The role of ichthyoplankton surveys in recruitment research and management of South African anchovy and sardine

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Abstract

Anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* are ecologically and economically important components of the southern Benguela upwelling ecosystem situated off the west coast of South Africa. The importance of these species has resulted in substantial research effort directed towards understanding their population dynamics, with much of this effort going into ichthyoplankton surveys. This review describes the methodologies used and results obtained from ichthyoplankton surveys conducted off South Africa during the past 50 years. This research has allowed the development of a detailed knowledge of the life history cycles of small pelagic species in the southern Benguela, particularly that of anchovy. Spatially distinct spawning and nursery areas have been identified, highlighting the critical influence that transport of eggs and early larvae from the spawning to nursery grounds has on subsequent recruitment strength. Temporal changes in the location of spawning habitat of both anchovy and sardine have been tracked, and environmental parameters characterizing spawning habitat differentiated. Frequent monitoring of early life history stages in the transport region shows promise as a predictor of recruitment success for anchovy but not necessarily sardine, although this predictor is not yet formally incorporated into management procedures. Insights gained from ichthyoplankton surveys have been used to develop individual-based models (IBMs) coupled with a 3D hydrodynamic model of the region; these have allowed the testing of various hypotheses concerning transport success and various physical and biological parameters through experimental simulation. Ichthyoplankton survey data have been used for stock management by application of the DEPM to estimate anchovy spawner biomass from 1986-1993; these absolute estimates were then used to calibrate relative estimates of anchovy biomass made using hydroacoustic methods. These examples demonstrate that ichthyoplankton surveys of anchovy and sardine are widely used off South Africa and have made a substantial contribution toward identifying key mechanisms impacting on recruitment success and hence management of these small pelagic species.

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Introduction

The oceanography off South Africa is dominated by two major current systems, the poleward flowing, warm Agulhas current off the east and south coasts, and the equatorward flowing, cool Benguela current off the west coast (Fig. 1). These current systems clearly influence the species diversity of the marine ecosystems in this region; the east and south coasts range from subtropical to warm temperate marine systems with a high diversity of fish species and a low productivity, whereas the west coast is characterized by a cool temperate upwelling system with relatively few fish species and a high productivity. This upwelling system is known as the southern Benguela, and is separated from the northern Benguela off Namibia by a perennial cell of intense upwelling off Lüderitz (26-27.5°S). The Benguela is one of the world's major eastern boundary upwelling

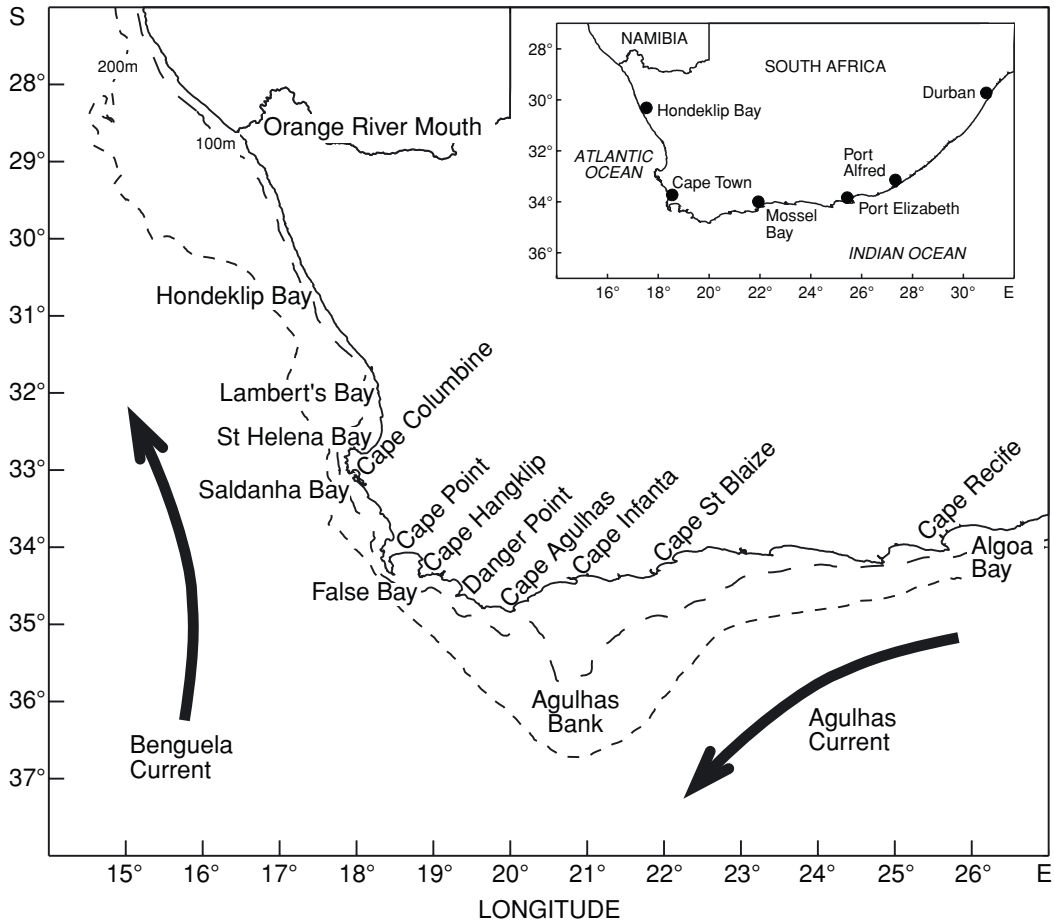

***Figure 1**: Map of southern Africa showing the continental shelf (the 100 m and 200 m isobaths are shown), the Agulhas and Benguela current systems, and places mentioned in the text.*

systems; in the southern Benguela intense coastal upwelling occurs from late spring (September to November) to early autumn (March to May). Detailed reviews of various aspects of the Benguela upwelling system may be found in Shannon (1985), Chapman and Shannon (1985), Shannon and Pillar (1986), and Crawford et al. (1987).

Like other upwelling systems (Schwartzlose et al. 1999), the southern Benguela supports large populations of small pelagic fish, principally anchovy *Engraulis encrasicolus* (formerly known as *E. capensis*; Grant and Bowen 1998) and sardine *Sardinops sagax*. These fish are small schooling species that occur in the upper water layers and are found primarily over the continental shelf. Both species are important prey items for fish, birds and marine mammals (Cury et al. 2000).

These large populations of small pelagic fish support a substantial fishery, South Africa's largest in terms of annual landings and the second-most valuable. Purse-seine fishing for sardine off South Africa commenced in the 1930s (Beckley and van der Lingen 1999), but only became commercial in 1943 following the war-time demand for canned fish (Crawford 1981a). The fishing industry expanded rapidly over the next few years and was landing 50-100 000 tons of fish annually during the late 1940s. Over the past 50 years the pelagic fishery has made large catches averaging around 300 000t annually (Fig. 2a). Sardine dominated the catches initially, but overfishing of this population in the early 1960s led to a stock collapse and the fishery changed to smaller-meshed nets in 1964 to target the smaller anchovy. Anchovy have dominated catches since, but catches of sardine have increased steadily since 1990. The fishery is located off the west and southwest coasts, with anchovy caught inshore, principally in St Helena Bay, whereas sardine are caught farther offshore and over a greater geographical range than anchovy (Fig. 2b). Most of the anchovy caught are less than one year old, and are reduced to fish meal and oil in industrial scale factories. Adult sardine are canned or frozen for human consumption in addition to being packed for bait; juvenile sardine that shoal together with anchovy are taken as bycatch in the anchovy fishery.

Hydroacoustic surveys to estimate the population size of anchovy and sardine have been conducted off South Africa since 1984 (Hampton 1987, 1992; Barange et al. 1999). Anchovy recruitment has been moderately variable over most of the time series, with consequent inter-annual fluctuations in stock size, but has been exceptionally strong since 2000 (Fig. 3). Sardine recruitment has also been variable, but has shown an increasing trend that has resulted in a steady growth of the sardine stock. The commercial importance of anchovy and sardine off South Africa, and the difficulties in managing stocks prone to such interannual variability in population size, has led to substantial research effort being directed towards these species, including a variety of ichthyoplankton surveys.

This review describes the methodologies used and results obtained from ichthyoplankton surveys conducted off South Africa over the past 50 years (see Table 1). The consequent increased knowledge of life history strategies of pelagic fish off South Africa, how this has improved understanding of recruitment variability, and examples of how survey data have been incorporated into methodologies attempting to predict pelagic fish recruitment strength or used directly for management, are discussed. Finally, the incorporation of ichthyoplankton survey data into individual-based models (IBMs) that encapsulate the understanding of the physical and biological processes impacting on recruitment variability, is described.

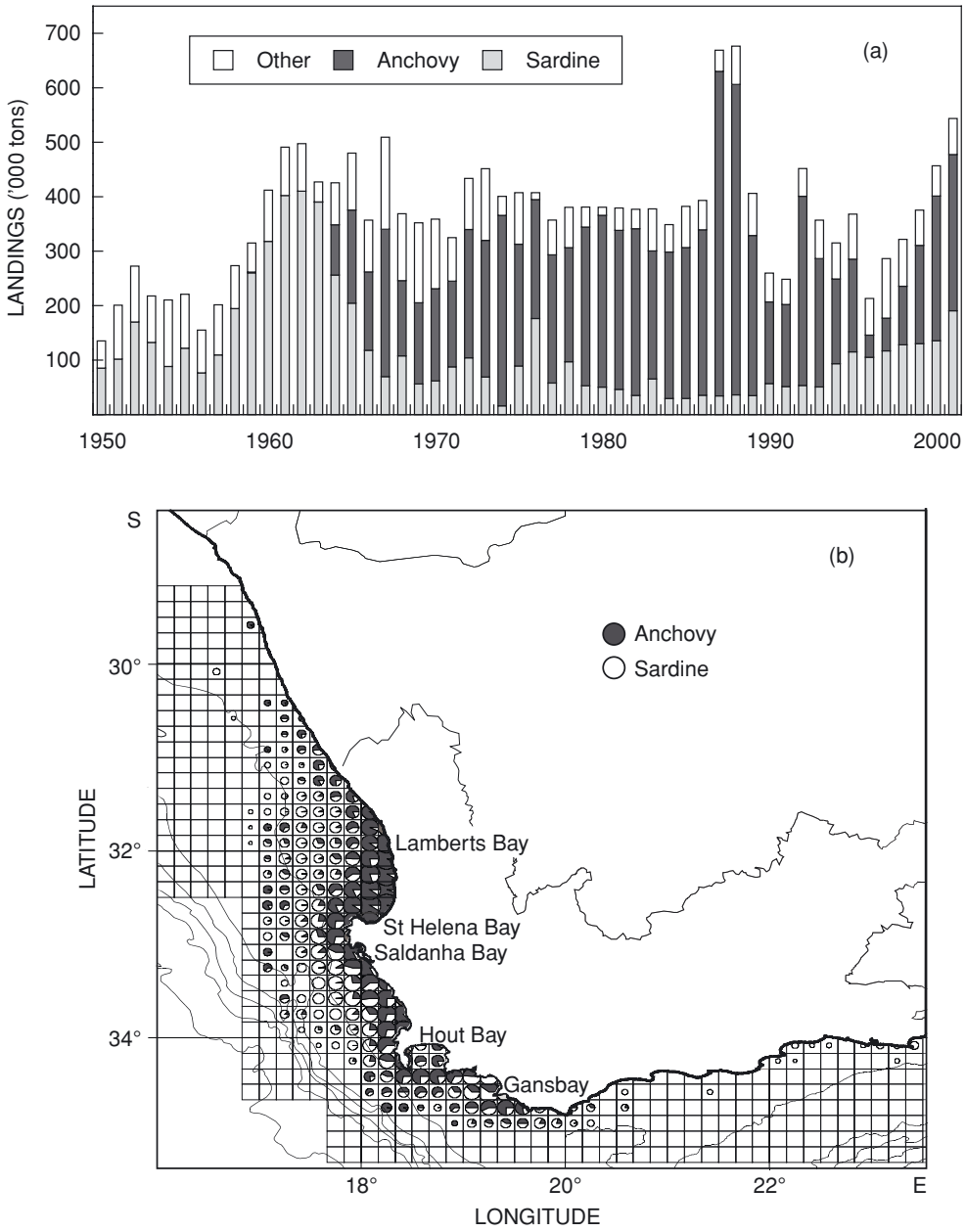

Figure 2: *(a) Time-series of annual landings of anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*) and other species (primarily round herring* Etrumeus whiteheadi *and Cape horse mackerel* Trachurus trachurus capensis*) made by South Africa's pelagic fishery, 1950-2001 (from Marine and Coastal Management, unpublished data). (b) Output from ArcView GIS showing anchovy and sardine catches by area (10' by 10'block) over the period 1987-1998. Circle size is proportional to average catch size, and landing sites are indicated (courtesy of L. Drapeau, IDYLE, IRD, Cape Town).*

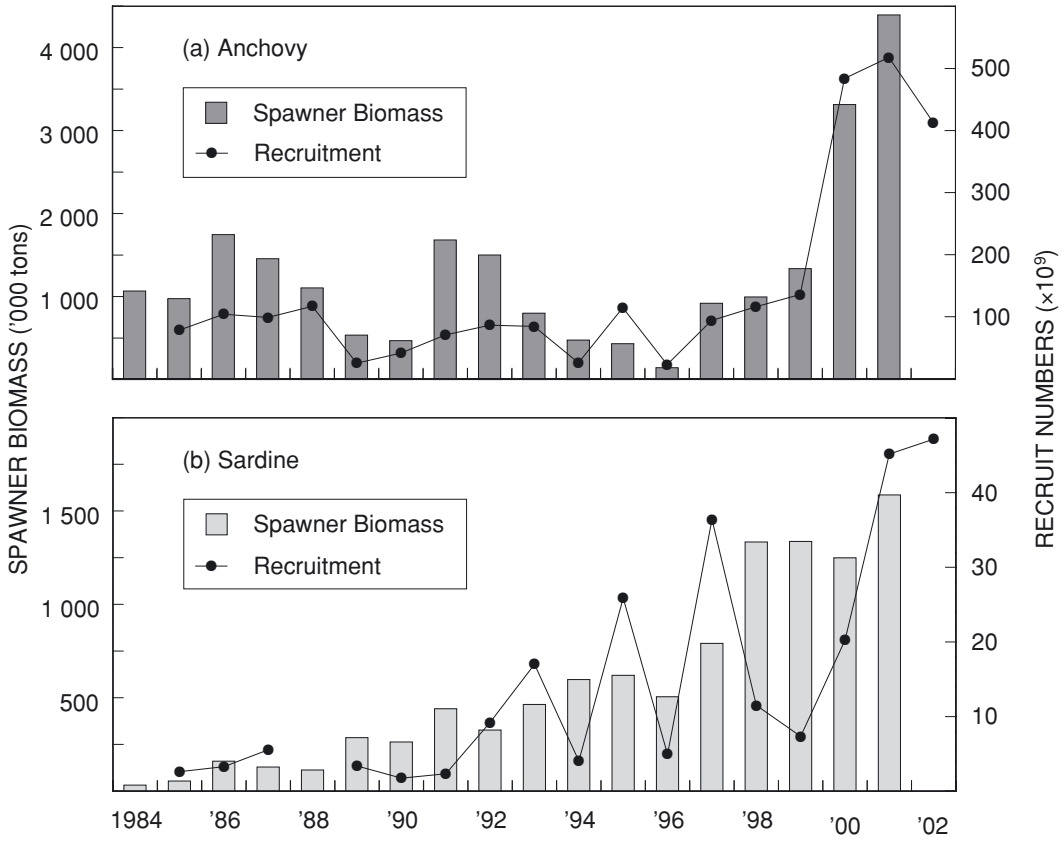

Figure 3: *Time-series of spawner biomass and recruitment strength (numbers of 0+ fish) of anchovy and sardine off South Africa derived from hydroacoustic surveys, 1984-2002 (updated from Barange et al. 1999).*

Early ichthyoplankton surveys. The rapid expansion of purse seine fishing for pelagic species during the 1940s prompted the introduction of a variety of research programmes, and in 1950 a sampling programme was initiated to locate the major spawning areas of sardine. A further aim was to determine both the extent of spawning and the survival of the larvae, with a view to forecasting future commercial catches (Davies 1954; de Jager 1954). From 1950-1953 the survey area comprised a small grid of stations off the west coast that were sampled monthly (Table 1). This sampling grid was gradually extended farther offshore and along the south coast (see Fig. 4). By 1960 a total of 80 stations over 16 lines between Lamberts Bay and St Sebastian Bay were being sampled quarterly, this sampling programme continuing until 1967. In 1964 sampling for the smaller, elliptical anchovy eggs was initiated, using a finer mesh net in conjunction with the coarser mesh used for sampling sardine eggs (Table 1).

