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7

CHARACTERIZING AND COMPARING THE SPAWNING HABITATS OF ANCHOVY (*Engraulis capensis*) AND SARDINE (*Sardinops sagax*) IN THE SOUTHERN BENGUELA UPWELLING ECOSYSTEM

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MASTER OF SCIENCE
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University of Cape Town

DECLARATION

I hereby declare that this thesis presents my own work. With respect to data collection, I could not participate in the surveys; all the samples were collected at sea by Marine & Coastal Management (MCM) scientists and technical staff. Data on egg abundance during the SARP study was arranged and provided by Justine Fowler. Carl van der Lingen provided egg abundance data for the November spawner biomass surveys. Nitrate concentrations used for analysis during the two survey programs were provided by Marcel van den Berg. Chris Duncombe Rae provided current speed and direction for SARP and November surveys. Betty Mitchell-Innes provided phytoplankton biomass and mixed layer depth data for both SARP and spawner biomass surveys. Zooplankton biomass and production data during SARP were obtained from Suzanne Painting. Hans Verheye and Anthony Richardson contributed with data on zooplankton biomass and production for analysis during spawner biomass surveys. Most of the data on physical variables (salinity and wind speed) during the two survey programs were extracted from the ship's data distribution system (DDS), arranged by MCM staff.

University of Cape Town

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Nandipha Monica Twatwa Date

CONTENTS

University of Cape Town

CHAPTER 3:

CHAPTER 4:

University of Cape Town

CHAPTER 5:

University of Cape Town

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ABSTRACT

The spawning habitats of anchovy (*Engraulis capensis*) and sardine (*Sardinops sagax*) in the southern Benguela upwelling ecosystem were characterized by comparing the data on abundance and distribution of eggs of the two species with environmental variables. Data were collected from two different survey programs: (a) 14 SARP (Sardine and Anchovy Recruitment Programme) cruises, conducted monthly for 2 spawning seasons between August 1993 and March 1994, and September 1994 and March 1995, off the west coast of southern Africa from Cape Columbine to Cape Agulhas; (b) annual November/December spawner biomass surveys conducted from 1984-1999 along the South African coast and covering the continental shelf between Hondeklip Bay on the West Coast and Port Alfred on the South Coast. A CalVET net was used to collect fish eggs at stations on a survey grid, and physical and biological data were collected concurrently with egg samples. Physical variables measured included sea surface temperature, nitrate concentration, water depth, salinity, current speed, wind speed and mixed layer depth, whereas biological variables included phytoplankton biomass (as 50m integrated chlorophyll *a*) and zooplankton biomass and production. The spawning habitats selected by anchovy and sardine were identified by constructing quotient curves derived from egg abundance data and individual environmental variables. Anchovy and sardine spawning probability with reference to the distribution of environmental variables was examined using overlay operation analysis. Relationships between eggs of the two species and the environmental variables were verified using multivariate coinertia analysis. Relationships among the environmental variables were examined through cluster analysis.

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During SARP surveys, single parameter quotient analysis indicated that the spawning habitats of these two species were most dissimilar in terms of water depth, sea surface temperature, current speed and zooplankton biomass, and most similar in terms of salinity and phytoplankton biomass. Coinertia analysis using all environmental variables as inputs showed a positive association between anchovy eggs and salinity and sea surface temperature, and a negative association between anchovy eggs and secondary production and phytoplankton biomass. Sardine eggs were strongly positively associated with phytoplankton biomass. During spawner biomass surveys, anchovy and sardine spawning habitats appeared to differ with respect to sea surface temperature, wind speed and current speed, and overlapped in terms of water depth, phytoplankton biomass, zooplankton biomass and production. Anchovy eggs were strongly positively associated with SST, salinity, mixed layer depth and zooplankton production. Sardine eggs were strongly positively associated with current speed and zooplankton biomass.

Although anchovy and sardine show some overlap in spawning habitat, sardine are less specific in their selection of spawning habitat than are anchovy. These results suggest that anchovy and sardine spawning habitats can be characterized in terms of environmental variables, and indicate that these two species show substantial differences in selection of their spawning habitat. Such characterizations may be used to demarcate potential spawning habitat when information on egg abundance is not available, through, for example, satellite-derived data. This will be useful in monitoring space-time variability in the dimensions and location of the spawning habitats of these two ecologically and commercially important species.

