EGG AND LARVAL ECOLOGY OF ANCHOVY (*Engraulis capensis)* AND SARDINE (*Sardinops sagax*) IN THE SOUTHERN BENGUELA ECOSYSTEM

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Supervisors: Dr. M.J. Gibbons and Prof. J.G. Field

To my parents, Peter and Audrey Fowler
and to Cameron Ewart Smith

"**The world is a messy laboratory for ecologists....................**"

- James Gleick in *Chaos*, 1987

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DECLARATION

I hereby declare that this thesis largely represents my own work. Although I participated in some of the cruises, the collection of samples at sea were primarily made by the technical staff at the Sea Fisheries Research Institute. Egg and larval samples were sorted in the laboratory by two technicians under my supervision. The computer programme for aging anchovy eggs was written by Ms. B. Roel. The egg abundance and distribution data presented in Chapter 3 were analyzed and written by myself as part of a paper entitled "Factors contributing to variability in anchovy and sardine spawning in the southern Benguela. III. Fish distribution and spawning success during SARP" which was coauthored with Dr. S. Painting and Ms. C. Coetzee and has recently been submitted for publication. The biomass of copepods and the sea surface temperature data used for the analyses in Chapter 4 were provided by Mr. A. Richardson and the integrated chlorophyll *a* concentration data was kindly provided by Mrs B. Mitchell-Innes. The relationships between anchovy egg abundance and sea surface temperatures in Chapter 4 are presented in a coauthored paper entitled "The effect of sea temperature and food availability on the spawning success of the Cape anchovy *Engraulis capensis* in the southern Benguela" which is currently in press. Most of this paper was written by the senior author, Mr. A. Richardson. Chapter 5, "The transport of anchovy and sardine eggs and larvae from the western Agulhas Bank to the west coast during the 1993/94 and 1994/95 spawning seasons" has been submitted for publication and my coauthor, Dr. A. Boyd was responsible for the description and interpretation of the current features and also assisted with editing draft copies. Egg abundance data from November biomass cruises were reworked from unpublished data provided by the Sea Fisheries Research Institute for the estimation of annual anchovy egg mortalities presented in Chapter 6.

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ABSTRACT

Temporal and spatial changes in the abundance and distribution of anchovy and sardine eggs and larvae in the southern Benguela ecosystem were investigated during 14 cruises over 2 consecutive summer upwelling seasons as part of the South African Sardine and Anchovy Recruitment programme (SA-SARP). Cruises were conducted each month between August 1993 and March 1994 (SARP I) and September 1994 and March 1995 (SARP II). Anchovy spawning was largely confined to the western Agulhas Bank, reaching a definite peak during spring (October and November). Sardine spawning extended up the west coast during periods when anchovy spawning reached a peak on the western Agulhas Bank. However, sardine eggs were dense on the western Agulhas Bank during peak spawning activity which appears to be bimodal, reaching a peak in the early spring (August/September) and again in late summer (February). Although the midshelf region on the WAB appeared to be the centre of both anchovy and sardine spawning in the southern Benguela ecosystem, these data suggest that anchovy and sardine spawning activity may be both spatially, and temporally separated to some extent. Mean anchovy egg densities on the WAB decreased by 53 % from 1993/94 to 1994/95 while a slight increase in mean sardine egg density (16 %) over the entire region was observed from one season to the next. Lloyd's Patchiness Index was used to investigate the distribution patterns of spawning products and the results showed that the distribution of both anchovy and sardine eggs and larvae was extremely patchy, but that the eggs of both species were more patchy than their larvae. Anchovy eggs were most abundant at sea surface temperatures ranging from 16-20°C. Changes in the extent of 16-19°C water (as a measure of spawning habitat) and the abundance of large copepods within this region reflect intra-annual changes in the intensity of anchovy spawning activity. Sardine eggs were found predominantly in water of between 14.5-21.5°C. The seasonal intensity of sardine spawning appears to vary independently of the area of 16-19°C water, but a positive correlation between the spawning activity of sardine and the monthly chlorophyll *a* concentrations on the WAB suggests that spawning may be related to their feeding conditions. A comparison of egg and larval distributions with current features from selected months during SARP supports previous studies which indicate that the frontal jet plays an important role in the transport of the early life history stages of anchovy and sardine but that the position of such transport can vary between the 200 m and 500 m isobaths. Areas of possible egg loss included the WAB, the offshore currents which can develop west of the Cape Peninsula and the outer branch of the jet off Cape Columbine. However, there is evidence that onshore currents further north may transport the eggs back to the region of the jet. The monthly estimates of anchovy egg mortality were highly variable and imprecise and these results were probably due to a combination of small sample sizes and reduced egg abundances, usually encountered at the start and end of the anchovy spawning season. The annual estimates of anchovy egg mortality during November between 1984 and 1994 were positively correlated with the patchiness of anchovy eggs during the same cruises. The effect of cannibalism in areas where eggs are particularly dense was invoked as a possible explanation for this result. It was concluded that the spawning behaviour of anchovy and sardine may be influenced by sea surface temperatures, feeding conditions for adult fish and advective processes in the southern Benguela ecosystem and these factors were discussed in terms of their possible impact on recruitment.

CHAPTER 1

Introduction

1.1 Clupeoid fisheries

Clupeoids, such as anchovies and sardines are small, relatively short-lived fish feeding mainly on plankton in shallow coastal regions of the world. As well as being an extremely important food base for larger fish, seabirds and marine mammals, clupeoids are of great commercial and socio-economic value worldwide (Hunter and Alheit 1995). These fish alone currently account for about 30% of the global yield of marine fish and contribute significantly to the global economy and overall protein resource (FAO 1995). Products such as oil, fish meal and human food derived from clupeoids are traded internationally and are important in the economies and cultures of many nations (Hunter and Alheit 1995). Clupeoids are therefore extremely important to marine fisheries as a whole and changes in population size and, consequently, the supply of these fish may have far reaching social and economic implications.

Clupeoid populations characteristically undergo fluctuations in stock size of great magnitude from time to time (Lasker and Smith 1976, Blaxter and Hunter 1982). Although often compounded by overfishing (Blaxter and Hunter 1982, Beverton 1990), historical evidence from fossil fish scales has shown that major changes in clupeoid populations can not always be attributed to fishing pressure (see Lasker 1985a for review, Shackleton 1987). Instead, most scientists agree that large interannual variations in clupeoid stocks are highly dependent on fluctuations in recruitment because of the short lifespan of these fish (Wooster and Bailey 1989, Leggett and Deblois 1994, Hunter and Alheit 1995). Large recruitments can be produced by small populations which suggests that recruitment fluctuations occur independently of changes in parent stock size (Anderson 1988, Wooster and Bailey 1989). Instead, environmental parameters, through their influence on the survival of early life stages, are the main cause of recruitment variability and concomitant fluctuations in population size (Saville and Schnack 1981, Blaxter and Hunter 1982, Lasker 1987, Bakun 1985, 1993, Cushing 1990, Armstrong and Shelton 1990).

1.2 Early life stages and recruitment variations

Clupeoids are extremely sensitive to changes in environmental conditions and are particularly vulnerable to the environment during their early life stages (Lasker 1985a, Armstrong and Shelton 1990, Leggett and Deblois 1994). Consequently, fluctuations in recruitment and ultimately population size, are likely to depend on the differential survival of the eggs and larvae (McCall 1980, Lasker 1985a, Houde 1987). Relatively high and variable mortality and growth rates are evident during these early stages in the life history of clupeoid fishes (Houde 1987). Growth rates can influence the overall survival of a cohort of developing larvae because the duration of the larval stage determines the period over which an individual is most vulnerable to environmental conditions (Pepin and Myers 1991, Leggett and Deblois 1994). Thus slight variations in the characteristically high rates of development, growth and mortality during the egg and larval stages of fish can result in tenfold or greater fluctuations in recruitment (Houde 1987).

The idea that recruitment is influenced by processes during the early life history stages of fish stems from the pioneering work of Hjort (1914). Through his research on North Sea cod (*Gadus mortura*) and herring (*Clupea harengus*) fisheries, Hjort (1914) suggested that recruitment strength is determined during a "critical period" of larval first feeding when larvae are particularly vulnerable to starvation. Hjort (1914) proposed that if food is limiting during the transition from yolk-sac to first feeding larvae, mortality would be high due to starvation. By contrast, if food is abundant during this period, larval survival would be high and recruitment would be good. Later, Hjort (1926) extended his ideas to include larval drift as a mechanism for carrying larvae out of favourable feeding areas which would lead to poor feeding conditions and consequently, to high larval mortality and poor recruitment.

Since then considerable attention has been focused on the egg and larval stages of fishes in an attempt to understand the mechanisms of recruitment. Although the "critical period" hypothesis is still highly regarded, field investigations of links between feeding conditions at the time of first feeding and either larval survival or recruitment strength are not conclusive (Anderson 1988). Several hypotheses have emerged in an effort to create generalisations which could be useful for prediction. The most well known of these are summarised in Table 1.1. Among those who attribute larval survival and recruitment success to starvation, Cushing (1973) established the "match-mismatch" hypothesis which draws attention to the overlap between the start of the annual production cycle in temperate regions and the appearance of fish larvae in the plankton. Cushing (1973) believes that recruitment variability is not restricted to a particular critical stage in larval development as suggested by Hjort (1914). He proposed that if the timing of the annual phytoplankton bloom and the subsequent production of copepod nauplii occurs either too early, or too late, then fish larvae will be mismatched with the abundant food supply, and high mortality and poor recruitment will result. Lasker's (1975) "stability" hypothesis emphasises that larval survival is determined by the presence of sufficient concentrations of food which are found only during calm periods when plankton patches are not disturbed. This concept was supported by field studies on the larvae of northern anchovy (*Engraulis mordax*) where it was observed that feeding success is greater during calm periods (Lasker 1975). Although Peterman and Bradford (1987) have also indicated that the survival of northern anchovy larvae may be associated with calm periods, larval abundance does not seem to be correlated with subsequent recruitment (Peterman *et al.* 1988). Thus the extent to which starvation alone controls larval survival and subsequent year class strength is unknown.

Table 1.1 Common hypotheses describing factors which may effect the survival of early life stages of fishes and subsequent recruitment (Anderson 1988).

Starvation hypotheses	**Author**
Critical period	Hjort 1914
Match-mismatch	Cushing 1975
Food production	Parrish &MacCall 1978, Bakun &Parrish 1980
Vertical stability	Lasker 1975, 1978
Resource use competition	Fraser 1970, van der Veer & Sadee 1984, Frank 1986
Growth-mortality	Ware 1975, Shepherd and Cushing 1980
Predation hypotheses	
Gelatinous predator	Fraser 1970
Fish predator/cannibalism	Oiestad 1985
Juvenile predation	Sissenwine 1984
Physical dispersal hypotheses	
Transport-retention	Hjort 1926, Parrish *et al.* 1981
Disease	
Transmission	Sindermann 1970
Temperature	Burreson 1981

According to the "larval transport" hypothesis of Parrish *et al.* (1981), advective processes are the primary agents of recruitment variability. These authors proposed that temporal and spatial variations in prevailing currents will result in variable egg and larval survival as spawning products are either retained in, or transported away from, areas suitable for growth. An extension of this idea was proposed by Iles and Sinclair (1982), from research on Atlantic herring. These authors suggested in their “larval retention” hypothesis that stock size is determined by the size of its larval retention area. Several authors have demonstrated that eggs and larvae are transported by currents and that spawning adaptations are linked to current features (Shelton and Hutchings 1982, Norcross and Shaw 1984). However, there is little or no evidence to suggest that transport into unfavourable areas will affect larval survival and subsequent recruitment strength (Wooster and Bailey 1989).

More recently, Cury and Roy (1989) proposed the “optimal environmental window” hypothesis which ties in both starvation and advective processes and relates recruitment success to upwelling intensity. These authors proposed that a dome-shaped relationship exists between recruitment success and upwelling intensity, where moderate upwelling provides the best suite of feeding and advective processes for the survival of developing larvae. These ideas are supported by an analysis of clupeoid stocks off Peru, West Africa and California which indicate that a consistent environmental “window” exists wherein optimal wind speeds of around 5-6 m. s^{-1} result in enhanced annual recruitment (Cury and Roy 1989). In the southern Benguela ecosystem, support for the “Optimal environmental window” hypothesis is provided by Waldron (1995) who showed that a dome-shaped relationship exists between annual potential new production and anchovy spawner biomass. This relationship indicates that both too little and too much upwelling is detrimental to the fishery.

Several authors however, indicate that predation of eggs and larvae by invertebrates (Hunter and Kimbrell 1980) and fishes (Pepin *et al.* 1987, Bailey and Houde 1989) and the incidence of cannibalism (Valdes *et al.* 1987, Valdes Szeinfeld 1993) cannot be ruled out as important regulators of population size. Nevertheless, few investigations have been able to measure predation rates in the field with any degree of accuracy and therefore the contribution of predation to recruitment variation is not known (Anderson 1988, Bailey and Houde 1989, Leggett and Deblois 1994).

Decades of research on the subject indicate that predation, starvation and advection are likely to be the main agents of mortality in the early life history stages of fishes and are therefore the primary causes of recruitment variations. However, it is not possible to highlight any one of these factors as a primary explanation for recruitment fluctuations. Evidently, a number of different factors must interact at several different temporal and spatial scales to influence larval survival and recruitment and there is no simple, unifying hypothesis which can be used to explain variations in year class strength for all species and in all systems (Wooster and Bailey 1989).

It is important to acknowledge that generalities with respect to recruitment mechanisms cannot be made across species groups because mechanisms for survival and recruitment are different for each group (Houde 1987). However, Bakun and Parrish (1991) have shown that comparisons between similar species inhabiting similar environments are useful for identifying the combination of environmental components which optimise recruitment success. In a study comparing fish populations inhabiting the California Current, the Benguela Current and the Southwestern Atlantic shelf ecosystems, Bakun (1993) identified a triad of three interacting factors which promote growth and survival of eggs and larvae and therefore contribute to successful recruitment. These factors include (i) enrichment of the system by physical processes such as upwelling; (ii) concentration of food particles through stable ocean conditions or strong convergence in frontal zones; and (iii) larval retention in, or transport to suitable habitats (Bakun 1993).

Although there is substantial evidence that recruitment may be enhanced by a certain constellation of three broad environmental conditions (Bakun and Parrish 1991), predictive models for individual systems have been difficult to obtain (Hunter and Alheit 1995). This is mainly due to a short time-series of data available and the lack of environmental information to accompany them.

1.3 The Sardine and Anchovy Recruitment Programme (SARP).

In recent years, there has been an increased interest in tackling the "stock-recruitment" problem of commercially important species in an interdisciplinary and international manner. Within this framework, an international Sardine and Anchovy Recruitment programme (SARP) was initiated in the mid 1980's by the Intergovernmental Oceanographic Commission (IOC) and the United Nations Food and Agricultural Organisation (FAO) to gain a better understanding of the biological-oceanographic processes which govern recruitment fluctuations of marine fishes (IOC/UNESCO 1990). SARP has received worldwide support because it offers the most promising approach presently available for addressing recruitment variability, and was selected as a central project of the International Recruitment Programme (IREP) (Bakun and Parrish 1991). The primary intention of SARP was for several nations to work simultaneously on the same fish species group inhabiting different regional ecosystems, so that data could be collected and compared worldwide. The rationale behind this is that the application of the comparative method (Mayr 1982) should facilitate the task of unravelling the common mechanisms which lead to recruitment variability (IOC/UNESCO 1990). The UK, Denmark and Germany were the first to implement SARP and investigated sprat (*Sprattus sprattus*) recruitment in the North Sea. Portugal and Spain are involved in a study of sardine (*Sardina pilchardus*) recruitment in Iberian waters while the recruitment of the Southwest Atlantic anchovy (*Engraulis anchoita*) is being investigated by Argentina, Uruguay, Brazil, Germany and Sweden. Anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) recruitment along the Chilean coast has also been addressed (IOC/UNESCO 1991).

The South African Sardine and Recruitment programme (SA-SARP) was launched in 1993 in response to wide variations in the annual recruitment of anchovy (*Engraulis capensis)* and sardine (*Sardinops sagax);* two pelagic species which are of great commercial and socio-economic value to the region. Despite the implementation of a conservative management strategy in 1984 (Cochrane and Hutchings 1995), dramatic fluctuations in the anchovy population was observed during the 1990's, and there has been a general decline between 1992 and 1996. Since the mid 1980's, the abundance of sardines has gradually increased and sardine spawner biomass was greater than anchovy spawner biomass during the period 1994 to1996 (Fig. 1.1). Although there is some doubt about the accuracy of these biomass estimates (as a consequence of biases caused by the target strength used in their calculation, Barange and Hampton 1997), the SA-SARP programme was implemented at a significant point in the history of pelagic stock fluctuations in the southern Benguela ecosystem. The main objective of SA-SARP was to identify the factors most frequently limiting recruitment in these species and to try and develop the ability to predict their spawning success from year-to-year (Painting 1993, Painting *et al.*

subm.a). To fulfil these objectives, the southern Benguela ecosystem was surveyed monthly over two consecutive anchovy spawning seasons (1993/94 and 1994/95).

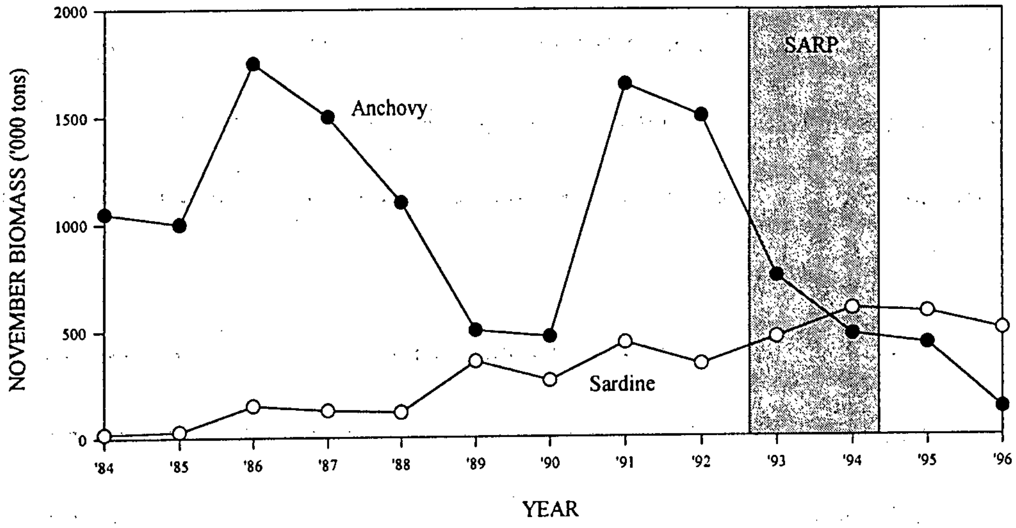

Figure 1.1 Estimates of anchovy and sardine spawner biomass in the southern Benguela ecosystem since 1984. The grey area indicates the the period over which SARP was conducted (SFRI unpublished data).

Although one of the main aspects of the international SARP initiative was to analyse events within the spawning season, South Africa was the first nation to adopt an intensive "within-year" approach to addressing the recruitment problem. Instead of averaging conditions over the entire spawning season, SA-SARP addressed the intra-annual changes in biological and physical processes in an attempt to reveal linkages and causal mechanisms of the recruitment process.

As it is largely accepted that recruitment is profoundly influenced by the impact of environmental factors on the differential survival of egg and larval stages, an integral part of SA-SARP was to specifically focus on these stages of anchovy and sardine. Therefore, based on intensive field collections made during SA-SARP (referred to as SARP hereafter), this thesis provides an insight into within-season variations in the abundance and distribution of the early life stages of the South African anchovy and sardine and the biological and physical factors influencing these variations.

1.4 Clupeoids in the Benguela Ecosystem

1.4.1 Previous research on the early life stages of anchovy and sardine.

Our knowledge of ichthyoplankton assemblages in the Benguela system as a whole is limited (Olivar and Shelton 1993). In the northern Benguela ecosystem, surveys of sardine and anchovy spawning have been conducted periodically since 1960 (Le Clus 1990), and the seasonal occurrence of sardine eggs there was first documented by Matthews (1963) and Stander (1964). An intensive sampling initiative known as the South West African Egg and Larval Survey (SWAPELS) was conducted monthly during the summers of 1972/73 and 1973/74 to assess the temporal and spatial spawning habits of anchovy and sardine, as well as other commercially important species (O'Toole 1977). Based on samples taken during SWAPELS, King (1977a) described the abundance and distribution of anchovy and sardine eggs, while O'Toole (1977) investigated larval populations to provide a comprehensive assessment of the spawning areas and seasons of anchovy and sardine in relation to sea surface temperatures and salinity. Although these early studies described the temporal and spatial characteristics of anchovy and sardine eggs and larvae in the northern Benguela system, no detailed knowledge of the physical and biological environment such as upwelling, primary production and current movements was available at the time (O'Toole 1977). Therefore, O'Toole (1977) concluded that these aspects required further investigation in order to gain a better understanding of the ecology of the early life history stages of anchovy and sardine. Consequently, SWAPELS commenced again in 1978 and the area between the Cunene River and Luderitz was sampled on a monthly basis during the 1978/79, 1979/80 and the 1981/82 spawning seasons (October to March) of anchovy and sardine (Olivar and Shelton 1993). Besides contributing to knowledge of spawning locations and seasonality, Badenhorst and Boyd (1980) used data collected over the first two seasons to examine the larval and juvenile distribution of anchovy in relation to hydrological features, while Boyd and Hewitson (1983) extended their own examination of larval distribution to include data collected during the following two seasons (1980/81 and 1981/82). More recent studies have addressed both the horizontal and vertical distributions of anchovy and sardine eggs and larvae in order to provide detailed knowledge of the spatial patterns of anchovy and sardine egg and larval distributions in relation to their environment off the Namibian coast (Olivar 1990, Olivar *et al.* 1992).

In the southern Benguela ecosystem, the longest consecutive time series for estimates of anchovy and sardine egg and larval abundance and distribution extends from 1950 to 1969, although these data were not quantitative and never fully documented. Preliminary descriptions of anchovy egg distribution were documented by Anders (1965) for monthly samples taken in 1964 and 1965. In his examination of the distribution of anchovy and sardine off South Africa, Crawford (1981a) and Crawford (1981b) present some of the egg and larval abundance and distribution data collected during this period. In October 1976, Shelton and Hutchings (1982) investigated the effect of water movement on the transport of anchovy eggs and larvae in the direction of the recruitment ground. These authors were the first to describe the transport of eggs and larvae in the southern Benguela and emphasised the role of the shelf-edge frontal jet off the Cape Peninsula in the movement of eggs and larvae from the western Agulhas Bank to the west coast of South Africa.

The most comprehensive data set for the southern Benguela region was provided by the Cape Egg and Larval Programme (CELP) which involved monthly surveys between Cape Agulhas and

Cape Columbine for the period August 1977 to August 1978 (Shelton 1986). CELP provided the best seasonal and spatial coverage and concurrent environmental data for the South African anchovy and sardine and provides a description of the spawning habits of these species and others (mainly redeye *Etrumeus whiteheadi,* lantern fish *Lampanyctodes hectoris* and hake *Merluccius spp*). Most of the egg and larval abundance and distribution data collected during CELP were documented by Shelton (1986), who described three life history "strategies" to cope with oceanographic variability *viz.* serial summer spawning (*e.g.* anchovy and sardine), winter spawning (*e.g.* hake) and spawning throughout the year (*e.g.* lantern fish). Besides Shelton's (1986) thesis, several publications emanated from the programme. In particular, Shelton and Hutchings (1990) summarised most of the environmental data, emphasising the conditions which favour anchovy spawning.

In the laboratory, King *et al.* (1977b) monitored the influence of sea temperature, dissolved oxygen and salinity on the development of sardine larvae caught off the Namibian coast. In South Africa, the development of anchovy eggs under different environmental conditions was investigated by King *et al.* (1978) and similarly, Brownell (1983) monitored the growth and development of anchovy and sardine eggs and larvae at different water temperatures.

Annual variations in anchovy and sardine egg abundance and distribution have been monitored since 1983 each year during November as part of the annual SFRI spawner biomass surveys. During these surveys, sampling is intensive (every 5 nm) and extends from the Eastern Agulhas bank to the Olifants River mouth on the west coast. Anchovy egg abundance estimates from these surveys have been used mainly to calculate egg mortality and egg production estimates for the calculation of the anchovy biomass (Armstrong *et al.* 1988, Shelton *et al.* 1993). Based on egg abundance estimates and current features measured during these surveys, Boyd *et al.* (1992) examined the movement of eggs over the entire southern Benguela region. Roel *et al.* (1994) used anchovy and sardine egg abundance data in relation to adult fish and the environment during selected November biomass cruises to examine the importance of the Agulhas Bank for spawning. Aside from studies on the abundance and distribution of eggs and larvae, several studies have investigated the predation and cannibalism of anchovy eggs in the southern Benguela (Valdes *et al.* 1987, Valdes Szeinfeld and Cochrane 1991 and Valdes Szeinfeld 1993).

Much of our current understanding of the abundance and distribution of anchovy and sardine ichthyoplankton stems from Shelton's (1986) work during CELP and the annual November surveys. Although the CELP survey shed much light on the spawning activities of both the anchovy and sardine, there is still much uncertainty in this regard. Also, little is known about the ecology of the eggs and larvae of these species and the variations which occur within the spawning season.

1.4.2 Current understanding of the life histories of anchovy and sardine in the southern Benguela ecosystem.

Like clupeoids in other eastern boundary systems, the southern subpopulations of anchovy and sardine in the Benguela Current are well adapted to their highly variable upwelling environment (Shelton 1986). As successful bet-hedgers, these small pelagic fishes spawn several times over an extended period during the austral summer (August to March; Melo 1994, Akkers *et al.* 1996) when the Agulhas Bank is characteristically structured by thermoclines and temperature fronts

(Shelton and Hutchings 1990). Anchovy spawning peaks in about November each year while sardine have a less clearly defined season with peaks in about August/September and February (Shelton 1986). Sardine and anchovy spawning is concentrated in a relatively stable, strongly stratified region on the Agulhas Bank where eggs develop in warm surface waters, prevalent during the summer months (Fig. 1.2, Shelton and Hutchings 1990, Hutchings 1992). Compared to anchovy however, sardine spawn over a wider area which occasionally includes the west coast (Crawford 1981a, Shelton 1986). Spawning products on the Agulhas Bank are transported westwards by convergent flow on the western Agulhas Bank and northwards from the spawning grounds by a jet current which usually tracks the shelf edge (Shelton and Hutchings 1982, Boyd *et al.* 1992). Although offshore losses may occur (Boyd *et al.* 1992, Hutchings 1992), the movement of eggs and larvae in the jet ensures that they are retained in the system and eventually reach the productive nursery grounds inshore on the west coast. Larvae continue to grow rapidly in the inner shelf region where feeding conditions are thought to be good throughout the year (Hutchings 1981). Young fish then move south to the spawning grounds on the Agulhas Bank and it is during this southward migration that anchovy and sardine recruit to the fishery in about April each year (Hutchings 1992). These behavioural adaptations allow anchovies and sardines to optimise their survival in the highly variable and unpredictable Benguela ecosystem.

1.5 Aims of this study

The primary goal of this project is to examine within-season variations in the abundance and distribution of the eggs and larvae of the South African anchovy and sardine throughout the spawning season (September to March) and to relate these variations to environmental conditions within the Benguela ecosystem for two such seasons. It was envisaged that links between

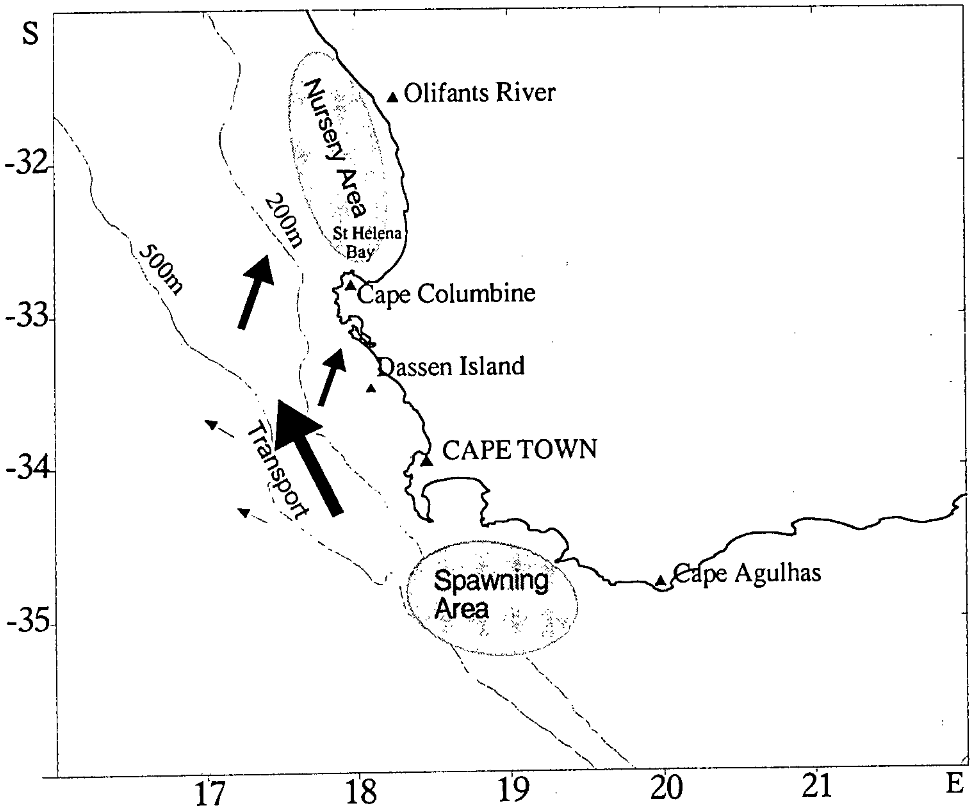

Figure 1.2 Schematic representation of the life history of anchovy in the southern Benguela Ecosystem (adapted from Painting 1993).

patterns in the ichthyoplankton and environmental conditions would provide greater insight into the processes which influence the survival of early life history stages, and possibly recruitment.

The first step in this sequence is to assess both the spatial and temporal patterns of anchovy and sardine egg and larval abundance each month throughout the spawning season. These patterns are then used to re-examine the distribution, duration and peaks in the spawning activities of these two species.

Secondly, as an indicator of spawning intensity, the spatial and temporal patterns in the abundance of anchovy and sardine eggs are related to the distribution of adults, sea surface temperatures and the feeding environment for adult spawners. In particular, the relationship between the distribution of eggs and the surface area of water between 16°-19°C is examined as it has been hypothesised (King *et al.* 1978, Armstrong *et al.* 1991. Richardson in press) that environmental conditions within this temperature range constitute a favourable habitat for anchovy and sardine spawning. The biomass of large copepods within this area is used as an indication of the zooplankton food environment for adult spawners, while chlorophyll *a* concentrations over the western Agulhas Bank are used to assess feeding conditions for phytoplankton feeders.

A comparison of egg and larval distributions with current features from selected months will be used to validate and elaborate the conceptual model of transport of pelagic eggs and larvae in the southern Benguela ecosystem by examining intra-annual variation in current features between Cape Agulhas and the Olifants River in relation to spawned products.

Month-to-month variations in the mortality rates of anchovy eggs are examined. These estimates are calibrated by comparing them with estimates calculated from the data sets for the two November surveys which are more comprehensive. The relationship between anchovy egg mortality estimates from November surveys since 1984 and the spatial distribution patterns of eggs during these cruises are examined in order to explain possible causes for inter-annual variations in egg mortality rates. To assess whether inter-annual variations in mortality rates of anchovy eggs are large enough to account for major recruitment fluctuations, annual mortality rates are compared with the anchovy recruitment biomass the following year.

Finally, these results are discussed in relation to their implications for recruitment success.

CHAPTER 2

Methods

2.1 General

Intensive field sampling during SARP was undertaken each month aboard either FRS *Algoa,* FRS *Africana* or the Norwegian vessel *Dr. Fidtjof Nansen*, from August 1993 to March 1994 (SARP I) and between September 1994 to March 1995 (SARP II). No cruise was undertaken during January 1995, because no research vessel was available. The study area extended from the mouth of the Olifants River on the west coast to Cape Agulhas on the south coast (Fig 2.1). This region included the anchovy spawning area on the western Agulhas bank (WAB), the transport area off the Cape Peninsula and Dassen Island on the west coast, and the major nursery area in St Helena Bay further north. A standardised survey grid, with transect lines perpendicular to the coastline, was adopted for all 14 cruises (Fig. 2.1). During SARP I, sampling stations were spaced every 10 nm along seven lines which extended from the coast to the 200 m or 500 m depth contour. Additional lines were sampled during SARP II to improve coverage of the area. Sampling along the Cape Columbine line was also intensified during SARP II and stations were spaced every 5 nm in order to identify the bifurcation of the Columbine Jet described by Shannon (1985). Monthly changes in the intensity of sampling can be seen from the egg and larval distribution maps in Chapter 3. Stations were identified by line and station number. A summary of the number of lines and stations where ichthyoplankton samples were taken each month is provided in Table 2.1. During November 1993 and November 1994, the SARP survey grid was incorporated into the expanded, more intensive survey grid of the annual Spawner Biomass survey conducted by the Sea Fisheries Research Institute (see Hampton 1987). The data sets from these two surveys are more detailed because information collected from both survey grids

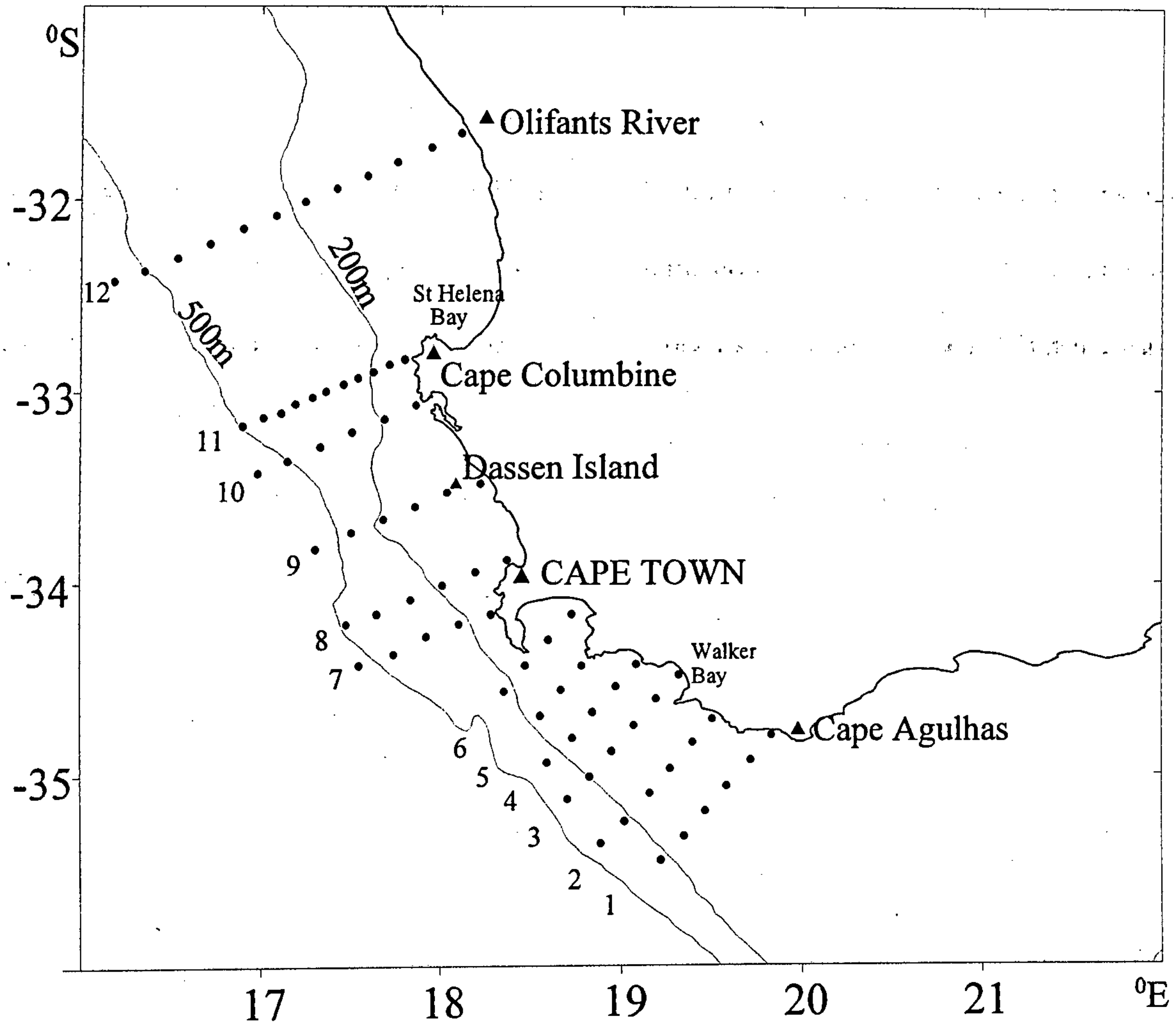

Fig. 2.1 Map showing the area which was sampled during SARP I and SARP II. Each transect is numbered and the dots indicate the positions for each station.

are included in this study.