The earliest surveys (1950-1953) showed dense concentrations of sardine eggs in the nearshore region (<20 miles) during early summer (Davies 1956). Extension of the survey grid between 1953

Table 1: Comparison of temporal and spatial coverage, sampling gear and tow profiles for ichthyoplankton surveys conducted off the coast of South Africa from 1950 to present.

Survey Programme	Period and frequency	Spatial coverage	Gear used	Tow profile	Reference
Early surveys	March 1950 – April 1969 (monthly). East coast: several cruises during 1951-1969; Jan, Jul, Aug & Dec 1973.	West and South-west coasts. Initially Lamberts Bay to Saldanha Bay, extended to Quoin Point in 1959, and to Cape Infanta in 1961 (80 stations). East coast: Algoa Bay to Tugela.	N100 net (950µm mesh; 100cm diameter; 0.78m^2 area). From 1964: N100/70 net (200µm mesh; 100cm diameter; 0.78m^2 area).	Horizontal tow (N100H) at surface for 10 mins; vertical haul (N70V) from 100-0m; oblique haul (N100B) from 150-0m.	Davies (1954, 1956); Anders (1965, 1975); King and Robertson (1973).
Drogue survey	October 1976 (68 hours).	10 stations off Cape Peninsula.	Array of 8 Miller nets (300µm mesh; 14.5cm diameter; 0.017m^2 area).	Horizontal tows (60 minutes at 3 knots); vertically stratified sampling from 85-0m.	Shelton and Hutchings (1981, 1982).
Cape Egg and Larval Programme (CELP)	August 1977 – August 1978 (monthly).	120 stations on West and South-west coasts extending 50 nm offshore.	Bongo (300µm mesh; 57cm diameter; 0.5m^2 area).	Double-oblique tows from 0-100m.	King and Robertson (1973); Shelton (1986); Shelton and Hutchings (1990).
Spawner Biomass surveys	November/ December 1984 onwards (annually).	~300 stations on West and South coasts, from Hondeklip Bay to Port Alfred.	CalVET net (300µm mesh; 25cm diameter; 0.05m^2 mouth area).	Vertical haul from 200-0m (earlier surveys) or 100-0m (recent surveys).	Armstrong et al. (1988); van der Lingen et al. (2001).
East coast larval surveys	May/June 1990, October 1990, February 1991.	36 stations from Algoa Bay to Tugela.	Bongo (500µm mesh; 57cm diameter; 0.5m^2 area).	Stepped oblique tows from 80-0m; 10 min tows; 5m spans.	Beckley and Hewitson (1994).
South African SARP	August 1993 – March 1994; September 1994 – March 1995 (monthly).	17-189 stations on West and Southwest coasts (Olifants River to Cape Agulhas).	CalVET net (as above) for eggs; Paired-bongo net (300µm mesh; 57cm diameter; 0.5m^2 area) for larvae.	CalVET: vertical haul from 70-0m. Bongo: oblique haul from 70-0m.	Fowler and Boyd (1998); Painting et al. (1998).
SARP Monitoring Line	August 1995 onwards (~ bimonthly).	12-20 stations, 3 n miles apart, off Cape Peninsula.	Paired mini-bongo net (200 and 300µm; 18cm diameter; 0.025m^2 area).	Oblique haul from 70-0m.	Huggett et al. (1998); Huggett (2002).
Pre-recruit surveys	March 1991 onwards (annually).	West coast (usually Orange River to Cape Point).	Methot frame trawl (5mm mesh; 0.9mm codend; 5m^2 area).	Stepped, oblique hauls from 35-0m.	Methot (1986); O'Toole and Crous (1989).

and 1961 revealed the occurrence of eggs up to 50 n.miles offshore of Cape Columbine, as well as high concentrations off Saldanha Bay and on the south coast.

Between 1961 and 1963 two main foci of sardine spawning were identified, one near Cape Columbine, and one between Cape Point and Danger Point (Crawford 1981a). From 1963 to 1967, sardine spawning activity declined off the west coast, coincident with the disappearance of adults in this region, but spawning was still evident on the south coast as far east as Cape Agulhas (Fig. 4a,b). This shift in spawning was thought to have resulted either from the disappearance of the west coast spawning population, had two separate populations previously existed, or else, a southward contraction of the range of adult sardine. Between 1951 and 1967 most sardine spawning took place between September and February (Crawford 1981a), with greatest densities of sardine eggs encountered during January and February, declining thereafter until June or August when egg production began to rise again (Fig. 4e). Most sardine eggs were collected at temperatures between 15 and 18 °C, with few eggs encountered at temperatures colder than 12 °C or warmer than 23 °C (Fowler et al. 1996).

Following the switch to smaller meshed sampling nets, anchovy eggs were found to be concentrated on the south coast between Cape Point and Cape Infanta, with few eggs collected on the west coast. Greatest concentrations of eggs occurred between Cape Point and Cape Agulhas (Fig. 4c,d) and were associated with relatively warm waters (Crawford 1981b). The absence of anchovy eggs off the west coast was considered to be a result of their low tolerance to cold water, anchovy eggs having a lower lethal limit of 14°C as opposed to 13°C for sardine (King et al. 1978). Anchovy spawning was most intense during early summer (November/December; Fig. 4f), declining rapidly with the advent of autumn (Anders 1965; Crawford 1981b).

Cape Point drogue study. Oceanographic studies conducted during the late 1960s and early 1970s indicated the presence of a strong northward-flowing jet current running from Cape Point along the shelf-edge, associated with a strong thermal front between cold upwelled water and warm oceanic water (Bang and Andrews 1974). The north-westward drift of anchovy eggs and early larvae toward the west coast was thought to be linked to this frontal jet current, and the effect of this water movement on the transport of anchovy eggs and larvae was investigated through the tracking of a free-drifting parachute drogue placed within a dense patch of anchovy eggs south of Cape Hangklip (see Fig. 1) in October 1976 (Shelton and Hutchings 1981, 1982).

The drogue drifted at a mean speed of 0.55 $m.s^{-1}$, and followed a northwesterly trajectory just offshore of the front (Shelton and Hutchings 1982). Whereas the wind speed decreased towards the end of the drogue track, the speed of the drogue increased, indicating that it was entrained by the jet current. The consistency of physical properties and zooplankton species composition along the drogue path supported the likelihood that the drogue closely approximated the drift of water in which high densities of anchovy eggs were initially located. Anchovy eggs and larvae (mostly <5 mm notochord length) were present throughout the drogue path, although they decreased in abundance with time, which was attributed to an expected high mortality rate. A nocturnal spawning rhythm was suggested by the incidence of newly-spawned eggs on two of the three nights, although early-stage eggs were abundant before sunset on the first night (Shelton and Hutchings 1981, 1982). Most anchovy eggs and larvae occurred above the thermocline, with larvae

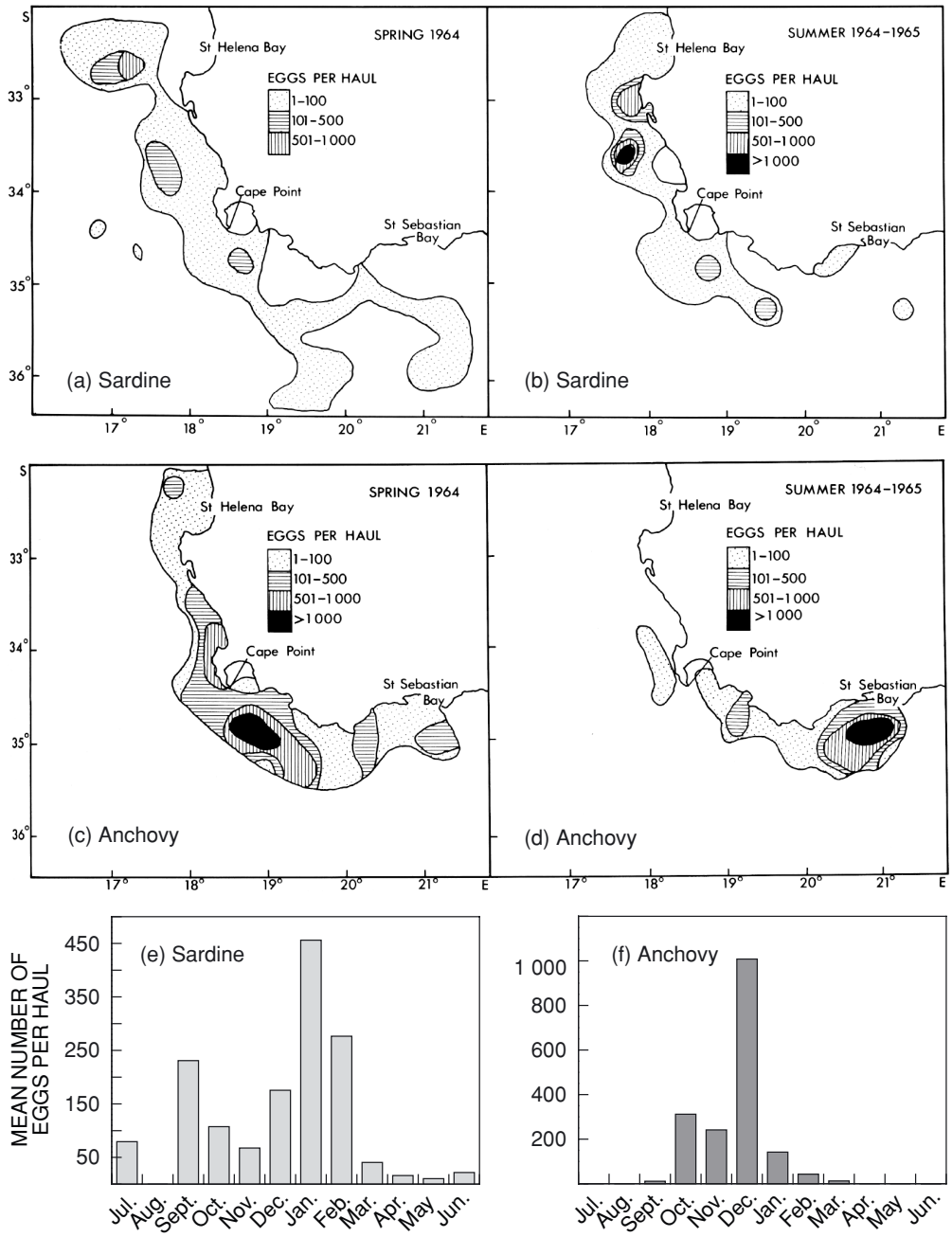

Figure 4: *Distribution of sardine eggs during (a) spring 1964 and (b) summer 1964/65, anchovy eggs during (c) spring 1964 and (d) summer 1964/65 (from Crawford 1981a, b), and monthly mean egg abundance for (e) sardine over the period 1955-1967 (redrawn from Crawford 1981a) and (f) anchovy over the period 1965-1967 (redrawn from Crawford 1981b).*

more dispersed than eggs in the water column and more abundant near the thermocline. Larvae displayed vertical migration, being closer to the surface at night. This study confirmed the ability of the jet current to entrain and transport eggs and larvae from the Agulhas Bank spawning ground towards the west coast recruitment ground, particularly during periods of southeasterly winds, the dominant wind direction during the anchovy spawning season. Although sustained northwesterly winds could reverse the direction of near-surface currents and hence transport eggs and larvae eastwards, the persistence of subsurface frontal features made it likely that the system could rapidly shift back to the more normal summer pattern of northerly transport (Shelton and Hutchings 1982).

The Cape Egg and Larval Programme. In 1977 the Cape Egg and Larval Programme (CELP) was initiated in order to investigate the composition, distribution and temporal variability of ichthyoplankton in the southern Benguela, thereby increasing understanding of the recruitment mechanisms of important fish species. Environmental and plankton sampling was conducted at monthly intervals from August 1977 to August 1978 over an extensive survey grid of 120 stations (Fig. 5a; Shelton 1986; Shelton and Hutchings 1990; also see Table 1).

Anchovy eggs were absent or rare in autumn and winter (June-August), but both egg and larval abundance increased rapidly with the onset of spring and peaked in late spring and early summer (Fig. 5b). Anchovy spawning was most intense on the Agulhas Bank, with eggs restricted almost entirely to the upper 50m above the thermocline. Anchovy eggs extended up the south-west coast whereas the larvae were dispersed more widely over the Agulhas Bank and extended further up the west coast than the eggs (Fig. 6a, b). Transects across the jet current showed that both anchovy eggs (Fig. 6c, d) and larvae were concentrated within the frontal zone. Sardine eggs and larvae were present during each month of the survey, but were more abundant from mid-winter to early summer (Fig. 5c), and both eggs and larvae were generally widespread over the survey grid (Shelton 1986).

The findings of the CELP surveys and the Cape Point drogue study, combined with commercial catch patterns of recruits on the west coast, provided new and significant insight into the life cycle of the Cape anchovy, and suggested the existence of separate spawning, transport and recruitment areas for this species. Current knowledge indicated spawning on the Agulhas Bank between October and January and transport of eggs and larvae to west coast nursery grounds via the jet current. Juvenile anchovy of approximately 4 months old appeared in commercial catches made off the west coast from March onwards, up to 250 km north of the spawning grounds. Juveniles then began a southerly return movement, against a food gradient, to the Agulhas Bank spawning grounds in spring (Fig. 7). At this time knowledge of the sardine life-cycle was less well understood, but indicated maximum spawning in warm water during spring and summer, subsequent recruitment to the west coast, and a return of mature fish to the Agulhas Bank in spring and summer, with an eastward migration beyond Cape Point in autumn (Crawford 1981a).

The implications of this knowledge of the anchovy life history in terms of understanding recruitment variability were substantial, since it highlighted the critical role of the transport process in determining recruitment success. Advective loss of anchovy eggs and early larvae through offshore divergence of the jet current was postulated as having a substantial, negative impact on re-

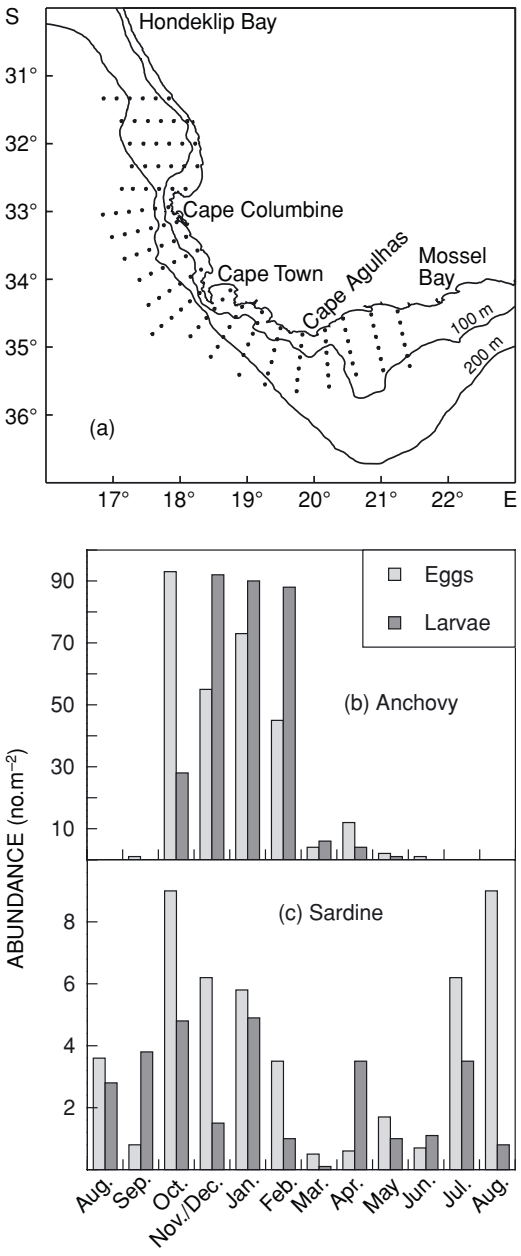

***Figure 5**: Schematic of Cape Egg and Larval Programme (CELP) surveys showing (a) the location of stations sampled each month using an oblique Bongo net, and monthly mean egg and larval abundance for (b) anchovy and (c) sardine over the period August 1977 to August 1978 (redrawn from Shelton 1986).*

cruitment success (Shelton and Hutchings 1982, 1990). With respect to management, understanding of the anchovy life history strategy, derived in part from ichthyoplankton surveys, was later used to set the timing of the pelagic spawner biomass surveys, which at that time (1984) were directed primarily at anchovy since sardine biomass was very low

Spawner biomass surveys. Pelagic spawner biomass surveys conducted annually since 1984 off South Africa's west and south coasts have provided a substantial amount of information on the distribution and abundance of anchovy and sardine eggs. Timed to coincide with peak anchovy spawning (November/December), as determined during the CELP survey, the spawner biomass surveys use hydro-acoustics to estimate the adult biomass of anchovy and sardine required for the setting of Total Allowable Catch (TAC) limits (Barange et al. 1999). The surveys cover an area of 100-150 000 km^2 extending from Hondeklip Bay on the west coast (31°S) to Port Alfred on the southeast coast (27°E), and sample a grid consisting of transects positioned perpendicular to the coastline and extending over the continental shelf. Sampling for biological and physical parameters is conducted at stations positioned 10 n.miles apart along transects, where approximately 300 ichthyoplankton samples are collected with a CalVET (California Vertical Egg Tow) net (Smith et al. 1985; see Table 1). Substantially more anchovy than sardine eggs are collected by the CalVET net during spawner biomass surveys, and anchovy eggs occur in a markedly higher percentage of CalVET samples than do sardine eggs.