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Chapter 1:

Introduction

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1.1:Eastern boundary current ecosystems

Coastal upwelling ecosystems, the so-called "eastern boundary current regions", are located on the eastern boundaries of the oceans where the equatorward trade winds induce offshore Ekman transport (Cury & Roy 1989; Fig. 1.1). These regions are the Benguela, California, Humboldt and Canary upwelling ecosystems (Jarre-Teichmann & Christensen 1998), and all share a number of common characteristics. The major descriptive feature about eastern boundary current ecosystems is the dominance of strong and variable physical processes of wind-driven upwelling (Parrish *et al.* 1981).

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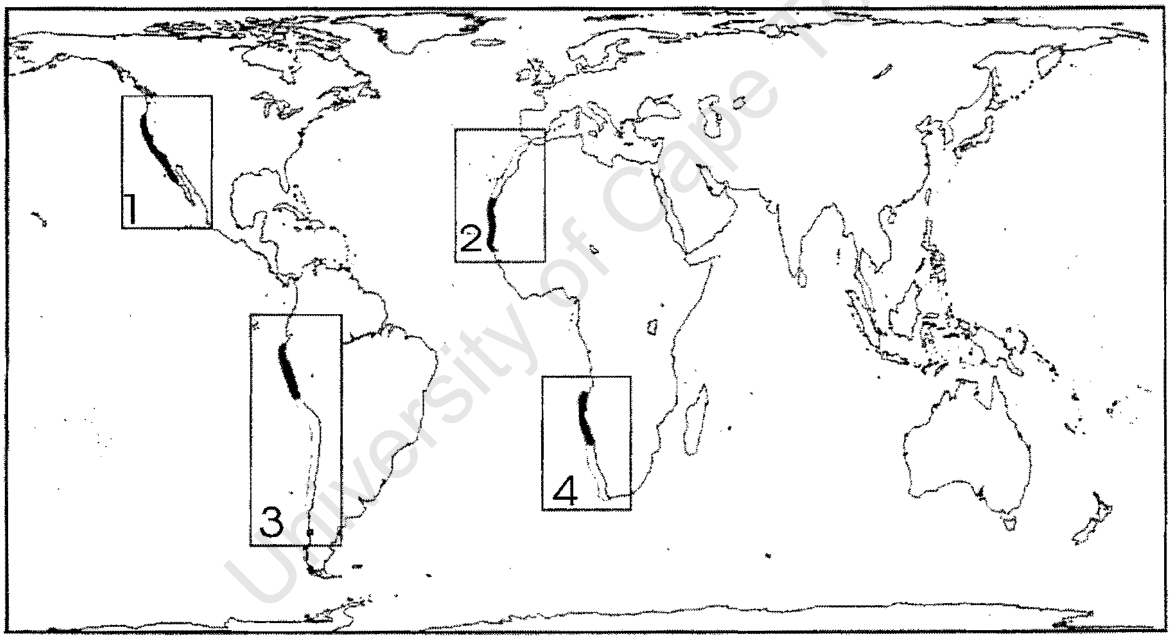

Fig. 1.1: Major upwelling ecosystems of the world (1. California, 2. Canary, 3. Humboldt and 4. Benguela (From Jarre-Teichmann & Christensen 1998)

Upwelling is the process whereby the surface water is blown offshore by strong winds along the coast, resulting in an inshore drop and offshore sea-level rise (Jarre-Teichmann & Christensen 1998). To compensate for this, cool bottom water that is rich in nutrients upwells inshore along the coastline, stimulating primary production because of high nutrient availability (Pitcher *et al.* 1996).

The upwelling process makes all the major upwelling ecosystems dispersive environments, where particles tend to be swept away from the coast by wind-induced offshore drift (Cury *et al.* 1998). The high primary production results in a plankton-dominant food environment with enhanced secondary production, which supports a large biomass of small pelagic fishes like anchovy and sardine (Cury & Roy 1989). According to figures given by Lluch-Belda *et al.* (1989) on anchovy and sardine catches in eastern boundary ecosystems up to 1986, the Humboldt Current was the only region with maximum catches of anchovy of more than 1.3m tonnes and those of sardine attained a maximum of more than 500 000 t.