2.2 Collection of Oceanographic data

Currents were measured while underway (10 knots) and on station using 150 kHz RDI narrow band Acoustic Doppler Current Profilers (ADCPs) mounted in the hull of the vessel. The ADCP resolves the Doppler shift of beam reflections from particles in different layers of the water column (depth "bins") and from the bottom. Data were recorded from 8 m depth "bins" and over several periods of 3 to 5 minutes at each position (Boyd *et al.* 1992).

Fish distribution and density was determined from hydro-acoustic surveys which were conducted while underway. Standard echo integration methods were used for this procedure (MacLennan and Simmonds1992, Hampton 1987). Fish were collected from *ad hoc* midwater trawls for the identification of target species and the collection of biological fish data.

Table 2.1 A summary of the total number of lines and stations where CalVET and Bongo net samples were taken during SARP I and SARP II.

SEASON	CRUISE	MONTH	CalVET		BONGO	
			LINES	STATIONS	LINES	STATIONS
SARP I	SARP 1	August 1993	3	17	0	0
	SARP 2	September 1993	5	21	3	10
	SARP 3	October 1993	5	35	5	38
	SARP 4	November 1993	15	178	4	21
	SARP 5	December 1993	5	41	5	22
	SARP 6	January 1994	4	28	4	23
	SARP 7	February 1994	5	35	5	26
	SARP 8	March 1994	4	24	4	22
SARP II	SARP 9	September 1994	10	52	10	47
	SARP 10	October 1994	12	87	12	81
	SARP 11	November 1994	20	189	7	37
	SARP 12	December 1994	9	39	9	36
	SARP 13	February 1995	12	76	12	70
	SARP 14	March 1995	12	72	12	71

At each station, a thermistor and Aquatracker fluorometer attached to a Magnum Rosette sampler were used to obtain vertical profiles of temperature and fluorescence. Water samples were collected from both the sea surface and the fluorescence maximum by means of 18 *l* Niskin bottles for nutrient and chlorophyll analysis.

Mesozooplankton in the upper 200 m, or from above 10 m off the bottom in shallower water, were collected using Bongo nets which were hauled vertically to the surface. These nets were fitted with 200 µm mesh and electronic temperature, depth and flow sensors. All samples were preserved in 5 % buffered saline formalin and the major copepod species were identified, staged and counted later in the laboratory.

2.3 Collection and processing of anchovy and sardine eggs

Sardine and anchovy eggs were collected by means of a CalVET net hauled vertically from a maximum depth of 70 m or from within 5 m of the bottom (Smith *et al.* 1985). The unit had a mouth area of 0.05 m^2 and was fitted with a 300 μm mesh. Samples were immediately preserved in 5% buffered formalin. In the laboratory, a total of 621 CalVET samples were sorted and anchovy and pilchard eggs were identified, and counted (King 1977b, King *et al.* 1978, Brownell 1979). Egg abundance at each station was quantified per m^2 for further analysis.

2.4 Collection and processing of anchovy and sardine larvae

Larvae were sampled at each station using a double-oblique Bongo net of 0.255 m^2 mouth area. Both units were fitted with 300 μm mesh. The nets were towed at a speed of 2 knots from a maximum depth of 70 m, or to within 5 m of the bottom where shallower and returned at a speed of 0.5 $m.s^{-1}$. Bongo nets were equipped with electronic sensors to measure depth and temperature, while the volume of water filtered during the tow was measured by means of a calibrated electronic flowmeter fitted in the mouth of one of the nets. On several occasions it was noted that the flowmeter was not operational. For these stations, the volume filtered by the nets was calculated from the linear regression equation 2.1 ($r^2 = 0.733$, $n = 507$):

$$V = 0.33\,D - 26.31 \text{ .... } \textit{Equation}\ 2.1$$

where: V = volume filtered (m^3)

D= duration of the tow (seconds)

This relationship was established by regressing the volume filtered by the nets and the duration of each tow for all samples taken during that cruise (see Table 2.1).

Both nets were rinsed as quickly as possible on retrieval and the sample collected from one net was preserved in 5% buffered saline formalin while the other sample was preserved in 95% ethanol. While formalin is a better fixative than ethanol, its low pH often leads to the dissolution, etching, pitting or discolouration of larval otoliths (Butler 1992). Although preservation in 95% ethanol ensured that the pH of most samples was maintained at pH 8, it often fell to below this level and larval otoliths were inadequately preserved. This was due either to dilution of the preservative with water in the tissues of gelatinous zooplankton in the samples, or to erroneous volumes of alcohol being added to the samples at sea. This reduced the number of samples with well preserved otoliths quite considerably.

The alcohol preserved samples were sorted in the laboratory except in cases where the larvae were not well preserved, in which case the formalin preserved replicas were sorted instead. All sardine and anchovy larvae were removed, identified and counted (King 1977b, King *et al.* 1978, Brownell 1979). The total length of anchovy and sardine larvae was measured with an ocular micrometer from subsamples containing no more than 200 larvae per species at each station.

To enable a comparison with other studies, larval lengths were corrected for shrinkage. Larvae are known to shrink substantially upon death when osmoregulatory processes cease and water loss occurs (Theilacker 1980, Mc Gurk 1985). This process is enhanced by abrasion against the net during capture and handling of the sample thereafter (Theilacker 1980). The degree of shrinkage caused by these processes depends both on larval size and the time period between capture and preservation. Assuming an average net-treatment and handling time of 10 minutes per sample, lengths of preserved larvae were adjusted to live lengths using the relationship and shrinkage factors (P_1, P_2 & P_3) reported by Theilacker (1980) for northern anchovy *Engraulis mordax* given by equation 2.2:

$$lnL = lnX_1 + P_1 \exp^{(-P_2 X_1 X_2^{P_3})} \text{ .... } \textit{Equation } 2.2$$

where: L is live size

$P_1 = 0.289$

$P_2 = 0.434$

$P_3 = -0.68$

X_1 = preserved size (mm)

X_2 = combined net treatment and handling time (minutes)

Although no further shrinkage is thought to occur for northern anchovy (*Engraulis mordax*) preserved in 90% ethanol, Theilacker (1980) has shown that the ratio of preserved length to live length was 0.92 for larval anchovy of all lengths preserved in 5% formalin. Corrections for preservative-related shrinkage were therefore also made for larvae preserved in formalin.

Length frequency distributions for both anchovy and sardine were obtained using 1 mm size classes (live-length). As larvae develop, they are able to visually detect the sampling gear during daylight hours and avoid the net by swimming out of its path (Hewitson 1987). Consequently, undersampling occurs during daylight hours and this increases with increasing larval size (Ahlstrom 1954, 1959, Hewitson 1987). In instances where Bongo samples were taken during daylight hours, larval abundances were corrected for net avoidance using size-specific day/night ratios for larvae between 8 mm and 22.5 mm (Hewitson 1987) and applying the correction factors detailed by Hewitt and Methot (1982). The relationship between these known day/night ratios and each millimetre size classes is given by equation 2.3 ($r^2 = 0.96$, $n = 10$):

$$R = 0.352l - 0.554 \text{ .... } \textit{Equation } 2.3$$

where: R = corrected length (mm)

l = captured length (mm)

Larval abundance is expressed as number. m^{-2} in order to allow for ready comparison with the egg data.

CHAPTER 3

Patterns in the abundance and distribution of anchovy and sardine eggs and larvae

3.1 Introduction

Spatial and temporal patterns in the abundance and distribution of planktonic fish eggs and larvae reflect the location, timing and mode of adult spawning, the rates of predation on the eggs and the influence of circulation features such as eddies, fronts and thermoclines (Chesney and Alonso-Noval 1989, Brodeur *et al.* 1996, Stabeno *et al.* 1996). These factors may interact on various scales to create a mosaic of egg and larval abundance and distribution patterns that vary both intra- and inter-annually (Brodeur *et al.* 1996). In order to understand the processes which influence these patterns, it is important to describe and analyse their spatial and temporal characteristics.

In the southern Benguela region, the spawning seasons and locations of the anchovy and sardine were first described by Anders (1965) and Crawford (1981a, 1981b), for the period 1950 - 1969. The spawning strategies of anchovy and sardine were re-examined each month between August 1977 and August 1978 by Shelton (1986). Although the distributions of anchovy and sardine eggs are documented each year during November (SFRI unpublished data), intra-annual variations in the patterns of abundance of anchovy and sardine have not been investigated since the late 1970's. This chapter examines the intra-seasonal and geographical distributions of anchovy and sardine eggs and larvae as estimated during SARP.

3.2 Data analysis

The total number of anchovy and sardine eggs and larvae for each month over the sampling area during SARP I and II are presented separately for the Western Agulhas Bank (WAB) and the west coast (WC) in order to analyse the anchovy spawning area (WAB) and transport region (WC) separately (Shelton 1986, Shelton and Hutchings 1990, Hutchings 1992). These estimates were based on the geometric mean of monthly egg or larval densities and the proportion of the total sampling area in which eggs or larvae were found. The total area sampled is the area enclosed by the southern-most and northern-most line, the coastline and a western boundary formed by joining the most offshore stations on each line. Since anchovy and sardine select specific areas for spawning (Shelton 1986), the data set consisted of a large proportion of empty samples which can be regarded as unoccupied 'habitat' (Pennington 1983). Thus, density estimates were calculated as the geometric means of non-zero samples (Pennington 1983). Arithmetic means were inappropriate in this case because the egg and larval data were not normally distributed (Zar 1984). Although mean densities are usually employed to represent abundance, during some months (*i.e.* January and February 1994) mean anchovy egg densities for non-zero samples were the same as the total number of eggs sampled, because all the eggs were found at a single station. In such cases, mean values are meaningless and total numbers provide a better estimate of abundance. Average seasonal egg and larval abundance over the WAB, the WC and both regions combined are presented as densities.

Differences in the mean abundances of anchovy and sardine eggs between SARP I and II were tested using a non-parametric Kruskal-Wallis test, because within-group variances of $\log_{10}$-transformed data were not equal (Levene's test, $p<0.05$) (Millikan and Johnson 1984) and therefore the data did not meet the requirements for performing parametric statistics.

Several measures were used to summarise the distribution of eggs and larvae. Firstly, the percentage occurrence of either eggs or larvae was used as an indication of whether the distributions of eggs and larvae were widespread or concentrated over the entire sampling grid during SARP. These monthly percentages were arcsine transformed (Zar 1984) to satisfy the assumptions of t-tests. The assumption of homogeneity of variance among groups was verified using Levene's test (Millikan and Johnson 1984). Based on these transformed data, a t-test for independent sample means (Zar 1984) was used to test whether the distributions of anchovy and sardine larvae were more widespread than their eggs during SARP.

Secondly, the ratio of the total number of eggs on the WAB to the total in entire sampling grid was calculated for both species to compare the distribution of anchovy and sardine eggs between the WAB and the WC. A Mann Whitney *U*-test was employed to test whether there was a significant difference between the average proportion of anchovy and sardine eggs on the WAB.

Lastly, Lloyd's patchiness index (Lloyd 1967), was used to assess statistical patterns of egg and larval abundance. As a density-independent measure of pattern, the use of this index allows a comparison between populations despite differences in their relative abundances (Hewitt 1981). In a randomly dispersed population the value of the index is equal to 1. For a uniform pattern the index is < 1 and for aggregated patterns the index is >1. Lloyd's patchiness index (LPI) is given by equation 3.1:

$$LPI = 1 + \frac{(s^2 - \bar{x})}{\bar{x}} \quad \text{............} \; \textit{equation } 3.1$$

where LPI = Lloyd's patchiness index

s^2 = sample variance

$\bar{x}$ = sample mean

The calculation of sample means used in the calculation of Lloyd's Patchiness Index included zero samples because the exclusion of such samples is not justified when assessing patchiness.

The monthly patchiness indices of anchovy and sardine eggs and larvae were $\log_{10}$-transformed to satisfy the assumptions of ANOVA (Zar 1984). A two-way ANOVA (Zar 1984) was performed on the transformed data to test the null hypothesis that there was no significant difference in the mean patchiness between species or between eggs and larvae during SARP I and II.

To assess within-season variations in the patchiness of eggs and larvae over the entire region, indices were grouped into three seasons which were defined by hydrographic conditions; *viz.* winter (August and September), spring (October to December) and summer (January to March) (Richardson *et al.* in press). The variables used to categorize the months included the minimum and maximum depth of the upper mixed layer (indicative of water column stability), the minimum and maximum sea surface temperature, the volume of water below 12 °C in the upper 200 m and the depth of the 10 °C isotherm (indicative of the ease in which upwelling may occur), and the volume of 16-19 °C water (a measure of the suitable spawning habitat for anchovy, see Chapter 4). The specific criteria used to distinguish these variables are detailed in Richardson *et al.* in press).

In order to assess whether the distribution of eggs differed between (August and September), spring (October to December) and summer (January to March) for either anchovy or sardine, a two-way ANOVA was performed on the transformed patchiness data grouped by the seasons described above. Tukey's multiple comparison test for unequal sample sizes was used to compare individual means (Zar 1984).

3.3 Results

3.3.1 Abundance and distribution of anchovy eggs and larvae

The monthly spawning activity of anchovy was consistent over the two seasons, with low egg and larval abundances at the start (August) and end (March) of each season (Fig. 3.1). Anchovy egg densities increased rapidly with the onset of spring reaching a peak during October and/or November (Figs. 3.1 a,b). Anchovy larval abundance reached a peak later in the season, during December/January of SARP I, and February 1995 of SARP II (Fig. 3.1 c,d). Larvae were relatively abundant in December 1994, suggesting that the peak in larval abundance may have been comparable over the two seasons. Firm comparisons were not possible however, as data were not collected during January 1995.

Maximum monthly egg and larval densities were higher during SARP I (1114 eggs m^{-2} and 1301 larvae. 10 m^{-2}) than during SARP II (311 eggs m^{-2} and 412 larvae. 10 m^{-2})(Table 3.1 and 3.2). The mean anchovy egg density during October of SARP I (Table 3.1, 1114 eggs m^{-2}) was considerably higher than any other density estimated during SARP, because an exceptionally high density (23 625 eggs m^{-2}) was measured at a single station on the WAB.

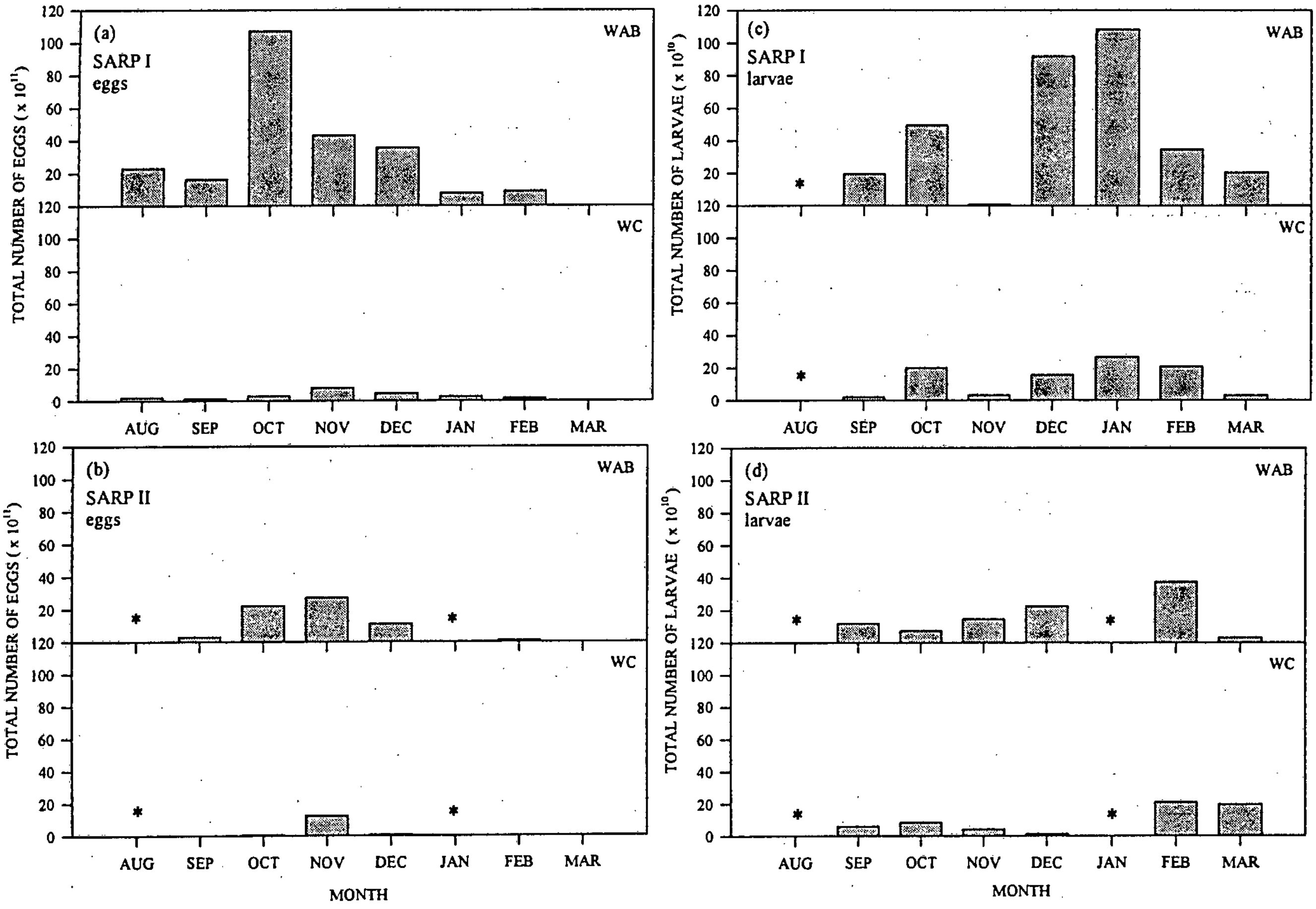

Fig. 3.1. The total number of anchovy eggs and larvae found on the westerm Agulhas Bank (WAB) and on the west coast (WC) each month during SARP I and II. (a,b) Eggs, (c,d) Larvae. * = no sample.

individual cruises, both eggs and larvae were generally more abundant on the WAB than on WC during SARP as a whole (Fig. 3.1). These differences are clear when the seasonal average egg and larval densities for both regions are compared (Fig. 3.2 a,b).

The overall mean density of anchovy eggs was significantly greater (300 eggs m^{-2}) during SARP I than SARP II (180 eggs m^{-2}; Fig. 3.2 a; Kruskal Wallis, $H = 4.56, p<0.05$). Because anchovy eggs occurred primarily on the WAB, mean densities in this region may provide a more realistic

Table 3.1. The number of stations where **EGGS** were found (n), their proportion of the total number of stations sampled (presence), the geometric means of egg density (m^{-2}) from positive stations, the coefficient of variation of the mean (cv) and the total area sampled during SARP. The cv's are based on the standard deviations of the log$_{10}$-transformed data. The area sampled on the WAB was consistent (16455 km2) but the area sampled on the west coast was variable. The dash (-) indicates those months that were not sampled.

	WAB				WEST COAST				
	n	presence (%)	mean	cv (%)	n	presence (%)	mean	cv (%)	area (km2)
ANCHOVY									
SARP I									
August	5	42	335	20	2	40	81	8	6467
September	6	35	280	39	3	75	30	19	6467
October	7	58	1114	33	2	9	111	29	30465
November	80	66	400	28	19	34	121	27	19400
December	6	40	541	18	5	18	85	53	30465
January	1	8	567	0	1	9	147	0	19400
February	1	8	651	0	4	17	47	24	19400
March	0	0	0	0	0	0	0	0	6467
SARP II									
August	-	-	-	-	-	-	-	-	-
September	7	28	64	37	0	0	0	0	19400
October	19	56	242	33	2	4	47	30	30465
November	57	53	311	26	26	37	111	32	30465
December	10	37	181	32	2	14	36	22	12934
January	-	-	-	-	-	-	-	-	-
February	5	17	30	15	0	0	0	0	30465
March	1	3	21	0	0	0	0	0	30465
SARDINE									
SARP I									
August	7	58	102	26	2	40	154	37	6467
September	4	24	90	39	2	50	30	14	6467
October	4	33	185	31	3	13	71	36	30465
November	36	30	68	28	14	25	131	32	19400
December	4	27	97	25	8	29	168	25	30465
January	4	33	205	56	2	18	199	42	19400
February	3	25	315	48	5	22	121	34	19400
March	3	30	65	28	2	10	30	14	6467
SARP II									
August	-	-	-	-	-	-	-	-	-
September	15	60	167	23	7	26	64	30	19400
October	19	56	234	19	13	25	77	30	30465
November	25	24	81	30	22	34	114	39	30465
December	6	22	164	36	4	29	143	32	12934
January	-	-	-	-	-	-	-	-	-
February	7	23	272	39	13	28	117	41	30465
March	4	13	64	32	4	10	33	16	30465

estimate of spawning intensity (Fig. 3.2 a). While the overall mean density of anchovy eggs decreased by 40 % from 1993/94 to 1994/95, a seasonal comparison of mean densities for the WAB only, indicated a 53 % decrease over the same period (426 to 216 eggs. m^{-2}). Even though

Table 3.2. The number of stations where **LARVAE** were found (n), their proportion of the total number of stations sampled (presence), the geometric means of larval density (10 m^{-2}) from positive stations, the coefficient of variation of the mean (cv) and the total area sampled during SARP. The cv's are based on the standard deviations of the $\log_{10}$-transformed data. The area sampled on the WAB was consistent (16455 km^2) but the area sampled on the west coast was variable. The dash (-) indicates those months that were not sampled.

	WAB				WEST COAST				
	n	presence (%)	mean	cv (%)	n	presence (%)	mean	cv (%)	area (km2)
				ANCHOVY					
SARP I									
August	-	-	-	-	-	-	-	-	-
September	4	57	206	47	2	67	48	33	6467
October	6	50	601	26	13	50	131	35	30465
November	3	27	20	19	2	20	81	25	19400
December	3	43	1301	22	14	93	55	36	30465
January	7	64	1033	18	8	62	223	26	19400
February	7	70	301	41	13	81	132	33	19400
March	3	30	414	12	10	83	56	28	6467
SARP II									
August	-	-	-	-	-	-	-	-	-
September	18	75	97	39	15	58	54	29	19400
October	10	34	130	37	19	36	78	19	30465
November	5	29	301	23	4	20	67	12	30465
December	13	50	274	40	3	25	38	34	12934
January	-	-	-	-	-	-	-	-	-
February	15	56	412	29	23	53	129	31	30465
March	7	24	73	43	17	40	159	26	30465
				SARDINE					
SARP I									
August	-	-	-	-	-	-	-	-	-
September	2	29	11	75	1	33	6	0	6467
October	3	25	13	21	11	42	93	25	30465
November	1	9	15	0	2	20	15	34	19400
December	0	0	0	0	2	13	10	16	30465
January	2	18	59	52	6	46	178	21	19400
February	1	10	8	0	9	56	18	29	19400
March	1	10	17	0	6	50	28	35	6467
SARP II									
August	-	-	-	-	-	-	-	-	-
September	20	83	159	35	21	81	96	30	19400
October	4	14	93	43	10	19	51	38	30465
November	2	12	8	34	0	0	0	0	30465
December	2	8	10	57	0	0	0	0	12934
January	-	-	-	-	-	-	-	-	-
February	9	33	59	41	25	58	206	27	30465
March	1	3	48	0	10	24	39	32	30465

the seasonal change in the abundance of anchovy larvae (19 %) was not as marked as the change in egg abundance, a significant decrease in mean density was observed (Fig. 3.2 b), from 157 larvae. 10 m^{-2} for SARP I to 126 larvae. 10 m^{-2} for SARP II (Kruskal-Wallis, $H = 0.75$, $p<0.05$).

The greatest anchovy egg densities (> 1000 eggs. m^{-2}) were found most frequently in the midshelf region on the WAB. This was particularly evident during November 1994 (Fig 3.3 k) when anchovy spawning was at a maximum. The proportion of samples with anchovy eggs (Table 3.1) was largest from September to December during both SARP seasons, when anchovy spawning was most intense, indicating that anchovy eggs were more widespread over the WAB during peak spawning periods.

Anchovy eggs were seldom found inshore where the sea surface temperatures were relatively cool (see Chapter 4). Although eggs were sometimes found offshore beyond the 500 m isobath (*e.g.* November 1993, Fig. 3.3 d), densities in this region were generally low (<100 eggs m^{-2}).

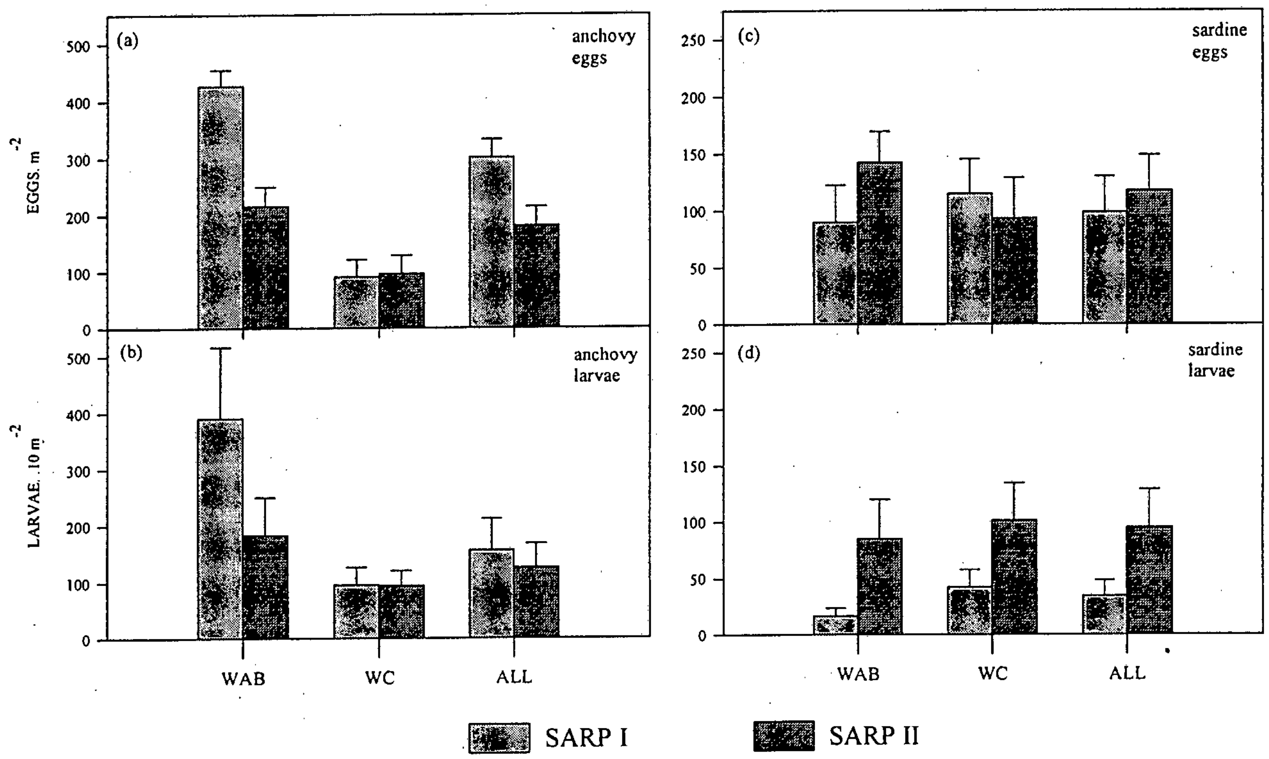

Fig. 3.2. Geometric means over the western Agulhas Bank (WAB), the west coast (WC) and the entire sampling region (ALL) for anchovy egg (a) and larval (b) densities and sardine egg (c) and larval (d) densities during SARP I (August 1993 - March 1994) and SARP II (September 1994-March 1995). The error bars indicate one standard deviation of the geometric mean.

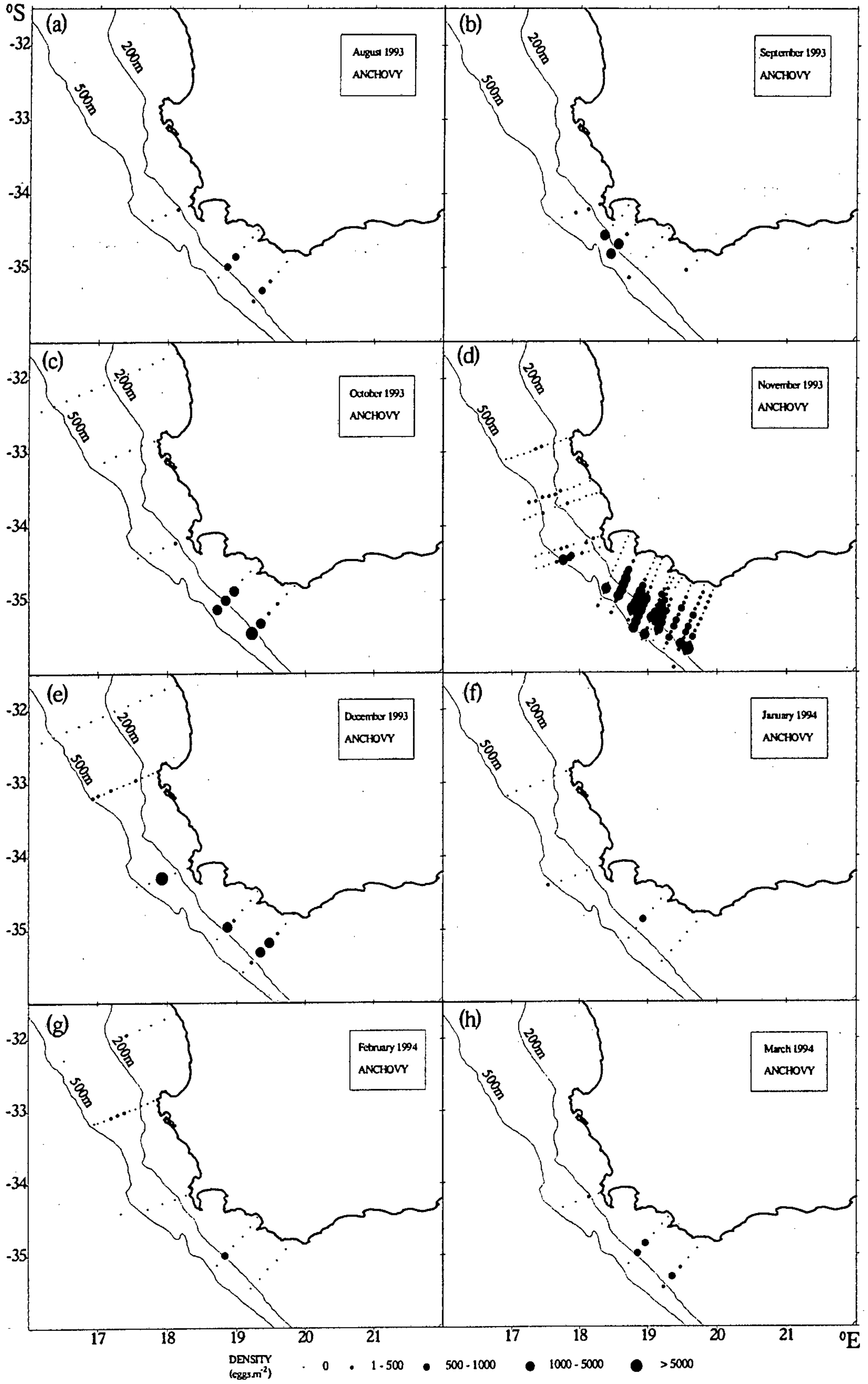

Fig. 3.3. The distribution of anchovy eggs between August 1993 (a) and March 1994 (h) during SARP I. Station positions and the 200m and 500 m depth contours are also shown. Line numbers are shown in Fig. 2.1.