The distribution of anchovy eggs in early surveys corroborated acoustically-derived spawner distribution maps, with high egg

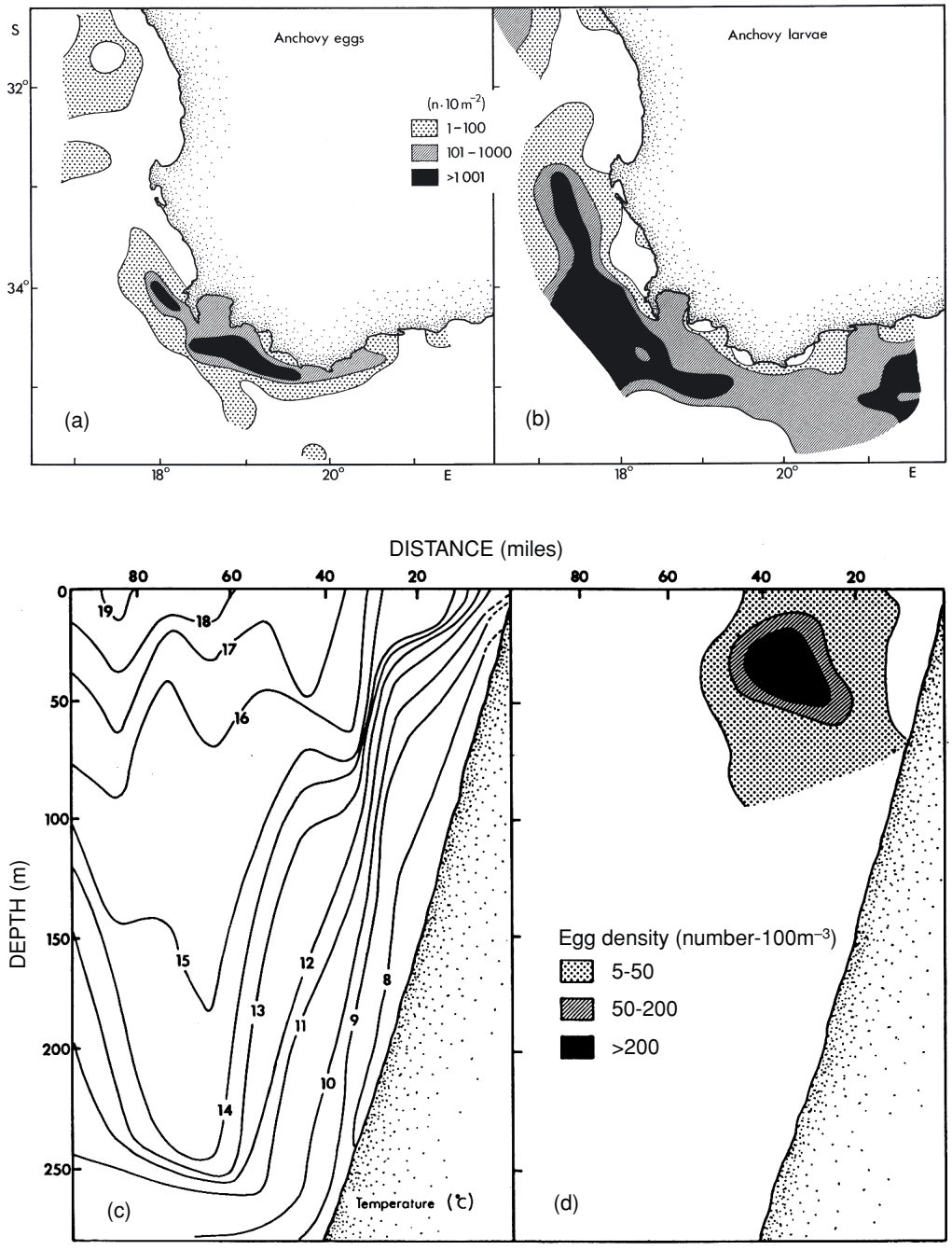

Figure 6: *Distribution of anchovy eggs (a) and larvae (b) in January 1978 (from Shelton and Hutchings 1990), and steeply shelving isotherms of the frontal region (c) off the southwest coast with which anchovy eggs (d) are closely associated (from Hutchings 1992; reproduced with permission).*

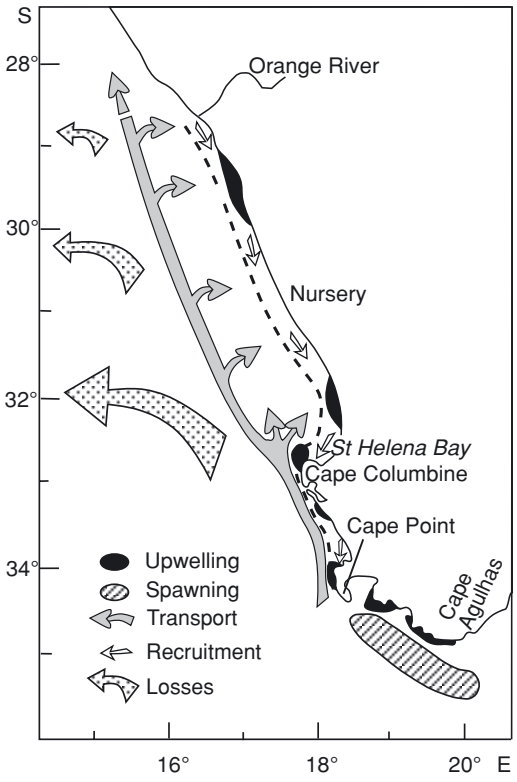

Figure 7: *Schematic of the present hypothesis on anchovy life history (from Hutchings et al. 1992; reproduced with permission).*

densities coinciding with high fish densities (Hampton 1987). Egg data therefore validated newly-developed acoustic methodology. Additionally, anchovy egg data collected during the surveys between 1984 and 1993 were used in the estimation of spawner stock size through the daily egg production method (DEPM; Armstrong et al. 1988; Shelton et al. 1993). Direct estimates of anchovy spawner biomass obtained using the DEPM compared well with indirect estimates derived from acoustic methods for most of the time series (Fig. 8). A combination of estimates from both methods produced a more accurate and reliable estimate than either method alone, with the two estimates being used together with catch data to set TAC levels (Shelton et al. 1993). The closer correspondence between the mean of the egg production estimates and the mean of acoustic estimates derived using a locally-developed anchovy target strength expression (Barange et al. 1996) compared to that derived using a target strength expression for Icelandic herring (Reynisson 1983; see Fig. 8) provided support for the former expression. Hence egg production estimates of anchovy biomass proved useful in scaling acoustic estimates during a period when there was no reliable information on the accuracy or applicability of the target-strength expression used (Hampton 1996). Because of its labour-intensive nature and the fact that the acoustic method is now considered to provide sufficiently robust estimates of anchovy biomass however, the DEPM is no longer used directly in management of the anchovy resource, and has yet to be used to estimate sardine spawner biomass off South Africa. Given that aspects of the behaviour of this species such as a patchy distribution, the formation of dense schools and near-surface schooling, all impact adversely on acoustically-derived biomass estimates, application of the DEPM for providing absolute estimates of the South African sardine population is imperative.

Daily egg production by anchovy measured during spawner biomass surveys was one of a suite of biological and environmental indicators investigated for use in forecasting subsequent anchovy recruitment (Cochrane and Hutchings 1995). Those authors reported a weakly-correlated, dome-shaped relationship between daily egg production and begin-year anchovy recruitment strength back-calculated from recruit survey data, but the relationship was insufficiently strong for daily egg production to be further considered for forecasting recruitment strength. Instead, parameters

or variables that could influence anchovy egg production (copepod biomass and production on the spawning grounds) or its cessation (incidence of gonad atresia), and the transport of eggs and larvae to the nursery grounds (the incidence of southerly winds at Cape Point and the distance of the 16°C isotherm from the coast at Cape Columbine during early summer, both of which are used as proxies for transport success) were considered more likely to be useful in predicting anchovy recruitment strength.

Despite Cochrane and Hutchings' (1995) reservations regarding the utility of anchovy daily egg production as a predictor of subsequent recruitment strength, it was incorporated into an expert system designed to provide a qualitative forecast of anchovy recruitment (Korrûbel et al. 1998). The expert system linked recruitment to environmental and biological parameters through a set of rules using predictor variables assumed to influence recruitment via the processes shown in Figure 9a. Four differentially-weighted indicator variables, including daily egg production by anchovy estimated during pelagic spawner biomass surveys, were used to provide forecasts of either average/above-average or three categories of below-average (possible, likely, or very likely) anchovy recruitment. Previous simulation studies (Cochrane and Starfield 1992) had indicated that management actions based on correct forecasts of either "below average" or "average or above" recruitment made at the start of the fishing season would result in a 16% increase in mean annual anchovy catches. Data collected from 1985 to 1993 were used to construct the expert system and a prediction of recruitment success was made for 1994. Hindcast and observed anchovy recruitment were closely matched (Fig. 9b), and the prediction of very likely below-

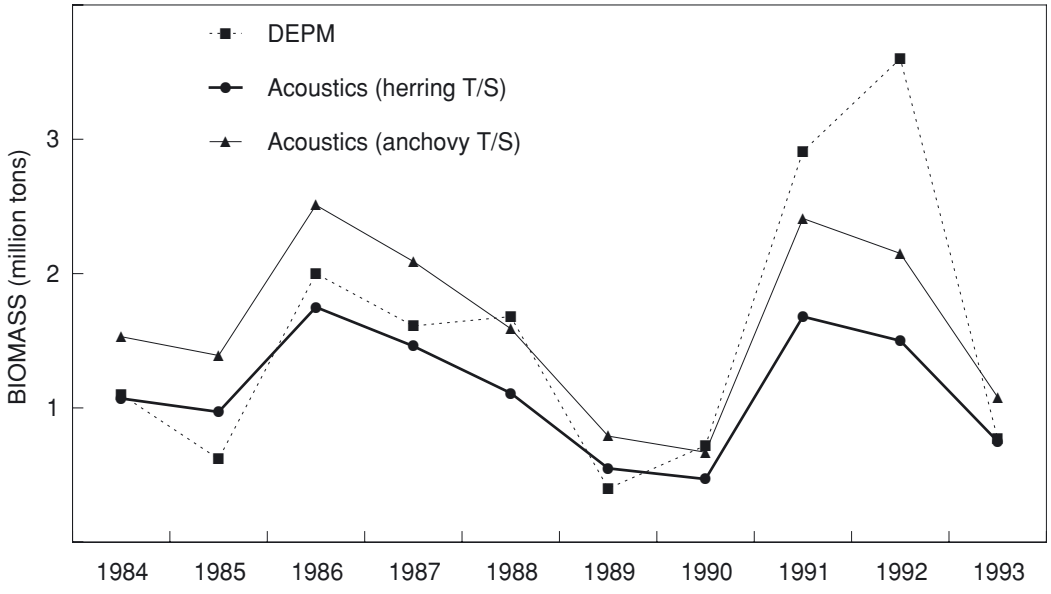

Figure 8: *Time-series of estimates of anchovy spawner biomass obtained using the daily egg production method (squares), and the hydro-acoustic method using the Icelandic herring target strength expression (circles) and the anchovy target strength expression (triangles; redrawn from Hampton 1996).*

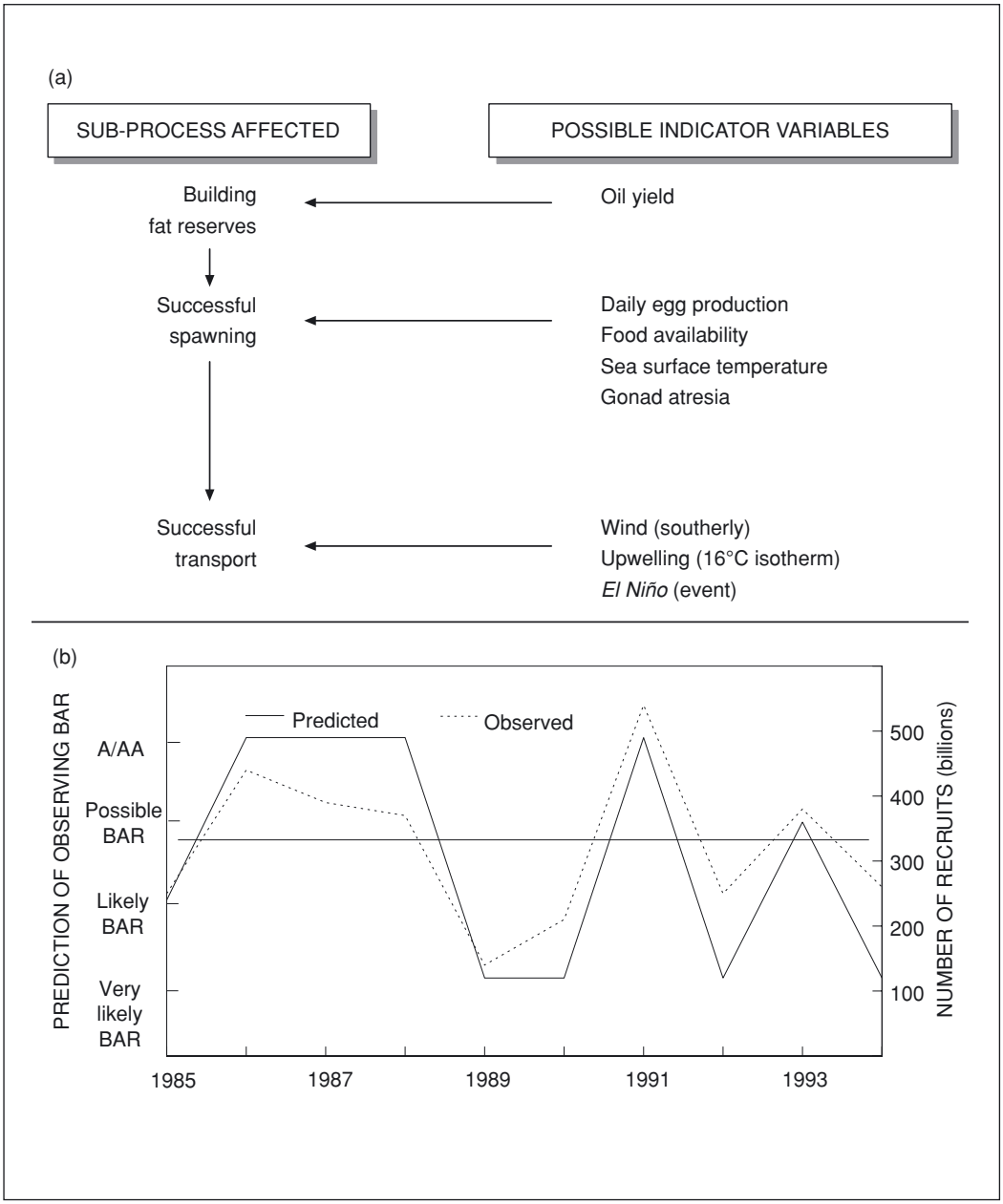

Figure 9: *(a) Conceptual model of the major sub-processes and possible indicator variables thought to influence anchovy recruitment used in an expert system; and (b) observed (in begin-year numbers derived from an anchovy population assessment model) and predicted (qualitative predictions of average/above-average [A/AA] and three categories of below-average recruitment [BAR]) anchovy recruitment from the expert system that used daily egg production and three other indicator variables measured during the anchovy spawning season to hindcast recruitment strength (redrawn from Korrûbel et al. 1998).*

average recruitment for 1994 was validated by the observation of recruitment that was slightly below long-term average recruitment. Unfortunately, validation of the model was only conducted for one year, owing to the loss of experienced personnel, a situation that has yet to be redressed. Nonetheless, this expert system is considered to have great potential for supporting future management of the anchovy fishery in the dynamic environment of the Benguela upwelling ecosystem (Korrûbel et al. 1998).