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The eastern boundary current ecosystems are also characterized by an unresolved problem of natural alternating abundance of anchovy and sardine populations (Baumgartner *et al.* 1992). Anchovy and sardine have been extensively fished and alternate in relative abundance in all eastern boundary current regions. The phenomenon of alternating high and low phases of abundance between the two species is known as a regime shift. The maximum catches of both species have never occurred simultaneously in any of these systems, when sardine population biomass is high, anchovy levels drop (Lluch-Belda *et al.* 1989). This has been observed on decadal scales in the absence of fishing through the study of fish scales preserved in anaerobic sediments (Baumgartner *et al.* 1992). These regime shifts are also indicated by commercial catch data for both species' landings and the availability of guano from guano-producing seabirds that feed on pelagic species (Schwartzlose *et al.* 1999). Both species have a tendency of changing their geographical ranges during periods of low and high abundance (Lluch-Belda *et al.* 1992). For example, sardine populations were restricted into one fixed location in the North of Chile when anchovy biomass was high off the Pacific coast of South America. During periods of high abundance of sardine, the sardine population extended along the whole coast (Lluch-Belda *et al.* 1992). There are two hypotheses regarding regime changes in anchovy and sardine populations (Schwartzlose *et al.* 1999). The first is that there may be continuous modifications in the habitat that favour one species relative to the other. Changes in food and temperature are two possible mechanisms that may sustain large shifts in abundance of sardine or anchovy populations over long periods. For example, anchovy populations tend to increase in the Pacific Ocean with increasing global air and sea temperature, while sardine tend to do the opposite (Lluch-Belda *et al.* 1992).

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Secondly, there may be episodic environmental events that trigger abrupt changes in populations and ecosystems in well-separated areas (Schwartzlose *et al.* 1999). Evidence of severe population reduction was observed from mass mortalities of sardine that were recorded off Australia in 1985 (Hyatt *et al.* 1997 cited by van der Lingen 1999), or changes in climate cause shifts in spawning habitats that may strongly affect recruitment (Huggett *et al.* 1998).

1.2: Spawning habitats of small pelagics in eastern boundary current ecosystems

Selection of spawning habitat appears to be based on good feeding for adults, the matching of larval stages with plankton production, and favorable temperatures (Blaxter & Hunter 1982). Spawning habitats of species in eastern boundary current ecosystems appear to be chosen such that they reduce periods of intense turbulent mixing and minimize offshore advection (Blaxter & Hunter 1982). Major pelagic fish spawning areas share a common feature of being located in places with a broad shelf where offshore flow from the coastal area is limited (Roy *et al.* 1992). These broad shelf areas chosen as spawning areas have boundaries that expand and contract from year to year depending on the fish population size and oceanic conditions (Blaxter & Hunter 1982). Despite high production at low trophic levels, major upwelling systems appear to be difficult reproductive habitats for fish (Laevastu 1993). As a result, most of the major small pelagic fish populations migrate in order to find suitable spawning habitats. Reproductive strategies of small pelagic fish populations appear to be tuned to minimize the detrimental effects of environment on larval survival (Jarre-Teichmann & Christensen 1998).

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The selection of spawning habitats is also related to good feeding conditions for adult spawners (Blaxter & Hunter 1982). Adult anchovy in the southern Benguela upwelling ecosystem are hypothesized to select the Western Agulhas Bank (WAB) for spawning because of successful transport to the West Coast (WC) despite the Eastern Agulhas Bank (EAB) being a better feeding environment (Hutchings *et al.* 1998). According to Laevastu (1993), in clupeoid fish populations the length of spawning season depends upon the frequency of spawning, and the annual frequency of spawning may depend upon the availability of food for the average spawning population. The timing of spawning of most clupeoid species appears to be a mechanism to match the frequency of occurrence of larval stages with the optimal phase of the annual plankton cycle (Laevastu 1993). It also ensures conditions favorable to survival of early life history stages either by avoiding starvation and predation, or by ensuring good retention and advection related mechanisms, or both (Motos *et al.* 1996). The timing of reproduction of sardines, sardinella or anchovies appears to occur over a wide range of upwelling intensity (Shin *et al.* 1998). The spawning success of clupeoid populations also depends upon the selection of spawning habitats with favorable temperatures to promote egg development. Unfavorable temperatures are responsible for regulation of duration of spawning such that adults stop spawning for the rest of the season (Richardson *et al.* 1998).