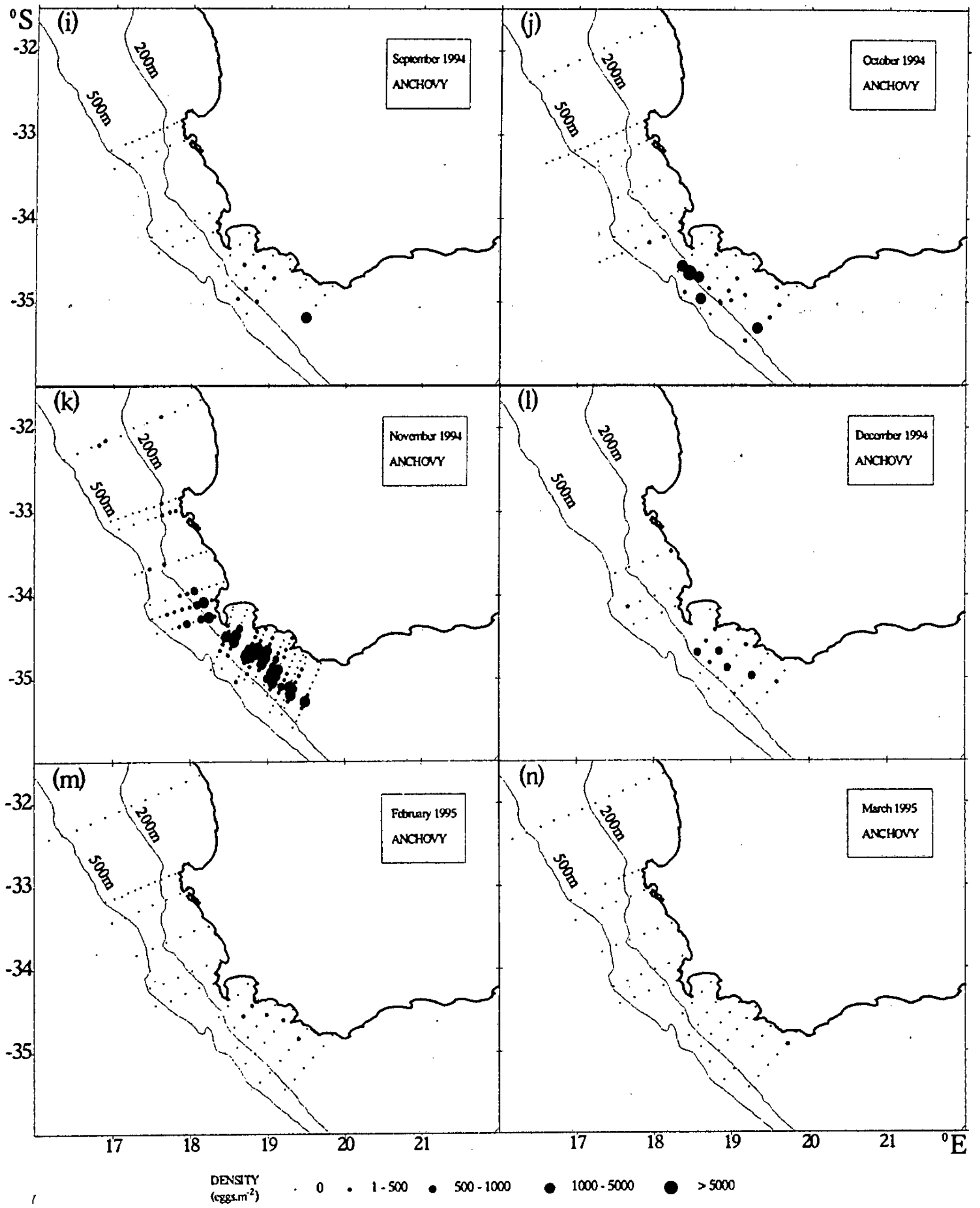

Fig 3.3 continued. The distribution of anchovy eggs between September 1994 (i) and March 1995 (n) during SARP II. Station positions and the 200m and 500m depth contours are also shown. Line numbers are shown in Fig. 2.1.

The cross shelf pattern of egg abundance on lines 1 and 3 (WAB) indicates that anchovy eggs were further offshore during SARP I than SARP II (Fig. 3.4 a,b). A similar pattern can be seen on the WC with a comparison of the average egg abundance per station on line 7 (Cape Peninsula) and line 11 (Cape Columbine)(Fig. 3.5 a,b). These data suggest a distinct change in the anchovy egg distribution between years. Where anchovy egg distributions extended as far north as Cape Columbine and the Olifants River (*e.g.* November 1993, Fig. 3.3 d and November 1994, Fig. 3.3 k), densities in these regions were relatively low (< 270 eggs m^{-2}).

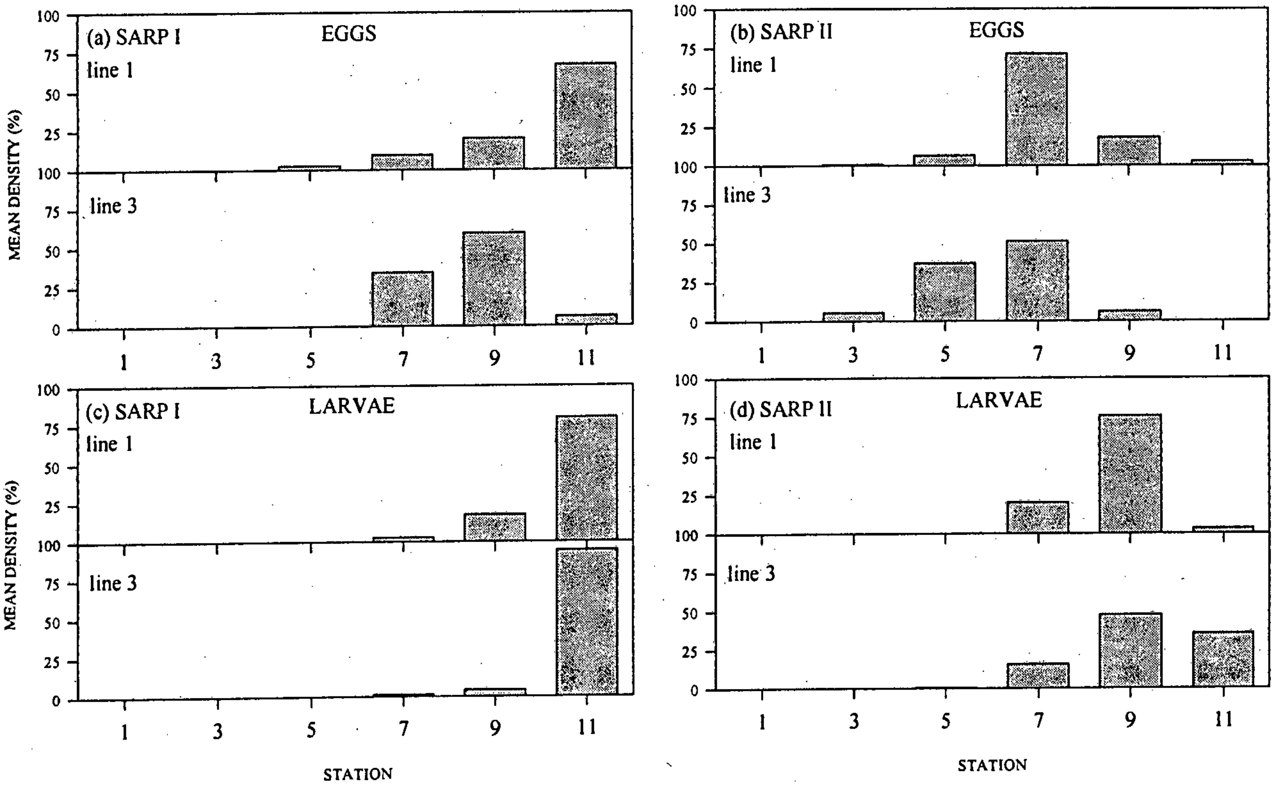

Fig. 3.4 Inshore-offshore distribution of anchovy eggs (a,b) and anchovy larvae (c,d) on line 1 (Cape Agulhas)and line 3 (Walker Bay) during SARP I (1993/94) and II (1994/95) given by the station averages as a percentage of the overall average of each line. The stations are numbered from inshore (1) to offshore (11) and the line positions are illustrated in Fig. 2.1.

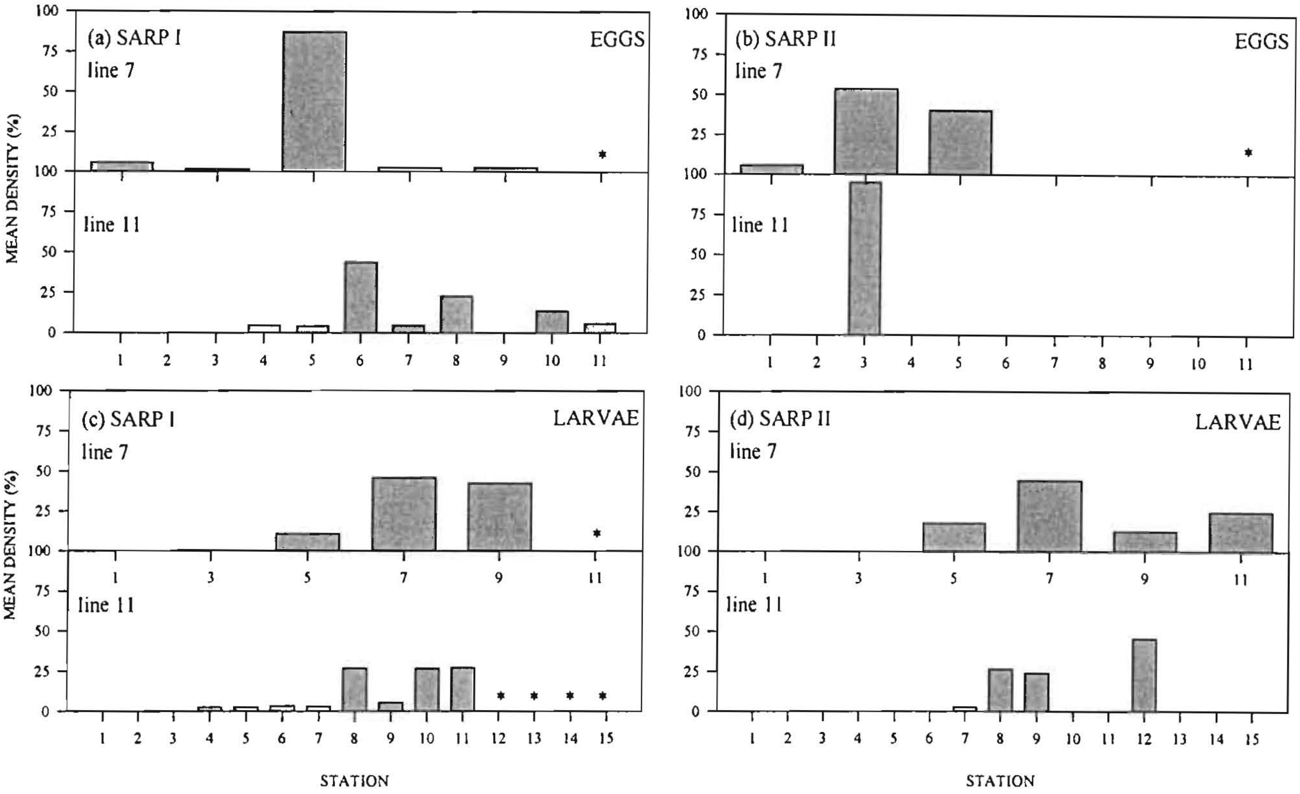

Fig. 3.5 Inshore-offshore distribution of anchovy eggs (a,b) and anchovy larvae (c,d) on line 7 (Cape Peninsula) and line 11(Cape Columine) during SARP I (1993/94) and II (1994/95) given by the station averages as a percentage of the overall averages of each line. The stations are numbered from inshore (1) to offshore (11) and the line positions are illustrated in Fig. 2.1 * = no sample.

Larvae often occurred densely (>500 larvae.10 m^{-2}) on the WAB and the WC during both spawning seasons (Fig. 3.6). The mean percentage of positive stations over the entire sampling area for anchovy larvae was significantly greater (51.32%) than that for anchovy eggs (24.63%) ($t = 3.77$, $df = 24$, $p < 0.001$) indicating that anchovy larvae were far more widespread over the area sampled than were their eggs.

Anchovy larvae were rarely found inshore on either the WAB or the WC but frequently occurred at offshore stations in both regions. This is particularly evident when examining station averages

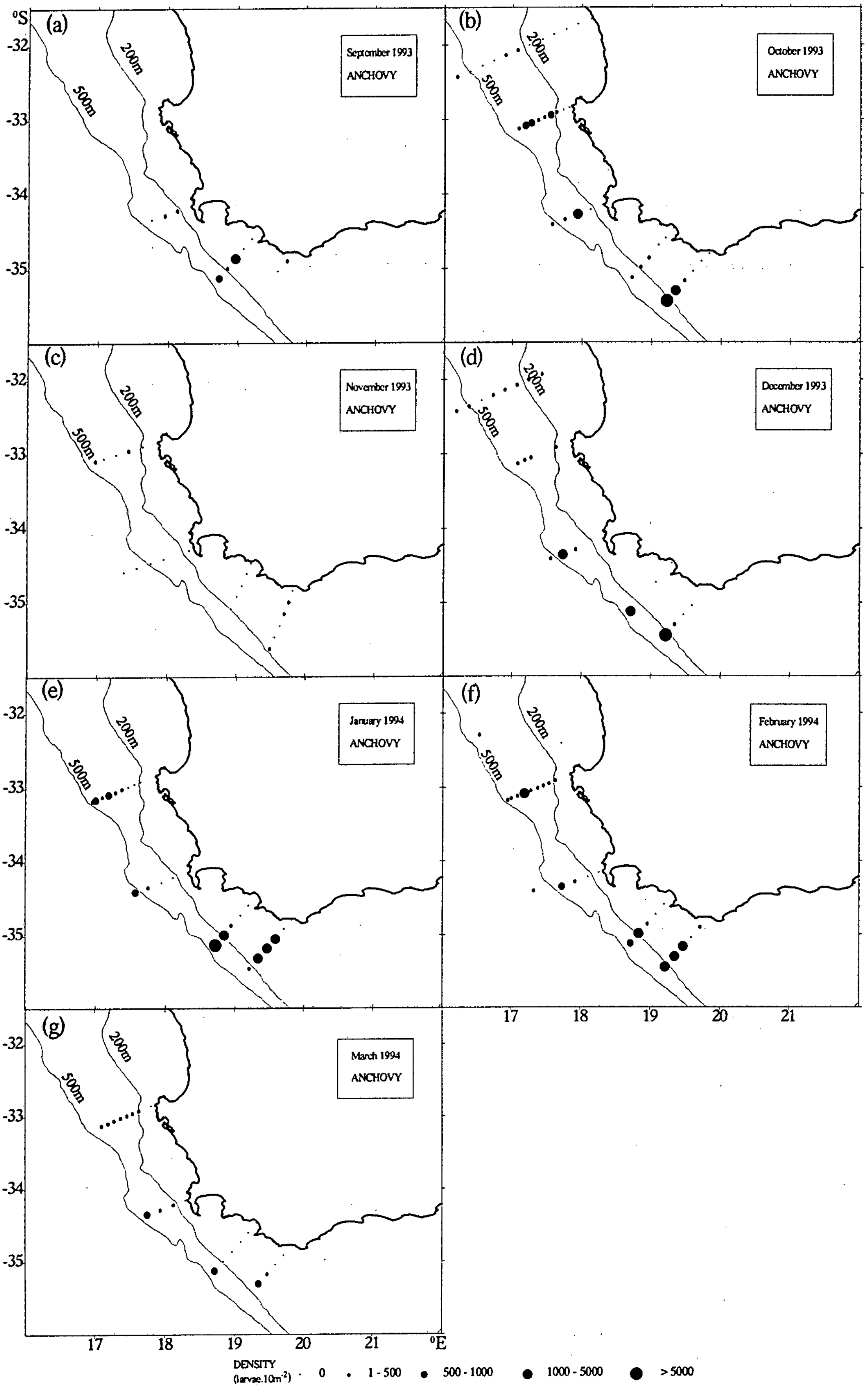

Fig. 3.6 The distribution of anchovy larvae between September 1993 (a) and March 1994 (g) during SARP I. Station positions and the 200m and 500 m depth contours are also shown. Line numbers are shown in Fig. 2.1.

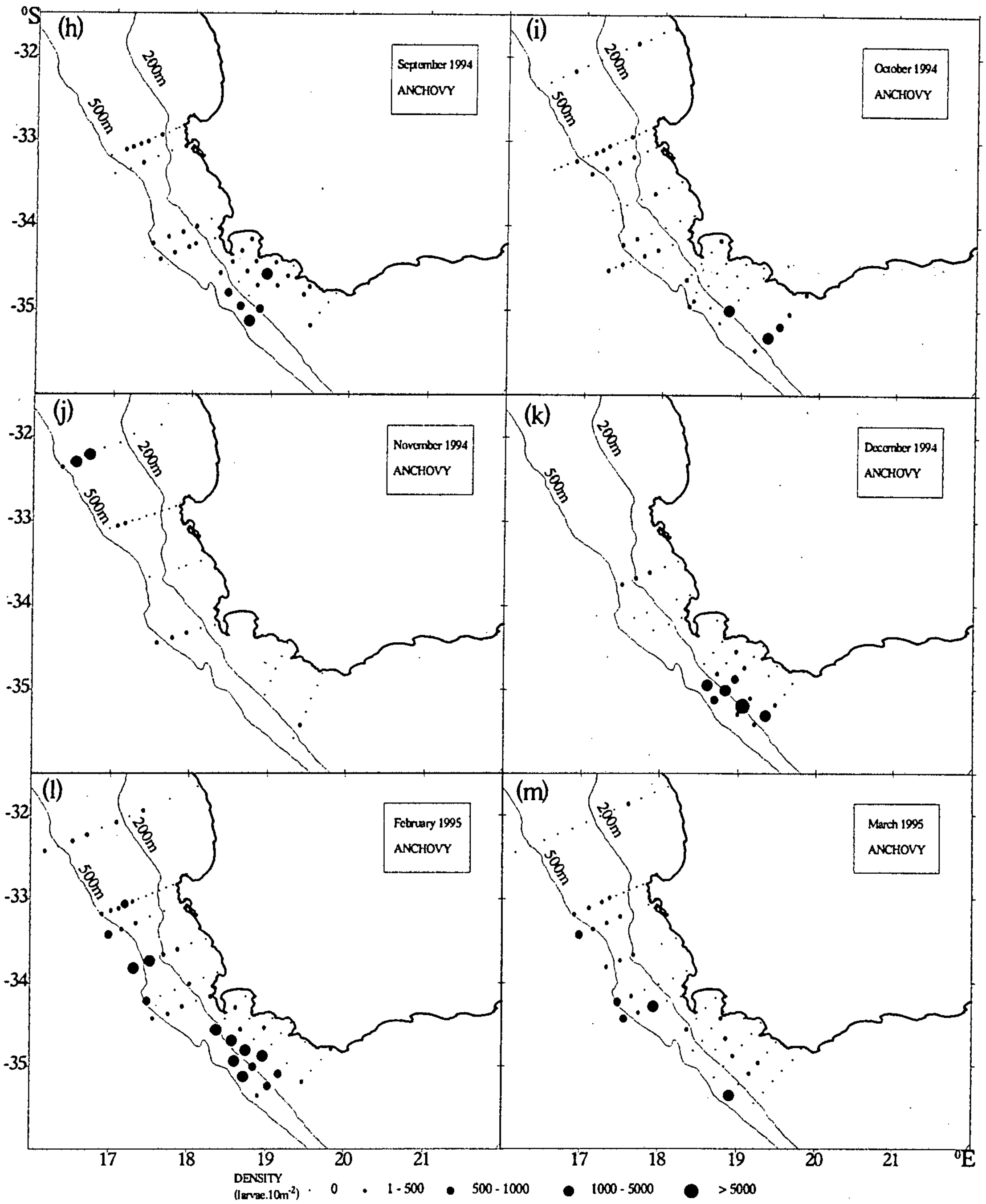

Fig.3.6 continued. The distribution of anchovy larvae between September 1994 (h) and March 1995 (m) during SARP II. Station positions and the 200m and 500 m depth contours are also shown. Line numbers are shown in Fig. 2.1.

on the WAB (Fig. 3.4 c,d) and the WC (Fig. 3.5 c,d) for both years. These data indicate that anchovy larvae occurred most frequently in the region of the 500 m isobath on the WAB (lines 1 and 3, stations 9 and 11; Fig. 3.4 c,d) and off the Cape Peninsula (line 7, stations 7 and 9; Fig. 3.5 c,d) and slightly further offshore off Cape Columbine (line 11, station 12; Fig. 3.5 c,d). This was particularly clear when larval abundances were high and relative densities in excess of 1000 larvae. 10 m^{-2} were found in the region of the 500 m isobath during January 1994 (Fig. 3.6 e) and February 1995 (Fig. 3.6 l). Larvae were usually further offshore than the eggs on the WAB and WC (see Fig. 3.4 and 3.5) and were further offshore during SARP I than SARP II in both regions (see Fig. 3.4 c,d and 3.5 c,d).

3.3.2 Abundance and horizontal distribution of sardine eggs and larvae

Sardine eggs were found throughout the sampling period. Elevated egg densities were recorded on the WAB during both August and October 1993 and again in January and February 1994 at a time when egg abundance reached a maximum during SARP I (Fig. 3.7 a). The seasonal pattern for larvae was similar to that of the eggs with two well defined peaks in abundance during October 1993 and January 1994 (Fig. 3.7 c).The pattern of sardine spawning activity during SARP II was generally consistent with that of the previous year (SARP I), and egg and larval abundances peaked in September/October 1994 and again in February 1995 (Fig.3.7 b,d). This pattern suggests that sardine spawning activity may not be confined to a single period over the summer.

Although sardine egg densities over the entire region were slightly higher (16 %) during SARP II (117 eggs. m^{-2}) than SARP I (98 eggs. m^{-2}), this inter-annual difference was not significant

(Fig. 3.2 c; Kruskal-Wallis, $H = 0.96, p > 0.05$). By contrast, the average larval density over the entire region increased by a significant 64 % from SARP I to SARP II (Fig. 3.2 d; Kruskal-Wallis, $H = 12.55$, $p < 0.05$).

Sardine eggs were widespread throughout the study area (Fig. 3.8), occurring on both the WAB and the WC. Although densities were highest on the WAB, eggs were always abundant on the WC. During some months (*e.g.* December 1993 and November 1994), the total number of eggs was much greater on the WC (Fig. 3.7 a,b) between the Cape Peninsula and Cape Columbine (Fig. 3.8 e,k) where adult fish were concentrated (Painting *et al.* subm.c).

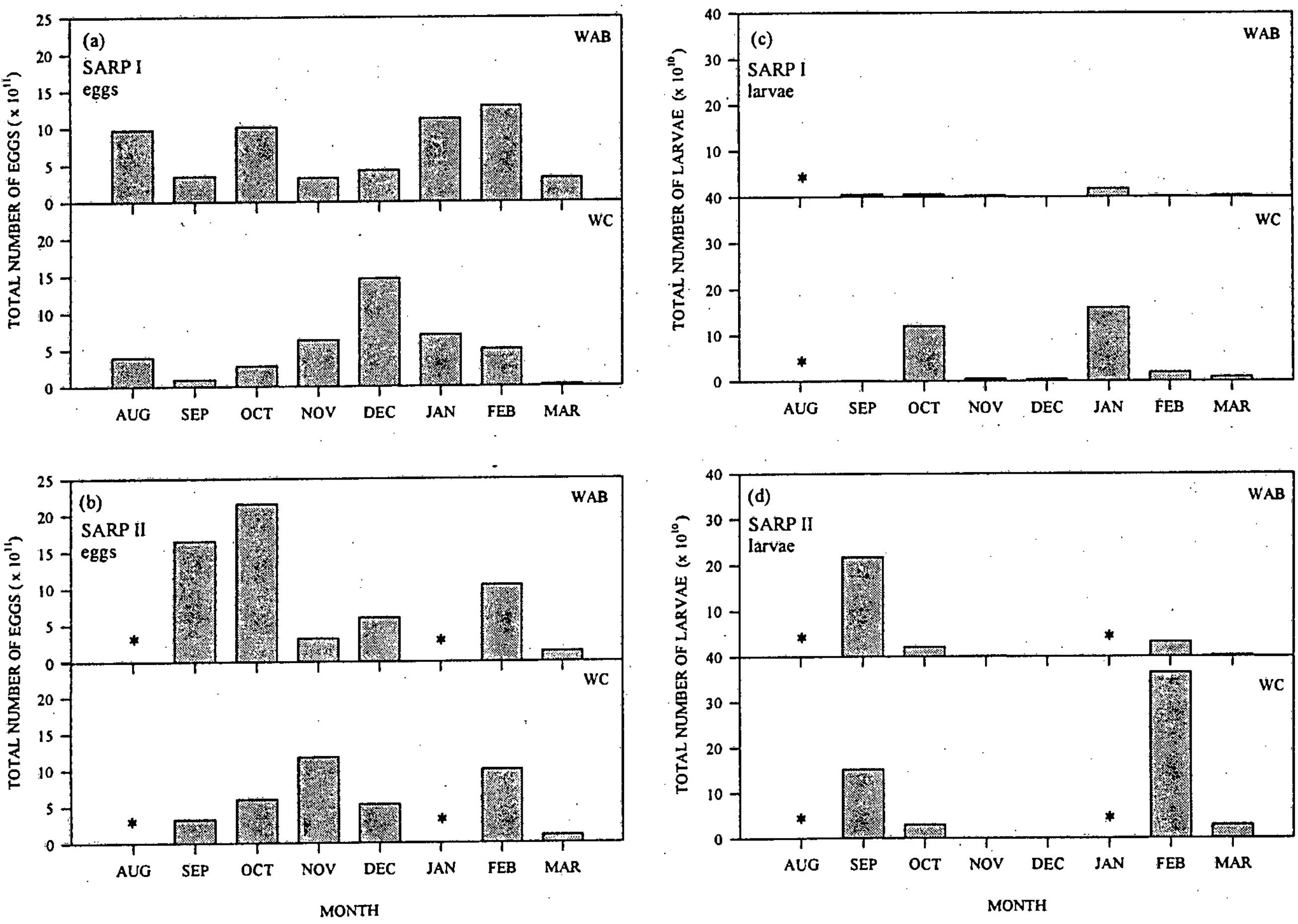

Fig. 3.7 The total number of sardine eggs and larvae found on the westerm Agulhas Bank (WAB) and on the west coast (WC) each month during SARP I and II. (a,b) Eggs, (c,d) Larvae. * = no sample.

The relatively large proportion of samples with eggs (Table 3.1) emphasises the consistently wide distribution of sardine spawning activity throughout the sampling period. Sardine eggs were particularly widespread during late winter and early spring of both years as indicated by the percentage of positive stations which were slightly higher during this period (Table 3.1). This pattern coincided with the spring peak in sardine eggs and larvae (Fig. 3.7) when conditions over the sampling area were fairly homogeneous (see Chapter 4). Sardine eggs were comparatively less widespread during the late summer (January/February) peak (Table 3.1, Fig. 3.7), when the eggs were concentrated in the upwelling front which was inshore during this period (see Chapter 5).

The inshore-offshore distribution of sardine eggs was not as clear as it was for anchovy, although a mid-shelf maximum was also apparent on the WAB (Fig. 3.8). Station averages indicate that the majority of sardine eggs occurred in the region of the 200 m isobath (stations 11 and 9 on lines 1 and 3 respectively) on the WAB during SARP I (Fig. 3.9 a). The distribution shifted inshore during SARP II however, and the majority of eggs occurred at stations 5 and 7 on lines 1 and 3 respectively (Fig. 3.9 b). Sardine eggs were not found inshore very frequently, but did extend into False Bay and Walker Bay during September 1994 and October 1994 (see Figs. 3.8i,j). On the WC, where inshore waters were cooler than on the WAB, sardine eggs were seldom found inshore. Average cross-shelf patterns on the WC for SARP I and II indicate that most sardine eggs were found just beyond the 200 m isobath off the Cape Peninsula (stations 3 and 5; Fig. 3.10 a,b). Although sardine eggs were found at almost all stations on line 11 (Cape Columbine) during SARP I, average egg densities were high from midway between the 200 m and 500 m isobath to the 500 m isobath (stations 7 to 11; Fig 3.10 a). In comparison with SARP

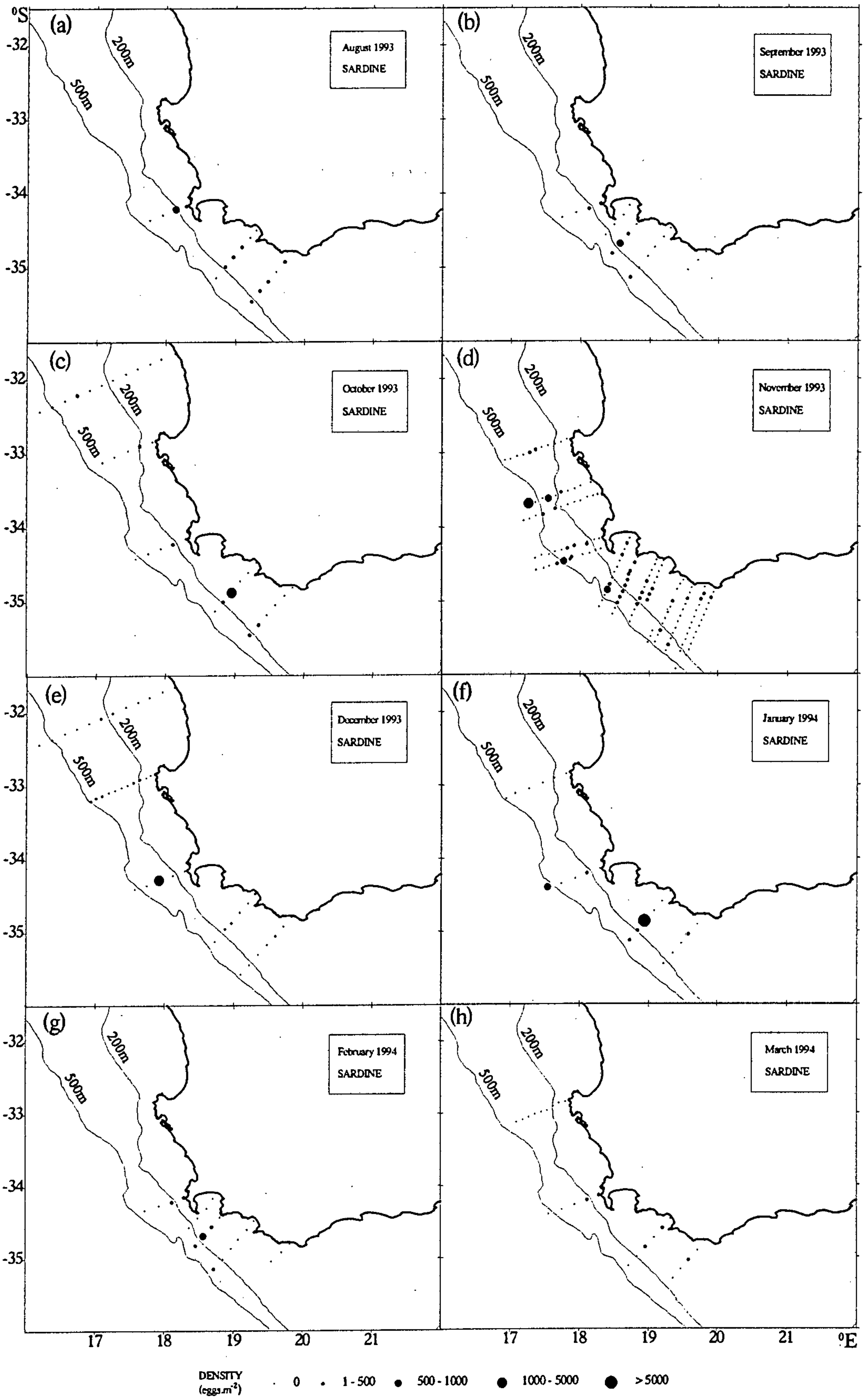

Fig. 3.8 The distribution of sardine eggs between August 1993 (a) and March 1994 (h) during SARP I. Station positions and the 200m and 500 m depth contours are also shown. Line numbers are shown in Fig. 2.1.

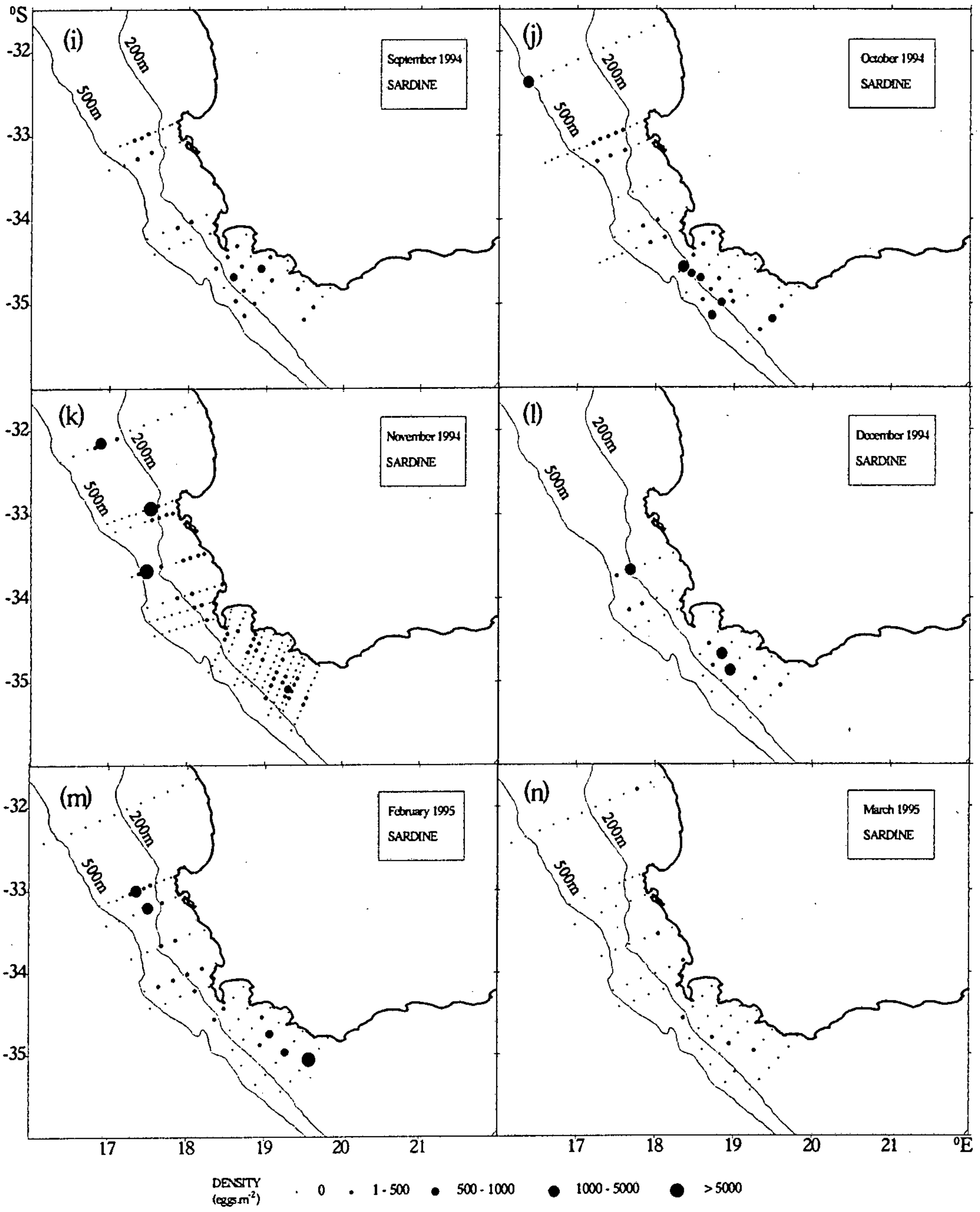

Fig. 3.8 continued.The distribution of sardine eggs between September 1994 (i) and March 1995 (n) during SARP II. Station positions and the 200m and 500m depth contours are also shown. Line numbers are shown in Fig. 2.1.