The relatively long time series of abundance and distribution data on anchovy and sardine eggs has facilitated a spatial comparison of the spawning habitats of these two species. Composite egg distribution maps derived from CalVET net samples collected during spawner biomass surveys over the period 1984-2000 have shown that anchovy eggs are typically found in a continuous band between Cape Point and Algoa Bay, with high concentrations occurring over most of the western Agulhas Bank, the offshore portion of the central Agulhas Bank and over much of the eastern Agulhas Bank (Fig. 10a). Sardine eggs are found from Hondeklip Bay to Algoa Bay, and probably extend farther east (Fig. 10b), with dense concentrations being found offshore of the west coast and over the shelf-edge region of the central Agulhas Bank.

Anchovy egg distributions have been relatively stable through time, showing consistent spawning east of Cape Point with occasional extensions up the west coast in years when Agulhas Bank water intruded north of Cape Point (van der Lingen et al. 2001). However, recent data have indicated an eastward shift in anchovy spawning habitat over the Agulhas Bank, with the offshore regions of the central and eastern Banks appearing to have become the primary anchovy spawning grounds in contrast to the previously dominant western Agulhas Bank (van der Lingen et al. 2002). The fate of eggs spawned in this region is uncertain, since they could either be (1) transported shorewards onto the western Agulhas Bank and so into the jet current to the west coast, (2) retained on the central and eastern Agulhas Banks and recruit on the south coast, or (3) entrained by the Agulhas Current and advected into the southern Indian or Atlantic Oceans where they would be unlikely to contribute to recruitment (Hutchings et al. 2002). In contrast to anchovy, sardine eggs have been more patchily distributed through time and have shown large-scale shifts in their distribution, with both the south and the west coasts comprising the major spawning grounds during different periods. Anchovy and sardine showed a broad overlap in spawning habitat during the 1980s and early 1990s, but their spawning habitats have diverged since 1994, with sardine spawning mainly off the west coast and anchovy still spawning off the south and east coasts (van der Lingen et al. 2001). This change in spawning habitat has been accompanied by a steady increase in sardine population size (from 34 000 tons in 1984 to 1.6 million tons in 2001; see Fig. 3), and the spawning by sardine off the west coast is reminiscent of the high egg concentrations observed there during the 1950s and early 1960s, a time of high sardine biomass and an expanded age composition (Beckley and van der Lingen 1999). Whilst the impact on recruitment of this shift in spawning habitat success is unclear, sardine eggs spawned off the west coast in summer will be subject to offshore Ekman drift during periods of strong equatorward winds and could be displaced far offshore. Hence the west coast may constitute a sub-optimal spawning habitat and the persistence of spawning there by older fish is considered unusual (Hutchings et al. 2002). Nonetheless, sardine recruitment has been higher since 1994 than before (see Fig. 3), although this is most likely a result of increased population size.

Egg data from spawner biomass surveys has also permitted a characterization of anchovy and sardine spawning habitats in terms of physical and biological parameters, such as sea surface temperature (SST). The preferred spawning range of anchovy ranges from 17.4 to 21.1°C, is unimodal, and peaks between 19.5 and 20.5°C (van der Lingen et al. 2001; Fig. 11). The preferred spawning range of sardine is greater than that of anchovy, ranging from 15.2 to 20.5°C, and is essentially bimodal with a major peak from 15.5 to 17.5°C and a secondary peak between 18.7 and 20.5°C. Anchovy therefore spawn preferentially in warmer waters than do sardine, and the broader SST range for sardine reflects spawning by that species on both the west and south coasts. Such characterization of spawning habitat will permit monitoring of the location and magnitude of suitable spawning habitat in the absence of egg data, through, for example, remote sensing of SST via satellite.

A recent addition to ichthyoplankton sampling during pelagic spawner biomass surveys has been the introduction of a continuous underway fish egg sampler (CUFES), first developed to sample eggs of Atlantic menhaden *Brevoortia tyrannus* (Checkley et al. 1997). The CUFES consists

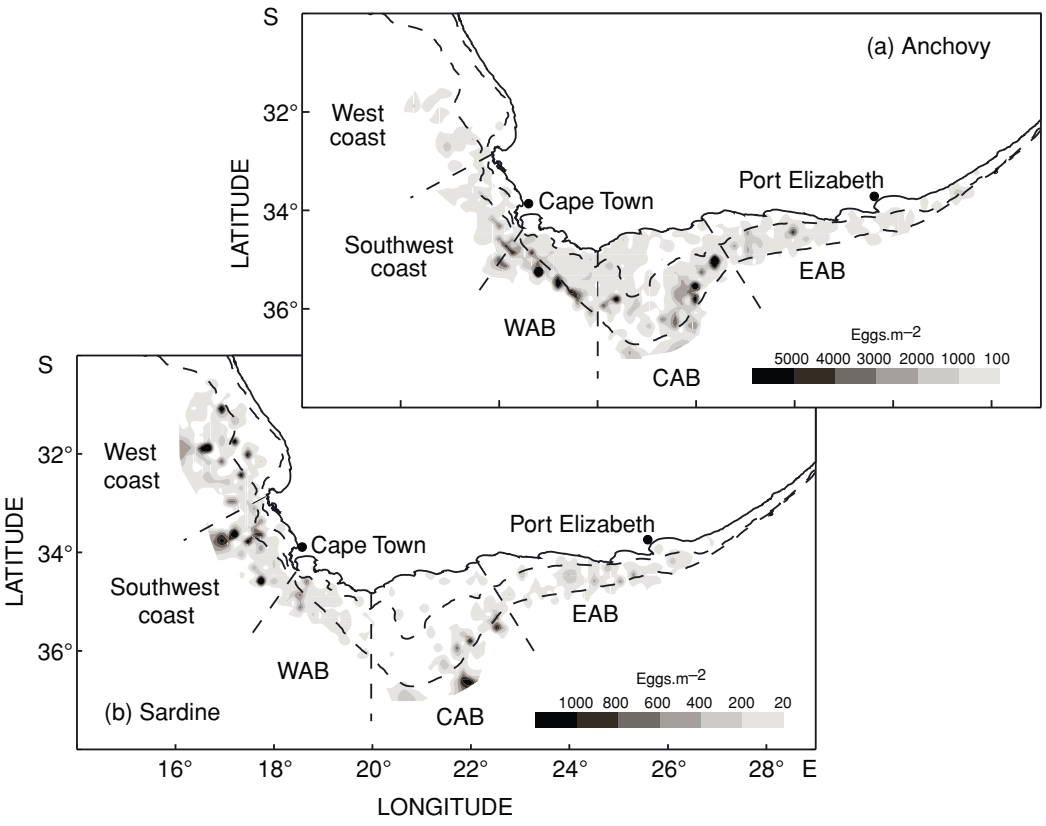

Figure 10: *Composite distribution maps for eggs of (a) anchovy and (b) sardine derived from CalVET net samples collected during spawner biomass surveys over the period 1984-2000 (CDvdL, unpublished data). The five survey strata are shown.*

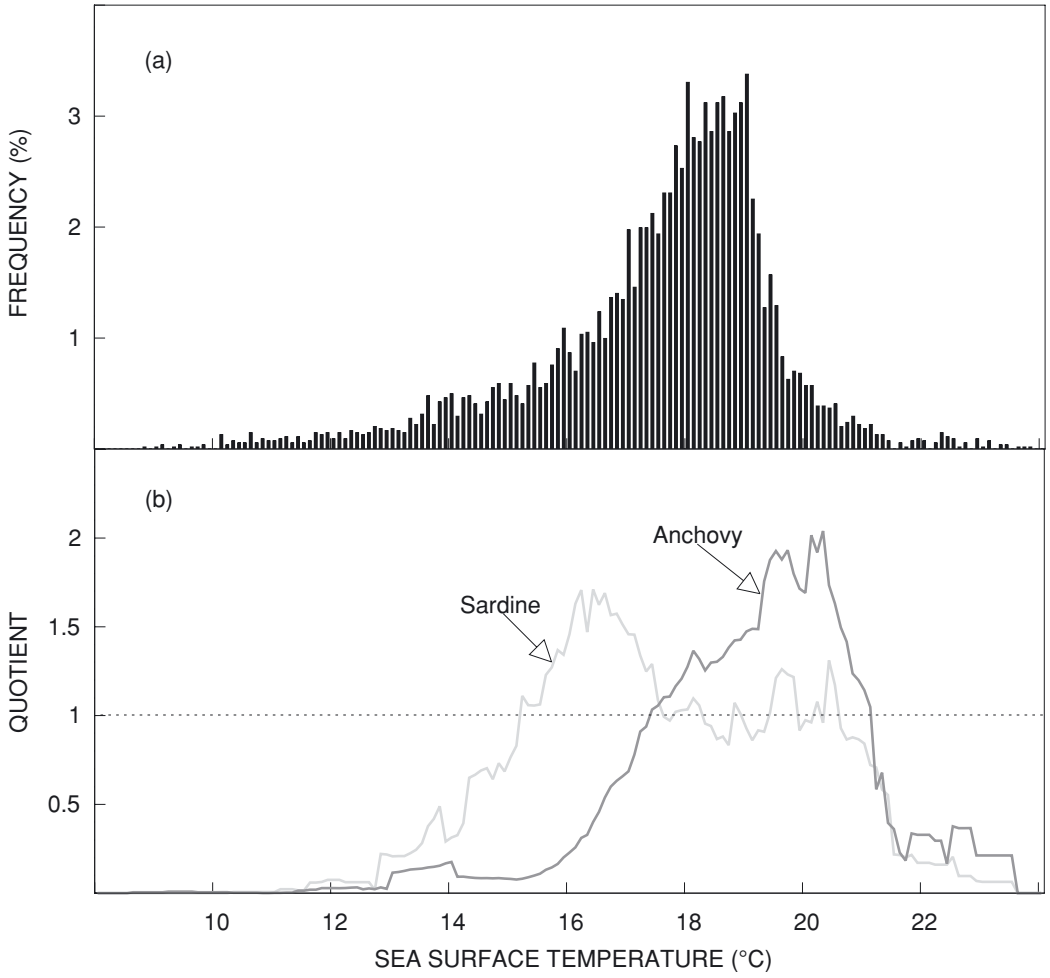

***Figure 11**: (a) Frequency distribution of sea surface temperature at all CalVET stations sampled during pelagic spawner biomass surveys conducted over the period 1984-1998 and (b) egg abundance/sea surface temperature quotients (the 11-point running means are shown) for anchovy and sardine egg samples collected during those surveys (redrawn from van der Lingen et al. 2001).*

of a submersible, high volume pump that can be used whilst the vessel is both on-station and underway; hence the CUFES collects many more samples and provides much higher spatial resolution than is possible using a CalVET net. In contrast to the CalVET net which collects a vertically-integrated sample at a single location however, the CUFES only samples at a fixed depth (usually 3m) and thus collects horizontally-integrated samples at that depth when used whilst underway. The CUFES is now used in many of the world's oceans, particularly for small pelagic species such as anchovy and sardine (see Checkley et al. 2000), and was first used off South Africa in 1996 (van der Lingen et al. 1998). The highly significant correlations observed between CUFES- and CalVET

Table 2: Total numbers of anchovy and sardine eggs collected and numbers of samples taken by the CalVET net, on-station (O-S_{CUFES}) and underway (U-W_{CUFES}) CUFES during pelagic spawner biomass surveys, 1998-2000.

			No. of anchovy eggs			No. of sardine eggs		
Year	No. of CalVET net and O-S_{CUFES} samples	No. of U-W_{CUFES} samples	CalVET	O-S_{CUFES}	U-W_{CUFES}	CalVET	O-S_{CUFES}	U-W_{CUFES}
1998	373	1 118	3 595	427	1 147	856	4 273	29 148
1999	314	716	6 025	1 804	4 752	577	2 488	22 321
2000	300	1 197	3 782	1 718	11 574	1 492	6 673	43 802
Total	987	3 031	13 402	3 949	17 473	2 925	13 434	95 271

net-derived density estimates for eggs of sardine and round herring proved the accuracy and demonstrated the suitability of the CUFES as a sampler of fish eggs under local conditions. Additionally, collecting CUFES samples while underway increased the precision of the estimate of mean egg density for sardine eggs, which was attributed to increased sampling effort and the consequent improved coverage of the highly patchy distribution of sardine eggs (van der Lingen et al. 1998). No increase in precision was observed for round herring eggs, most likely due to their less-patchy distribution.

The CUFES has been used on spawner biomass surveys since 1998 and collects substantially more sardine eggs that does the CalVET net during these surveys (van der Lingen and van der Westhuizen 2000; Table 2), indicating that it is particularly well-suited to sampling eggs of this species. This is in contrast to anchovy eggs which are under sampled by the CUFES, most likely due to the 500µm mesh of the concentrator which, because of their elliptical shape and small size, does not retain anchovy eggs with 100% efficiency. For both anchovy and sardine eggs however, the increased small-scale resolution provided by the CUFES will improve our understanding of fish spawning processes, and of the dispersion of eggs following spawning. The high spatial resolution afforded by the CUFES resolves the problem of a highly patchy egg distribution characteristic of sardine, hence this methodology shows substantial promise for incorporation into the DEPM for this species, possibly being used to adaptively establish sampling strata for CalVET net hauls. Such an approach has been used for sardine off California, where it reduced the number of CalVET samples taken (which reduced ship-time costs per survey mile) and increased the percentage of egg-positive CalVET hauls (Lo et al. 2001). Hence the CUFES is likely to prove useful to the DEPM in that it should increase the precision of biomass estimates, reduce survey costs, and, because of the near-real-time information it provides, reduce the potential bias of not enclosing the entire population within the survey grid.

