the 1950s, when sardine dominated the pelagic catches. Most of the catch then was adult fish >20 cm long, taken within the St Helena Bay area mainly between March and July each year. That is currently the peak period of anchovy recruitment within St Helena Bay, and it is difficult to envisage large populations of juvenile anchovy and adult sardine cohabiting the area simultaneously. This may be a further factor in ensuring that a switch from anchovy to sardine will be sustained. However, despite the increase in size of the sardine population, adults have not re-occupied the inshore West Coast niche to any great extent, but have increased their densities farther east, particularly on the eastern Agulhas Bank.

CONCLUSION

Events within all of the spawning, transport and

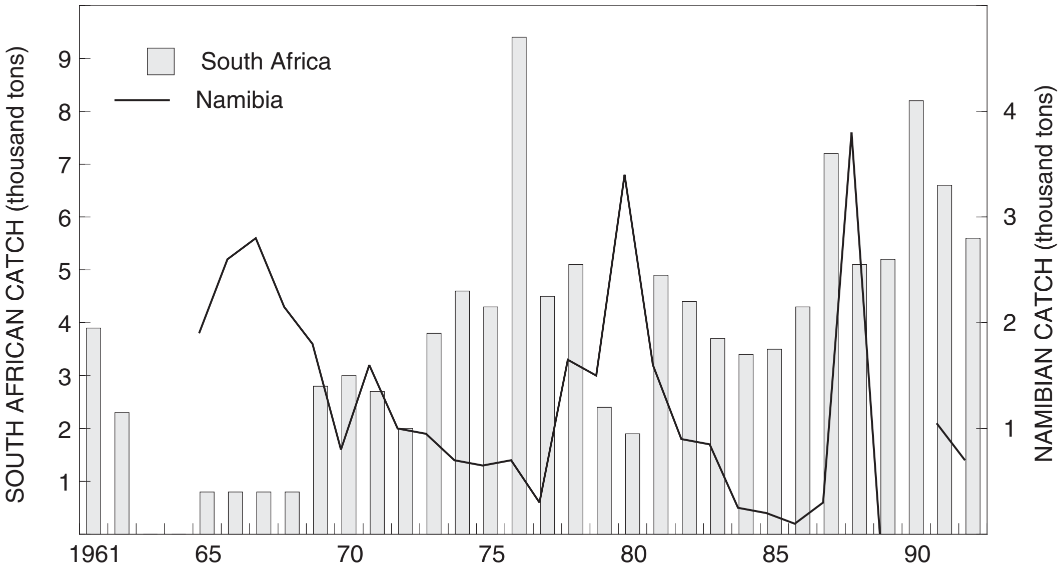

Fig. 15: South African and Namibian catches of handlined snoek, 1961–1992 (modified after Crawford *et al.* 1995)

nursery areas of anchovy appear to have contributed to the recruitment strength to both the fishery and the spawning population over the past 13 years. In any one year, several plausible, but different, factors appear to operate, making it difficult to generalize and to design a simple monitoring programme that will supply the information necessary to predict recruitment strength with sufficient certainty. Lasker (1985) pointed to the multiplicity of factors that can affect recruitment strength. The original comprehensive list of some 20 environmental and biological factors that have been monitored during research cruises in the past has been reduced to four or five, but it has proven necessary to invoke additional factors, such as the duration of the spawning season, the extent of 16–19°C water on the western Agulhas Bank and predator abundance.

At present, funding and manpower constraints do not allow adequate monitoring of these extra parameters. The change in relative species dominance from anchovy to sardine is an additional complication. The spawning habitat and season of sardine are considerably larger and longer than for anchovy, and length frequencies of sardine recruits suggest multiple within-season spawning successes and failures. Prediction of recruitment strength of sardine is less pressing, in terms of the directed catch, which targets 2–3 year-old fish, but it is necessary for managing the bycatch in mixed shoals of juveniles of both species.

A large number of potentially limiting factors may help explain why recruitment is relatively invariant in the southern Benguela, where the potential for order-of-magnitude changes must exist, yet four to five fold variation is the maximum observed (except in 1996). However, even a two fold variation is important in terms of yields, and if predicting recruitment is to continue to be an objective, comprehensive monitoring programmes are required. The expert system approach is flexible in that it does not require that all variables be measured every year, but some judgement has to be made as to which ones are likely to be operating in any particular year. The approach should be developed further and vigorous attempts made to utilize newer (and cheaper) technology to monitor proxy variables such as SST and ocean colour from satellites, zooplankton numbers and size from optical counters, and fish egg counts from continuous surveys in particular regions, at space- and time-scales appropriate to both the short-term changes in upwelling frequency and the seasonal scale of the spawning season.

The prognosis for forecasting appears positive in the southern Benguela, where mechanisms affecting recruitment processes are quite well understood. Whereas the cost of monitoring is considerably high, simulation studies (Cochrane and Starfield 1992) indicate a cost-efficient improvement in average yield if predictions are correct 70% of the time. Better predictability of recruitment six months ahead of time also benefits the pelagic fishing industry in terms of operational logistics of factories and fleets, and in terms of forward sales of meal and oil.

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