I, sardine eggs were further inshore at Cape Columbine during SARP II with the highest average density occurring at station 5 on line 11 (Fig. 3.10 b). In agreement with these seasonal average densities, the greatest egg densities (> 1000 eggs m^{-2}) were usually found between the 200 m and 500 m isobath (Fig. 3.8). During October 1994 and November 1993 and 1994, however, high egg densities (> 1000 eggs.m^{-2}) were also further offshore on the WC, beyond the 500 m isobath (see Fig. 3.8 d,j,k).

Relatively few sardine larvae were encountered during SARP I (see Figs. 3.2 d and Fig. 3.11) and were largely confined to the region off Cape Columbine on the WC during October 1993 (Fig. 3.11 b) and January 1994 (Fig. 3.11 e) when peak abundances were recorded (see Fig. 3.7c).

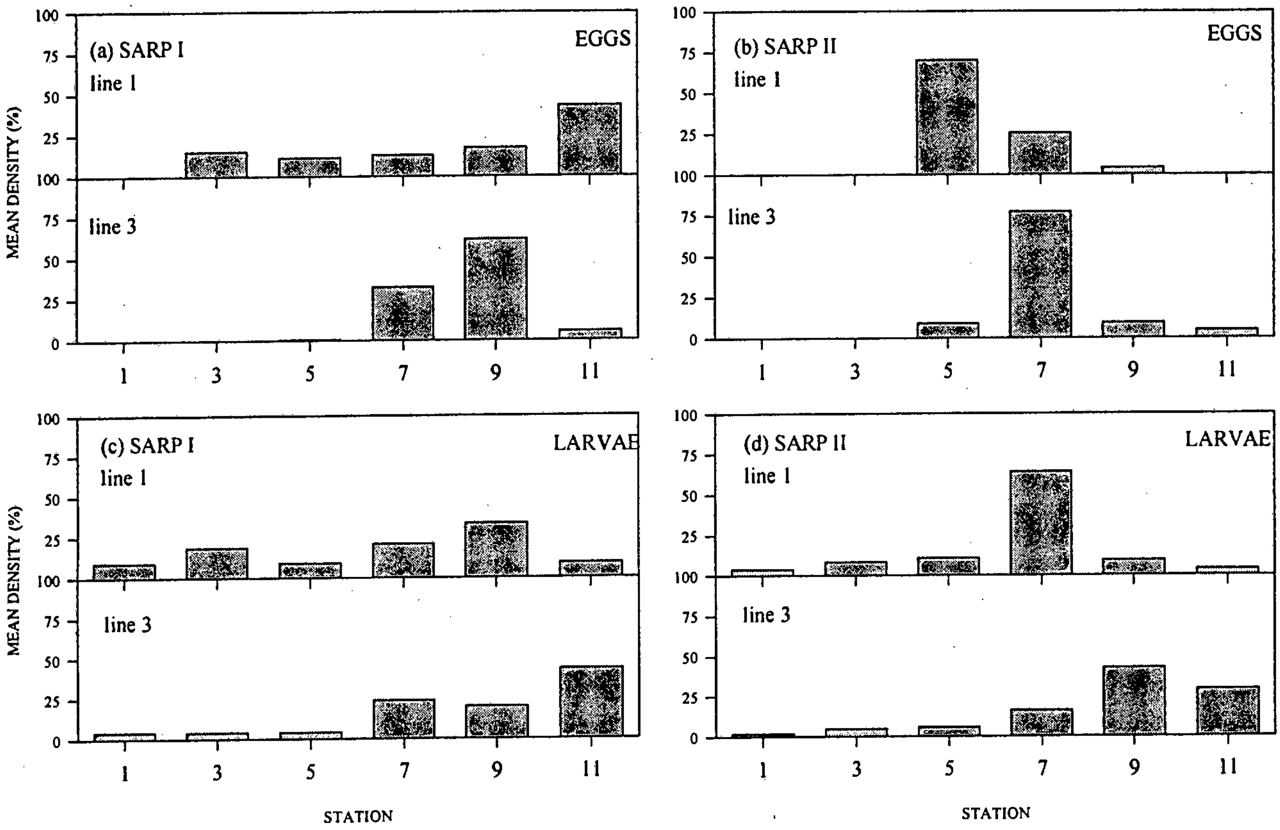

Fig. 3.9 Inshore-offshore distribution of sardine eggs (a,b) and sardine larvae (c,d) on line 1 (Cape Agulhas) and line 3 (Walker Bay) during SARP I (1993/94) and II (1994/95) given by the station averages as a percentage of the overall averages of each line. The stations are numbered from inshore (1) to offshore (11) and the line positions are illustrated in Fig. 2.1.

Sardine larvae were rarely found inshore, although September and October 1994 were exceptions to this pattern as larvae occurred inshore on the WAB (Fig. 3.11 h,i). Station averages on the WAB indicated that sardine larvae occurred predominantly in the midshelf region (stations 9 and 11 on line 1), occurring slightly offshore on line 3 (Fig. 3.9 c,d). However, sardine larvae were widespread over the sampling area during September and October 1994 when larval abundance was high (Fig. 3.11 h,i). These widespread distributions are clearly indicated by the high percentage of positive stations recorded during these months (Table 3.2). Despite the formation of a strong front during the late summer, sardine larvae were fairly widespread over the WC during this period (Table 3.2). A comparison of the mean percentage of positive stations over the entire sampling area for sardine larvae indicated that there was no significant difference between

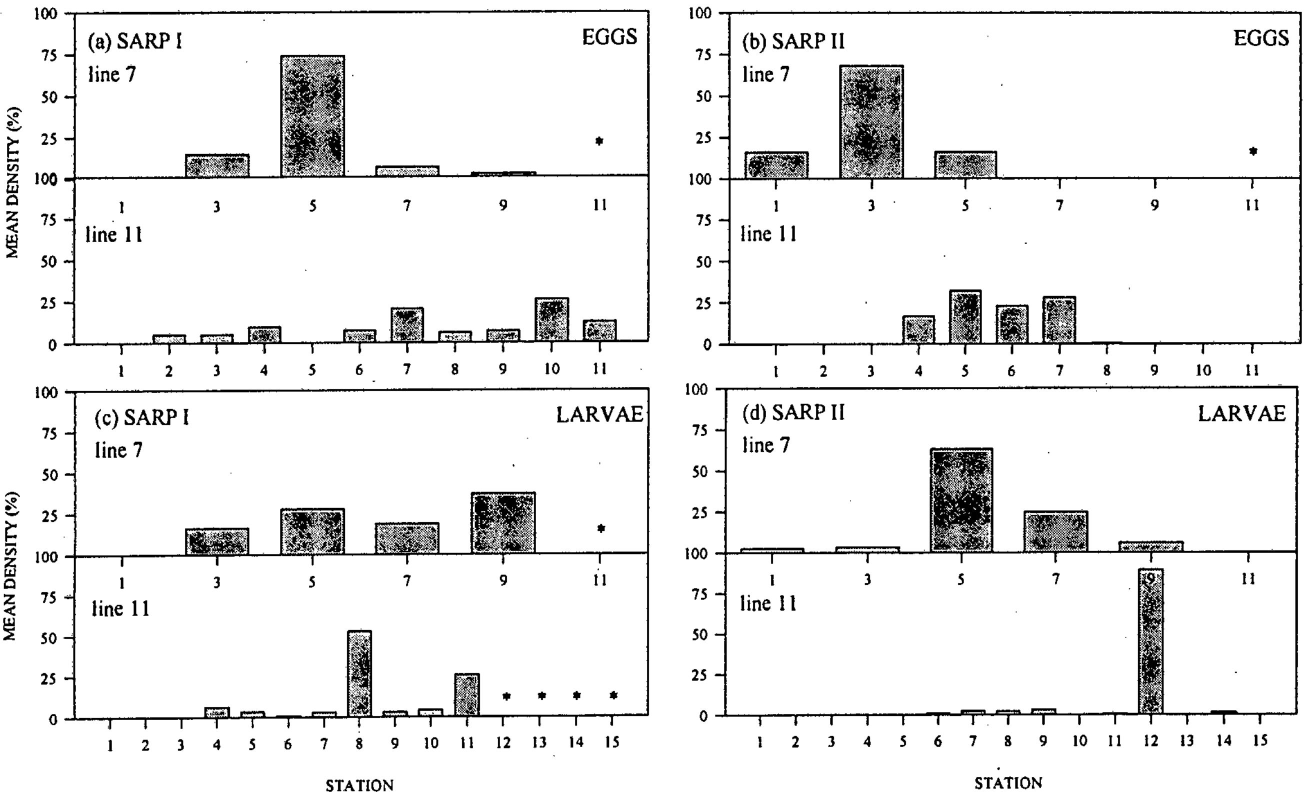

Fig. 3.10 Inshore-offshore distribution of sardine eggs (a,b) and sardine larvae (c,d) on line 7 (Cape Peninsula) and line 11 (Cape Columine) during SARP I (1993/94) and II (1994/95) given by the station averages as a percentage of the overall averages of each line. The stations are numbered from inshore (1) to offshore (11) and the line positions are illustrated in Fig. 2.1 * = no sample.

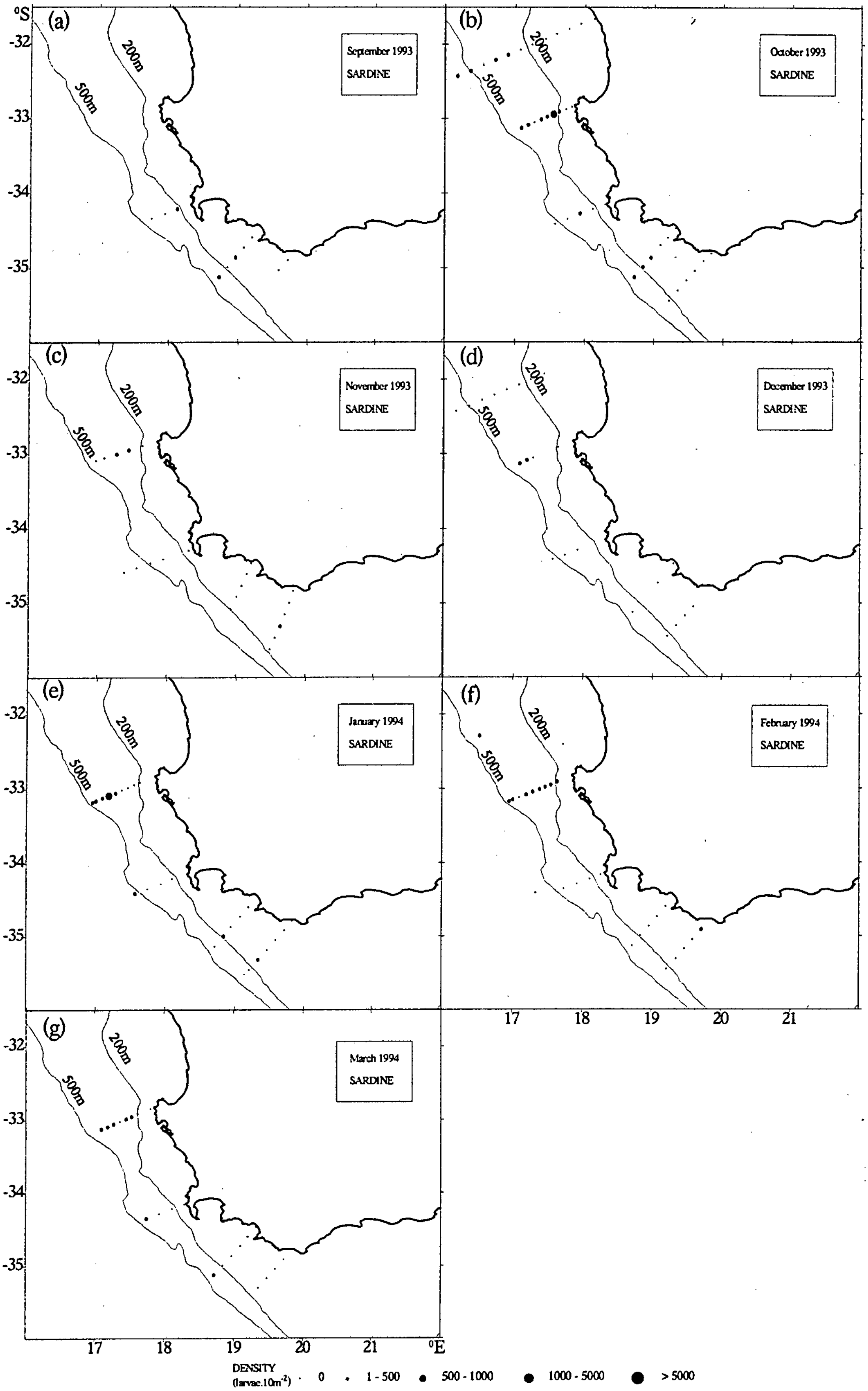

Fig. 3.11. The distribution of sardine larvae between September 1993 (a) and March 1994 (g) during SARP I. Station positions and the 200m and 500 m depth contours are also shown. Line numbers are shown in Fig. 2.1.

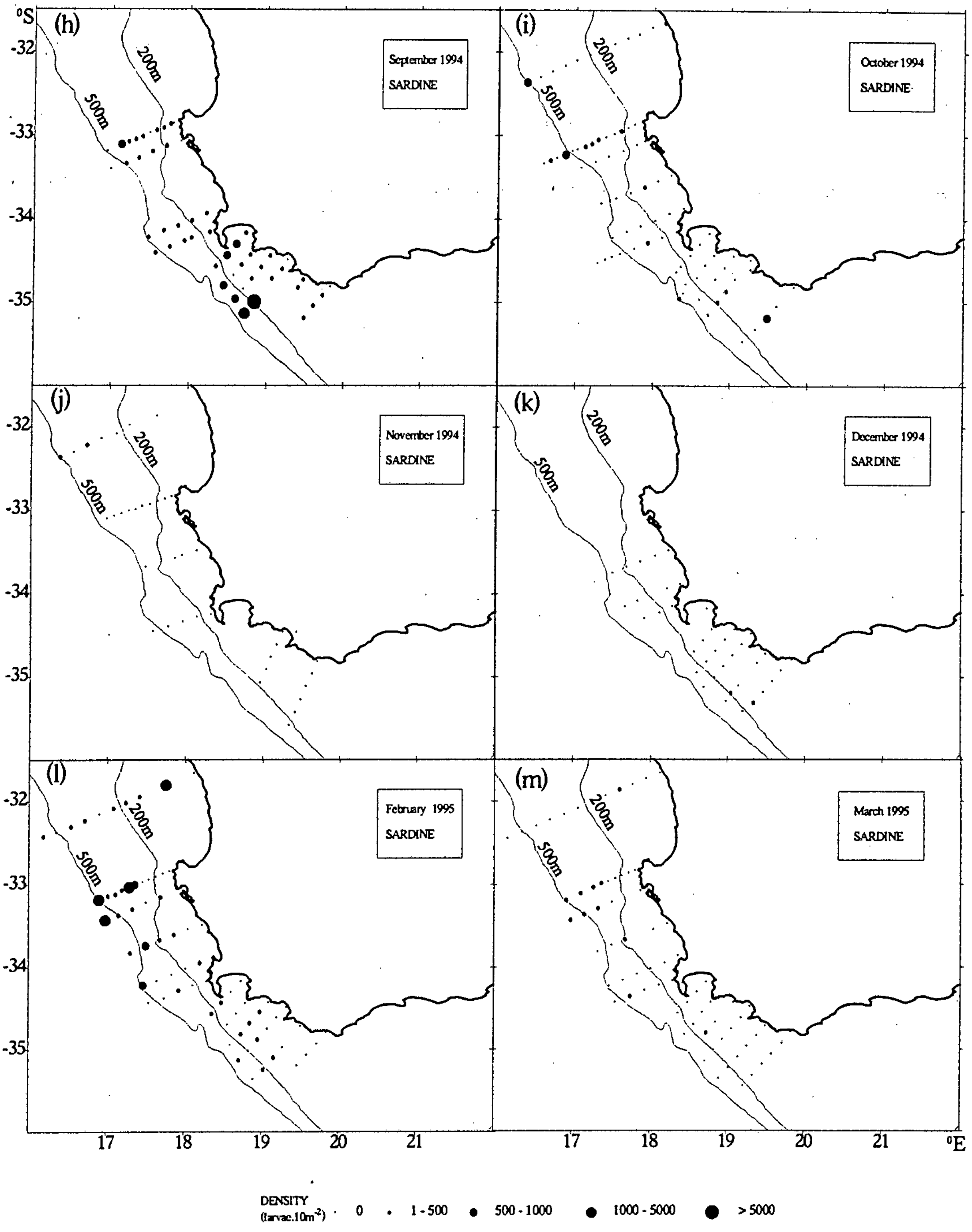

Fig. 3.11 continued. The distribution of sardine larvae between September 1993 (h) and March 1994 (m) during SARP I. Station positions and the 200m and 500 m depth contours are also shown. Line numbers are shown in Fig. 2.1.

sardine eggs (27 %) and larvae (28 %) ($t = 0.018, df = 24, p > 0.05$) which suggests that sardine eggs were as equally widespread as their larvae. This provides further evidence to suggest that sardine spawning is not confined only to the WAB, but frequently occurs on the WC.

Sardine larvae were fairly widespread over the Cape Peninsula line with the highest average abundance occurring beyond the 500 m isobath during SARP I (Fig. 3.10 c). This contrasts with the situation during SARP II when sardine larvae were more concentrated in the midshelf region off the Cape Peninsula (Fig. 3.10 d). Larval densities were often further offshore than the egg distributions, occurring in high densities (> 1000 larvae 10 m^{-2}) on the shelf break or beyond the 500 m isobath (*e.g.* September 1994, October 1994 and February 1994). The cross-shelf distribution of sardine larvae off Cape Columbine during SARP I indicated that larvae occurred mainly in the mid to outer shelf region although their distribution extended further offshore during SARP II with the highest average abundance at station 12, beyond the 500 m isobath (Fig. 3.10 c,d).

3.3.3 A comparison between the spatial patterns of anchovy and sardine eggs and larvae

Based on a comparison of the ratio of eggs on the WAB to the total number of eggs sampled during SARP for anchovy and sardine, it is evident that the average proportion of anchovy eggs (84 %) on the WAB was significantly greater than that for sardine eggs (68 %) (Mann-Whitney *U* Test, $Z=2.57$, $p<0.01$). Evidently, sardine spawning activity was more widespread over the sampling area than that of anchovy which appear to spawn primarily on the WAB.

The eggs and larvae of both anchovy and sardine were not uniformly distributed over the area studied. The patchiness index was >1 for both anchovy and sardine eggs and larvae for all samples during both SARP seasons (Table 3.3). This indicates that egg and larval distributions during each survey were aggregated and not random.

Table 3.3. Lloyd's patchiness index (LPI) calculated for monthly anchovy and sardine egg and larval distributions over the entire sampling area during SARP I (1993/94) and II (1994/95). The average LPI's are in bold font. The dash (-) represents months that were not sampled. The star (*) indicates that no eggs/larvae were found during that particular cruise.

	anchovy eggs	anchovy larvae	sardine eggs	sardine larvae
SARP I				
August	3.9	-	3.7	-
September	7.0	3.8	10.8	0.9
October	17.8	10.6	12.3	1.6
November	7.5	9.4	18.4	2.1
December	13.7	8.1	15.9	*
January	16.1	4.8	19.2	6.2
February	19.7	4.1	24.1	4.4
March	*	4.5	12.2	6.0
mean LPI	**12.2**	**6.5**	**14.6**	**3.5**
SARP II				
August	-	-	-	-
September	31.1	9.0	5.0	10.6
October	22.0	12.1	6.0	17.2
November	8.1	11.7	38.5	21.2
December	7.1	12.9	9.8	28.4
January	-	-	-	-
February	18.8	4.7	36.0	6.4
March	68.6	8.1	21.2	16.3
mean LPI	**26.0**	**9.7**	**19.4**	**16.7**

A comparison between species and spawning products (eggs and larvae) for all 14 cruises using a 2-way ANOVA showed that there was no significant difference in the patchiness of anchovy and sardine spawning products (F=0.12; df= 1, 13; p>0.05). However, the egg distributions of both species together were significantly more patchy than their larval distributions (F = 10.45; df=1,13; p<0.01). There was no significant interaction between species and spawning products (F = 0.04; df=1,13; p>0.05).

By pooling monthly egg samples into the three seasons (see section 3.2), a 2-way ANOVA comparing seasons and species, shows that there was no significant difference in the seasonal pattern of patchiness between species ($F=0.02$; $df=1,2$; $p>0.05$), although both sardine and anchovy egg distributions were significantly more patchy in summer (January - March; mean LPI = 13.35) than in spring (October- December; mean LPI = 6.86) ($F = 4.44$; $df=1,2$; $p<0.05$). There was no significant interaction between species and egg distributions ($F = 1.05$; $df = 1,2$; $p>0.05$)

3.4 Discussion

As planktonic organisms, the eggs and early larval stages of pelagic fish such as anchovy and sardine are patterned according to the specific spawning strategies of the adult fish (Hewitt 1981, Loeb *et al.* 1983, Stabeno *et al.* 1996). Shelton (1986) stated that anchovy, and to a lesser extent sardine, select specific environmental windows for spawning in order to optimise reproductive output and survival through to recruitment. In agreement with Shelton (1986), the spatial and temporal patterns of egg and larval abundance observed during this study clearly indicate that the spawning behaviours of anchovy and sardine are both seasonally and geographically distinct.

3.4.1 Monthly variations in the abundance and distribution of eggs and larvae

The indication that anchovy spawning occurs mainly during the spring months, reaching a maximum in October and November, is similar to the findings of Anders (1965) and Crawford (1981b). These authors showed that anchovy spawning in the southern Benguela ecosystem occurred predominantly in the spring and summer with a peak in December between 1964 and 1969. Shelton (1986) too found that anchovy eggs and larvae were completely absent in the southern Benguela during winter but increased rapidly during spring, to reach a peak in October.

Whereas anchovy spawning is highly seasonal, sardine eggs and larvae have been found throughout the year (Crawford 1981a, Shelton 1986), which suggests that sardine do not confine their spawning activity to a single period as do anchovy. Before the collapse of the sardine stocks in the 1960's, sardine egg abundance showed a minor peak in spring (September) and a higher peak in late summer (January and February, Crawford 1981a). During the CELP survey when sardine were scarce, egg and larval densities reached a peak in August 1978 although densities were low in August 1977 (Shelton 1986). More recently, an examination of sardine gonad mass by Armstrong *et al.* (1989) between 1976 and 1987 indicated that sardine spawning activity peaks in both August and January. In agreement with the findings of Armstrong *et al.* (1989) and those of Crawford (1981a) from the late 1950's and early 1960's, the current study shows that sardine spawning activity was consistently elevated during late winter or spring and again in late summer of both SARP I and II. Also consistent with these findings are the results obtained by recent investigations as part of SARP III (Huggett *et al.* in press) which indicate that sardine eggs and larvae are found throughout the year with greater densities in August and January each year.

Although there is some temporal overlap in the occurrence of sardine and anchovy eggs and larvae, the spawning peaks of these two species appear to occur at different times. This finding contrasts with that of Shelton (1986) who suggested that the temporal spawning strategies of these two pelagic species were the same, distinguishing them from species with midwater and demersal modes of existence in the adults. However, Shelton's (1986) results were drawn from surveys undertaken during a period (1978/79) when the sardine biomass in the southern Benguela region was reduced and small sample sizes may have influenced the true pattern during this period. A study of sardine *(Sardinops sagax)* and anchovy (*Engraulis mordax*) spawning off the

Californian coast has shown that in this system, these species spawn at different times and in different areas (Hernandez-Vazquez 1994), which supports the current findings.

In contrast to the geographically distinct spawning centres of anchovy and sardine in the California Current (Hernandez-Vazquez 1994), the midshelf region on the WAB appears to be the centre of both anchovy and sardine spawning in the southern Benguela ecosystem (Anders 1965, Shelton 1986, this study). However, both the monthly egg distribution maps and the monthly ratio of eggs on the WAB for anchovy and sardine indicate that anchovy spawning is more localized than that of sardine which frequently also spawn on the west coast (WC). Shelton (1986) also reported that sardine eggs occurred up the WC, but noted that the highest concentrations of sardine eggs during the 1978/79 CELP survey were on the WAB. Before the collapse of the sardine in 1962-64, however, sardine eggs were abundant offshore at Cape Columbine (Crawford 1981a). Sardine eggs were particularly abundant on the WC between the Cape Peninsula and Cape Columbine during the spring and summer (*e.g.* December 1993 and November 1994) when anchovy spawning was intense on the WAB. Also, a comparison of the average inshore-offshore pattern of sardine and anchovy egg distribution shows that anchovy eggs were slightly further offshore compared with sardine eggs during both SARP I and II. There is therefore, some evidence to suggest that the spawning strategies of sardine and anchovy are both temporally and spatially separated. The environmental conditions which possibly determine the spawning adaptations of anchovy and sardine will be dealt with in more detail in Chapter 4.

In accordance with the findings of Shelton (1986), it would appear from the analysis using

Lloyd's Patchiness Index (LPI) during this study, that the distribution of both anchovy and sardine eggs and larvae was not uniform, but highly aggregated. These conclusions were also reached by Barange and Hampton (1997) who used geostatistical analyses to investigate patterns of sardine and anchovy egg abundances during selected November Biomass cruises, spanning the entire spawning area of both species. The observed patchiness of anchovy and sardine eggs may be explained as the result of adult social behaviour to reduce predation and to achieve efficient fertilisation (Hewitt 1981, Shelton 1986).

Although the distribution of young eggs reflects the chosen spawning location of the adults, older eggs and young larvae tend to disperse and are usually less patchy (Hewitt 1981). In support of Hewitt's (1981) contention that larvae disperse and become less patchy relative to their initial intensity of pattern, this study shows that both anchovy and sardine larvae in the southern Benguela ecosystem are less patchy, more widespread and further offshore than the eggs. However, Hewitt (1981) points out that over and above the role of adaptive spawning behaviour of the adults, spatial patterns of egg and early larval abundance could also be the result of circulation features such as fronts and eddies which concentrate spawn (see Chapter 5), or as consequence of differential mortality (see Chapter 6). Evidently, anchovy and sardine eggs were significantly more patchy in summer (January - March) when frontal conditions were far more structured, than in spring (October - December) (Painting *et al.* subm.b).

3.4.2 Seasonal changes in the abundance and distribution of egg and larvae

The reduced anchovy egg and larval abundances in 1994/95 compared with 1993/94 corresponds to a decrease in the biomass of adult anchovies from one season to the next (Painting *et al.* subm.

c). Also, sardine egg and larval abundance was greater during 1994/95 than 1993/94 and this pattern corresponds to an increase in the biomass of adult sardine spawners (Painting *et al.* subm. c). Despite the decrease in both anchovy spawners and their eggs and larvae from SARP I to SARP II, both anchovy and sardine recruitment was better after SARP II (1994/95) than SARP I (1993/94) (SFRI unpublished data). This suggests that environmental conditions during SARP II may have been more favourable for the growth and survival of eggs and larvae through to recruitment of both anchovy and sardine. Environmental conditions which favour anchovy and sardine spawning and the survival of eggs and larvae are therefore addressed in Chapter 4. Both eggs and larvae of anchovy and sardine were further offshore during SARP I than SARP II, which suggests that egg and larval transport was more efficient during the second season and this may have contributed to better anchovy and sardine recruitment in 1995. The role of water currents in the transport of eggs and larvae during SARP are discussed in more detail in Chapter 5.

CHAPTER 4

Relationship of sardine and anchovy egg abundance to sea temperatures and the availability of food for adult spawners.

4.1 Introduction

Like most other coastal upwelling areas, the southern Benguela region is highly variable in terms of both the physical and biological environment (Hutchings 1992). In order to optimise their survival to recruitment in such a dynamic environment, anchovies and sardines are thought to select specific seasons and locations for spawning. Consequently, spatial and temporal patterns of egg abundance (see Chapter 3) should reflect the spawning behaviour of the adults. However, as planktonic organisms, the abundance patterns of older eggs and larvae are also influenced by physical features such as currents and fronts (see Chapter 5).

A great deal of attention has been focussed on the physical and biological processes which control the population dynamics of anchovy (Roel *et al.* 1994, Cochrane and Hutchings 1995). Of these, sea temperature is generally considered to be one of the most important factors influencing the spawning behaviour of anchovy (Shelton 1986, Armstrong *et al.* 1987, Shelton and Hutchings 1990, Richardson *et al.* in press). Indeed, it has been suggested that anchovy spawn primarily in water with a temperature range of 16-19°C (King *et al.* 1978, Armstrong *et al.* 1991, Richardson *et al.* in press) since both adult fish (Hampton 1987) and their eggs (Anders 1965) are commonly found in this temperature range. Besides the influence of sea temperatures on the spawning behaviour of anchovies, it has been shown that the frequency of spawning events is dependant on the availability of food (Hunter and Leong 1981, Peterson *et al.* 1992). This implies that adequate food may be necessary to ensure successful spawning throughout the season. By contrast, the environmental conditions that favour sardine spawning in the southern Benguela ecosystem are poorly understood.

This chapter investigates spatial and temporal variations in anchovy and sardine egg abundance in relation to both sea surface temperatures and the distribution of adult spawners. The relationship between intra-annual changes in the availability of food for adult spawners and the abundance of eggs will also be investigated in order to assess the relative importance of the food environment to the choice of spawning ground for these two species.

4.2 *Data analysis*

The total number of anchovy and sardine eggs collected each month during SARP I and II (Chapter 3, section 3.2) was used as an index of spawning success. Because the western Agulhas Bank (WAB) is the major centre of both anchovy and sardine spawning during peak periods (Chapter 3), monthly average egg abundance over the WAB was examined together with sea temperatures, the biomass of adult fish, large copepods, and integrated chlorophyll *a* concentrations from the sample region. These environmental parameters were collected simultaneously with the egg samples and the procedures for their collection have been described in Chapter 2.

In order to assess the preferred temperature range over which anchovy and sardine spawned most frequently during SARP, both the density of anchovy and sardine eggs and the biomasses of adult anchovy and sardine for all 14 SARP cruises were summed within bins of temperature. Within each temperature range, the density of eggs and the biomass of adult fish were divided by the number of stations for all 14 SARP cruises sampled in each temperature range in order to reduce biases in the interpretation caused by sampling at specific sea temperatures. Thus, an "index of occurrence" was derived for anchovy and sardine eggs and adult fish within each temperature range.

In order to investigate the temporal changes in the spawning habitat of anchovy and sardine, the density of eggs and the biomass of adult fish collected each month during SARP I and II were summed within bins of temperature. Each temperature range was weighted according to either the density of eggs or the biomass of fish within that range in order to calculate the average temperature at which either eggs or adults occurred most frequently each month during SARP I and II. These procedures were also performed on the number of stations sampled within each temperature range in order to compare temporal changes in the average sea surface temperatures at which samples were most frequently collected.

As a measure of intra-annual variation in suitable spawning habitat, the area of the WAB occupied by water of between 16-19°C was calculated from temperature sections in SURFER v.6 (Golden Software Inc., USA) (Richardson *et al.* in press). Temperature data were collected from continuous ship-board measurements during each cruise.

Copepod numbers were converted to biomass as mg dry weight. m^{-2} using published data (Verheye 1991, Peterson *et al.* 1992). Since adult anchovy prefer large copepods as a food source (James and Findlay 1989) and because anchovy spawn predominantly in water between 16-19°C (King *et al.* 1978, Armstrong *et al.* 1991, Richardson *et al.* in press), the biomass of large copepods (>1.5 mm, Richardson *et al.* in press) within the area of 16-19°C water was used as a measure of the food available to anchovy. These estimates were calculated each month from stations on the WAB, and average biomass estimates were used to explore the relationship between spawning activity and anchovy feeding conditions during SARP I and II.

Whereas anchovy are primarily zooplanktivorous, adult sardine can feed on microzooplankton, as well as phytoplankton (van der Lingen 1994). Both the monthly average chlorophyll *a* concentrations and the average copepod abundances over the WAB were compared with monthly sardine egg abundances to investigate the relationship between sardine spawning activity and feeding conditions over the WAB during SARP I and II.

4.3. Results

4.3.1. Anchovy eggs in relation to adult fish distribution and sea surface temperatures during SARP.

Anchovy eggs occurred predominantly in water with a sea surface temperature of between 16-19°C (Fig 4.1). While anchovy eggs were sometimes found in either cooler water (*ca* 15 °C) or warmer water (*ca* 21 °C, Fig. 4.1), their abundances at these temperatures were usually low (<300 eggs m^{-2}). Stations with the greatest abundance of anchovy eggs had similar sea surface temperatures on both the WAB and the west coast (Fig. 4.2). However, anchovy eggs at sea surface temperatures less than 16 °C tended to be found on the west coast, while anchovy eggs in warmer water (*i.e.* > 20°C) were found on the WAB (Fig. 4.2).