East coast larval surveys. Several surveys were conducted along the east coast between 1951 and 1969 (Anders 1975). Sardine eggs were not found there until 1960, but the time of year of these cruises is uncertain. Subsequent cruises timed to coincide with the annual "Sardine Run" off Durban in winter (June/July) revealed concentrations of sardine eggs south of Durban (~27-29°E),

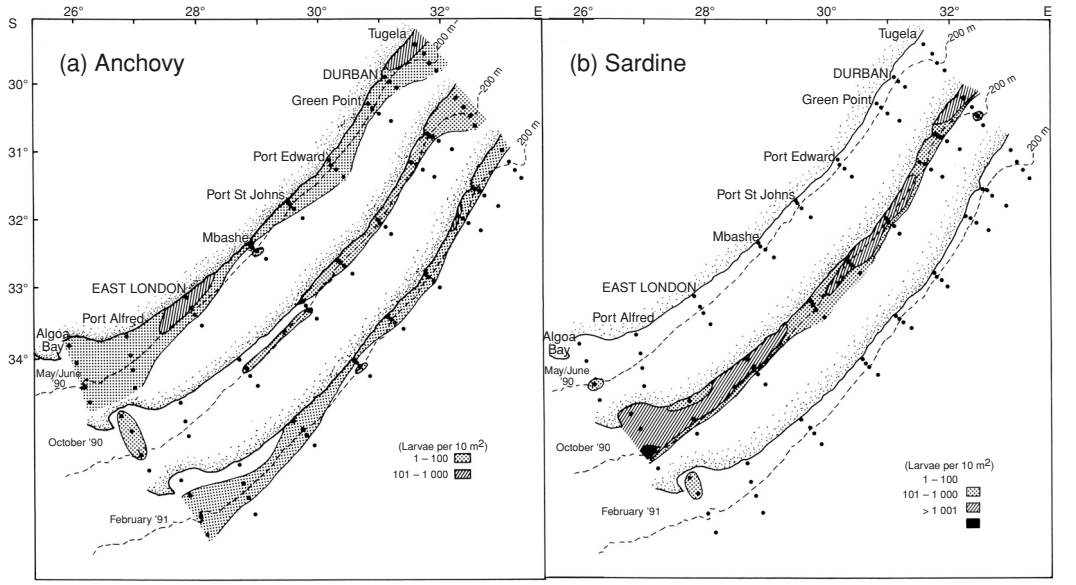

Figure 12: *Abundance of (a) anchovy and (b) sardine larvae along the east coast of South Africa in the period 1990/91 (from Beckley and Hewitson 1994; reproduced with permission).*

but only in the vicinity of Durban itself immediately following the sardine run. No anchovy eggs were found during these cruises (Anders 1975). Additional surveys along the east coast during January, July, August and December 1973 revealed dense concentrations of sardine eggs in August and of anchovy eggs in December, although eggs of both species were found during both months (Anders 1975). Greatest concentrations of both species were found in the coastal waters north of East London, and anchovy eggs were also collected north of Durban, where the continental shelf widens. These findings of widespread spawning by both anchovy and sardine along the east coast provided the first real indication of the suitability of this region as a spawning habitat.

No further ichthyoplankton surveys were conducted along the east coast until 1990/1991, when three cruises (May/June 1990, October 1990 and February 1991) were undertaken to investigate the distribution and abundance of clupeoid larvae in this relatively under explored part of the coastline (Beckley and Hewitson 1994).

Anchovy larvae were fairly widespread on all three cruises, with greatest abundance off East London and Tugela (north of Durban) during the May/June cruise (Fig. 12a). Sardine larvae were only abundant during the October cruise, when they were found along the entire survey area, with greatest densities near the shelf-break off Algoa Bay (Fig. 12b; Beckley and Hewitson 1994). In addition to these surveys, studies of seasonal variability in sardine egg abundance south of Durban have shown peaks in sardine egg abundance in June/July and again in November/December, which were attributed to the northward and southward (return) migrations associated with the sardine run (Connell 1996). Very few sardine eggs were found between January and May. Together, these

findings complement the earlier discovery of anchovy and sardine spawning along the east coast by Anders (1975), and support the hypothesis of Armstrong et al. (1991) that this region forms an extension of the spawning environment of South African temperate clupeoids.

South African Sardine/Anchovy Recruitment Project surveys. In the late 1980s, the international Sardine/Anchovy Recruitment Project (SARP) was initiated by IOC/UNESCO and FAO in order to investigate biological and physical oceanographic processes governing recruitment fluctuations in marine fish stocks, in particular, factors causing mortality of early life stages (IOC/UNESCO 1990). South African SARP (SA SARP) was initiated in 1993 and comprised monthly cruises from spring through autumn to investigate within-season variability in factors thought to affect sardine and anchovy recruitment (Painting 1993). Sampling details are given in Table 1. SA SARP extended over 2 consecutive spawning seasons, namely 1993/1994 and 1994/1995 (Painting et al. 1998).

A comparison of egg and larval distributions with water current features during individual cruises corroborated the important role of the frontal jet current in transporting eggs and early larvae from the south coast spawning grounds to the west coast nursery area (Fig. 13), supporting the hypothesis originally proposed by Shelton and Hutchings (1982). Convergent flow south of the Cape Peninsula merged into the fast-flowing jet current, the location of which was found to vary between the 200 and 500 m isobaths. Generalized flow patterns indicated that transport was favoured in spring compared to summer, suggesting that eggs spawned earlier in the spawning season would be more likely to reach the nursery grounds than those spawned later (Fowler and Boyd 1998). Currents beyond the 500 m isobath had a much stronger offshore component in some months during the first season (e.g. November 1993; Fig. 13c) compared to the second, suggesting that offshore advection of the spawning products of both species may have been higher in the first season. The increased anchovy and sardine recruitment in 1995 compared to 1994 (see Fig. 3) appears to be consistent with this observed disparity in advective processes. Despite the potential for losses of spawning products through offshore divergence of the jet current, flow patterns observed during some of the SA SARP surveys indicated that eggs and larvae advected offshore could be returned to the system farther north via onshore flow. Hence, whereas some eggs and larvae could be lost by offshore flow, others could reach the nursery grounds via a delayed route farther offshore (Fowler and Boyd 1998).

Richardson et al. (1998) used data collected during the SA SARP programme to examine the effect of SST and food availability (copepod biomass, consistency of copepod biomass, and daily copepod production) on anchovy spawning success. Total anchovy egg abundance over the western Agulhas Bank (WAB) was used as an index of spawning intensity, and was substantially higher during spring and early summer compared to winter or late summer. Total anchovy egg abundance was also significantly related to the area of 16-19°C water over the WAB (Fig. 14a). The disparity between this SST range and that estimated from spawner biomass surveys (17.4-21.1°C) is a result of the extension farther east of the spawner biomass surveys compared to the SARP surveys, which only extended as far as Cape Agulhas. Richardson et al's (1998) results led to the conclusion that the WAB was a more suitable spawning area than the southwest coast because of its greater thermal stability, a larger area of 16-19°C water, and a more consistent food environment having high copepod production, and to the hypothesis that anchovy spawning success was dependent on the extent of such suitable spawning habitat.

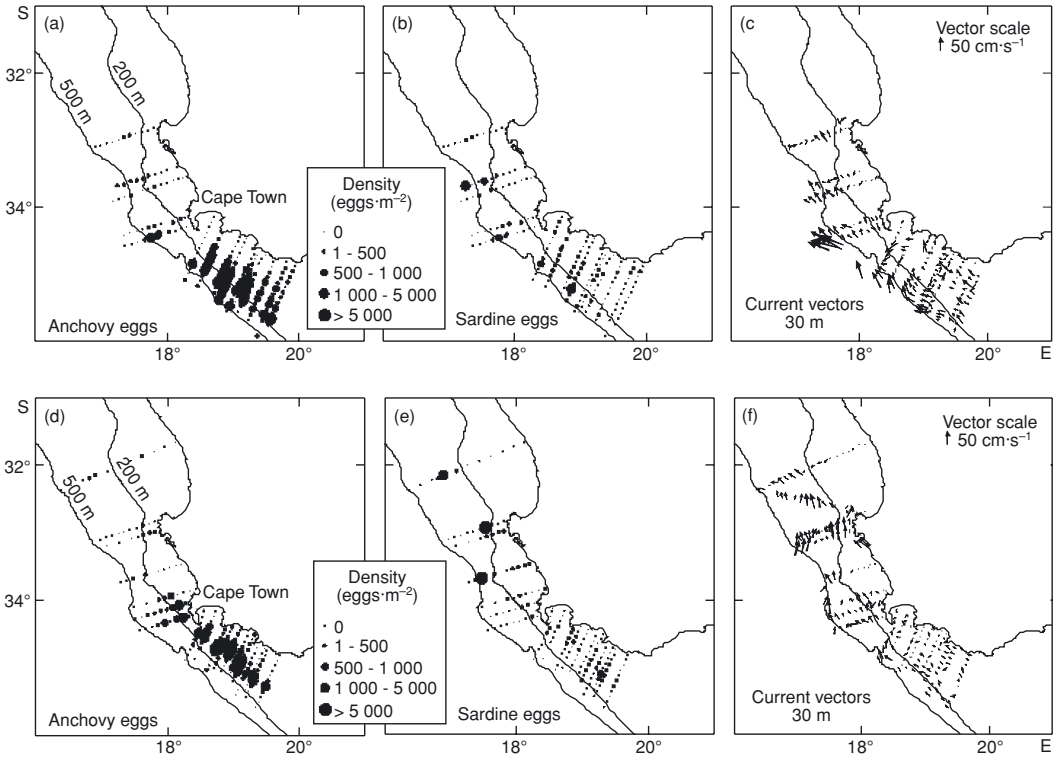

Figure 13: *Density of (a) anchovy and (b) sardine eggs, and (c) current vectors at 30m depth during the SA SARP survey of November 1993; and (d) anchovy and (e) sardine eggs, and (f) current vectors at 30m depth during the SA SARP survey of November 1994. Redrawn from Fowler and Boyd (1998).*

The seasonal intensity of sardine spawning varied independently of the area of 16-19°C water, suggesting that the thermal conditions that define suitable spawning habitat for sardine are not necessarily the same as for anchovy, or that sardine spawning is less restricted by temperature than is that of anchovy (Fowler 1998). However, intensity of sardine spawning was positively correlated with integrated chlorophyll *a* on the WAB, with highest egg abundance values occurring during early spring (Fig. 14b). This coincidence between spawning intensity and the spring bloom over the WAB, during which there is enhanced phytoplankton, microzooplankton and mesozooplankton production over the inner shelf (Mitchell-Innes et al. 1999), suggests that sardine spawning activity may be related to feeding conditions (Fowler 1998). The decrease in sardine spawning intensity on the WAB during summer when chlorophyll *a* concentrations are low, coupled with the second sardine spawning peak in late summer (February) that coincides with maximal upwelling (Fowler 1998) and increased primary production, lend support to this hypothesis. Hence the temporal pattern of sardine spawning behaviour may be related to the availability of food for spawners, but in terms of phytoplankton as opposed to zooplankton for anchovy.

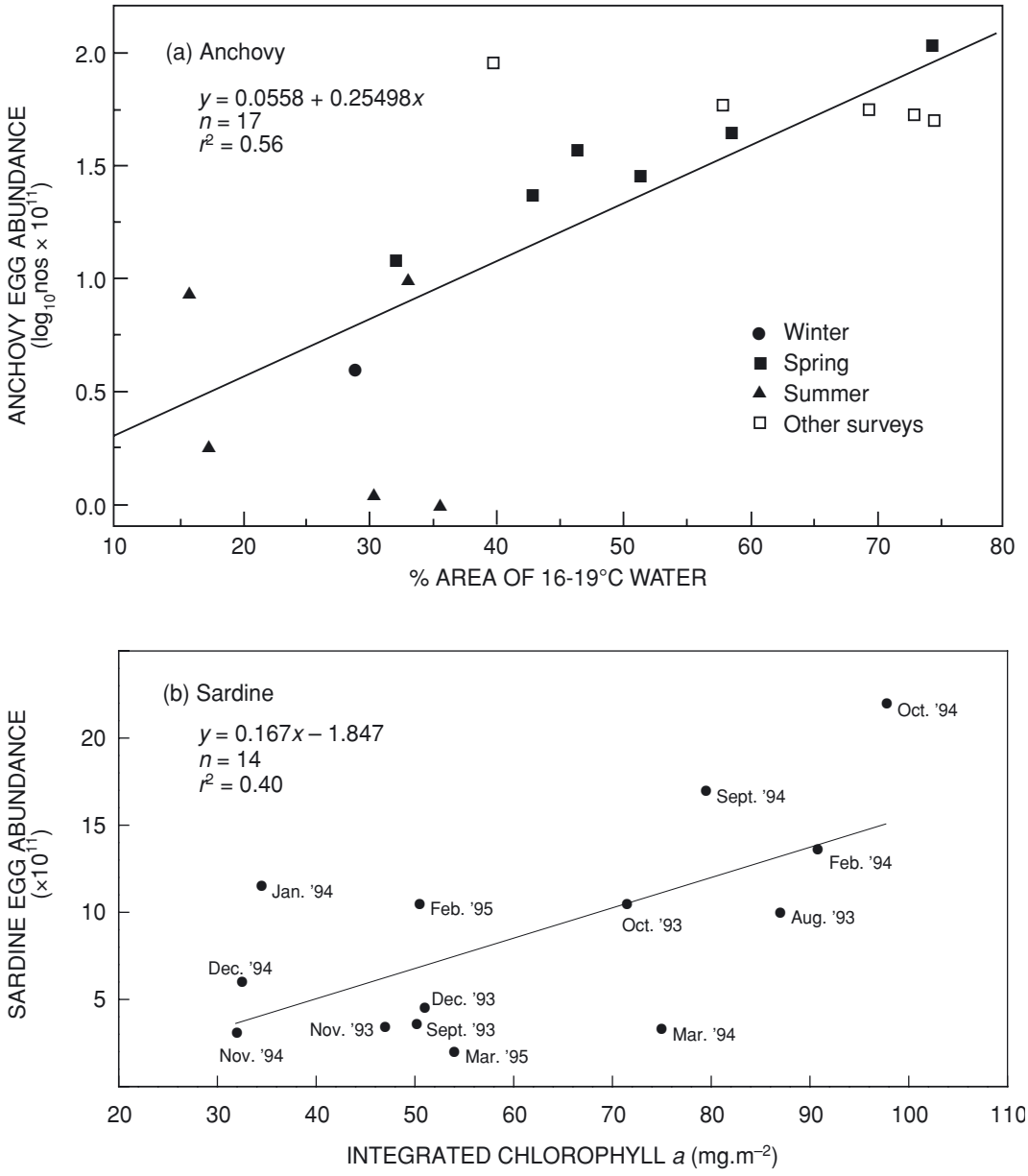

***Figure 14**: Relationships between (a) total anchovy egg numbers on the western Agulhas Bank and the area of 16-19°C water (arcsine transformed to improve normality) during SA SARP surveys (winter, spring and summer) and five pelagic spawner biomass surveys (November 1988-1992; from Richardson et al. 1998; reproduced with permission), and (b) total sardine eggs numbers on the western Agulhas Bank and the concentration of chlorophyll a (integrated over the WAB) during SA SARP surveys (redrawn from Fowler 1998).*

A modified expert system was examined for suitability in forecasting anchovy recruitment strength from data collected during the monthly surveys of SA SARP (Painting and Korrûbel 1998). Since construction of the original expert system model was not based on SARP field data, the use of those data provided an independent test of the expert system and also allowed for a comparison between predictions based on data from a single annual survey (*e.g.* Korrûbel et al. 1998; see section on pelagic spawner biomass surveys) and those resulting from surveys conducted at regular intervals throughout the spawning season. In this instance six indicator variables were considered in the analysis: (1) distance offshore of the 16°C isotherm, (2) southerly wind stress, (3) anchovy egg abundance (no.m^{-2}), (4) the incidence of oocyte atresia in adult females, (5) an index of adult fish starvation derived from estimates of fish density and copepod biomass, assuming a P:B ratio of 0.2 day^{-1} for copepods and a fish daily maintenance ration of 2% dry body mass.day^{-1}, and (6) oil : meal ratios obtained from anchovy processing factories that were used as an index of fish condition (Painting and Korrûbel 1998). Since forecasts of anchovy recruitment would be required at the start of the fishing season (January) in order to make the results useful for management, only those SA SARP data from the first part of the spawning season (August/September up to and including December) were used in the procedure. In the model, data for each variable were assessed against a threshold value; "active" variables were assumed to contribute towards below-average recruitment (BAR) by being either above or below threshold values, as defined by model rules. If there were no active variables then "average/above-average recruitment" was forecast; if the number of active variables was between one- and two-thirds of the number of variables used then "likely below-average recruitment" was forecast; and if the number of active variables was greater than two-thirds then "very likely below-average recruitment" was forecast.

Egg abundance (daily egg production was not estimated during the SA SARP surveys) was used as a predictor of recruitment based on the assumptions that this index was one step shorter in the causal chain than the classic stock-recruit relationship, and that a low egg abundance implied an increased chance of a BAR event (Painting and Korrûbel 1998). Mean monthly egg abundance during the SA SARP surveys was less than the threshold value of 300 eggs.m^{-2}, and hence indicative of a BAR event, in only three of the nine surveys from which data were used. Nonetheless, forecasts of anchovy recruitment made from the SA SARP data were for below-average recruitment for both 1994 and 1995. For 1994, all the monthly forecasts fell in the BAR category (including two possible, two likely and one very likely forecast of BAR), and both observed (direct survey estimate; see Fig. 3) and estimated (from an anchovy assessment model) recruitment was below average. For 1995, three of the four monthly forecasts fell into the BAR category (two possible and one very likely) and the other into the "average/above-average recruitment" category; observed recruitment that year was above average but recruitment estimated using the assessment model was below average.