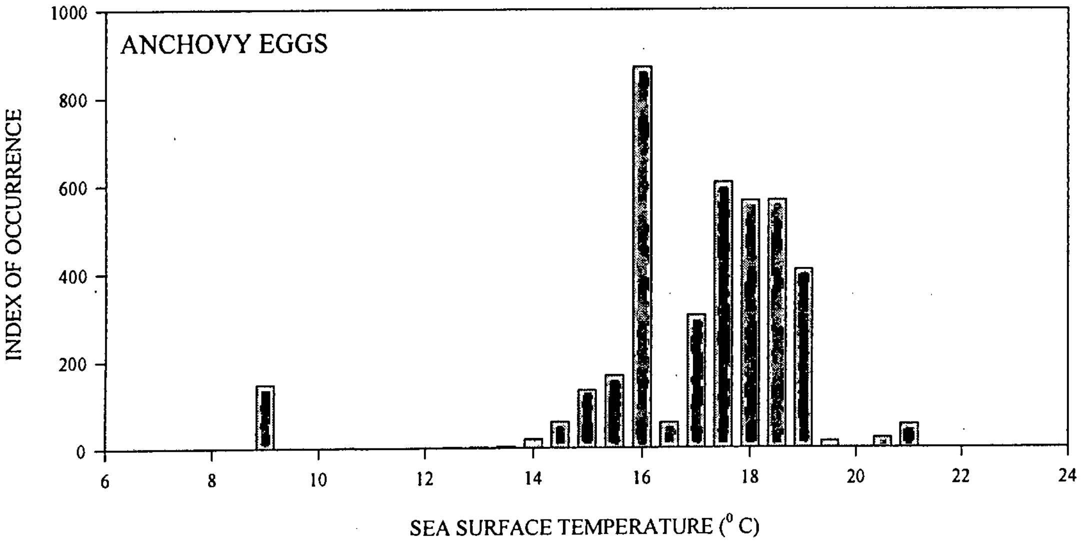

Fig. 4.1 Anchovy egg occurence in relation to sea surface temperature during SARP. The index of occurrence is calculated as the number of eggs in each temperature range divided by the number of stations sampled in each temperature range in order to reduce sampling bias.

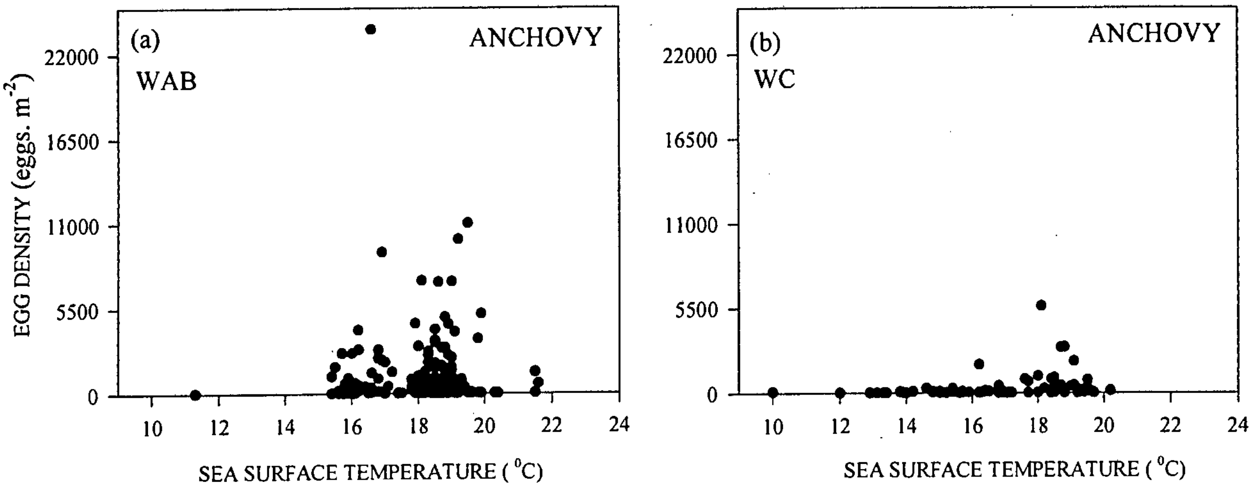

Fig. 4.2. Scattergrams showing the relationship between anchovy egg abundance and sea surface temperature on (a) the western Agulhas Bank (WAB) and (b) the west coast (WC) during SARP I and SARP II.

During peak anchovy spawning (Chapter 3), eggs were found on average between 17 °C (*i.e.* October) and 19.5 °C (*i.e.* December). This pattern was consistent between seasons (Fig. 4.3). The average sea surface temperature at which samples were collected each month during SARP indicates that intense spawning activity coincided with a period (*i.e.* October to December) when

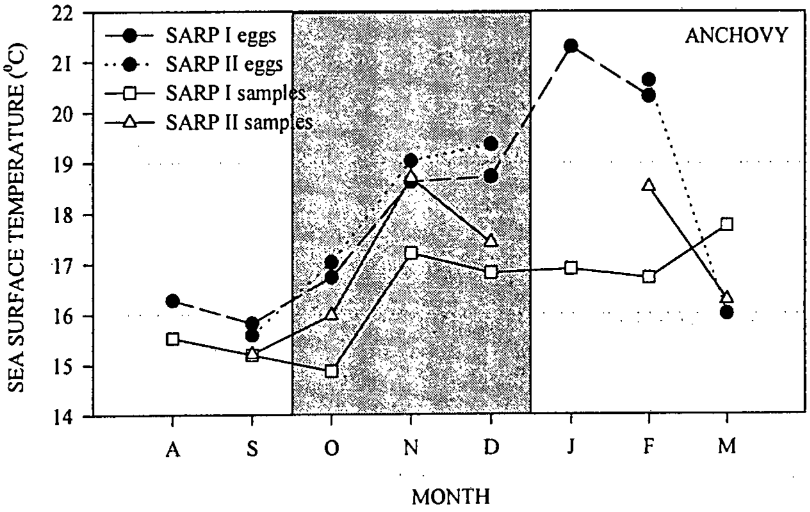

Fig. 4.3 The weighted mean sea surface temperatures at which anchovy eggs were most frequently found each month during SARP I and II. These are compared with the mean sea surface temperatures of all samples collected each cruise. The grey shaded area indicates the peak spawning period as defined in Chapter 3.

sea surface temperatures between 16-20 °C were widespread (Fig. 4.3). Anchovy eggs at the cooler end of the range occurred most frequently during spring (*i.e.* September 1993 and September 1994) whereas eggs in warmer water occurred in late summer (*i.e.* January 1993, February 1993 and 1993, Fig 4.3).

Whereas anchovy eggs were confined to a relatively narrow temperature range, adult anchovy where found in water ranging from 11.5 °C to 22 °C (Fig. 4.4). However, during months of peak spawning (*i.e.* October and November of both SARP I and II), adult anchovy were found most frequently in sea surface temperatures between 16 and 19 °C (Fig. 4.5). Although adult anchovy were seldom found in water warmer than 20 °C, peak adult biomass in January 1994 occurred at 22 °C (Fig. 4.4). Nevertheless, adult fish in January 1994 occurred most frequently at *ca* 17 °C (Fig. 4.5) and were confined to a narrow band close to the coast (Painting *et al.* subm. c).

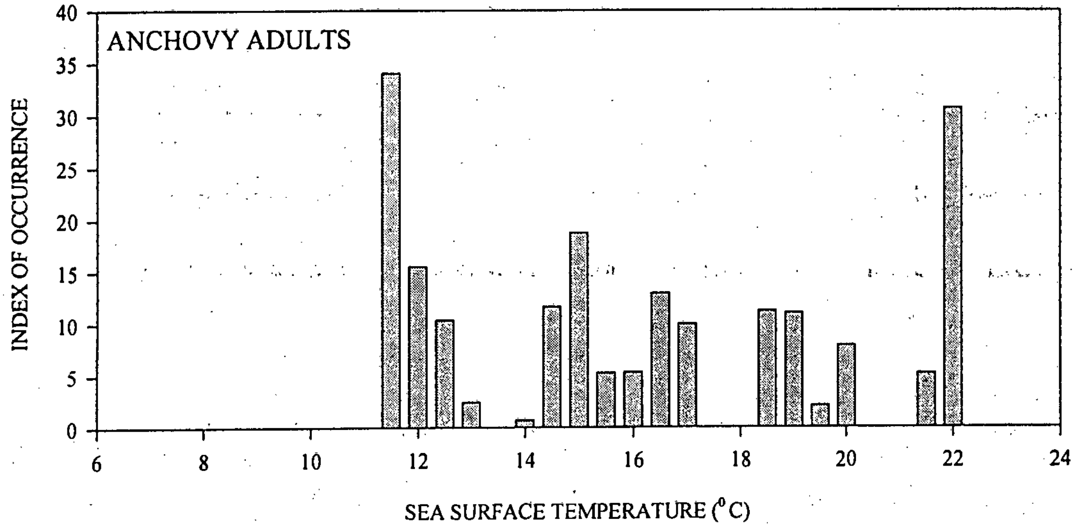

Fig. 4.4 Adult anchovy occurence in relation to sea surface temperature during SARP. The index of occurence is calculated as the biomass of adult fish in each temperature range divided by the number of stations sampled in each temperature range in order to reduce sampling bias.

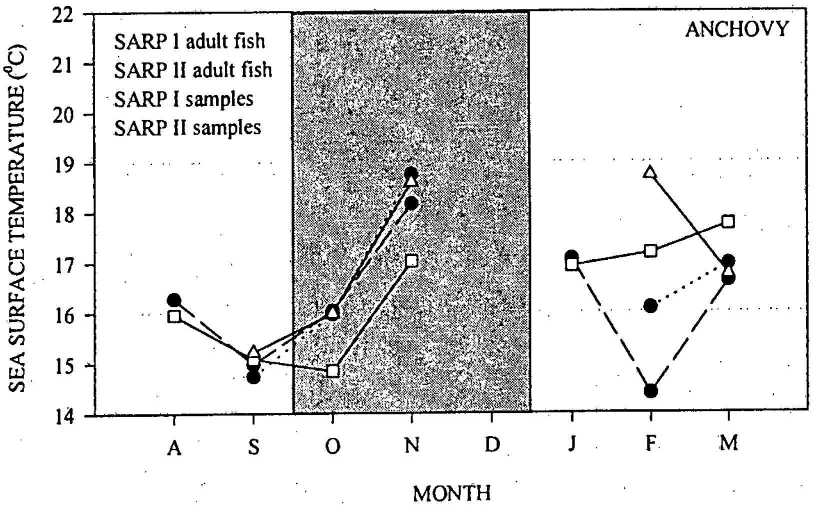

Fig. 4.5 The weighted mean sea surface temperatures at which adult anchovy were most frequently found each month during SARP I and II. These are compared with the mean sea surface temperatures of all samples collected each cruise. The grey shaded area indicates the peak spawning period as defined in Chapter 3.

Adult anchovy were found in cooler water (*ca* 11.5°C to 15°C, Fig. 4.4) during September 1993 and 1994 and during February 1993 (Fig. 4.5) when spawning intensity was at a minimum over the season (Chapter 3).

4.3.2. Sardine eggs in relation to adult fish distribution and sea surface temperatures during SARP.

Sardine eggs were found predominantly in water of between 14.5 - 21.5 °C (Fig. 4.6) Very dense sardine eggs (5000 to 19000 eggs m^{-2}) were found in warm water (*ca* 21.5 °C) on the WAB during late summer (i.e. January 1994 and February 1994, 1995, Fig. 4.7a) when spawning

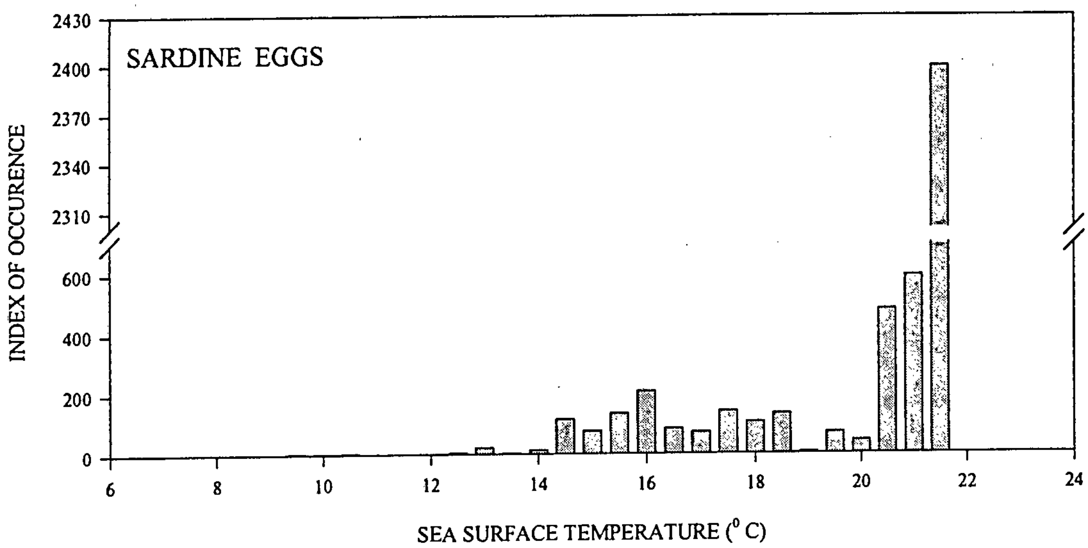

Fig. 4.6 Sardine egg occurence in relation to sea surface temperature during SARP. The index of occurence is calculated as the number of eggs in each temperature range divided by the number of stations sampled in each temperature range in order to reduce sampling bias.

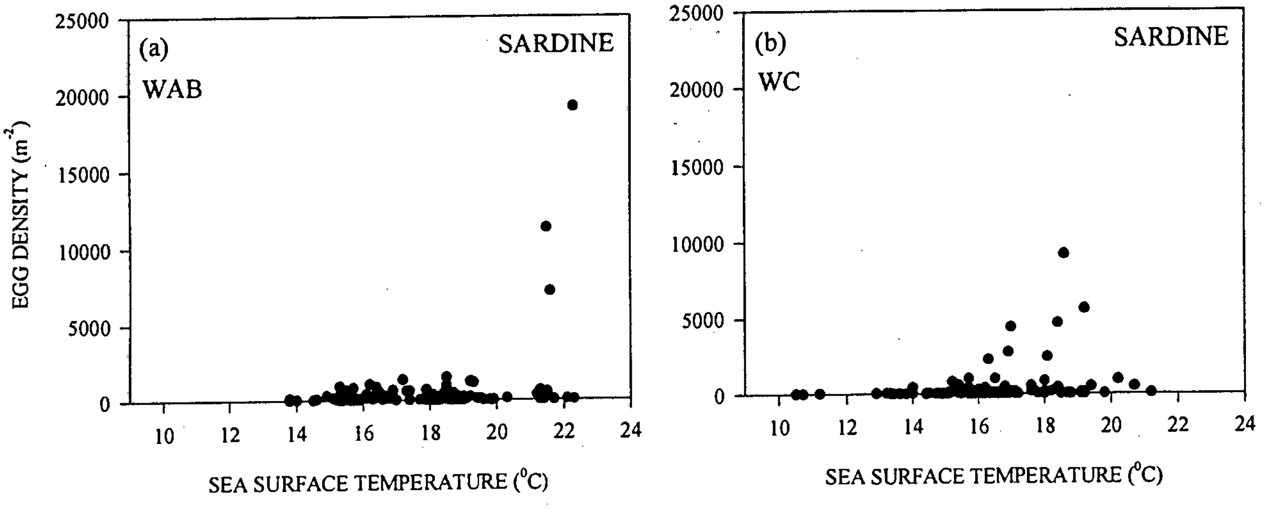

Fig. 4.7. Scattergrams showing the relationship between sardine egg abundance and sea surface temperature on (a) the western Agulhas Bank (WAB) and (b) the west coast (WC) during SARP I and SARP II.

activity was at a peak. During the spring/early summer peak in spawning activity, the weighted mean temperature at which sardine eggs were most frequently found ranged from 15.5 -16.5 °C (Fig. 4.8).

Although sardine spawned over a wide temperature range, adults were found predominantly between 14.5 -20 °C (Fig. 4.9). Adult sardine were found in water of 10.5 -21 °C (Fig. 4.9) during January 1994, and during February 1994 and 1995 when sardine spawning was at a maximum (Fig. 4.10). Despite the wide range in temperatures at which adult sardine were found, the greatest biomass of adults occurred most frequently between 16.5 -18.5 °C during the late summer period.

4.3.3 A comparison between anchovy and sardine eggs in relation to sea surface temperatures.

A significant positive correlation was observed between the area of 16-19 °C water and the abundance of anchovy eggs during SARP (Fig. 4.11a, $r^2 = 0.51, p<0.05$, N = 13). September

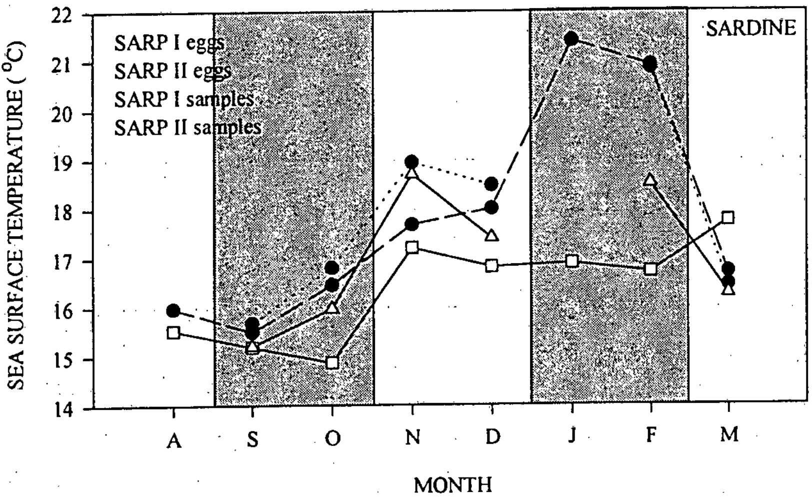

Fig. 4.8 The weighted mean sea surface temperatures at which sardine eggs were most frequently found each month during SARP I and II. These are compared with the mean sea surface temperatures of all samples collected each cruise. The grey shaded area indicates the peak spawning period as defined in Chapter 3.

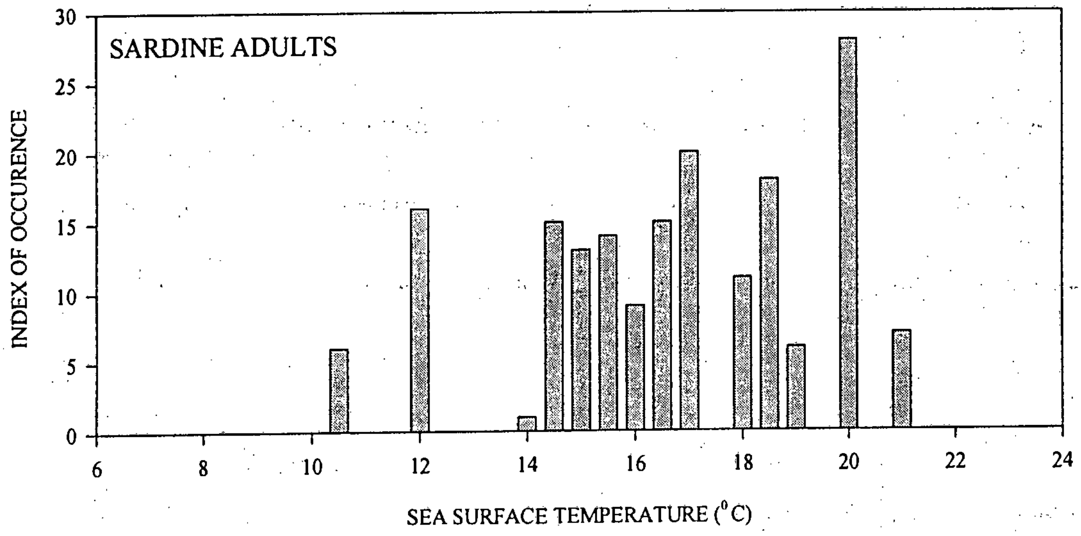

Fig. 4.9 Adult sardine occurence in relation to sea surface temperature during SARP. The index of occurence is calculated as the biomass of adult fish in each temperature range divided by the number of stations sampled in each temperature range in order to reduce sampling bias.

1993 was omitted from the analysis because only the inshore stations on the Walker Bay line were sampled and therefore the area of 16-19 °C water could not be accurately measured. Inclusion of estimates from the November biomass surveys between 1988 and 1992 improved

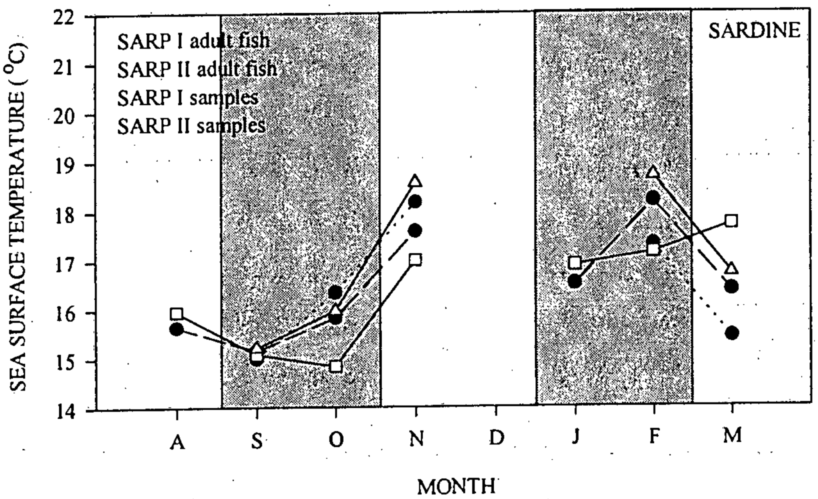

Fig. 4.10 The weigthed mean sea surface temperatures at which adult sardine were most frequently found each month during SARP I and II. These are compared with the mean sea surface temperatures of all samples collected each cruise. The grey shaded area indicates the peak spawning period as defined in Chapter 3.

the relationship (Fig. 4.11b, $p<0.05$, $r^2 = 0.63$, N = 18). Months of peak anchovy spawning (*i.e.* October and November) were at the higher end of the regression suggesting a possible link between area of suitable spawning habitat and the intensity of anchovy spawning (Fig. 4.11b).

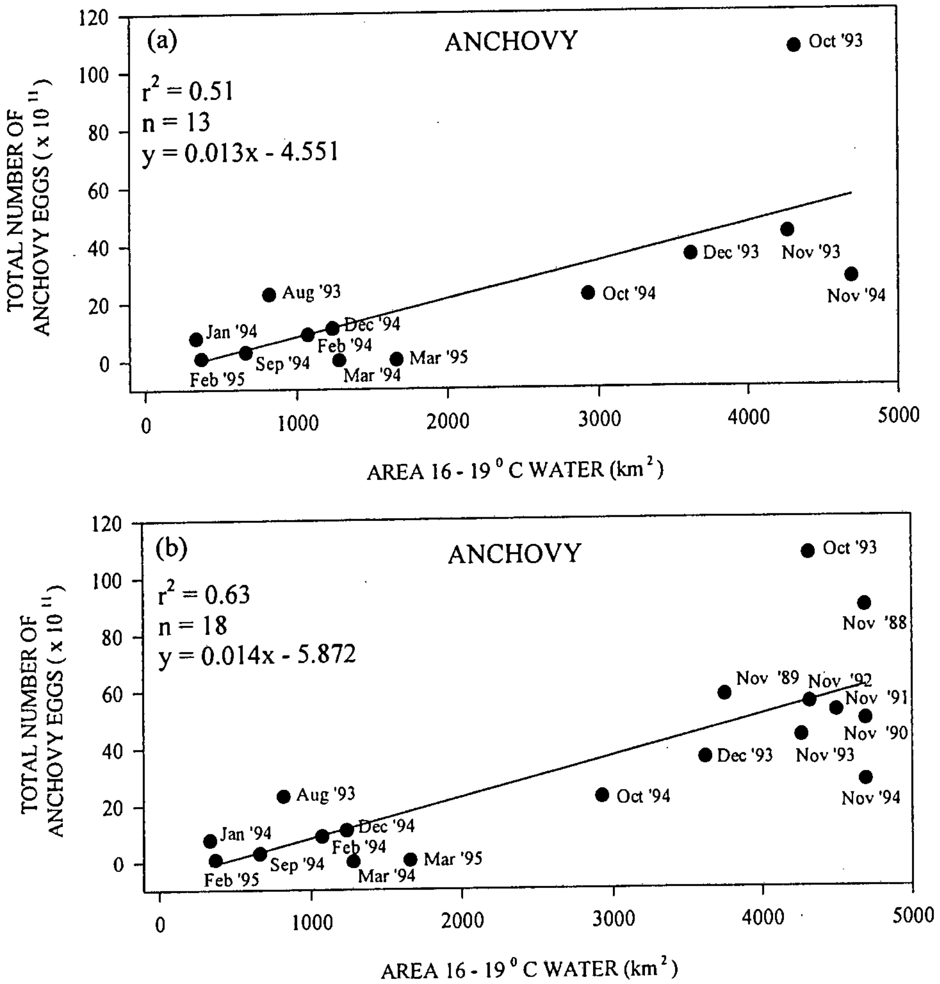

Fig. 4.11 The regression relationship between the area of 16 - 19 ° C water (km^2) and the total number of anchovy eggs (x 10 ^{11}) found each month on the WAB during (a) SARP I and SARP II and (b) SARP I & II together with data from November cruises

The spawning intensity of sardine did not appear to be related to the area of suitable spawning habitat identified for anchovy, as no significant relationship was found between sardine egg abundance and the area of 16-19 °C (Fig. 4.12, $p>0.05$, $r^2 = 0.082$, N = 13).

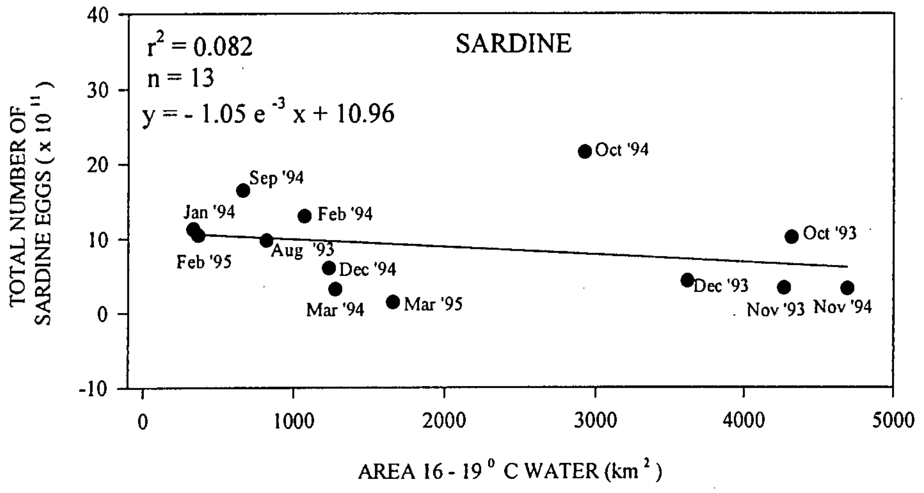

Fig. 4.12 The regression relationship between the area of 16 - 19 ° C water (km^2) and the total number of sardine eggs (x 10^{11}) found each month on the WAB during SARP I and SARP II.

4.3.4 Anchovy and sardine spawning activity in relation to the adult food environment during SARP.

The significant positive relationship between anchovy egg abundance and the area of 16-19 °C water on the WAB during SARP suggests that these hydrographic conditions favour anchovy spawning. Therefore, in order to understand the factors which may influence the spawning activity of anchovy, it is useful to consider the different environmental conditions within that area. The relationship between the biomass of large copepods in 16-19 °C water and the monthly abundance of anchovy eggs yielded a significant positive correlation (Fig. 4.13a, $r^2 = 0.35$, $p<0.05$, N = 11). For this analysis, data from September 1993 were excluded because of poor sampling, while data from both March 1994 and March 1995 were excluded because these two surveys marked the end of the anchovy spawning season when either no eggs (*i.e.* March 1994) or very few eggs (*i.e.* March 1995) were found. These data were excluded before the regression was undertaken. The inclusion of data from the November biomass cruises between 1989 and 1992 improved the relationship slightly (Fig. 4.13b, $r^2 = 0.41$, $p<0.05$, N = 15), suggesting that

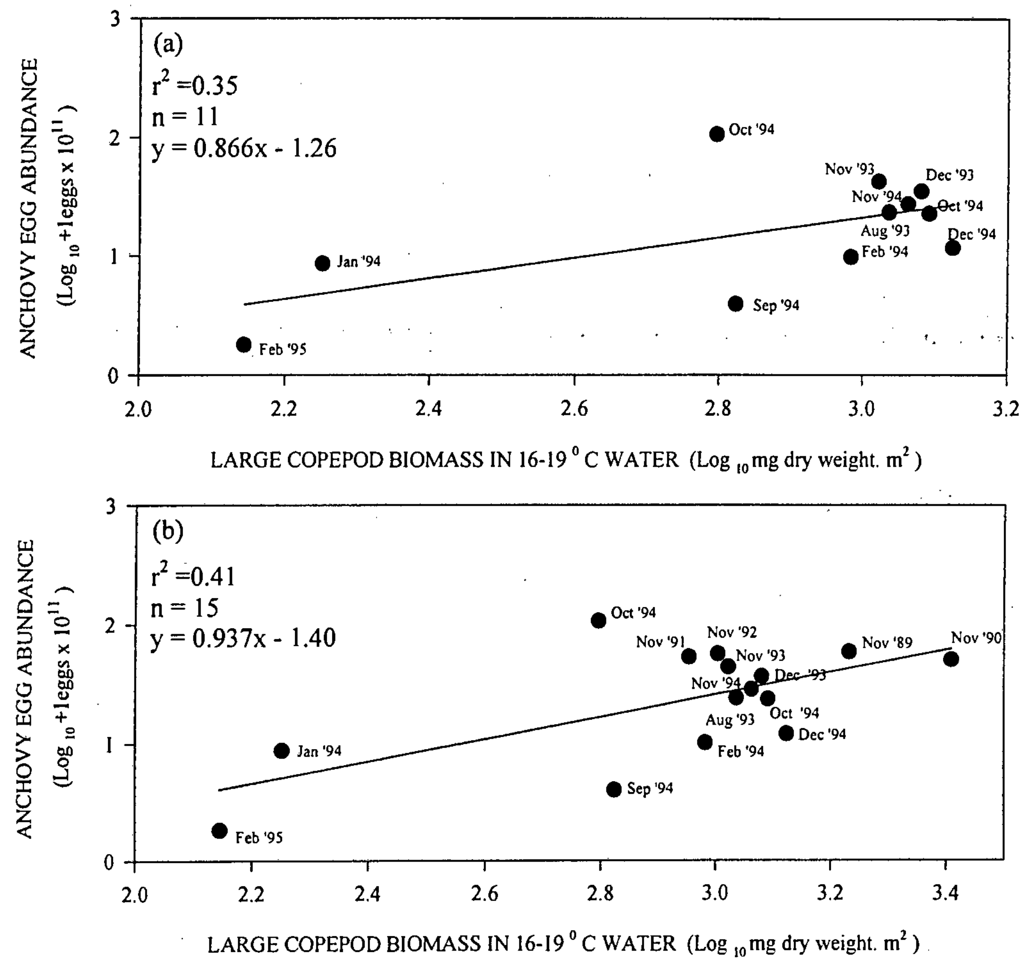

Fig. 4.13 The regression relationship between the biomass of large copepods in 16 - 19° C water (Log_{10} mg dry weight. m^2) and the total number of anchovy eggs (log_{10}+1eggs x 10^{11}) found each month on the WAB during (a) SARP I and II and (b) SARP I and II together with November cruise data.

the intensity of spawning by adult anchovy may be linked to the availability of large copepods during the spawning season. No significant relationship was found between sardine egg abundance and the biomass of copepods (y = 0.002x + 4.26; $r^2 = 0.064$, $p>0.05$, N = 14), suggesting that the spawning activity of sardine may not be influenced by the availability of copepods during the spawning season.

The average chlorophyll *a* concentrations over the WAB were positively correlated with the abundance of sardine eggs during SARP (Fig. 4.14a, $r^2 = 0.40$, $p<0.05$, N = 14). This relationship was improved by excluding the estimates for March 1994 and March 1995 when very few sardine eggs were found (Fig. 4.14b, $r^2 = 0.55$, $p<0.05$, N = 12). Evidently, periods of intense sardine spawning activity coincided with elevated integrated chlorophyll *a* values. The spawning intensity of anchovy did not appear to be related to the concentration of chlorophyll *a*, as no significant relationship was found between anchovy egg abundance and the monthly average chlorophyll *a* concentrations on the WAB during SARP ($y = 0.087x + 16.54$; $r^2 = 0.0048$, $p>0.05$, N = 14).

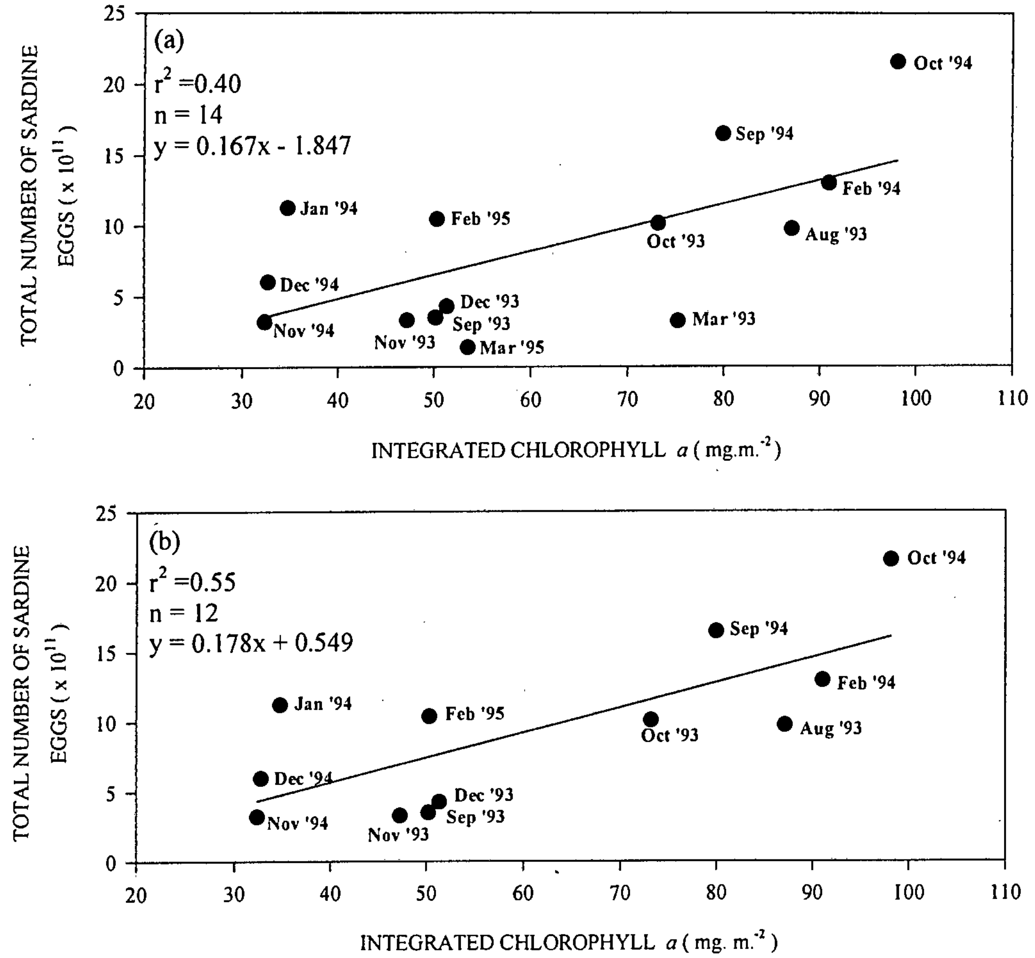

Fig. 4.14 The regression relationship between the concentration of chlorophyll *a* and the total number of sardine eggs (x 10^{11}) found each month on the WAB during SARP I and SARP II. (a) includes all 14 cruises, (b) excludes March 1994 and March 1995.

4.4 Discussion

Although it is possible to analyse the relationship between the distribution and abundance of eggs with regard to a number of physical and biological factors within the environment, this study has shown that sea surface temperatures and the availability of food for adult spawners may influence the area, timing and frequency of spawning by adult fish.

4.4.1 Anchovy and sardine egg abundance and distribution at specific sea surface temperatures in relation to the adult fish.

Although adult anchovy were found over a wider temperature range than their eggs, the peaks in adult biomass at cool temperatures and warm temperatures are driven mainly by their occurrence during periods of reduced spawning activity, either at the beginning or the end of the spawning season. However, during periods of peak spawning activity, both adults and eggs tended to be found at similar water temperatures.

Despite the predominance of sardine eggs in warm water (*ca* 20.5-21.5 °C, Fig. 4.6), the temperature range at which sardine eggs occurred was closely mirrored by the range at which the adult sardine were found. Without reference to sea surface temperature data, Hampton (1987) showed that the distribution of anchovy eggs during November (1983, 1984 and 1985) closely approximated the distribution of adult fish. The fact that the eggs extended slightly further offshore than the adults was explained by Roel *et al.* (1994) as probably due to the influence of offshore advection. Despite the influence of the physical environment, the spatial and temporal overlap between adults and eggs at certain temperatures supports the hypothesis that egg distributions give a relatively good indication of the spawning habitat of the adults. This provides further justification for the use of egg abundance estimates as an indicator of spawning activity.

4.4.2 Anchovy spawning in relation to environmental conditions during SARP.

Environmental conditions which may determine the choice of the WAB as the primary spawning area for anchovy, and to some extent sardine, have been the subject of much discussion over the years (Shelton and Hutchings 1990, Hutchings 1992, Peterson *et al.* 1992, Roel *et al.* 1994, Cochrane and Hutchings 1995). Parrish *et al.* (1983) and Shelton and Hutchings (1990) have suggested that, despite strong wind stress, anchovy spawn mainly on the WAB during the summer months in order to take advantage of seasonal patterns in water column stability in this region. In terms of the thermal stability on the WAB, Shelton (1986) showed that anchovy spawning appears to be related to the increase in mean sea surface temperatures at the onset of summer. King *et al.* (1978) suggested that the preferred sea temperatures for anchovy spawning are between 16 and 18 °C, which approximate the average summer temperatures in the midshelf region of the WAB. It is evident from this study that anchovy egg abundance reached a maximum in the midshelf region on the WAB during October and November where and when sea surface temperatures were within the range of 16-20 °C. Similar results were reported by Anders (1965) who found that 75 % of anchovy eggs were found on the midshelf WAB within the temperature range of 16-19 °C between September 1964 and February 1965.

The area of water between 16-19 °C provides a good measure of the size of the anchovy spawning habitat because anchovy spawn primarily in areas within this temperature range. It is therefore not surprising that changes in the extent of 16-19 °C water on the WAB reflect intra-annual changes in the intensity of anchovy spawning activity. This is exemplified here by a comparison of the 1993/94 and 1993/95 spawning seasons. During the spring and early summer months when anchovy spawning was at a maximum (Chapter 3), the WAB was characterised by infrequent surface upwelling during both seasons (Painting *et al.* subm.b) and a large area of 16-19 °C water. As upwelling activity on the WAB increased towards late summer (Painting *et al.* subm.b), persistent SE winds promoted the offshore migration of the upwelling front. The simultaneous advection of warm Agulhas Current water into the southern Benguela region caused a reduction in the area of 16-19 °C water as it was "squeezed" between the upwelling front and the oceanic front during January and February (Painting *et al.* subm.b). This reduction in the size of the anchovy spawning habitat coincided with a decrease in egg abundance during late summer (see Chapter 3).

Laboratory studies have shown that the normal development of anchovy eggs does not occur at temperatures below 14 °C (King *et al.* 1978). Thus, anchovy may select the WAB as the primary spawning habitat because the thermal stability of the region is conducive to rapid egg development.

Although previous studies have shown that the WAB is a food poor environment relative to the west coast, these findings were based on comparisons of total copepod biomass between the two areas. However, if copepod biomass is considered on a spatial scale relevant to anchovy, such as in 16-19 °C water, the food availability is similar in the two regions. Furthermore, Richardson *et al.* (in press) found that in 16-19 °C water, the food environment on the WAB was more stable than that of the west coast, and the production of large copepods greater than in cooler waters. Thus, the area of 16-19 °C water during SARP can be considered as a food-rich environment.

Evidently, spawning intensity during SARP was enhanced during periods when the biomass of large copepods in the area of 16-19 °C was at a maximum. Hunter and Leong (1981) have shown that although the northern anchovy (*Engraulis mordax*) obtain 66 % of their energy for spawning from fat reserves, the remaining third is taken up during the spawning season. Consequently, the intensity and duration of spawning is dependant on the availability of food for adults (Alheit 1989). Thus, the suitability of the area of 16-19 °C water for anchovy spawning may be related to the food conditions within this area. Besides the benefits of enhanced egg development and survival derived from stable sea surface temperatures on the WAB, adult anchovy may select the WAB as the primary spawning area because of the favourable feeding conditions in the area of 16-19 °C water which dominates the midshelf region during the summer. Thus, the duration of the summer period as defined by area of 16-19 °C water may be critical to the spawning success of anchovy (Richardson *et al.* in press).

4.4.3 Sardine spawning in relation to environmental conditions during SARP.

In accordance with the findings for anchovy, the simultaneous increase in the spawning activity of sardine and the occurrence of warmer water (*ca* 16 °C) on the WAB during spring (*i.e.* October) suggests that spawning of sardine may also be a response to water temperature (Shelton 1986). The reason for this phenomenon is unclear but may be related to enhanced egg development. King (1977b) showed that the survival of sardine eggs was greatest in water between 16-21 °C, although successful development could be achieved between 13-22 °C. Eggs kept at temperatures beyond this range, did not develop normally, which reduces their survival considerably (King 1977b). It is interesting to note that elevated sardine spawning did occur in warmer waters (*ca* 22 °C) on the WAB during late summer (*i.e.* January and February). These findings suggest that while anchovy and sardine spawning may be defined by a lower threshold sea temperature (*ca* 13 °C), sardine are able to spawn over a much wider temperature range than anchovy.

The seasonal intensity of sardine spawning seems to vary independently of the area of 16-19 °C water, which suggests that the conditions which define the suitable habitat for anchovy spawning are not necessarily the same for sardine. Despite the great abundance of sardine eggs at these temperatures, however, sardine spawning in warm water was not widespread. Most of the adult sardine were found in cooler upwelled water (*ca* 11 °C) close to the coast during this period, although some were found in temperatures of about 22 °C and could possibly have been spawning in this region. However, it seems that while anchovy spawning may be limited both temporally and spatially by a confined spawning habitat defined by sea temperatures, sardine spawning is less restricted by temperature.

The two peaks in sardine spawning activity (see Chapter 3) occur under totally different thermal conditions. Alheit (1989), suggests that under certain circumstances, the secondary peak can become the main peak if unfavourable conditions persist. This would allow sardine to optimise reproductive output during favourable conditions. The data presented in this study suggest that sardine may be able to utilise other environmental conditions to optimise spawning in areas and at times when temperatures are slightly higher than those defined for anchovy.

The relatively good positive correlation between the spawning activity of sardine and the monthly chlorophyll *a* concentrations on the WAB suggests that sardine spawning activity may be related to feeding conditions. As westerly winds decrease at the end of winter, the depth of the upper mixed layer is reduced, the surface water warms and stabilises (Shelton and Hutchings 1990), and phytoplankton production begins to increase (Richardson *et al.* subm.). The levels of chlorophyll *a* increased on the WAB during the spring of 1993 and 1994, and coincided with peaks in sardine spawning activity. As the nutrient levels are depleted during the summer, the concentration of chlorophyll *a* decreases (Richardson *et al.* subm.). This pattern coincided with a decrease in the intensity of sardine spawning activity during SARP. As upwelling intensity increased to a reach a maximum in late summer (Painting *et al.* subm.b), nutrient rich water was brought to the surface and phytoplankton production increased. This pattern was mirrored by an increase in the spawning intensity of sardine, which reached a second peak during this period.

Although both sardine spawning activity and chlorophyll *a* concentrations were intense during February 1994, the relationship between sardine spawning and the average chlorophyll *a* concentration each month during SARP seems to driven mainly by the spring peak in sardine spawning activity (September and October) when average chlorophyll *a* concentrations were elevated. However, the level of chlorophyll *a* varies according to the phase of upwelling. Because of the high turnover rate in phytoplankton production, chlorophyll a concentrations can change considerably within days. Consequently, monthly sampling only provides a "snap-shot" of the processes which occur throughout the month, and elevated concentrations of chlorophyll *a* may have been missed. In their review of primary production on the Agulhas Bank, Probyn *et al.* (1992) indicate that primary production is far greater at the end of summer than during spring and early summer. Although adult sardine also feed on microzooplankton, the diets of spawners may be supplemented by a fairly stable, uniform phytoplankton biomass during the spring and a productive, patchily distributed phytoplankton resource during late summer. Like other clupeids, (see Alheit 1989 for examples) it has been suggested that sardine in the Benguela ecosystem are able to reabsorb their eggs (atresia) during starvation and can rebuild their ovaries over a very short time when feeding conditions improve (Le Clus 1989). Alheit (1989) suggests that this tight relationship between food availability and spawning activity may explain the occurrence of two spawning maxima per season in clupeiform species such as sardine. Therefore, these intra-seasonal changes in the pattern of food availability for adult sardine may have contributed to the processes which shape the spawning behaviour of sardine.

It is evident that both the production and biomass of chlorophyll *a* is greater on the west coast compared with the WAB (Brown *et al.* 1991). This suggests that the choice of the WAB as the primary spawning ground is probably not driven by the availability of adult food. As the sea temperatures on the west coast are frequently below the threshold limit for normal egg development (King 1977b), the choice of the WAB for spawning may be related to optimum temperatures for egg and larval survival. Nevertheless, the data presented here suggests that the temporal pattern of sardine spawning behaviour may be related to the availability of food for the adult spawners.

4.4.4 Possible influences of anchovy and sardine spawning success on recruitment

The clearly defined temporal and spatial pattern of spawning in anchovy and to a lesser extent sardine suggests that the spawning strategies of these species are adapted to predictable intra-annual environmental processes. This study suggests that both sea temperatures and food conditions for adults influence their spawning behaviour. Although it is thought that recruitment variability depends partly on the survival of eggs and larvae, there is some evidence to suggest that fecundity influences recruitment in some fish e.g. the Baltic sprat *(Sprattus sprattus balticus)*and the Baltic herring (*Clupea harengus nembras*)(Nikolsky 1969). Thus, a reduction in the availability of food may influence recruitment strength the following year.

Nevertheless, environmental conditions which promote good feeding conditions for the adults may also enhance egg and larval survival. Although no clear relationships were evident between the larval food environment and the abundance of larval fish during SARP, Shelton (1986) found that anchovy larvae were abundant during months of enhanced concentrations of potential food particles. In line with Cushing's (1973, 1978, 1990) match/mismatch hypothesis, Shelton (1986) suggested that the availability of food particles suitable for larval feeding may be important in determining their spawning season. In order to make use of enhanced plankton standing stocks on the west coast (Shelton 1986), and to reduce the effects of cannibalism (Valdes Szeinfeld and Cochrane 1991) eggs and larvae need to be transported a considerable distance northwards. The importance of the north flowing currents in the southern Benguela upwelling system for the survival of anchovy and sardine eggs and subsequent recruitment will be addressed in the following chapter.

CHAPTER 5

The transport of anchovy and sardine eggs and larvae from the western Agulhas Bank to the west coast during the 1993/94 and 1994/95 spawning seasons.

5.1 Introduction

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

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

A study of within-season variations in the processes most likely to influence pelagic fish recruitment has been the central focus of the South African Sardine and Anchovy Recruitment Prediction programme (SARP). This has afforded us the opportunity to validate and elaborate the conceptual model of transport of pelagic eggs and larvae in the southern Benguela by examining intra-annual variations in current features between Cape Agulhas in the south and the Olifants River on the west coast in relation to the distribution of spawned products. This work expands on previous studies by not only including data for anchovy eggs but anchovy larvae as well as sardine eggs and larvae.

5.2 Data analysis

5.2.1 Current data recordings

Currents were measured at a depth of 30 m using 150 kHz RDI narrow band Acoustic Doppler Current Profilers (ADCPs) mounted in the hulls of the FRS *Africana* and FRS *Algoa*. Methods of data collection are described in Chapter 2. In October 1994, the data were collected on the *Dr Fridtjof Nansen* using a similar broadband profiler. Measurements were made on station and augmented on certain lines by underway measurements between stations.

The quality of the current data collected varied substantially throughout the programme. The two November surveys conducted on FRS *Africana* yielded the best data because the performance of the profiler enabled bottom-referenced currents to be measured from the coast to the shelf-edge at 500 m depth with an accuracy better than 5 cm.s^{-1} (Boyd *et al.* 1992). The performance of the profiler on the FRS *Algoa* was poorer in 1993/94, but better results were achieved in 1994/95 following the use of the new "Transect" software which allowed bottom-tracking solutions to be obtained if only 3 of the 4 beams tracked the bottom. Bottom referenced currents could be obtained in depths close to 300 m on the FRS *Algoa* in most instances in 1994/95.

5.2.2 Selection and presentation of data for analysing egg and larval transport

Although current flow and ichthyoplankton data were collected simultaneously from a total of 14 monthly cruises, only data from selected months will be described individually. The strength and direction of currents as well as the abundance and distribution of anchovy and sardine eggs (nos. m^{-2}) and larvae (nos. 10 m^{-2}) collected at each station over the study area (Chapter 2) are presented as horizontal plots using SURFER v.6 (Golden Software Inc., USA). These data will be used to highlight certain features in the southern Benguela ecosystem which influence the transport of eggs and larvae from spawning to recruitment grounds. In particular, the data from October 1994 and February 1995 depict early summer and late summer features respectively, while the data from both November cruises were chosen because of good spatial coverage during these months. Prolonged SE winds prior to sampling in January 1994 resulted in extreme conditions during this cruise and therefore these data are included as an example. Data from all 14 cruises have been averaged to illustrate transport of spawned products over the whole spawning season.

5.3 Results and Discussion

5.3.1 Transport of eggs and larvae from the WAB past the Cape Peninsula

A comparison between egg and larval distributions and current data for October 1994 provides evidence for current features which promote the rapid movement of spawned products to the west coast (Fig. 5.1 a-e). Convergent flow just south of Cape Point (Fig. 5.1 e) coincided with the majority of both anchovy and sardine eggs on the WAB (Fig. 5.1 a,b). Consequently, eggs were entrained in the jet current, which was typified by very strong NNW flow inshore off the Peninsula in the region of the 200m isobath. Similar flow patterns were measured repeatedly in the spring of 1995 by Boyd and Nelson (in press). Relative to anchovy eggs, anchovy larvae were found further offshore of the Cape Peninsula (Fig. 5.1 c) suggesting either that currents had been more offshore-directed prior to sampling, or that spawning had taken place further offshore. The presence of adult spawners (Painting *et al.* subm.c) as well as young larvae (5-6 mm) on the outer WAB supports the latter argument. However, a substantial proportion of larvae in this region were between 8 and 13 mm with some as large as 23 mm (Fig. 5.2), suggesting that currents had been more offshore-directed prior to sampling or possibly that larger larvae were spawned further east and had moved along- and offshore with the currents. Convergent flow on the WAB was also noted during November 1993 (Fig. 5.3 e), although it occurred further offshore between the 200 m and 500 m isobaths. The jet current off the Cape Peninsula was also comparatively far

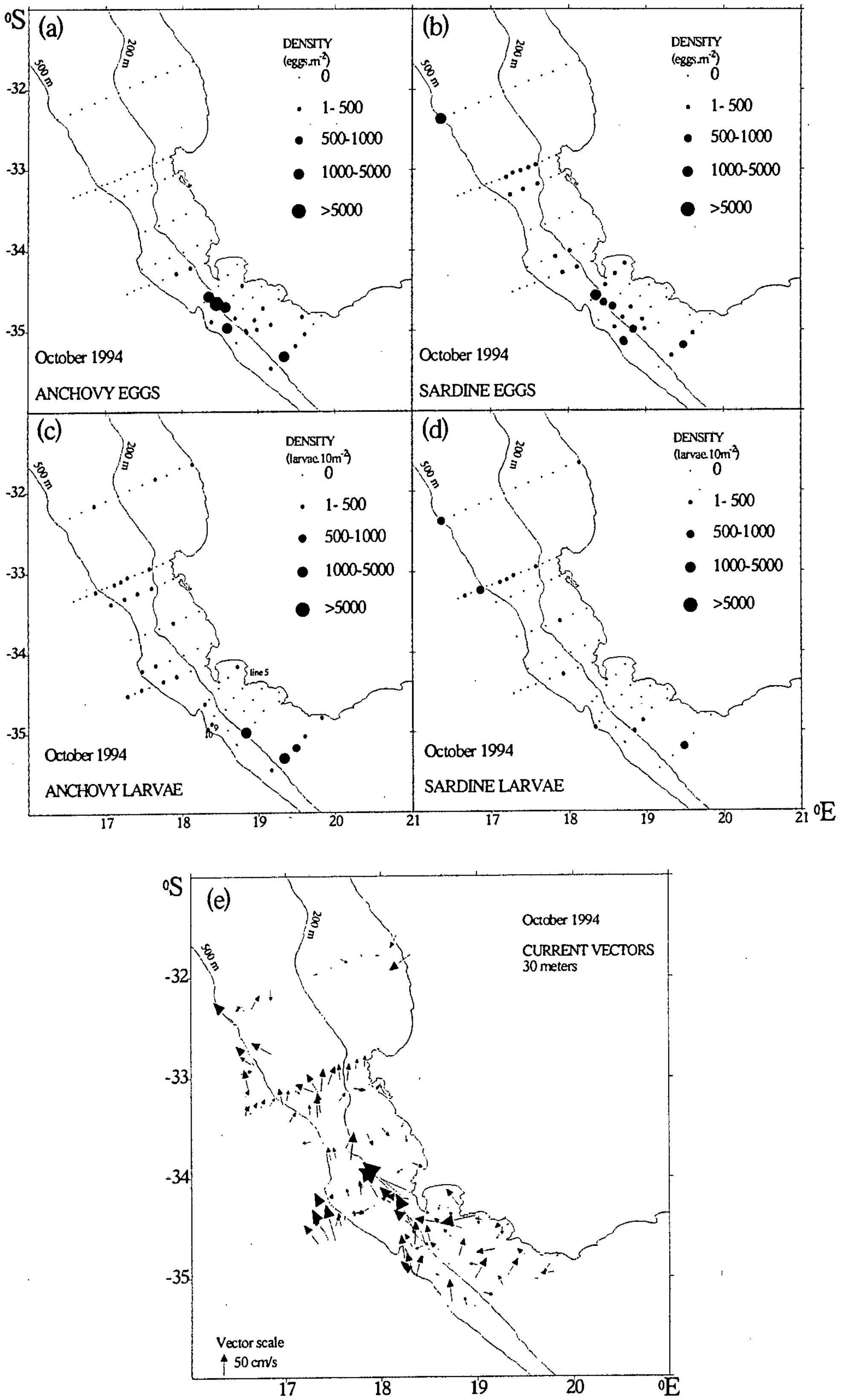

Fig. 5.1 The west coast of South Africa showing the relative density of anchovy and sardine eggs and larvae (a-d) and current vectors at 30 m depth (e) during October 1994.

offshore during this period. Both anchovy and sardine eggs were found in the vicinity of the jet suggesting rapid transport to the west coast (Fig. 5.3 a,b). Eggs and larvae of neither species were recorded in the strong currents on the outer stations offshore of the 500 m isobath, both south and west of the Peninsula, suggesting no losses in these regions at that time.

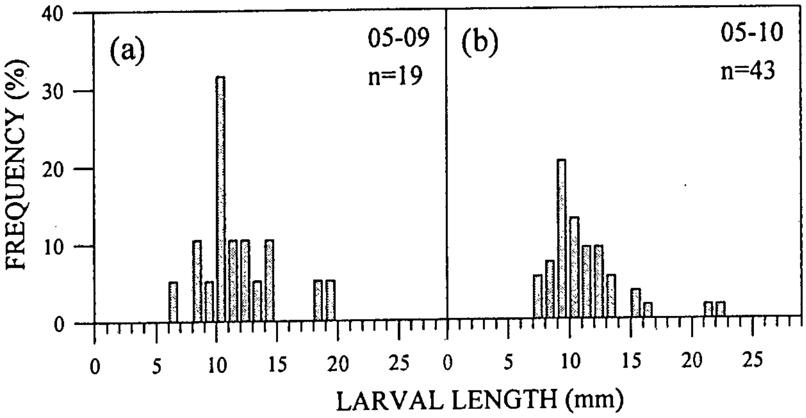

Fig. 5.2 Size frequency distributions of anchovy larvae observed at (a) station 9 and (b) station 10 on the outer WAB 9line 5) during October 1994. See Fig. 5.1c for the line and station positions.

The front on the WAB was clearly discernable in the midshelf region during January 1994 (Fig. 5.4 e). Erratic current vectors were observed in the region of the 500 m isobath (Fig. 5.4 e) and these could be due to both the convoluted nature of the front and the less-than-optimal set-up of the ADCP Navigation interface parameters. Areas of maximum northerly flow appeared to coincide with the thermal front (Fig. 5.4 e) and the majority of adult sardine and some adult anchovy were also found in this region (Painting *et al.* subm.c). The presence of large concentrations of eggs in this midshelf region suggests that adult fish were spawning in an area which coincided with the inner margin of the NNW flowing current (Fig. 5.4 a,b,e). These data suggest that the position of adult spawners in relation to certain current features is important in ensuring efficient entrainment of spawned products by the jet. This phenomenon has been confirmed by biophysical modelling (Lynne Shannon *et al.* 1996).

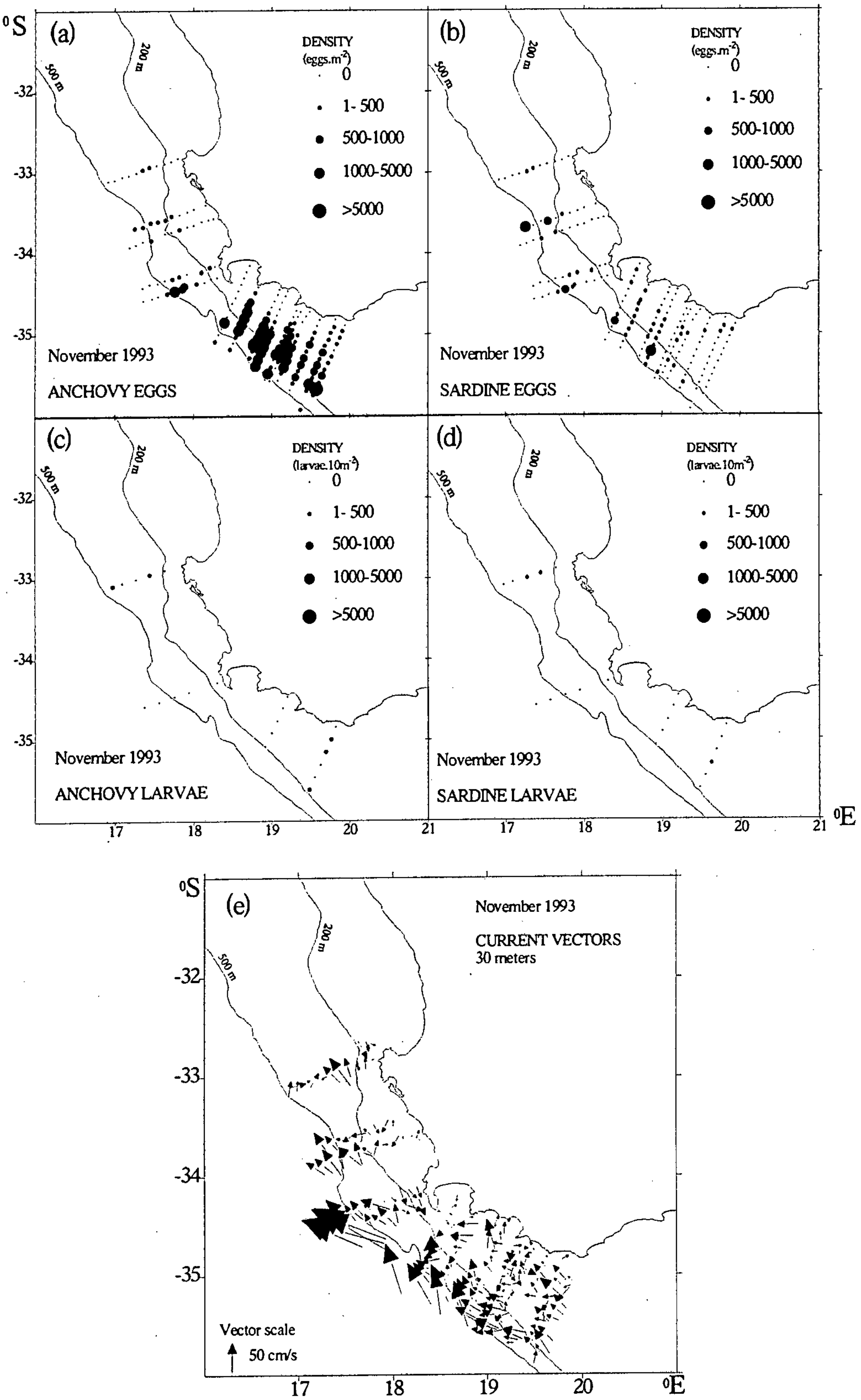

Fig. 5.3 The west coast of South Africa showing the relative density of anchovy and sardine eggs and larvae (a-d) and current vectors at 30 m depth (e) during November 1993.

Biological and hydrographic features observed during November 1994 (Fig. 5.5) show that prevailing conditions during the anchovy spawning season do not always favour speedy transport of spawned products from the WAB to the west coast. In contrast to the October 1994 survey, the WAB and Peninsula regions during November 1994 were characterised by weaker currents resulting from successive weak atmospheric cold fronts and north westerly winds (Richardson *et al.* in press). Despite these conditions, currents were still predominantly to the NW, and no losses were indicated. While the prevailing current features on the WAB would not stop the movement of spawned products to the west coast, transport during this period would have been slower than during October 1994. This may have resulted in increased cannibalism and predation (Valdes *et al.* 1987) particularly by adult spawners during this time (Painting *et al.* subm.c). Indeed, very few larvae were found on the WAB in November 1994 and only a few anchovy larvae were encountered on the eastern margin of the grid (Fig. 5.5 c). The absence of larvae was also noted in November 1993 (Fig. 5.3 c,d). While transport may have been slow during November 1994, there might also have been a sustained break in spawning prior to both these cruises. Given the high density of sardine spawners on the west coast during November 1994 (Painting *et al.* subm.c), and the large number of sardine eggs found north of the Peninsula, it is likely that the spawning of sardine had shifted northwards. This would have reduced the relative importance of the contribution from the WAB for this species.

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

The characteristic twin jet that occurs off Cape Columbine (and occasionally off the Cape Peninsula), was clearly observed during some cruises. The jet comprises a major arm on the outer shelf (often with an offshore component of flow) and a minor northward arm further inshore.

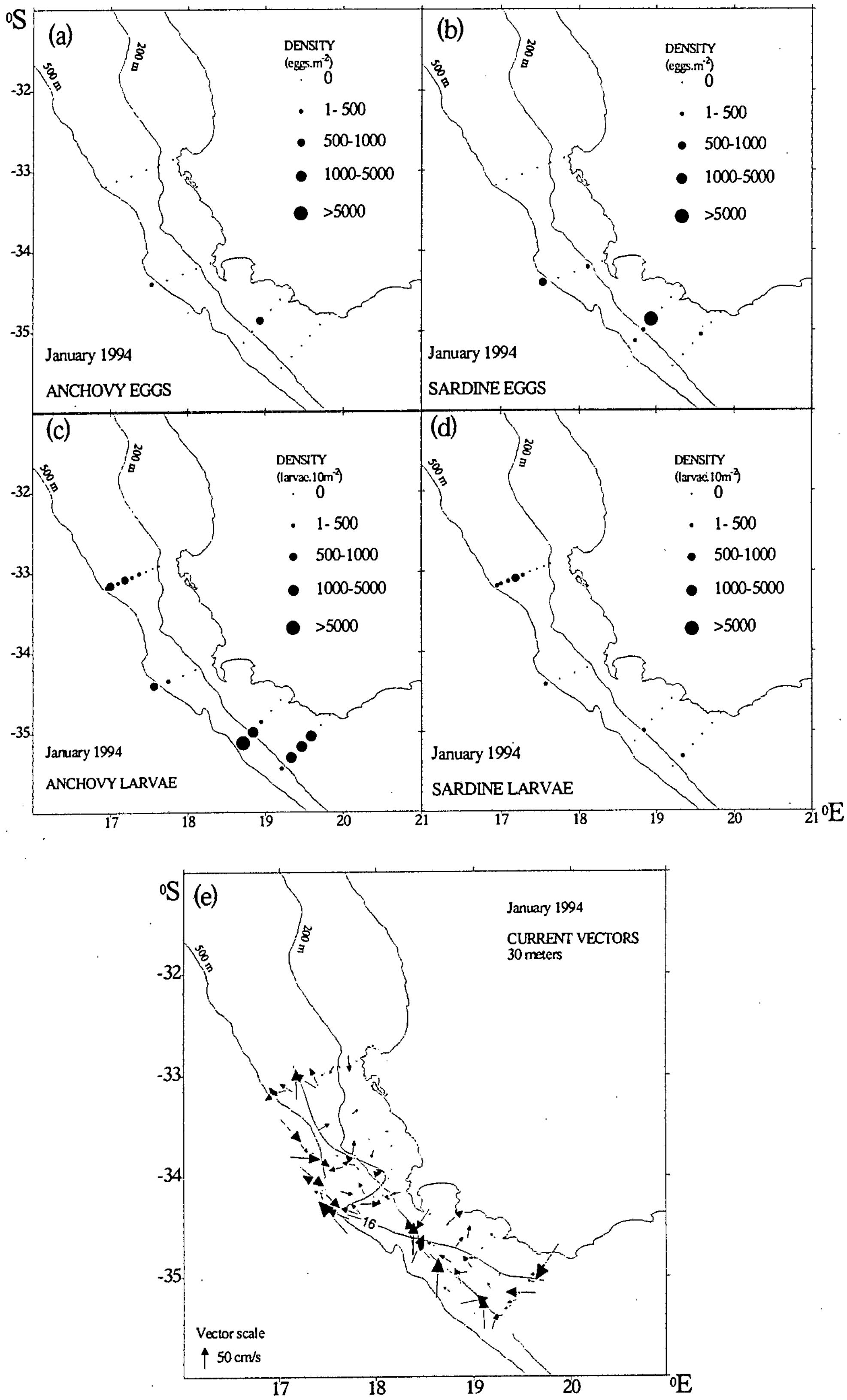

Fig. 5.4 The west coast of South Africa showing the relative density of anchovy and sardine eggs and larvae (a-d) and current vectors at 30 m depth, together with the 16^0 C isotherm showing the position of the front (e) during January 1994.