Painting and Korrûbel (1998) found that predicted and observed/estimated anchovy recruitment compared favourably, and suggested that field measurements of biological and environmental variables could thus be used in a structured manner to obtain timely forecasts. They emphasized that recruitment may be impacted by a suite of variables, which could vary in importance from year to year and which could act in isolation or conjunction. Nonetheless, those authors deemed two of their six variables to be essential, namely the position of the 16°C isotherm (which they used as a proxy for upwelling intensity and strength of the frontal jet current, and considered to be

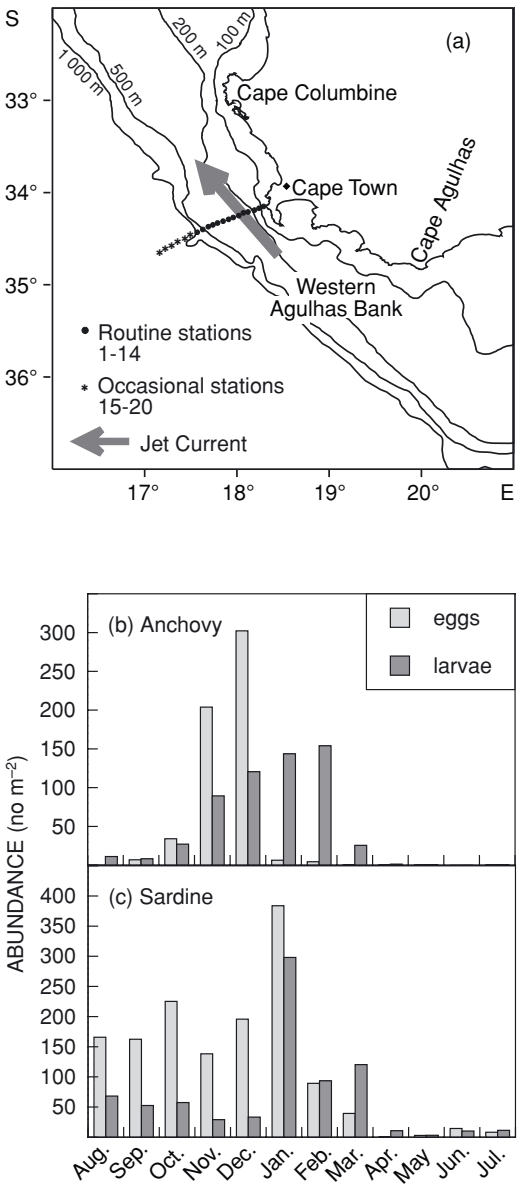

Figure 15: *Schematic of the SARP Monitoring Line showing (a) the location of stations sampled along the line using an mini-Bongo net and the approximate position of the shelf-edge jet current (from Huggett 2002), and monthly mean egg and larval abundance for (b) anchovy and (c) sardine over the period August 1995 to July 2001 (JAH, unpublished data).*

a driving variable in the recruitment process) and the index of southerly wind stress. Given this complexity in the processes impacting on recruitment, Painting and Korrûbel (1998) concluded that rule-based models provided a particularly appropriate system, since rules may be added easily with little disturbance to the system.

SARP Monitoring Line. The monthly SA SARP surveys provided valuable insight into processes affecting recruitment but were too labour intensive to maintain, leading to the decision to constrain regular ichthyoplankton sampling to a more focused objective. The SARP Monitoring Line programme was initiated in August 1995, with the aim of providing increased temporal coverage of the transport of early life history stages by the Benguela jet current. Given the role of the shelf-edge jet current in the concentration and transport of eggs and larvae from the western Agulhas Bank spawning grounds to the west coast nursery area (Shelton and Hutchings 1990), regular monitoring of this critical gateway during the spawning season was considered useful in attempting to predict recruitment success (Hutchings 1992). Sampling along the SARP Monitoring Line, which crosses the jet current off the Cape Peninsula (Fig. 15a), began in August 1995 and is ongoing; sampling frequency is effectively bimonthly (Table 1; Huggett et al. 1998). Ichthyoplankton collected along this transect primarily reflect spawning on the western Agulhas Bank, as the relatively small mouth area of the mini-Bongo net (Table 1) only samples eggs and small larvae (mainly <20mm *TL*), and larger larvae advected from farther east would be able to avoid the net.

Spawning seasonality inferred by egg and larval abundance along the SARP monitoring line has largely supported the findings of the

earlier studies. Monthly averages from 1995 to 2001 indicate that anchovy eggs were most abundant from November to December, and anchovy larvae from November to February (Fig. 15b). Sardine eggs and larvae were most abundant from August to March, peaking in January, but were found throughout the year (Fig. 18c). Eggs and larvae of both species showed different patterns of abundance from year to year, emphasizing the within-season variability in spawning patterns observed during the monthly SA SARP surveys. Similar variability was observed in the position and strength of the jet current, which was usually located close to the coast during spring, moving farther offshore in early summer (Huggett et al. 1998; Huggett 2002). This observation led Boyd and Nelson (1998) to suggest that the first part of the spawning season (October-December) was more favourable for transport to the nursery area than the second part (January-March), supporting the findings of Fowler and Boyd (1998) for the SA SARP surveys.

An important objective of the SARP Monitoring Line originating from the initial aims of the SA SARP surveys was to investigate within-season variability in spawning and transport success by comparing monthly egg and larval abundance along the SARP line to the birth date distributions of subsequent recruits. Mean monthly anchovy (August-March) and sardine (September-February) egg abundances from 1995/1996 were significantly correlated with the estimated birth date distribution of the 1996 recruits (Huggett et al. 1998; Painting et al. 1998), suggesting promise in this approach. However, the birth date distributions were only rough estimates derived from length frequency distributions of the 1996 recruits and average growth rates from 1993/94, and the lack of routine daily ageing and growth studies in the region since 1994 has hampered the further pursuit of such relationships. This has been a lost opportunity, as discrepancies between recruit or pre-recruit birth dates/hatch dates and monthly egg abundance along the SARP line would have facilitated the identification of event-related differential survival or mortality in relation to the transport process.

The within-season variability in the timing, duration and extent of spawning on the western Agulhas Bank, as indicated by the SARP Monitoring Line, invites comparison between years of low and high anchovy recruitment. Low anchovy recruitment in the winter of 1996 was preceded by a brief warming period along the monitoring line during the summer of 1995/1996, and a narrow window of anchovy eggs and larvae from late October to early December (Fig. 16a). In contrast, high anchovy recruitment in winter 2001 was preceded by an extended period of warm water along the monitoring line, and greater and more persistent abundance of anchovy larvae in particular, as well as eggs, which were associated with the warm water (Fig. 16b). Annual indices of mean egg and larval abundance ($no.m^{-2}$) along the monitoring line (Fig. 17a, b) have yielded positive linear correlations between eggs, larvae, and eggs and larvae combined, and the subsequent number of recruits for both anchovy and sardine over the 7 years sampled. Whereas most correlations were not significant, there was a significant correlation between anchovy eggs and subsequent numbers of recruits (Fig. 17c), indicating the potential of this index for use in forecasting anchovy recruitment strength before the final TAC revision. Nevertheless, it should be cautioned that the time-series is still very short, and correlations could change with the addition of future data points. The usefulness of these data for forecasting sardine recruitment is doubtful (Fig. 17d), most likely due to the considerable portion of sardine spawning that has taken place in recent years on the west coast, to the north of the SARP Monitoring Line (van der Lingen et al. 2001; see section on pelagic spawner biomass surveys).

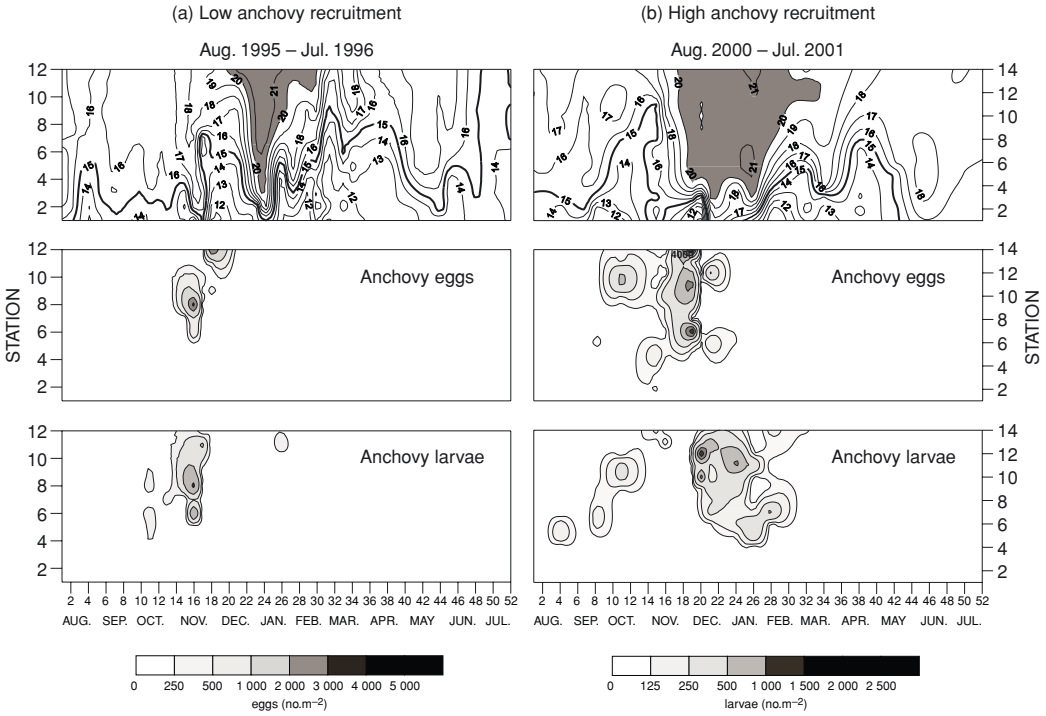

Figure 16: *Contoured plots of SST (°C), and anchovy eggs and larvae (no.m^{-2}) across the SARP Monitoring Line (station numbers are shown on the y-axis) during (a) 1995/1996, a year of low anchovy recruitment, and (b) 2000/2001, a year of high anchovy recruitment. Week number is shown on the x-axis (from Huggett 2002).*

Post-larval and pre-recruit surveys. Extensive datasets now exist concerning intra- and interannual changes in the abundance and distribution of eggs and early larvae of anchovy and sardine, but information for late and post larvae is relatively limited. Boyd and Hewitson (1983) described the distribution of anchovy larvae of a wide size range (3 to 42 mm standard length; *SL*) off the west coast between Lüderitz and Cape Columbine over the period 1978 to 1982, derived from oblique Bongo net tows made at 15 and 60 n.miles offshore at intervals approximately 30 n.miles apart along the coast. Their results showed that there was a rapid decrease in the abundance of larvae <20mm *SL*, and an increase in larval mean length, with decreasing latitude (Fig. 18). Their results supported the existence of a nursery ground north of Cape Columbine for larvae spawned off the south coast as proposed by Shelton and Hutchings (1982), and further suggested that there was some degree of northward transport or migration of larvae.

Surveys to assess the abundance and distribution of pre-recruit anchovy and sardine have been conducted off South Africa's west coast since 1991. Whilst not strictly ichthyoplankton surveys, since sampling is aimed at larval and juvenile fish that are active swimmers as opposed to passive drifters, the pre-recruit surveys have provided useful knowledge on these early life history stages of

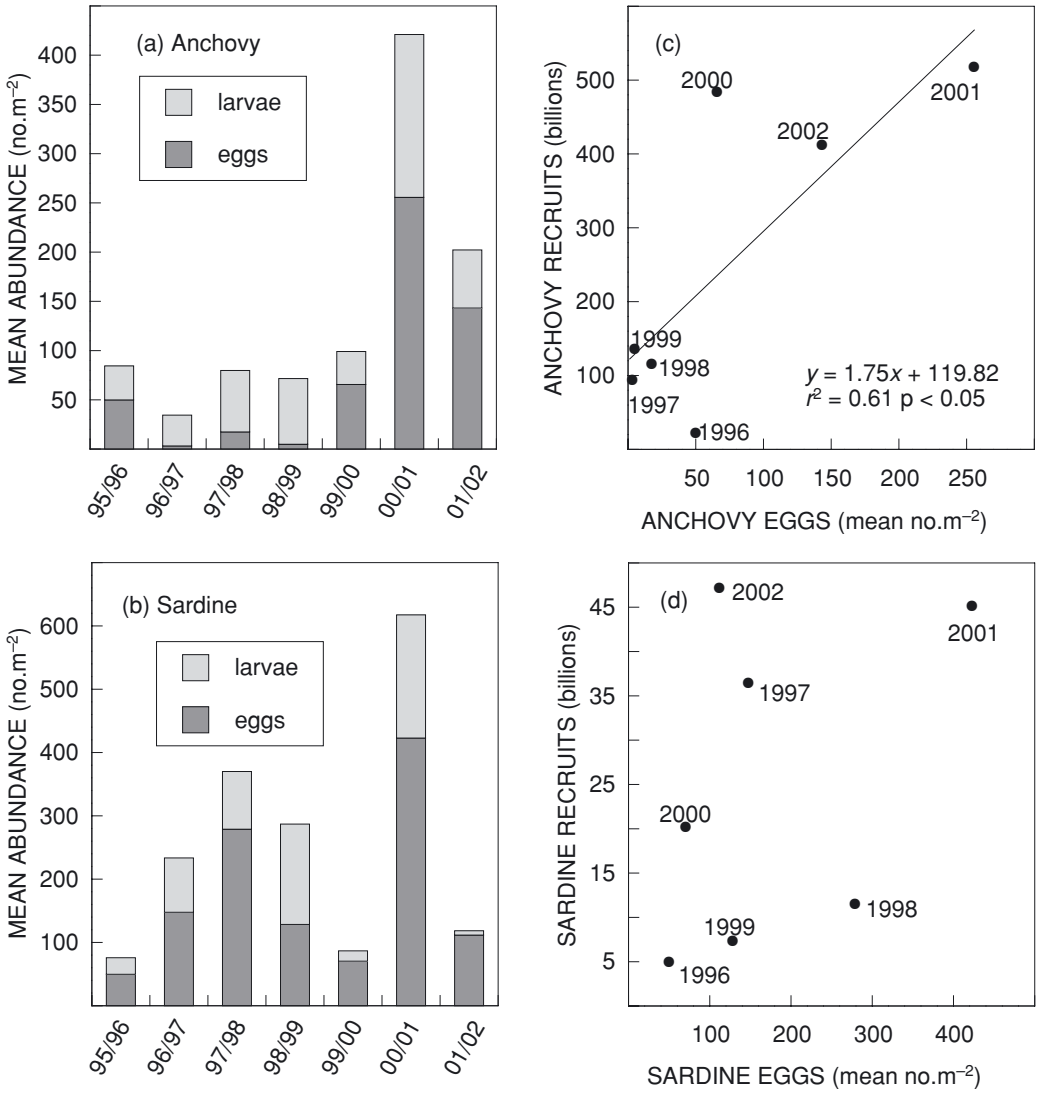

***Figure 17**: Indices of mean (a) anchovy and (b) sardine egg and larval abundance (no.m^{-2}) along SARP Monitoring Line between September and March each year from 1995/96 to 2001/02, and scatterplots between mean abundance of (c) anchovy and (d) sardine eggs across the SARP Monitoring Line and subsequent numbers of recruits (billions; JAH, unpublished data).*

anchovy and sardine. Designed to obtain an indication of forthcoming recruitment strength, primarily for anchovy (O'Toole and Hampton 1989), and timed so that such information would be obtained sufficiently early in the fishing season to be useful for management (Cochrane and Starfield 1992), pre-recruit surveys are conducted during March, when surviving fish from eggs spawned in summer are 2-5 months old.