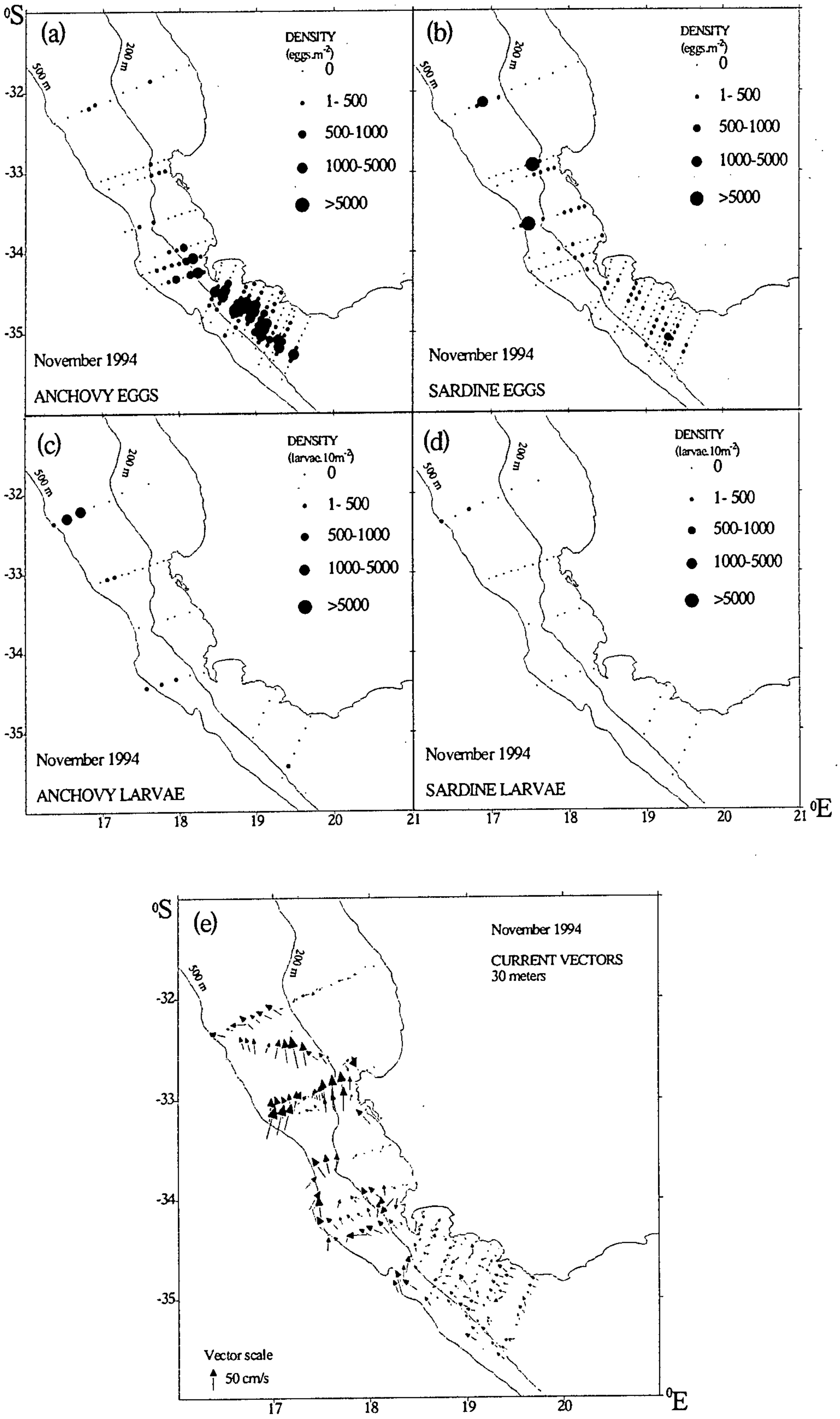

Fig. 5.5 The west coast of South Africa showing the relative density of anchovy and sardine eggs and larvae (a-d) and current vectors at 30 m depth (e) during November 1994.

During October 1994, anchovy larvae were contained in the offshore branch of the current both off the Peninsula and Cape Columbine in the region of the 500 m isobath (Fig. 5.1 c-e). Very few larvae were found on the shorter Dassen Island line which suggests that larval transport may be continuous along the offshore margin of the grid. Anchovy larvae were also absent from the Dassen Island line during November 1994 although they were found at the offshore stations along the Peninsula, Cape Columbine and Olifants River lines (Fig. 5.5 c). During February 1995, high concentrations of sardine and anchovy larvae were observed on the mid and outer shelf off Cape Columbine (Fig. 5.6 c,d) due to transport from the Dassen Island region where the flow was onshore (Fig. 5.6 e). The presence of larvae along the offshore margin of the grid was also observed during January, February and March 1994 and March 1995, and suggests that transport along the offshore margin of the grid may occur fairly regularly during summer. A biophysical model of the influence of the mean advection field on anchovy recruitment (Lynne Shannon *et al.* 1996) has shown little loss in this region, despite the offshore flow at Cape Columbine. Losses were found to be important only when additional offshore vectors are added to simulate the effect of strong SE winds, as was postulated to have occurred in 1993/1994 (Lynne Shannon *et al.* 1996, Boyd *et al.* in press).

The inner branch of the Columbine jet generally entrained a substantial number of sardine eggs, together with some sardine and anchovy larvae. This was particularly evident during October 1994 (Fig. 5.1). Although densities were low, the presence of anchovy and sardine larvae in the nearshore and midshelf regions off the Olifants River during this period indicates that entrainment by the inshore branch of the jet would favour the retention of spawned products. Despite the potential of the inshore arm to transport larvae to the inner/mid shelf region, the

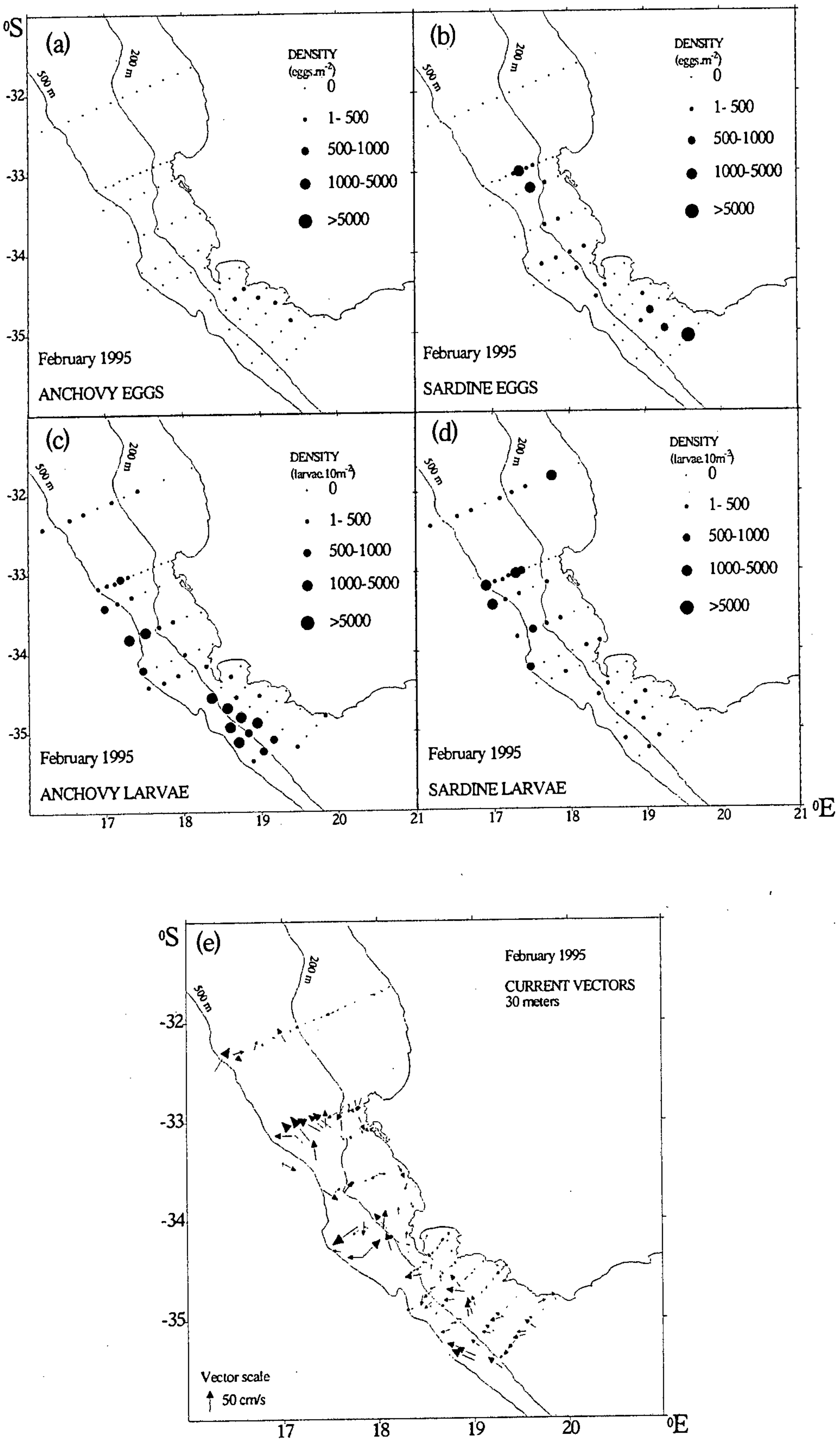

Fig. 5.6 The west coast of South Africa showing the relative density of anchovy and sardine eggs and larvae (a-d) and current vectors at 30 m depth (e) during February 1995.

presence of eggs or larvae inshore off the Olifants River was rarely observed. The exception to this observation occurred in February 1995 when larvae were distributed along most of the Olifants River line (Fig. 5.6 c,d). During this sampling period, the majority of both anchovy and sardine larvae were between 8-17 mm in length and there was no clear change in size distribution offshore (Fig. 5.7). Some 6-7 mm sardine larvae were found inshore (Fig. 5.7 d) and this suggests that spawning may have occurred on the west coast. Thus, the coincidence of sardine eggs and early larvae together with older larvae in the mid-shelf region off Cape Columbine (Fig. 5.6 b,d) suggests local spawning as well as advection from the south.

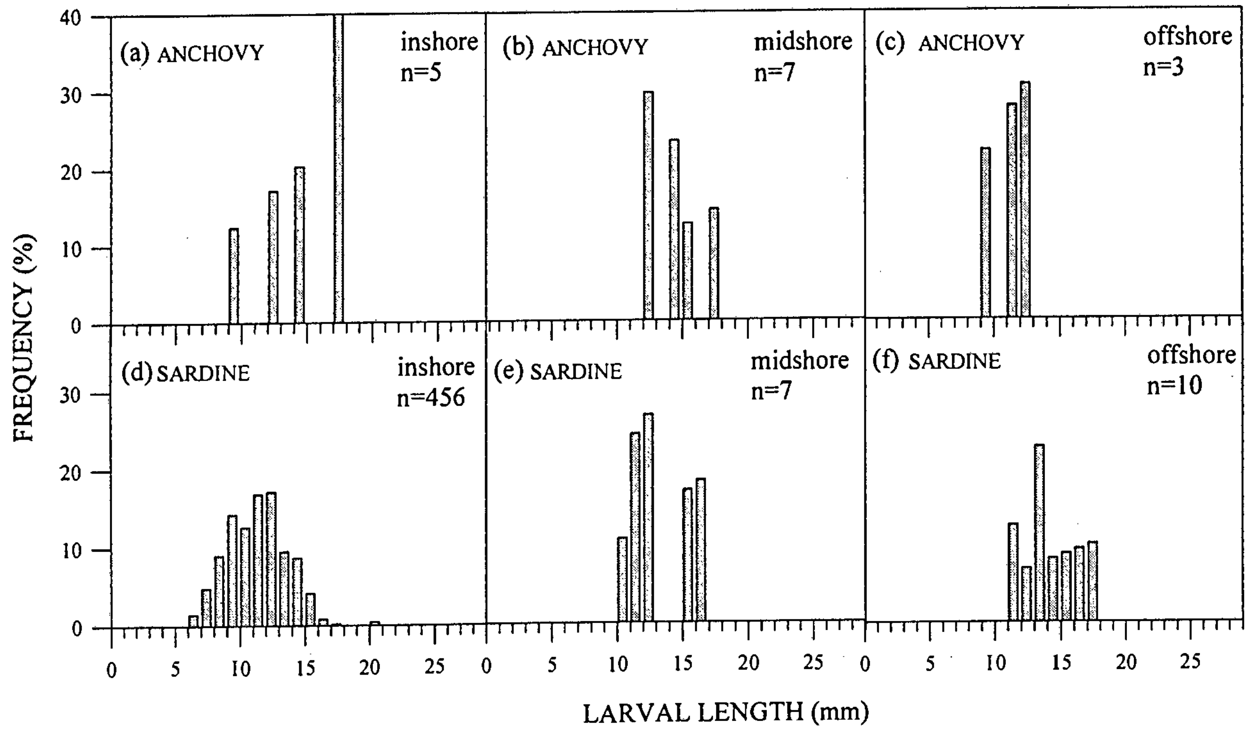

Fig. 5.7 Size frequency distributions of anchovy larvae (a-c) and sardine larvae (d-e) in the inshore, midshore and offshore regions along the Olifants River line during February 1995 .

5.3.3 Examples of potential egg and larval losses from the shelf system

Based on the data from individual cruises, areas of potential egg and larval loss could be identified. Offshore transport of eggs and larvae occasionally occurred on the outer margin of the WAB suggesting potential loss as indicated by Boyd *et al.* (1992). This was particularly evident during February 1995 when large densities of anchovy larvae (Fig. 5.6 c) appeared to be entrained by relatively strong offshore flow between the 200 m and 500 m depth contours off Cape Agulhas in the region between 18^0 and 19 ^{0}E (Fig. 5.6 e). This pattern of offshore distribution was not confined to the WAB however, and extended to the Cape Peninsula where sardine eggs and larvae also coincided with strong westerly flow (Fig. 5.6 b,d,e). This again suggests a potential source of loss. Consistently strong offshore currents were recorded off the Cape Peninsula during the late summer (i.e. January 1994, February 1995). As identified by Boyd *et al.* (in press) a significant negative relationship between recruitment and cumulative SE wind during the anchovy spawning season provides evidence for advective losses of eggs and larvae. Seasonal wind patterns in 1994, 1995 and 1996 have all shown intensification of SE winds at Cape Point in late summer (Richardson *et al.* in press, Boyd and Nelson in press), thus losses on the outer WAB may be most marked during the latter part of the spawning season. Evidently, anchovy and to a lesser extent sardine may spawn primarily in early summer (Shelton 1986, Huggett *et al.* in press, Chapter 3) because hydrographic conditions during this period may favour effective transport to the nursery grounds.

Although the eastern Agulhas Bank region was not sampled during the SARP surveys, there is evidence that spawned products were probably transported to the WAB from areas further east. During January 1994, for example, relatively high densities of anchovy larvae were sampled east of the egg distribution (Fig. 5.4 c). Previous studies have indicated that strong offshore flow from the southern tip of the Agulhas Bank is a regular feature and may contribute to substantial loss. Thus, eggs spawned on the south-east Agulhas bank probably do not contribute significantly to recruitment (Boyd *et al.* 1992). However, it appears that under some circumstances, these eggs may be advected inshore and that current features may then promote transport to the west coast (Largier *et al.* 1992, Boyd and Shillington 1994). Although the movement of eggs from the eastern Agulhas Bank to the west coast nursery grounds may augment recruitment on the west coast (Boyd *et al.* 1992), the SE winds which normally favour such movement are also likely to lead to higher advective losses on the west coast (Lynne Shannon 1996, Boyd *et al.* in press).

The most obvious area of potential egg and larval loss on the west coast initially appeared to be the outer branch of the Columbine jet, since it had a strong offshore component during a number of the SARP cruises. The potential for loss by the offshore arm of the Columbine jet can be seen by the presence of larvae on the outer stations of the Columbine line (*e.g.* January 1994, Fig. 5.4 c,d), and the Olifants River line (*e.g.* November 1994, Fig. 5.5 d), where flow was directed offshore (Fig. 5.4 e and Fig. 5.5 e).

Despite the potential for offshore losses at various localities between the spawning and nursery grounds, flow patterns observed during some surveys suggest that eggs and larvae may be returned to the system following their offshore advection and continue their journey northwards. Data form January, October and November 1994 suggest that spawned products which had been swept offshore near the Peninsula may have been transported back to the region of the jet by onshore currents further north. During both October and November 1994 (Figs. 5.1 and 5.5) anchovy larvae were entrained in the offshore margin of the NW flow positioned beyond the 500 m isobath off the Peninsula. Although these larvae could potentially have been advected offshore (particularly in October 1994), the presence of larvae in the coherent onshore flow in the region of the 500 m bottom contour off Cape Columbine suggests that a substantial portion of these larvae might rejoin the jet. Furthermore, the size distribution of anchovy larvae along the offshore margin during November 1994 was broader off the Olifants River line and Cape Columbine compared to the Peninsula region (Fig. 5.8). Moreover, larval lengths at offshore stations along the Olifants River line (Fig. 5.8 c) show small larvae together with larger ones (12-17 mm) which would have been spawned either in late October or on the eastern Agulhas bank and transported northwards. This provides further support for the idea that while some larvae may be lost by offshore flow, others may actually reach the nursery grounds on the west coast via a delayed route further offshore.

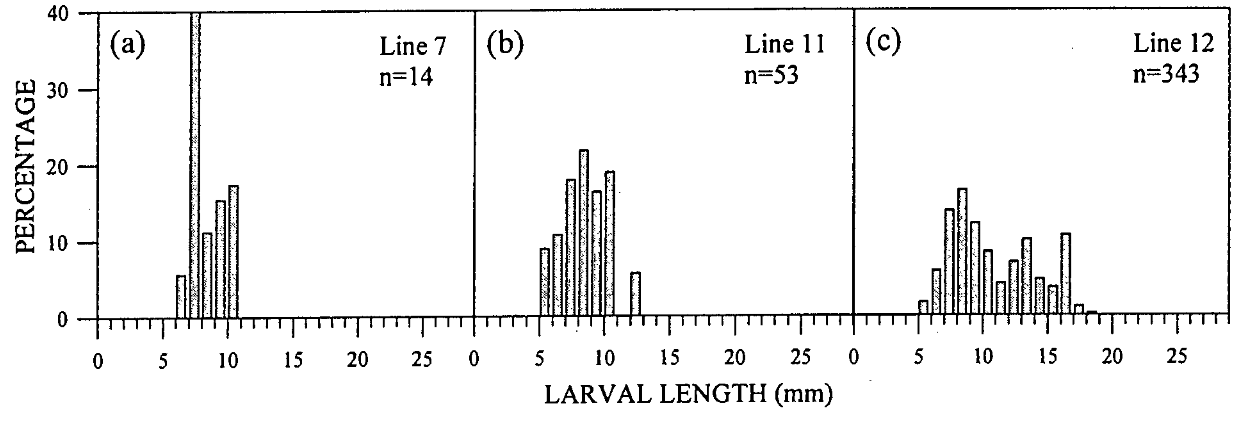

Fig. 5.8 Size frequency distributions of anchovy larvae averaged over (a) the Cape Peninsula line, (b) the Cape Columbine line (c) and the Olifants River line during November 1994 showing an increase in the size range moving northwards.

Similarly, eggs and larvae may be transported offshore at Cape Columbine but returned to the system by onshore flow further north, off the Olifants River. Current features during February 1995 in particular (Fig. 5.6 e), indicate offshore flow on the outer margin of the Columbine line and onshore flow at 500 m of the Olifants River line. Although the majority of sardine larvae and some anchovy larvae were found inshore off the Olifants River during this period, both anchovy and sardine larvae were entrained by the offshore currents at Cape Columbine and the onshore flow further north. A similar flow pattern was evident from the average current field recorded by Boyd and Oberholster (1994). Because of the potential for onshore flow and the sporadic sampling of the Olifants River line, the loss of reproductive products in this region was difficult to confirm. However, the potential for offshore flow in the Dassen Island region was examined by Boyd *et al.* (1992) and Nelson (1985) who suggested that short time-scale features could divert eggs and larvae to the outer branch off Cape Columbine, or indeed move them onshore under certain circumstances as described by Nelson *et al.* (in press). Such offshore and onshore transport appears to arise through the interaction of upwelling plumes and shelf waves (Nelson *et al.* in press).

5.3.4 Integration of the transport of spawned products during SARP over the whole spawning season: the mean picture

In order to complement the selected individual cruise data, mean flow patterns together with mean larval densities for all the 1993/1994 and 1994/1995 SARP cruises are presented in Figs. 5.9 and 5.10. Both data sets show a similar onshore flow pattern between 34 and 33 ^{0}S whereby currents follow the 200 m and 500 m isobaths. During 1993/1994 there was greater mean offshore flow from both the WAB (at 19^{0}E) and north of Cape Columbine (Fig. 5.9 c), than was observed during 1994/1995 (Fig. 5.10 c). Consequently, current conditions during the first SARP season may have promoted more offshore advection of eggs and larvae than during the second season but too few cruises were averaged for definite conclusions. Nevertheless, the increase in

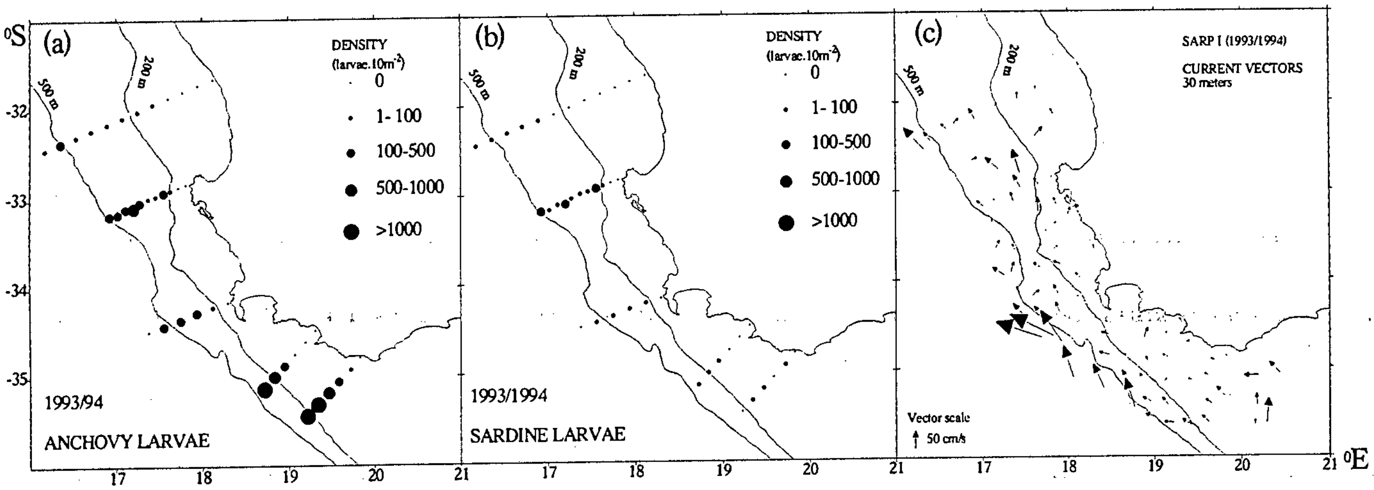

Fig. 5.9 The relative density of (a) anchovy larvae and (b) sardine larvae together with current vectors (c) averaged for SARP I between September 1993 and March 1994.

both anchovy and sardine recruitment from 1994 to 1995 (SFRI unpublished data) appear to be consistent with inter-annual variability in advective processes during SARP.

The distributions of the mean density of anchovy and sardine larvae (Figs. 5.9 a,b and 5.10 a,b) was not discernibly different between years, although sardine larvae were much less abundant during 1993/1994. For both species there was a shift from 1993/94 to 1994/95 in the region of maximum larval abundance away from the 200 m isobath on the WAB, towards the 500 m

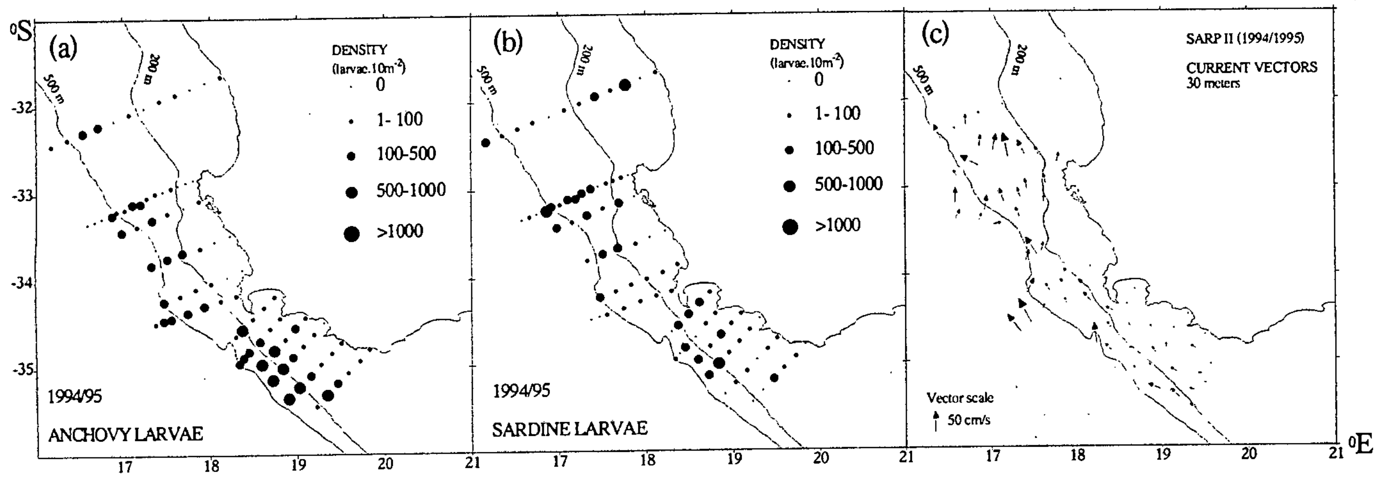

Fig. 5.10 The relative density of (a) anchovy larvae and (b) sardine larvae together with current vectors (c) averaged for SARP II between September 1994 and March 1995.

isobath off Cape Columbine. This emphasises the importance of the "offshore transport" path as well as the need to know more about onshore movement in the nursery region (Hewitson 1991).

5.4 General discussion

The results presented here reflect the efficiency of surface circulation patterns within the southern Benguela ecosystem to entrain eggs and larvae. This provides further support for Shelton and Hutchings' (1982) hypothesis that the shelf-edge frontal jet is responsible for the transport of eggs and larvae to nursery grounds on the west coast. Convergent flow south of the Peninsula, merging into the typically fast-flowing jet off the Peninsula appears to effectively funnel eggs and larvae to the west coast particularly during the early summer months, for example October 1994 and November 1993 (Figs. 5.1 and 5.2). Nevertheless, the probable loss of considerable numbers of both eggs and larvae was frequently observed during the survey particularly when offshore distributions of spawning products coincided with strong SE winds (Richardson *et al.* in press). This generally occurred later in the season (January, Fig. 5.4 and February, Fig. 5.6) when loss from the outer WAB was most marked. Entrainment in the Benguela jet current early in the summer spawning season may therefore enhance reproductive success, whereas later in the season, it may have the opposite result. Because the spawning activity of anchovy and, to a lesser extent sardine, peaks in early summer (Chapter 3, Shelton 1986, Huggett *et al.* in press), it is possible that advective processes might exert a particularly strong control on the spawning strategies adopted by these species. As documented by Parrish *et al.* (1981) and Bakun and Parrish (1982) for fish species in the Californian Current, a wide variety of fish stocks in upwelling systems generally avoid spawning during periods when intense offshore flows prevail.

Although conditions in the early part of the spawning season may be "ideal" for maximising reproductive success, mitigating circumstances during periods of apparent offshore larval loss may have a positive influence on recruitment. Observations from satellite images (Agenbag 1992) indicate situations in which offshore flow rejoins the main frontal region in areas on the WAB and the west coast. The possibility of onshore flow entraining eggs and larvae from earlier offshore movement, as observed during January 1994 and February 1995 in the region between the Cape Peninsula and Cape Columbine, would result in fewer losses due to transient features than those associated with semi-permanent features such as the offshore divergence off Cape Columbine.

Using a biophysical advection model, Lynne Shannon *et al.* (1996) found that anchovy recruitment is influenced by the position of adult spawners in relation to currents. During several cruises (e.g. November 1994, February 1995), adult sardine spawners and sardine eggs and larvae were found between Cape Columbine and the Cape Peninsula on the west coast. Spawning in this region implies that the journey of egg and larvae to favourable grounds is shortened so that the chances of being transported offshore are greatly reduced. In addition, the close proximity to highly productive feeding grounds implies that larval survival rates may be enhanced. Crawford (1981a) reported that before the collapse of the sardine in 1962-1964, when recruitment was considerably greater than in subsequent years, sardine eggs were frequently found on the west coast off Cape Columbine. Consequently, recruitment may be enhanced in years when the spawning on the west coast is frequent. This argument may partially explain the increase in sardine recruitment from 1994 to 1995 (SFRI unpublished data) which corresponds with an increase in the average sardine egg and larval abundance on the west coast from the 1993/1994 season to the 1994/1995 season.

Advection is one of many factors that determine the fate of developing eggs and larvae and subsequent year class strength. Bakun (1993) proposed that recruitment is associated with a combination of production, concentration and retention processes. Although these factors are not simultaneously compatible, temporal and spatial lags in these three factors may act together to promote successful recruitment. Whereas Richardson *et al.* (in press) and Chapter 4 of this thesis indicate that copepod production on the spawning grounds may mediate anchovy recruitment through spawning success, this study provides evidence for the influence of retention processes on recruitment of anchovy and sardine in the southern Benguela ecosystem.

CHAPTER 6

Intra- and inter-annual estimates of instantaneous anchovy egg mortality rates.

6.1 Introduction

Fast mortality rates during the egg phase are common among clupeoids because the adults release millions of pelagic eggs which are extremely vulnerable to predation (Smith 1985, Houde 1987), particularly through cannibalism (Hunter and Kimbrell 1980, Valdes *et al.* 1987). Lasker (1985a) and Smith (1985) proposed that recruitment variability in clupeoids is due to variable stage-specific mortality. Consequently, high and variable mortalities during the egg phase of anchovies and sardines can potentially influence the level of recruitment and contribute to fluctuations in stock size (Houde 1987, Dorsey *et al.* 1996). Accurate estimates of egg mortality are therefore valuable in recruitment studies.

In the southern Benguela ecosystem, anchovy egg mortality rates have been calculated annually from data collected over the entire spawning area during November since 1983 as part of the process for estimating spawner biomass using the Daily Egg Production Method (Armstrong *et al.* 1988 and Shelton *et al.* 1993). Apart from these estimates, the only other estimate of anchovy egg mortality was calculated by Valdes *et al.* (1987) for a limited area of intensive spawning over the western Agulhas Bank (WAB) during November 1984 as part of a study on egg cannibalism.

In an attempt to examine the magnitude and variability in anchovy egg mortality during the spawning season, this study investigates anchovy egg mortalities calculated from the monthly egg abundance data sets collected during SARP I and SARP II. Annual anchovy egg mortality rates over the SARP grid since 1984 are related to the spatial distribution of the eggs, and to recruitment the following year in order to determine whether recruitment in the South African anchovy is regulated by mortality at this developmental stage.

6.1 Data analysis

In order to calculate egg mortality rates for each month over the two spawning seasons, a total of 6 536 anchovy eggs from all 14 SARP cruises were sorted into 11 stages of embryonic development (Moser and Alstrom 1985). Because egg development is temperature dependant (King *et al.* 1978), staged eggs were assigned an age on the basis of the ambient sea surface temperature measured on station. The temperature-development relationship employed for this procedure was obtained by means of egg rearing experiments for *Engraulis capensis* described by Valdes *et al.* (1987). This relationship is given by the equation 6.1:

$$t_p = \exp^{(A_p - B_p V)} \text{ .... } \textit{Equation } 6.1$$

where: t_p = average age of an egg in development stage p

V = the ambient temperature in ^{0}C

A_p and B_p = constant parameters for egg stages 2 to 10 (Table 6.1)

Table 6.1 Parameters for egg stages 2 to 10 used in equation 6.1 for estimating the average age of an egg in development stage p. These parameters were calculated from egg rearing experiments during the November 1984 Spawner Biomass survey and the table is taken from Armstrong *et al.* (1988).

	Constant Parameters	
Egg stage (p)	*Ap*	*Bp*
2	3.755	0.1183
3	5.197	0.1576
4	5.559	0.1586
5	5.941	0.1600
6	5.875	0.1390
7	5.915	0.1286
8	5.914	0.1206
9	6.387	0.1428
10	6.215	0.1298

Based on histological studies, it is evident that an anchovy spawns over a short period of time at night with a peak in spawning activity at 22h00 (Melo 1992). Hatching takes place approximately three days later at a temperature range of 15 - 20^{0}C (King *et al.* 1978). According to their estimated ages, eggs at each developmental stage could therefore be grouped into two or three categories each representing eggs spawned one to three nights previously. The mean age of eggs in each group was re-estimated as the time difference between spawning at 22h00 and the time of the tow. Estimates of egg abundance at a maximum of three specific ages were therefore provided by each sample. In order to allow for the greater area represented by stations spaced every 10 nm, egg abundance at each station was weighted according to the distance between stations. Stations which were spaced at 10 nm intervals received twice the weighting of stations spaced every 5 nm (Armstrong *et al.* 1988). These procedures were performed by the programme detailed in Appendix I. The natural logarithms of the abundance estimates of anchovy eggs were then regressed against age in 1-hour age classes between 5 h and 50 h. Eggs younger than 5 h or older than 50 h were excluded from the regression to avoid biases caused by incomplete recruitment of the eggs to the plankton or hatching of older eggs. The slope, Z of the regression provided estimates of the hourly instantaneous rate of egg mortality used for further analyses.

Instantaneous rates of egg mortality were also calculated for egg data collected during each November Biomass survey between 1984 and 1994. These surveys cover the entire spawning area from Port Elizabeth on the Cape east coast, to the Olifants River mouth on the west coast and samples are collected at regular, 5 nm intervals. Anchovy egg mortality estimates based on these data have been calculated by Armstrong *et al.* (1988) for the period 1984 to 1986 and

Shelton *et al.* (1993) for the period 1987 to 1990. These authors used the estimates of instantaneous egg mortality in application of the Daily Egg Production Method for estimating spawner biomass (Lasker 1985b). For this study, only those samples collected over the SARP grid during each November Biomass cruise between 1984 and 1994 were analysed for comparison with the SARP data.

To compare the degree of patchiness in the distribution of anchovy eggs with the yearly estimates of hourly instantaneous egg mortality, Lloyd's patchiness Index (LPI), as described in Chapter 3, was calculated for each of the surveys between 1984 and 1994. LPI values were regressed against the hourly instantaneous egg mortality estimates to identify the relationship between these two variables. Smith *et al.* (1989) has suggested that the intensity of patchiness can be indicated by the maximum values for egg counts (*i.e.* the largest number of eggs found in any one sample over a given area). Therefore, the maximum values for anchovy egg counts per cruise were regressed against the hourly instantaneous egg mortality estimates for each of these surveys as an alternative method of assessing the relationship between egg mortality rates and spatial patchiness.

6.2 Results

6.2.1 Monthly estimates of anchovy egg mortality

Estimates of mean hourly instantaneous anchovy egg mortality rates and their 95 % confidence intervals for each month surveyed during SARP I and II are presented in Table 6.2. In all cases the 95 % confidence limits were very wide and the variances were very large, which indicates that a great deal of uncertainly is associated with these measurements. Furthermore, positive slopes were fitted to the abundance-at-age curves for six of the 11 data sets analysed during SARP (Table 6.2), which gives cause for concern regarding their precision. In particular, positive egg mortality slopes were associated with cruises which had very few positive CalVET samples (Table 6.2). This was due either to insufficient sampling (e.g. August 1993 and September 1993) or to the paucity of anchovy eggs during some months (particularly at the beginning and the end of the spawning season, Chapter 3). Zero egg mortality was included within the 95 % confidence limits in most cases, which further discredits the validity of these mortality estimates. A precise estimate of egg mortality rates requires that a large number of samples be used (Smith *et al.* 1989, Dorsey *et al.* 1996) and this was clearly not the case during the SARP surveys (Table 6.2).

Table 6.2. Total number of CalVET samples and the number of positive CalVET samples together with estimates of hourly instantaneous mortality rate (Z) for anchovy eggs sampled monthly during SARP I and II. - indicates those months that were not sampled and ~ indicates that the data set for that cruise was on adequately sampled for the analysis.

Year	CalVET samples	positive CalVET samples	-Z (h^{-1})	variance (10^{-5})	95 % confidence limits lower	upper
SARP I						
August	17	7	0.016	132.699	0.00000018	0.0326
September	21	9	0.082	357.353	-0.00000013	0.1634
October	35	10	0.027	211.784	0.00000010	0.0547
November (all)	178	99	-0.012	25.850	0.00000015	-0.0233
November (sarp)	47	26	-0.035	101.978	-0.00000049	-0.0691
December	41	11	-0.009	116.417	0.00000000	-0.0186
January	28	2	0.009	681.566	0.00801093	0.0098
February	35	5	~	~	~	~
March	24	0	~	~	~	~
SARP II						
August	-	-	-	-	-	-
September	52	7	-0.011	158.978	-0.00000003	-0.0230
October	87	21	-0.063	66.044	0.00000139	-0.1254
November (all)	189	83	-0.023	25.645	-0.00000072	-0.0458
November (sarp)	113	52	-0.046	37.419	-0.00000117	-0.0924
December	39	12	0.005	68.906	0.00000008	0.0101
January	-	-	-	-	-	-
February	76	5	0.013	60.295	0.00000011	0.0250
March	72	1	~	~	~	~

Wide 95 % confidence limits were also associated with the mortality rate estimates calculated during November 1993 and 1994, but the variances ($25.85*10^{-5}$ and $25.65*10^{-5}$ respectively) observed were relatively small. This suggests that the estimates from November 1993 and 1994 are probably the most reliable of any of the estimates calculated during SARP. A number of reasons can be put forward to explain this. Firstly, more samples (178 in November 1993 and 189 in November 1994) were collected during these two surveys than during other SARP surveys and secondly, these surveys coincided with a peak in anchovy spawning activity (Chapter 3). Consequently, a larger number of positive samples were encountered (99 in November 1993 and 83 in November 1994) which reduces problems associated with small sample sizes. As a means of calibrating the estimates obtained during the other SARP surveys, egg mortality estimates were recalculated for these two November surveys, using only the samples collected on the SARP lines. A comparison of these two estimates for each November cruise shows that the SARP grid subsample resulted in egg mortality estimates for November 1993 and 1994 that were three times and twice faster respectively than those based on the full set of samples (Table 6.2).

6.2.2. Interannual estimates of anchovy egg mortality

Table 6.3 provides the hourly instantaneous anchovy egg mortality estimates, their variances and their 95 % confidence intervals for the samples collected over the SARP grid during November between 1984 and 1994. Egg mortality rates were not constant from year to year but ranged between 0.012 h^{-1} (25 $\%.d^{-1}$) and 0.042 h^{-1} (64 $\%.d^{-1}$) (Table 6.3). The mean anchovy egg mortality over the 11 year period was 0.024 h^{-1}. The estimates obtained during 1988 and 1989 exhibited the smallest variances ($12.27*10^{-5}$ and $12.54*10^{-5}$ respectively), although these were still larger than those recorded by Shelton *et al.* (1993) between 1984 and 1990 over the entire spawning area.

The slopes of the mortality curves obtained from the November egg data were negative in all years (Fig. 6.1). The variance associated with each mortality estimate measured during November was considerably lower than that associated with the monthly mortality estimates of SARP (Table 6.2 and Table 6.3). These results lend some credibility to the estimates. However, there is a large amount of scatter around the fitted slopes and the 95 % confidence intervals of the mortality estimates are very wide, encompassing zero mortality in six of the 11 years sampled. This places some doubt on the adequacy of these results for reliable estimation of the instantaneous egg mortality rate.

Table 6.3. Total number of CalVET samples and the number of positive CalVET samples together with estimates of hourly instantaneous mortality rate (Z) for anchovy eggs sampled between Cape Agulhas and the Olifants River mouth during November between 1984 and 1994. The shaded area indicates the two years sampled during this study.

Year	CalVET samples	positive CalVET samples	-Z (h^{-1})	variance (10^{-5})	95 % confidence limits lower	upper
1984	110	63	-0.015	27.331	-0.0304	-0.00000032
1985	83	52	-0.027	15.171	-0.0549	-0.00005853
1986	153	124	-0.023	22.162	-0.0463	0.00000027
1987	171	123	-0.017	35.029	-0.0349	0.00000078
1988	284	151	-0.026	12.270	-0.0518	0.00000105
1989	214	87	-0.018	12.537	-0.0354	0.00000020
1990	252	99	-0.032	21.494	-0.0643	0.00000058
1991	203	111	-0.030	23.486	-0.0591	-0.00000084
1992	238	87	-0.042	25.335	-0.0846	-0.00000006
1993	178	99	-0.012	25.850	-0.0233	0.00000015
1994	189	83	-0.023	25.645	-0.0458	-0.00000072

The relationship between Lloyd's patchiness index and the yearly egg mortality estimates measured during November yielded a significant positive correlation (Fig. 6.2, $r^2 = 0.54$, $N = 11$, $p<0.05$). This indicates that the more patchy the anchovy egg distribution, the greater the mortality. It is evident however, that this relationship is primarily driven by data from two years,

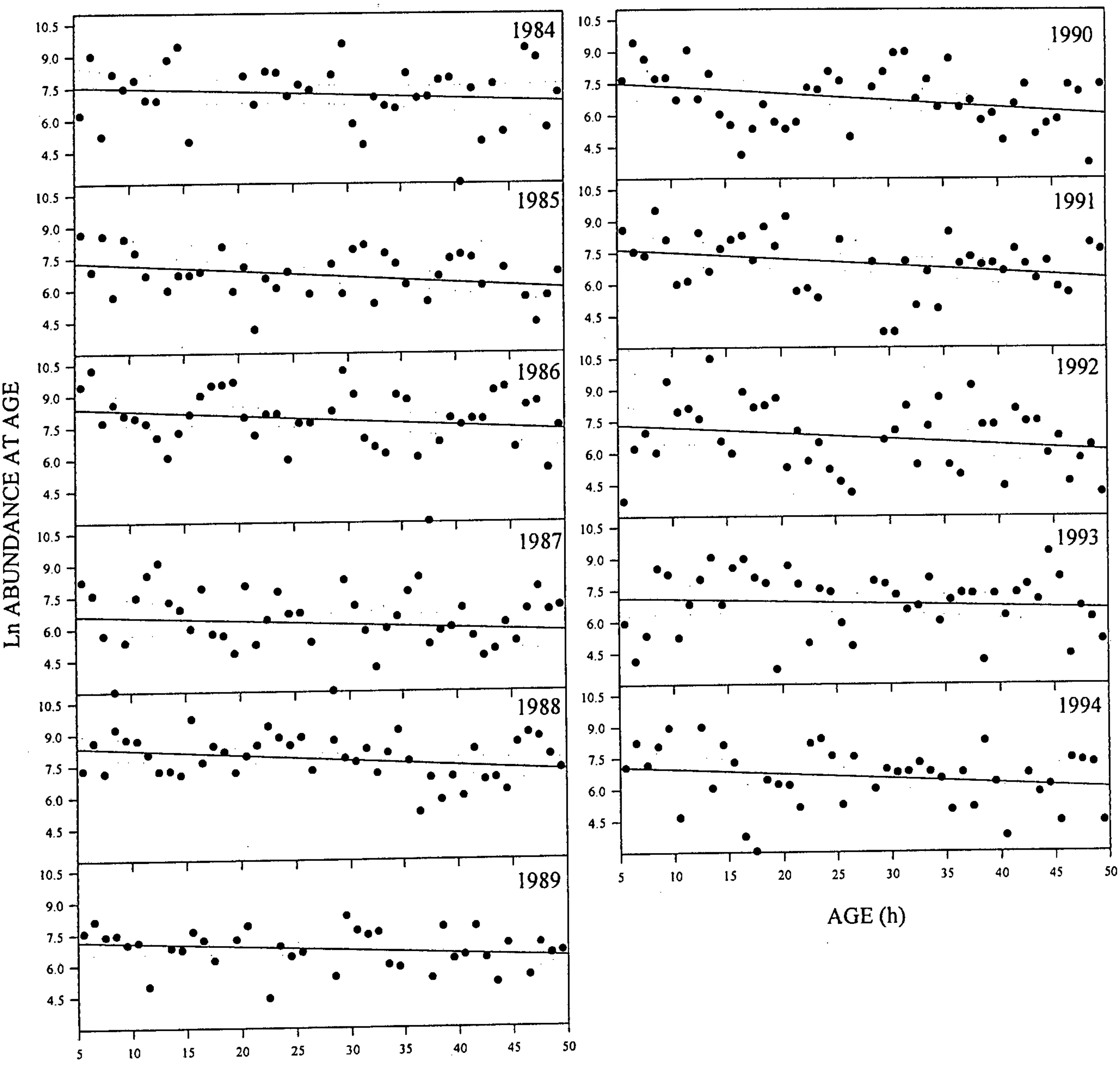

Fig. 6.1 Data points and mortality fits for anchovy eggs sampled between Cape Agulhas and the Olifants River mouth during November surveys for the period 1984 to 1994.

namely 1990 and 1992 when heavy mortality was associated with extreme patchiness (Fig. 6.2). Considering the error involved in measuring both patchiness and egg mortality rates, the fit of the data is fairly good. Although the slope of the regression between the maximum value of egg counts and the mortality rate of anchovy eggs is not significantly different from zero (Fig. 6.3,

$r^2 = 0.31$, N = 11, $p = 0.07$) an increase in the maximum was associated with an increase in the rate of egg mortality between 1984 and 1994. This provides further support for the positive relationship between spatial patchiness of eggs and their mortality rate.

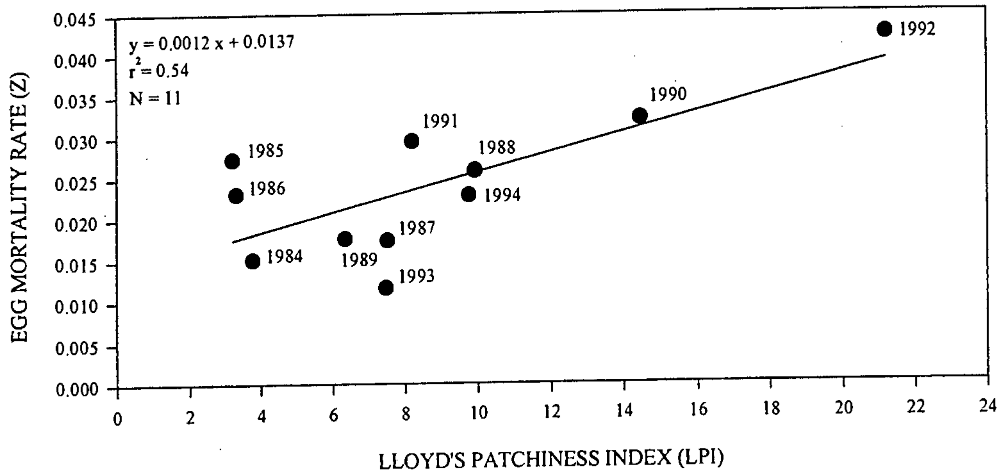

Fig. 6.2. The regression relationship between Lloyd's Patchiness Index (LPI) and the hourly instantaneous anchovy egg mortality estimates during November between 1984 and 1994.

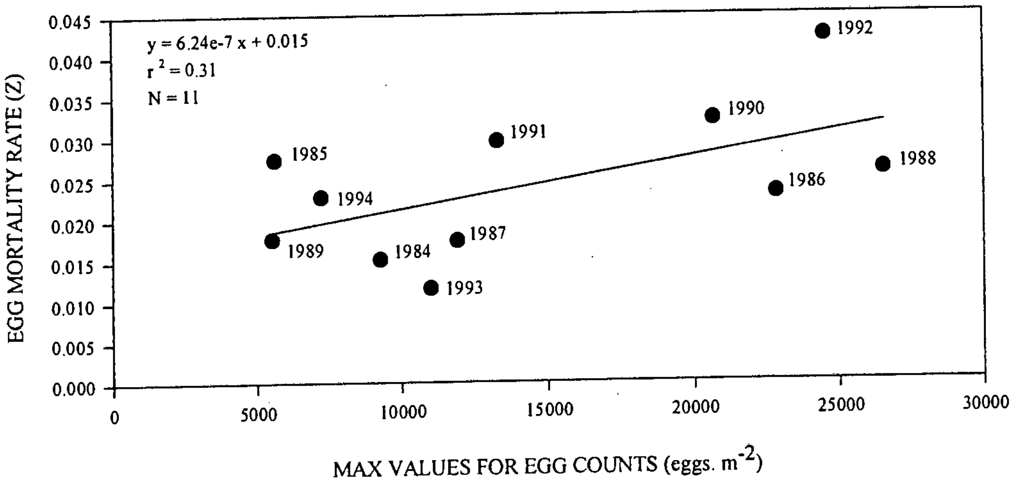

Fig. 6.3. The regression relationship between the maximum value for egg counts (eggs. m^{-2}) and the hourly instantaneous anchovy egg mortality estimates during November between 1984 and 1994.

There is no significant relationship between anchovy egg mortality (measured in November) and the biomass of anchovy recruits measured during May or June the following year (Fig.6.4, r^2 =

0.052, N = 11, $p>0.05$). This suggests that recruitment is independent of mortality during the egg phase of the anchovy as measured during peak spawning activity. However, this analysis is simplistic because parent stock size should be included and the relationship should be modelled using both factors (*i.e* egg mortality estimates and parent stock size). Nevertheless, the poor relationship observed in this study could be due to the quality of the egg mortality estimates.

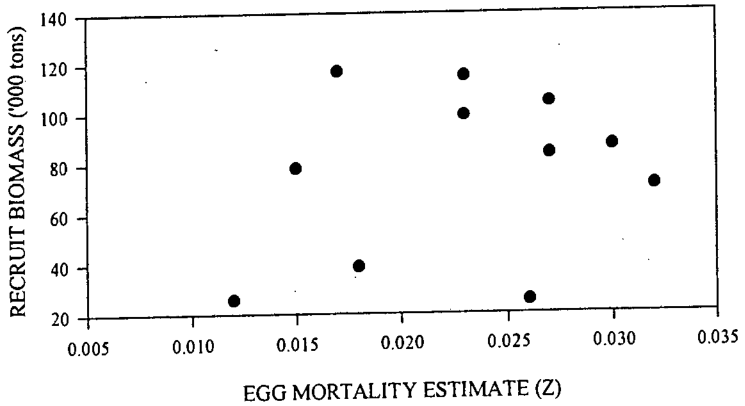

Fig. 6.4. Scattergram showing the relationship between anchovy egg mortality measured during November between 1984 and 1994 and the biomass of anchovy recruits measured during either May or June the following year.

6.3 Discussion

The estimates of anchovy egg mortality calculated each month during SARP were highly variable and imprecise. This was clearly demonstrated by the large variances and wide confidence intervals associated with these estimates. Estimation of *in situ* egg mortality rates has always been problematic, because egg distribution is extremely patchy in both space and time (Smith 1973, Hewitt 1981, Smith and Hewitt 1985a). Such spatially intense distribution patterns (Chapter 3) result in large sample variances and this problem is intensified when estimating egg mortality rates because the intensity of patchiness changes with age (Smith and Hewitt 1985, Mc Gurk 1987, Smith *et al.* 1989, Dorsey et *al.* 1996). From their study on the egg production of Pacific sardine (*Sardinops sagax*), Bentley *et al.* (1996) indicate that the large degree of scatter surrounding the mortality curve is due to the highly patchy distribution of young eggs.

Consequently, either very small or very large catches of young eggs, leading to extreme levels of variance, are particularly common when few samples are taken or when egg abundances are low (Bentley *et al.* 1996). Both these situations were encountered during SARP (see Table 6.1 and Appendix 2). At the start and end of the anchovy spawning season, egg abundances were very low (see Chapter 3) and during some months (e.g. August and September 1993) both reduced abundances and the paucity of samples were probably responsible for imprecise egg mortality estimates. In some cases this situation led to such poorly fitted mortality curves that positive slopes were measured for more than half of the SARP cruises (Table 6.3).

As indicated by the reduced variances exhibited by the egg mortality estimates from all the samples collected over the SARP grid during November 1993 and November 1994, large sample numbers during peak spawning periods increases the credibility of egg mortality estimates. Nevertheless, large variances and imprecise egg mortality estimates have been reported for studies where the positive sample numbers are far greater (Smith *et al.* 1989, Armstrong *et al.* 1988, Shelton *et al.* 1993). From estimates of anchovy egg mortality for egg distributions over the entire spawning area in the southern Benguela, Shelton et *al.* (1993) indicated that, despite positive sample numbers ranging from 166 to 277, egg mortality estimates are still associated with wide 95 % confidence intervals and large variances. Smith and Hewitt (1985b) found that 1 666 positive samples were adequate to estimate egg mortality of *Engraulis mordax* for inclusion in the daily egg production method. These estimates came from data assembled from 5 years of egg distribution observations. It is therefore unlikely that the method of estimating egg mortality on a monthly basis used in this study could provide useful estimates of anchovy egg mortality rates. To obtain reliable estimates of egg mortality of the bay anchovy (*Anchoa* *michilli*), Dorsey *et al.* (1996) repeatedly sampled a cohort of eggs or yolk-sac larvae throughout a 24 hour period. By simultaneously measuring biotic and abiotic variables, they were able to determine which factors affected variability in the rate of bay anchovy egg mortality. Thus, the approach of Dorsey *et al.* (1996) in future studies in the southern Benguela may provide better estimates of anchovy egg mortality for elucidating which factors influence the survival of eggs and to what extent these factors impact on the survival of anchovy during the egg phase.

The annual estimates of anchovy egg mortality and their variances during November between 1984 and 1994 over the SARP grid (Table 6.3), were larger than those obtained for the whole survey grid as reported by Shelton *et al.* (1993) for the period 1984 to 1990. Since anchovy spawning is concentrated on the WAB (see Chapter 3), mean anchovy egg densities over the entire spawning area during most years were lower than densities over just the SARP grid (Table 6.4) because the WAB is a major component of the latter. Valdes *et al.* (1987) provide evidence that the rate of anchovy egg mortality due to cannibalism in the southern Benguela varies according to the density of eggs. Also, these authors estimated that cannibalism accounted for about 70 % of the total egg mortality within an intensive area of spawning on the WAB. Because cannibalism seems to be the primary cause of egg mortality, greater egg mortality rates over the SARP grid may be related to high rates of cannibalism over the WAB due to larger mean egg densities in this region compared with the entire sampling region (Table 6.4). Since anchovy spawning is concentrated in the mid-shelf region on the WAB (see Chapter 3), density-dependant processes such as cannibalism probably have their greatest effect in this region but may be less important in surrounding areas where anchovy spawning is less intense.

Hunter and Kimbrell (1980) have also observed that the mean number of eggs in northern anchovy (*Engraulis mordax*) stomachs increased exponentially with an increase in egg density. They attributed this relationship to the patchiness of anchovy egg distributions because laboratory observations of cannibalism on northern anchovy eggs indicated that filtration may be intensified when egg patches are encountered. Mc Gurk (1986, 1987) has used a model of pelagic egg and larval mortality rates, which combines both size-dependence and spatial patchiness of the egg and larval distributions, to show that mortality rates are directly and positively correlated with the patchiness of their spatial distribution. In support of Mc Gurk's (1986) mortality-patchiness hypothesis, the significant positive relationship between anchovy egg mortality and the patchiness of their distribution observed during this study (Fig.6.2 and 6.3) suggests that egg mortality may vary according to the intensity of patchiness in their distribution. Maximum egg mortality was recorded in 1992 (64%.d^{-1}) and likewise the pattern of egg distribution indicated that they were most patchy during this period. Like Hunter and Kimbrell (1980), Mc Gurk (1986) suggest that the these differences are caused by the feeding of predators on patches of eggs and larvae. As the feeding rate of predators on eggs and young larvae is limited by the time required to find them rather than the time required to capture and eat them, eggs and larvae are particularly vulnerable to predation when their spatial distribution is highly patchy. Consequently, mortality rates are likely to be greater when and where eggs are concentrated in patches.

The hourly instantaneous egg mortality estimates for *Engraulis capensis* measured during this study are generally larger (25 - 64 %.d^{-1}) than those measured for *Engraulis mordax* (between 13 and 36 %.d^{-1}) off California (Stauffer and Picquelle 1981, Stauffer and Charter 1982, Picquelle and Hewitt 1983, 1984, Hewitt 1985, Bindman 1986) but smaller than those measured for *Engraulis ringens* (between 59 and 88 %.d^{-1}) in the Humbolt system off Peru (Smith *et al.* 1989). Whereas Valdes *et al.* (1987) have suggested that differences in the rates of cannibalism and therefore anchovy egg mortality between California, Peru and South Africa are probably due to differences in egg densities at the time of sampling, Smith *et al.* (1989) have attributed differences in egg mortality rates to the density of adult spawners in each region. Evidently, the average biomass density of adult anchovy over the sampling period in this study is greater (9 g. m^{-2}) than that for adult northern anchovy off California between 1980 and 1985 (6 g. m^{-2}) but smaller than that for adult *Engraulis ringens* during 1981 off Peru (40 g. m^{-2}) (Smith *et al.* 1989). In addition to the relationship between egg mortality rates and the density and spatial pattern of their distribution, the rate of egg mortality may also be influenced by differences in the rate of cannibalism imposed by varying densities of adult spawners.

Although the patchy release of eggs by extremely aggregated spawners such as anchovies seems counter intuitive for their survival during the egg phase, the advantages of aggregated spawning to avoid predation on adult fish may outweigh the disadvantages of heavy cannibalism (or other forms of predation) during the egg phase. Mc Gurk (1986) points out that upwelling events and turbulent mixing promote the dispersal of eggs and larvae which decreases the impact of predation. In the southern Benguela, anchovies spawn primarily on the WAB which is characteristically well stratified and stable throughout the summer (Chapter 3, Shelton and Hutchings 1990). Although these conditions contrast with those described by Mc Gurk's (1986) model for reduced predation rates, anchovy eggs and larvae are rapidly transported away from the spawning area by the shelf-edge frontal jet during the spring and summer when anchovy spawning is at a maximum (Chapter 5). Thus the choice of spawning area by the anchovy may be an adaptive strategy to separate spawners from their eggs and larvae and thereby reduce cannibalism on the eggs and early larvae (Cochrane and Hutchings 1995).

In his synthesis on the management of the Peruvian pelagic fishery, Pauly (1987) concluded that recruitment in the Peruvian anchovy (*Engraulis ringens*) is primarily regulated by egg mortality due to cannibalism as a density dependant control. By contrast Smith *et al.* (1989) state that it is unlikely that interannual variations in mortality rates of sardine and anchovy eggs due to cannibalism are large enough to account for major recruitment fluctuations in the Humboldt system. Peterman *et al.* (1988) argue that stock size is not influenced by the number of surviving eggs or early larvae but that recruitment success is determined later in the life history of the northern anchovy (older than 20 days). The anchovy egg mortality estimates presented in this study do not seem to affect the level of recruitment the following year (Fig. 6.4), supporting the views of Smith *et al.* (1989) and Peterman *et al.* (1988). Although interpretation is complicated by the large variances associated with the estimates in this study, these results suggests that factors other than egg mortality during the egg phase influence recruitment processes in the southern Benguela ecosystem.

CHAPTER 7

7.1. Conclusions

Anchovy and sardine in the southern Benguela ecosystem spawn in areas and at times when environmental conditions are optimal for maximising reproductive output and for ensuring survival to recruitment (Parrish *et al.* 1983, Shelton 1986, Shelton and Hutchings 1990). This statement is supported by the seasonal and geographic patterns of anchovy and sardine eggs and larvae in relation to their environment observed during SARP I and II.

The western Agulhas bank is clearly the centre of both anchovy and sardine spawning activity in the southern Benguela during peak times, and several possible causes have been invoked to explain this phenomenon. The simultaneous increase in both anchovy and sardine spawning and the occurrence of warmer water on the WAB during October of both seasons suggests that spawning is related to sea surface temperatures. This study confirms previous observations (Shelton and Hutchings 1990) which indicate that anchovy spawning is confined to 16-19°C surface water which prevails over the WAB during the summer months. Conversely, sardine spawning occurs over a much broader temperature range and is therefore is not related to the area of 16-19 °C water. Thus the area of suitable habitat defined for anchovy spawning is not necessarily the same as that for sardine. Nevertheless, the choice of the WAB as the primary centre for spawning may be related to optimum temperatures for egg and larval survival, because sea temperatures on the west coast are frequently below the threshold limit for normal egg development (14°C and 13°C for anchovy and sardine respectively).

Although it has been suggested that the choice of the WAB as the major spawning grounds for anchovy is independent of the food environment for adults (Roel *et al.* 1994, Cochrane and Hutchings 1995), this study provides evidence to the contrary. A positive relationship between the intensity of anchovy spawning activity and the biomass of large copepods in the area of 16-19°C water suggests that adult anchovy may select the WAB as the primary spawning area because of favourable feeding conditions in the area of 16-19 °C water which dominate the midshelf region on the WAB during the summer. Temporal changes in the spawning activity of sardine appear to be related to chlorophyll *a* concentrations on the WAB, suggesting that the diets of sardine spawners may be supplemented by an enhanced phytoplankton resource during both the spring and late summer peaks.

In their comparative examination of clupeoids in the four major eastern boundary current regions of the world, Parrish *et al.* (1983) found that temperatures characterising spawning habitats showed a much less coherent pattern, and suggested that selection of spawning habitat for any particular optimum temperature may be less important than minimizing turbulent mixing or offshore transport. Indeed, the ability of the NNW flowing jet current to entrain eggs and larvae during peak spawning periods was evident during SARP I and II. However, the efficiency of currents to transport eggs and larvae to the west coast did vary over the spawning season and there is evidence to suggest that losses on the outer WAB may be most marked during the late summer when SE winds are intensified at Cape Point. It is evident therefore that advective processes early in the summer spawning season may reduce offshore loss and, through rapid movement of eggs and larvae to the west coast, reduce cannibalism. This process would undoubtedly enhance reproductive success and it is possible that summer anchovy spawning and the spring peak in sardine spawning may be related to advective processes which might exert a strong control on the spawning strategies adopted by these species.

From the SARP data it therefore appears that sea temperatures, feeding conditions for adults and advective processes in the southern Benguela ecosystem influence the spawning behaviour of both anchovy and sardine. Besides these environmental processes which operate both spatially and temporally, it is possible that biotic factors such as competition may influence finer scale patterns in the spawning behaviour of these species. This study shows that the spawning peaks of anchovy and sardine occur at different times, although there is some temporal overlap in the occurrence of sardine and anchovy eggs and larvae. Also, anchovy spawning is far more localised than sardine spawning which extended up the west coast during November and December when anchovy spawning reached a peak on the WAB. Based on the temporal and spatial separation of anchovy and sardine spawning behaviour during SARP, it is possible that these species may be adapted to reduce the effects of interspecific competition. The relative importance of any one of these factors is not easily discernable, but it is likely that these and other factors interact at several different spatial and temporal scales to influence the overall spawning strategy of these species.

Conditions addressed in this study, together with recruitment the following year are summarised in Table 7.1. Although the decrease in anchovy spawner biomass and the availability of food was consistent with a decrease in the production of eggs from SARP I to SARP II, the apparent increase in recruitment from 1994 to 1995 suggests that anchovy recruitment during these years was driven primarily by processes acting on the eggs and larvae. Despite the problems associated with calculating egg mortality rates from survey data, it appears that mortality during the egg phase does not influence recruitment. Changes in both anchovy and sardine recruitment are consistent with interannual variability in advective processes during SARP. This study therefore supports the hypothesis that recruitment is regulated by variations in advective processes which are responsible for the transport of eggs and larvae. Although this study has contributed to our understanding of the factors which influence recruitment in these two species, definite conclusions regarding the recruitment process cannot be drawn from only two years of data.

Figure 7.1 A summary of the average conditions during SARP I and SARP II which could potentially have impacted on recruitment the following year. The sign indicates whether the condition could possibly promote (+) or weaken (-) recruitment the following year. The 0 indicates that no significant change was evident from one season to the next and therefore its impact on recruitment could not be considered. * Egg mortality is not averaged over the season but is represented by the November estimate in each case.

		SARP I	SARP II
Chlorphyll *a* concentration		0	0
Large copepods in 16 ^{0}-19^0 C water		+	-
Spawner biomass	*anchovy*	+	-
	sardine	-	+
Egg production	*anchovy*	+	-
	sardine	0	0
Egg mortality*	*anchovy*	+	-
Transport		-	+
Next year's recruitment	*anchovy*	-	+
	sardine	-	+

Even though the monthly estimates of anchovy egg mortality were plagued with a great deal of uncertainty, changes in interannual mortality rates have improved our understanding of this phenomenon and its importance for recruitment. In order to obtain a better understanding of the complex of ecological relationships into which the early life stages of anchovy and sardine are integrated, it is important to overcome biases in sampling and the difficulties associated with estimating growth and mortality of eggs and larvae in the field. Considerations of this nature are crucial to the prediction of anchovy and sardine recruitment in the southern Benguela ecosystem. However, this thesis has advanced our current knowledge of the spawning duration, seasonal intensity and geographic extent of anchovy and sardine. Conditions which favour the spawning success of these species have been successfully identified, and the extent of intra-annual changes in hydrographic conditions which influence the fate of developing eggs and larvae have been described. Incorporation of these findings into models such as the expert system suggested by Cochrane and Hutchings (1995) may be useful in predicting recruitment success which will enable improved management of these valuable resources in the future.

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Appendix 1. The programme written in SAS (Roel, unpublished SFRI data) which assigns ages to staged eggs according to the ambient sea surface temperature and then allocates aged eggs to one of three nights spawnings.

```
/*
INFILE WEIGHT CONTAINS THE WEIGHT OF THE STATIONS
SWT 1 IS 5 MILES, SWT 2 IS 10 MILES STATION
*/
DATA WEI;
    INFILE 'A:\WEIGH01';
    INPUT LIN STNO SWT;
PROC SORT;
    BY LIN STNO;

DATA EGGS;
    INFILE 'A:\EPAN01';
    INPUT LIN 1-2 STNO 4-5 TEMP  7-10 TIM 12-15  TOTEGG 19-24 (E1-E11) (5.);

PROC PRINT;

PROC SORT;
    BY LIN STNO;
DATA EGGWT;
    MERGE WEI EGGS;
    BY LIN STNO;

DATA FINAL;
    SET EGGWT END=EOF;

ARRAY ME{50} ME1-ME50;
ARRAY FG{50} FG1-FG50;
ARRAY EGGS{11} EGGS1-EGGS11;
ARRAY E{11} E1-E11;
ARRAY AGE{11} AGE1-AGE11;
ARRAY H{3} H1-H3;
ARRAY C{3} C1-C3;
ARRAY NE{50} NE1-NE50;
ARRAY ET{50} ET1-ET50;
ARRAY NEGG{50} NEGG1-NEGG50;

SPPEAK=22;
RF=21;
AMIN=5;
AMAX=50;

FILE 'A:\AGES01';

    DO J=1 TO AMAX;
        ME{J}=0;
        FG{J}=0;
        END;

DO L=1 TO 3;
    C{L}=0;
```

```
    END;

TOTEGG=TOTEGG*RF;

DO K=1 TO 11;
    EGGS{K}=E{K}*RF;
    END;
DAM=DAM*RF;
TOTSTAGE=0;
DO J=1 TO 11;
    TOTSTAGE+EGGS{J};
    END;

TIM = TIM/100;
MIN = TIM - INT(TIM);
DMIN = MIN * 100/60;
TIM = INT(TIM) + DMIN;

AGE{2}=EXP(3.755-0.1183*TEMP);
AGE{3}=EXP(5.1966-0.1576*TEMP);
AGE{4}=EXP(5.5591-0.1586*TEMP);
AGE{5}=EXP(5.9412-0.16*TEMP);
AGE{6}=EXP(5.875-0.139*TEMP);
AGE{7}=EXP(5.9154-0.1286*TEMP);
AGE{8}=EXP(5.9139-0.1206*TEMP);
AGE{9}=EXP(6.387-0.1428*TEMP);
AGE{10}=EXP(6.215-0.1298*TEMP);

IF TIM LE SPPEAK THEN H{1}=TIM+(24-SPPEAK);
    ELSE H{1}=TIM-SPPEAK;
H{2}=H{1}+24;
H{3}=H{1}+48;

DO J=2 TO 10;
    IF AGE{J} LE (H{1}+5) THEN AGE{J}=H{1};
    IF AGE{J} GT (H{2}-19) AND AGE{J} LE (H{2}+5) THEN AGE{J}=H{2};
    IF AGE{J} GT (H{3}-19) AND AGE{J} LE (H{3}+5) THEN AGE{J}=H{3};

    IF AGE{J}=H{1} THEN C{1}+EGGS{J};
    IF AGE{J}=H{2} THEN C{2}+EGGS{J};
    IF AGE{J}=H{3} THEN C{3}+EGGS{J};
    END;

DO X=1 TO 3;
    J = ROUND(H{X});
    IF J LT AMIN THEN GO TO K3;
    IF J GT AMAX THEN GO TO K3;
    ME{J}+SWT*C{X};
    FG{J}+SWT;
    NE{J}+1;
    PUT LIN 1-2 STNO 4-5 H{X} 9-15 C{X} 17-25 SWT 27;
K3:   END;
```

```
DO J=AMIN TO AMAX;
     IF ME{J}=0 THEN GO TO K4;
     ME{J}=ME{J}/FG{J};
     ET{J}+ME{J};
K4:   IF EOF THEN DO;
          NEGG{J}=ET{J};
          END;
     END;
IF EOF THEN OUTPUT;

PROC PRINT;

DATA PLOTT(KEEP=AGE LNAA);
     SET FINAL;

ARRAY NEGG{50} NEGG1-NEGG50;
ARRAY NE{50} NE1-NE50;

FILE 'A:\EGABU01';

DO J = 5 TO 50;
     LNAA=LOG(NEGG{J});
     NOBS=NE{J};
     AGE=J+0.5;
     PUT AGE NOBS LNAA NEGG{J};
     END;

RUN;
```

Appendix. 2 Frequencies of anchovy eggs at each developmental stage during SARP I and SARP II.