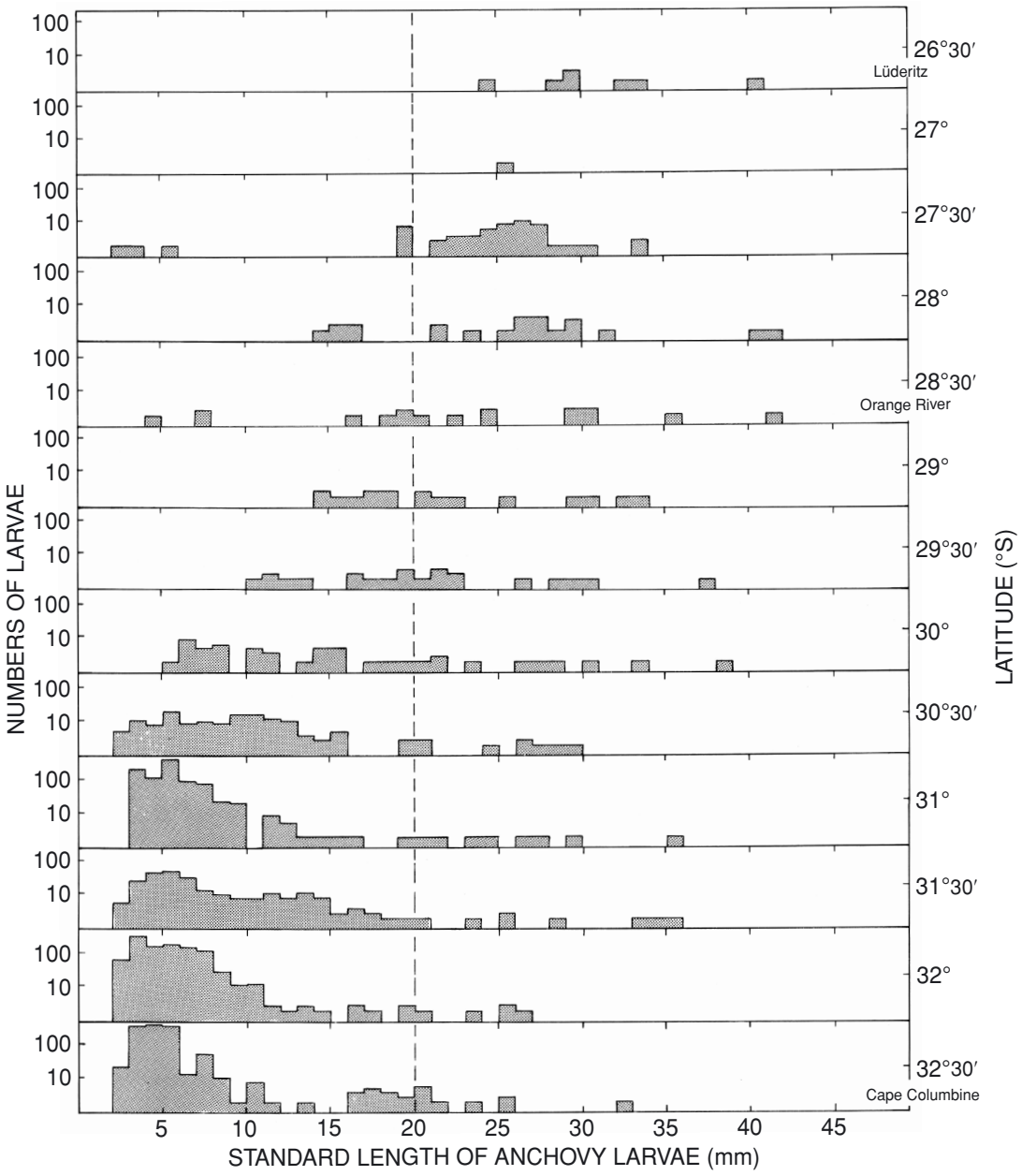

***Figure 18**: Size frequency distributions of anchovy larvae and caught with an obliquely-towed Bongo net per half degree of latitude between 26°30' and 32°30'S, 1979-1982 (from Boyd and Hewitson 1983; reproduced with permission).*

Surveys sample a grid of randomly-positioned transects, orientated perpendicular to the coast and extending across the continental shelf over the west coast nursery grounds between the Orange River mouth and Cape Point. Stepped, oblique hauls of a modified Methot frame trawl (Methot 1986; O'Toole and Crous 1989) from 35m depth to the surface are performed at 5-9 stations along survey transects, sampling being conducted at night when fish are dispersed near the surface and avoidance of the sampling gear is likely to be substantially reduced compared to day-time sampling.

Anchovy pre-recruits have been collected more frequently and at substantially higher densities than sardine pre-recruits during all surveys (Fig. 19). Survey mean density for anchovy pre-recruits has shown a 35-fold variation over the time-series, with peak densities observed in 1991 and 2001. Survey mean density for sardine pre-recruits has varied by 10-fold, and sardine have shown a slight increase in their frequency of occurrence during the time-series.

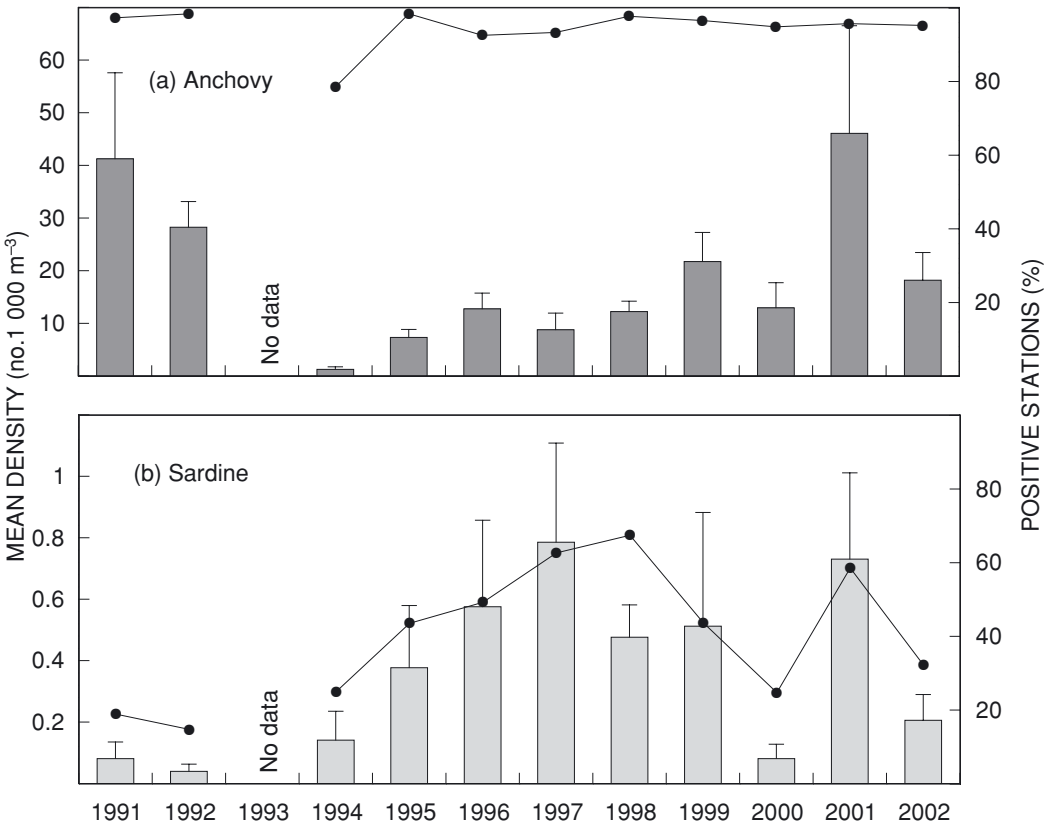

Figure 19: *Survey mean density (number.1000m^{-3}) and frequency of occurrence (percent positive stations) for anchovy and sardine pre-recruits surveyed between the Orange River mouth and Cape Columbine over the period 1991-2002. Vertical bars indicate the coefficient of variation (CV) of the mean; note that the density axes for anchovy and sardine are not to the same scale (CDvdL, unpublished data).*

Both anchovy and sardine pre-recruits show distinct distribution patterns according to size, although the picture is clearer for anchovy as a result of the greater numbers captured. Smaller (<35mm total length; *TL*) anchovy pre-recruits are found offshore of the continental shelf, predominantly in the south of the survey area (Fig. 20a, b), whereas larger (>35mm *TL*) pre-recruits are found closer inshore (Fig. 20c, d). This cross-shelf gradient in pre-recruit size is annually consistent, and indicates that early anchovy larvae are not transported by the jet current directly to the inner continental shelf of the west coast. However, the mechanisms by which larvae are transported shoreward, growing as they go, are unclear, and require further research. Active swimming seems probable, since larvae longer than 7mm *TL* can swim sufficiently well to avoid a bongo net during daylight (Badenhorst and Boyd 1980). An anchovy larva of 20mm *TL* swimming at a cruising speed of 1 body length s^{-1} (Hunter 1972) for 12 $h.d^{-1}$ would take 105 days to swim the 180 km from offshore of the continental shelf to the coast, if water movement either toward or away from the coast were zero. However, this is probably too long a period for active swimming to be solely responsible for onshore movement of larvae. Hence, passive transport is likely too, particularly in the region where the shelf narrows (approximately 31°S) and onshore movement of surface waters could transport larvae and pre-recruits shoreward. Similarly, the relaxation of upwelling-favourable southeasterly winds during late summer could promote a shoreward movement of the upwelling front.

Estimates of mean pre-recruit density are not correlated with subsequent estimates of recruit numbers made two months later during winter (May) recruit surveys for either anchovy or sardine. The lack of significant relationships between pre-recruit abundance and subsequent recruitment strength may be indicative of inadequate sampling, most likely due to insufficient temporal coverage, but may also be due to the short time-series of available data. However, whilst the pre-recruit surveys may not have provided the forecast of anchovy recruitment strength anticipated of them, they have provided a wealth of new information regarding these early life history stages, raised new ecological questions, and indicated new avenues of research.

Discussion

Ichthyoplankton surveys off South Africa have underpinned understanding of the life history cycles of anchovy and sardine in the southern Benguela. These surveys have also played an important role in the management of the anchovy fishery through, for example, application of the DEPM to estimate spawner stock size, and in identifying key mechanisms thought to impact on anchovy recruitment success. The latter is an important management consideration since most of the catch consists of young of the year. Management of the anchovy fishery consists primarily of the setting of total allowable catch (TAC) levels (Geromont et al. 1999). An initial anchovy TAC is set at the beginning of the year (Fig. 21), derived from a constant proportion formula that uses estimates of adult biomass obtained from the spawner biomass survey conducted in November of the preceding year and assumes that forthcoming recruitment will be the median of observed values. To counter possible poor recruitment, a scale-down factor of approximately 0.7 is applied to the derived value. Following the May/June recruit survey during which anchovy recruitment strength

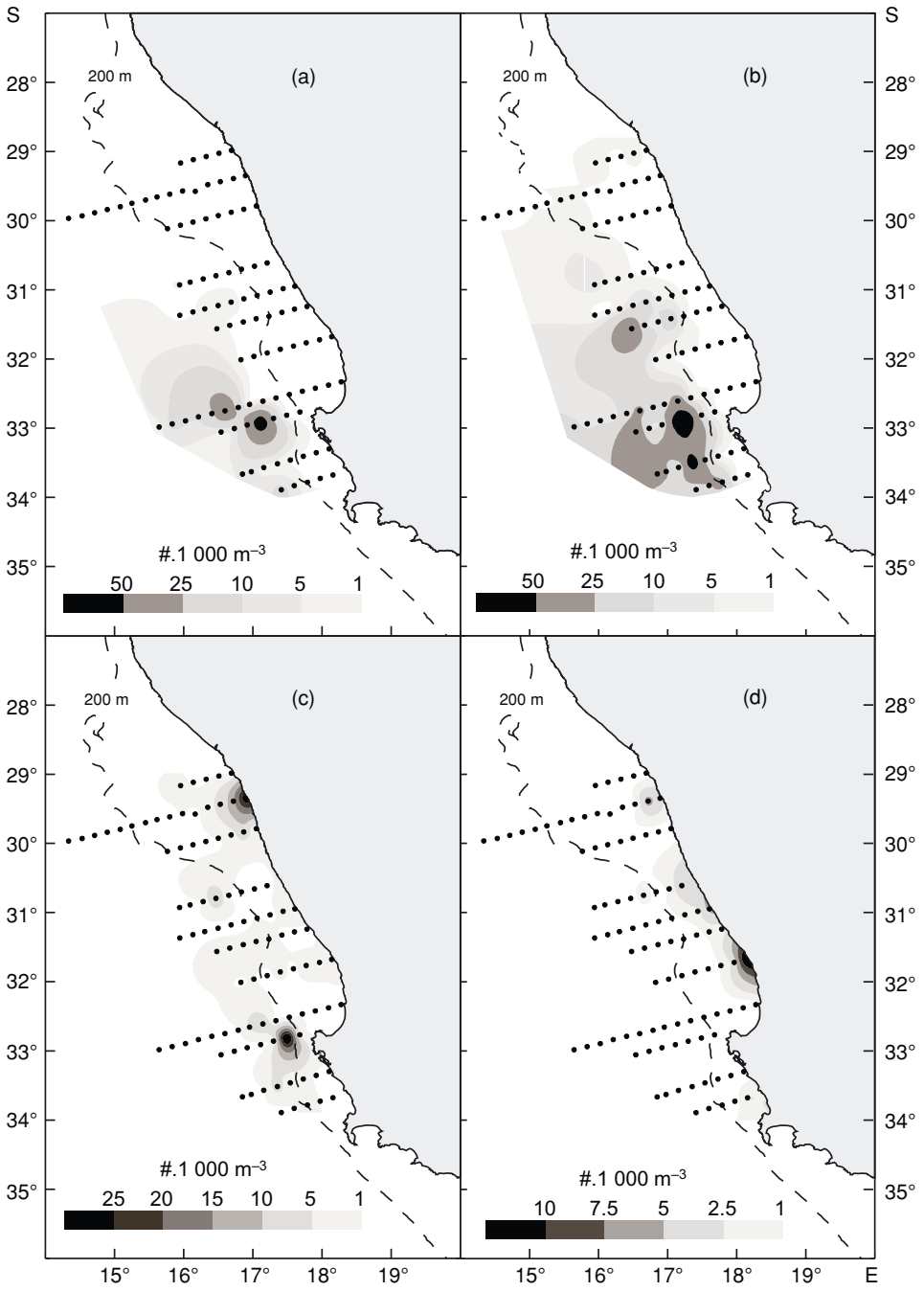

Figure 20: *Distribution by size class of anchovy pre-recruits collected using a Methot frame trawl during the March 1998 survey; (a) <20mm TL, (b) 20-34mm TL, (c) 35-50mm TL and (d) >50mm TL. Dots indicate the positions of Methot stations. Note that the density scales differ between size classes (CDvdL, unpublished data).*

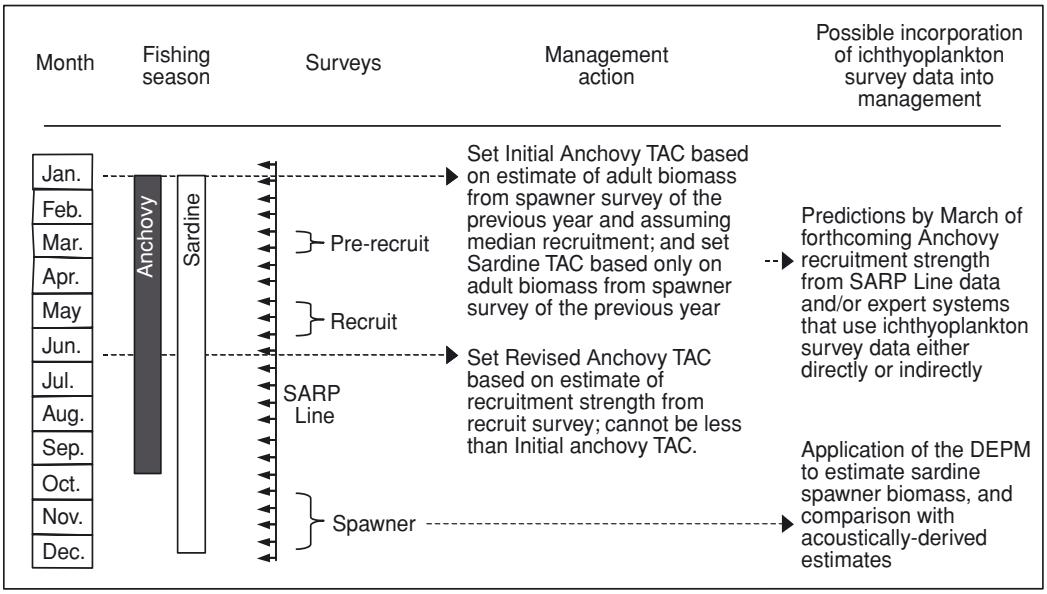

***Figure 21**: Schematic indicating the annual sequence of fishing, surveys, and management actions pertinent to management of South Africa's pelagic fishery, and how and when ichthyoplankton survey data can be incorporated into management procedures.*

is estimated acoustically, a revised (or final) anchovy TAC is set, depending on recruitment strength. If recruitment is higher than median the TAC is increased; if recruitment is median or lower the TAC remains unchanged.

Only one of the current ichthyoplankton survey programs, the SARP Monitoring Line, shows promise as a predictor of anchovy recruitment success. Simulation studies (Cochrane and Starfield 1992) have shown that predictions of anchovy recruitment that are correct 70% of the time and are made at the start of the fishing season could allow an increase in mean annual anchovy catch for the same level of risk under which the fishery is managed. Although some fishing for adult anchovy takes place during January and February, recruits are only caught in significant quantities towards the end of March. Hence predictions of anchovy recruitment strength would have to be made by the end of March at the latest in order to be of benefit to management (Fig. 21). The SARP Monitoring Line is also the only ichthyoplankton survey that provides an index that explains over 50% of the total variation in recruitment, the minimum percentage for the incorporation of such indices into management procedures for South African anchovy to show benefits in terms of risk and average catch (Barange 2001).

Despite substantial development of expert systems to forecast anchovy recruitment in the southern Benguela, and indications of their likely usefulness, these systems have yet to be incorporated into management procedures. The most recent expert system (Miller and Field 2002) is a deterministic model that uses five predictors that cover the spawning, transport and nursery areas of the anchovy life cycle to provide a qualitative (below median, median, and above median) forecast

of forthcoming anchovy recruitment strength. Two of the predictors are related to ichthyoplankton, namely an index of thermally suitable (16-19°C; Richardson et al. 1998) spawning area on the Agulhas Bank, and an index of wind velocity over the transport area between Cape Point and Cape Columbine. This system correctly predicted recruitment for 89% of the 18 year time-series, including two test years that were not used in model construction. The high success rate of this, and other expert systems, motivates strongly for their inclusion into management procedures.

Ichthyoplankton survey data have not provided substantial input into management of the South African sardine fishery. The DEPM has yet to be used to estimate sardine spawner biomass off South Africa, despite concerns regarding current acoustically-derived estimates of biomass, and its use in estimating population sizes of this species elsewhere (e.g. off California [Lo et al. 1996] and Peru [Alheit 1993]). Since only one sardine TAC is set annually (Fig. 21), predictions of recruitment strength for this species are not as important for management as they are for anchovy, but would be useful for predicting bycatch levels of juvenile sardine in the anchovy fishery.

A substantial amount of research effort has gone into attempts to understand variability in anchovy recruitment, using data derived from ichthyoplankton surveys as well as other sources (Hutchings et al. 1998). A decade ago, a multidisciplinary South African research program called the Benguela Ecology Program (BEP; Moloney et al. in press) that was primarily focused on pelagic resources was credited with having a "level of understanding of the ecosystem [that] is as good as anywhere in the world", and as being "close to resolving the recruitment problem of the anchovy" (Rothschild and Wooster 1992). A breakthrough in anchovy recruitment prediction has yet to be achieved, despite further research and promising empirical relationships. For example, observations that higher than average southeasterly (SE) winds during the October-March spawning season were followed by poor anchovy recruitment over the period 1984-1994 (Boyd et al. 1998) led to the development of a statistically significant relationship relating anchovy recruitment success to the cumulative SE wind anomaly at Cape Point (Fig. 22a). This inverse relationship was thought to occur because more wind resulted in an offshore displacement of the jet current, which increased advective loss of anchovy eggs and early larvae. However, the addition of subsequent data to this relationship removed its significance (Fig. 22b), with high SE anomalies (in 2000 and 2001) associated with exceptionally high recruitment success. This suggests a more complex relationship between seasonal wind patterns and recruitment strength than previously thought. Roy et al. (2001) proposed that a succession of weak and strong upwelling periods, and the appropriate timing of these events within the anchovy life cycle, represents the canonical pattern of environmental variability for maximizing anchovy recruitment success. This premise reconciled previous findings and provided a plausible explanation for the exceptional anchovy recruitment in 2000, but does not explain the high recruitment success recorded since 2001.

The collapse of such empirically-derived relationships both here in the Southern Benguela and elsewhere (Myers 1998) is not surprising, considering that many factors may affect the recruitment process, and any one variable may vary in relative importance from year to year in a dynamic system. For example, variability in spawning success and productivity of the west coast nursery area are both likely to contribute significantly to recruitment variability. Additionally, non-stationarity in the responses of fish populations to fishing or environmental pressure, such as regime shifts (Schwartzlose et al. 1999), changes in spawning habitat location (van der Lingen et al.

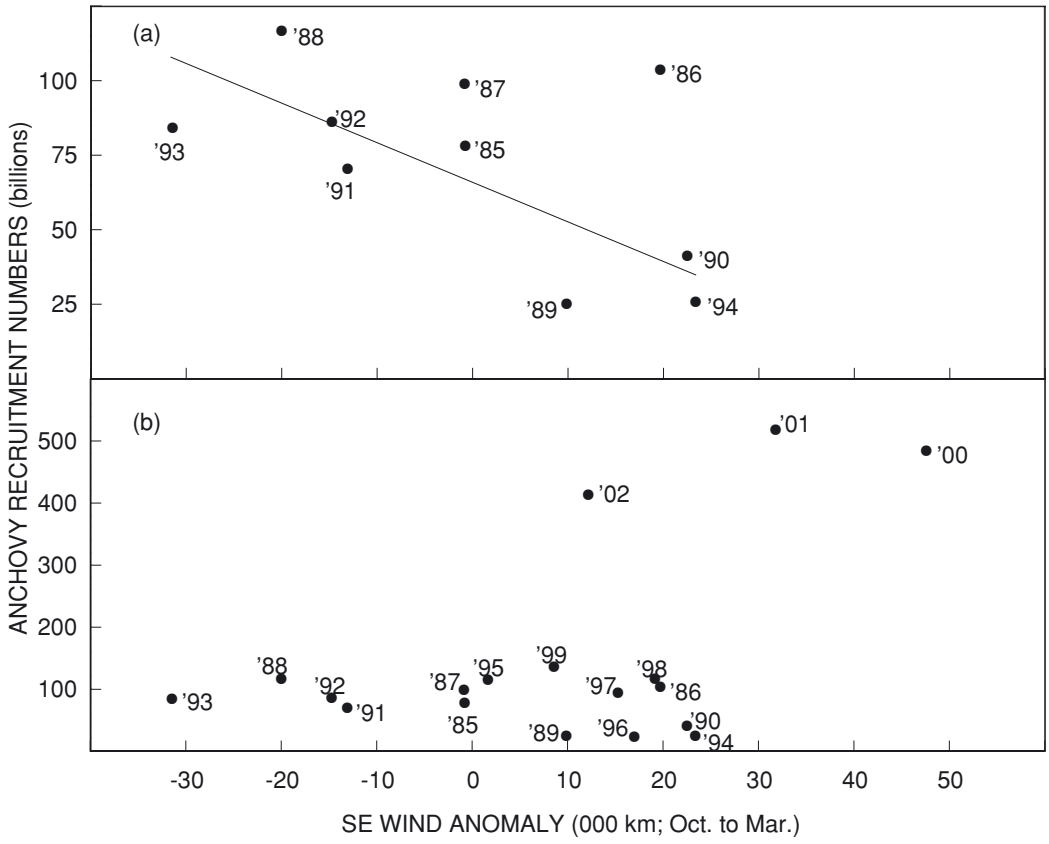

Figure 22: *Relationship between anchovy recruitment numbers and the southeast wind anomaly at Cape Point for (a) the period 1985-1994 (note that the data-point for 1986 was not included in generating the linear regression [see Boyd et al. 1998]), and (b) the period 1985-2002.*

2001), and other behavioural responses may invalidate the assumptions of long-term system stationarity that underlie conventional empirical analyses (Bakun 2002). A further complicating factor is that the understanding of micro- and mesoscale physical processes and their impact on recruitment variability in the southern Benguela is poor. For example, turbulence has been shown to have a substantial impact on survival of clupeid larvae elsewhere (see references in Bakun 1996), and offshore mesoscale eddies have been identified as areas of exceptional pre-recruit survival and production for sardine off California (Logerwell et al. 2001). A firm adherence to empirical relationships between physical and/or biological parameters and anchovy recruitment in the southern Benguela may thus be misplaced; such relationships may be spurious or transitory.

These problems suggest that a more integrative approach is required to address the "recruitment problem", such as that provided by expert systems or modeling. Ecosystem and holistic modeling

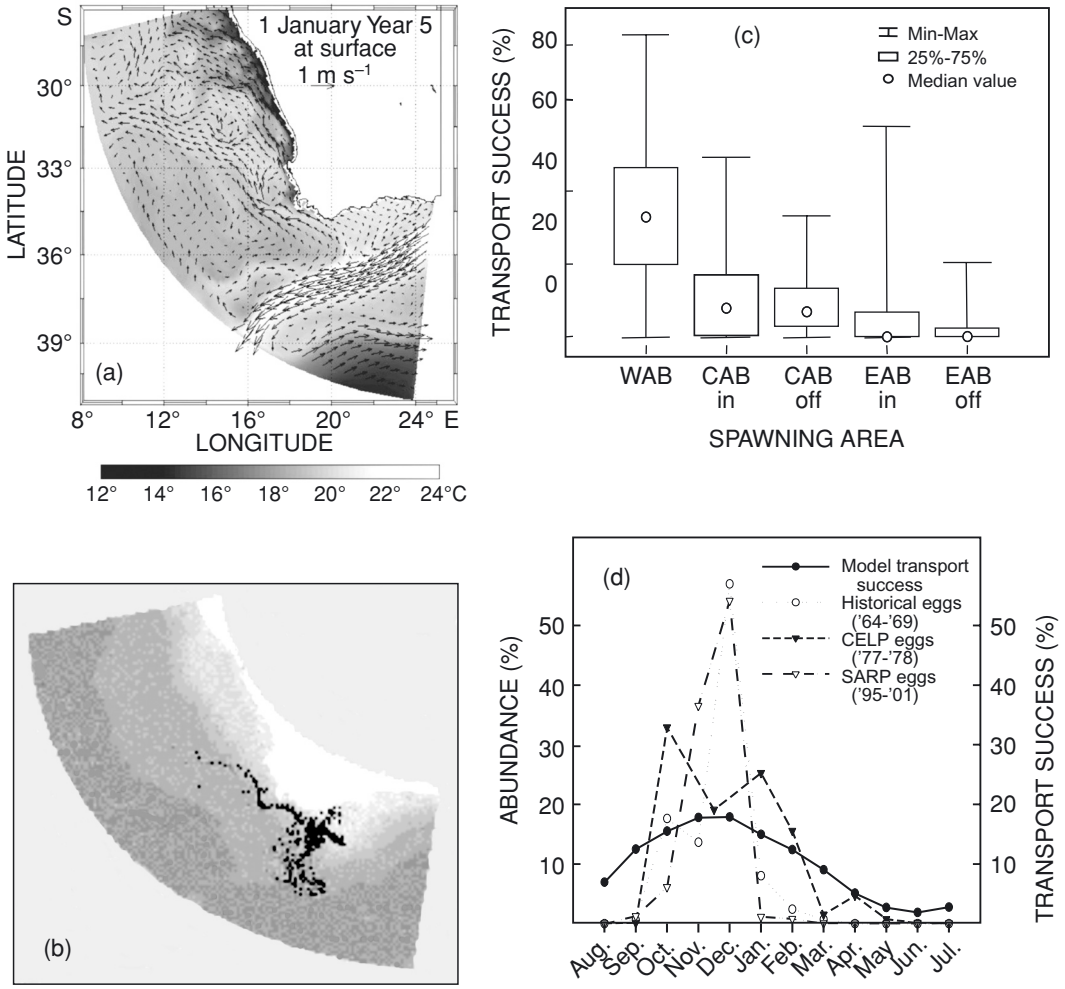

***Figure 23**: Examples of (a) the surface structure of the temperature and currents (arrows, only drawn every 3rd vector) in the Southern Benguela region simulated by a 3D hydrodynamic model (the snapshot of the 1st January of Year 5 shows the main oceanographic features of the region, including the warm, westward-flowing Agulhas Current and coastal upwelling off the West Coast; from Parada et al. 2003), and (b) output from an IBM experimental simulation showing the position of individual particles in the 3D hydrodynamic model (courtesy of C. Parada, IDYLE, University of Cape Town); results from an IBM showing transport success of particles representing anchovy eggs and early larvae as a function of (c) spawning area (the western Agulhas Bank [WAB], and the inshore [in] and offshore [off] regions of the Central (CAB) and Eastern Agulhas Banks [EAB]); and (d) a comparison between modeled transport success and observed patterns in anchovy egg abundance from three ichthyoplankton survey programmes (c and d from Huggett et. al. 2003).*

studies have recently been initiated for the southern Benguela, and provide an opportunity for improved understanding of recruitment variability through computer simulation. An example of this is the individual based model (IBM) approach, whereby the output (temperature, salinity and velocity fields) of a 3D hydrodynamic model of the sub-region is coupled to a model that tracks particles representing anchovy eggs and early larvae that have been allocated biological properties (Fig. 23a, b). Such coupling has enabled quantification of the effect of varied physical and biological parameters on the transport of particles from spawning to nursery grounds. In the southern Benguela, IBMs have been used to assess the effect of spatio-temporal variability in anchovy spawning on transport success (Huggett et al. 2003), to examine the influence of egg buoyancy on transport success (Parada et al. 2003), and to explore environmental constraints that select for observed spatial and temporal anchovy spawning patterns on an evolutionary time-scale (Mullon et al. 2002). Results from these IBMs have matched our knowledge of the spawning habits of anchovy in the southern Benguela to a large degree (Fig. 23c, d). Such agreement provides confidence that inferences made from these IBMs are meaningful, and that these experimental simulations are likely to improve our understanding of the key processes responsible for anchovy recruitment success in relation to their spawning strategy, a major step in predicting fluctuations in stock size.

Ichthyoplankton survey data from the southern Benguela have been used for management purposes to a lesser extent compared to other eastern boundary current systems where large populations of clupeids occur. Ichthyoplankton data from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys were used to develop the DEPM to estimate spawner biomass of anchovy *Engraulis mordax,* in response to perceived problems with traditional methods of stock assessment, such as acoustic surveys (Lasker 1985). It has since been used to estimate population size of clupeids in many other areas, such as Peru and the Bay of Biscay (Alheit 1993). However, more research aimed at relating clupeoid early life history stages to recruitment variability appears to have been conducted in the southern Benguela than in other eastern boundary systems. This is probably due to the large separation between anchovy spawning and nursery areas, a feature that is unique to the southern Benguela, and the consequent pivotal role of the transport process to recruitment variability in this region.

Future research concerning ichthyoplankton surveys off South Africa should be directed at obtaining a better understanding of the life history strategy of sardine, including an assessment of the south coast as a nursery area and an examination of spatio-temporal variability in spawning over the central and eastern Agulhas Banks. Additionally, research for both anchovy and sardine should be directed at assessing the effects of parental condition on egg quality and subsequent recruitment success; examining offshore retention and onshore movement of pre-recruits off the west coast; determining annual hatch date distributions; examining vertical distribution of eggs, larvae and pre-recruits off the west coast; and determining larval diets and the effects of frontal concentration mechanisms. Such research will help to improve our knowledge of factors influencing recruitment variability of these species and may assist in management of the fisheries they support.

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