1.3: Southern Benguela upwelling ecosystem

The Benguela upwelling ecosystem off Southern Africa extends from southern Angola (15°S) to Cape Agulhas (35°S) and is divided into northern and southern parts by a zone of intense perennial upwelling near Lüderitz (26-27.5°S; Shannon 1985). The Benguela ecosystem supports a highly productive assemblage of epipelagic fish, among which sardine *Sardinops sagax* and anchovy *Engraulis capensis* have periodically dominated the purse-seine fisheries of the region since the early 1940s (Armstrong *et al.* 1991). Together, these species constitute more than 80 % of the total national pelagic purse-seine catch (Barange *et al.* 1999). They are important as a source of protein for humans and energy transfer in marine pelagic ecosystems (Armstrong & Thomas 1989).

Sardine landings reached a peak of about 0.41 million tons in 1962, then the stock collapsed in the mid 1960s (Crawford *et al.* 1987). At this time the fishery began to use small-mesh nets to target anchovy, and anchovy showed a steady increase as an

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alternative resource supporting the purse-seine fishery from the mid 1960s (Armstrong & Thomas 1989). Between 1965 and 2001, anchovy catches fluctuated between 410 000 and 596 000 metric tons (Barange *et al.* 1999). Anchovy dominated the purse-seine fishery for a period of about 30 years up to 1995, with sardine showing an increase from 1997 onwards (Schwartzlose *et al.* 1999).

1.4: Anchovy and sardine in the southern Benguela upwelling ecosystem

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An important feature about this system is that spawning and nursery grounds of sardine and anchovy are spatially distinct. The spawning grounds are located away from the upwelling (north-south) orientated coast and rather concentrated poleward along the east-west orientated coast (Shin *et al.* 1998), with anchovy and sardine spawning predominantly in spring-summer on the Agulhas Bank (van der Lingen *et al.* 2001). More recently however, anchovy and sardine spawning habitats have became spatially distinct, with the main spawning area of sardine being west of Cape Point and that of anchovy east of Cape Point (van der Lingen *et al.* 2001). The spawning habitats of the two species also extend into waters off the East Coast, as their eggs are often dominant in ichthyoplankton surveys in this region (Beckley & van der Lingen 1999). Selection of spawning habitats by the two species in the southern Benguela upwelling ecosystem also depends on transport mechanisms.

According to Laevastu (1993), spawning and distribution of early life stages are affected by surface current anomalies through passive transport from spawning grounds to nursery grounds. This might also serve as a means of orientation of counter-current migration of adults from feeding to spawning grounds. In the southern Benguela, the transport of eggs and larvae of anchovy from the spawning grounds to nursery grounds is due to equatorward alongshore transport in the frontal jet system (Boyd *et al.* 1992)); the same is assumed to apply to sardine. The transport of anchovy eggs from the WAB to the WC appears responsible for an offshore loss of eggs from this region (Boyd *et al.* 1992).

Although both species spawn in summer, sardine start to spawn in spring and continue through autumn. Their prolonged spawning season has two peaks, the first one between September and October and the second between February and March (Fowler 1998). In contrast, the anchovy peak spawning season lies within October-November when the oceanographic conditions are presumably most suitable for their successful spawning (Armstrong & Thomas 1989). Understanding the spawning pattern is a fundamental element in understanding fish-stock predictability in the framework of life–history strategies in which individuals reproduce (Ichiro & Murayama 1993).

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Anchovy and sardine are both pelagic spawners, and a large proportion of their eggs and larvae are transported from the spawning grounds in a north-westerly direction to the nursery grounds off the West Coast (Shannon *et al.* 1996). It is during this transport period that eggs and larvae are highly vulnerable to offshore advective losses caused by strong southeasterly winds (Hutchings *et al.* 1998). After approximately three months, larvae undergo metamorphosis. On reaching the area between Cape Columbine and the Orange River, juveniles move inshore to feed on rich food concentrations (Shannon *et al.* 1996). A schematic diagram of the life history of anchovy is given in Fig. 1.2, and it may be similar for sardine although there is no clear evidence for that. Juvenile fish recruit to the pelagic fishery at about 6 months of age while still on the West Coast, and later migrate back to the spawning areas (Hutchings *et al.* 1998). On their way down to the spawning grounds the shoals pass the West Coast fishing grounds where anchovy are heavily targeted between May and August by both the purse-seine industry and their natural predators (Armstrong & Thomas 1989).

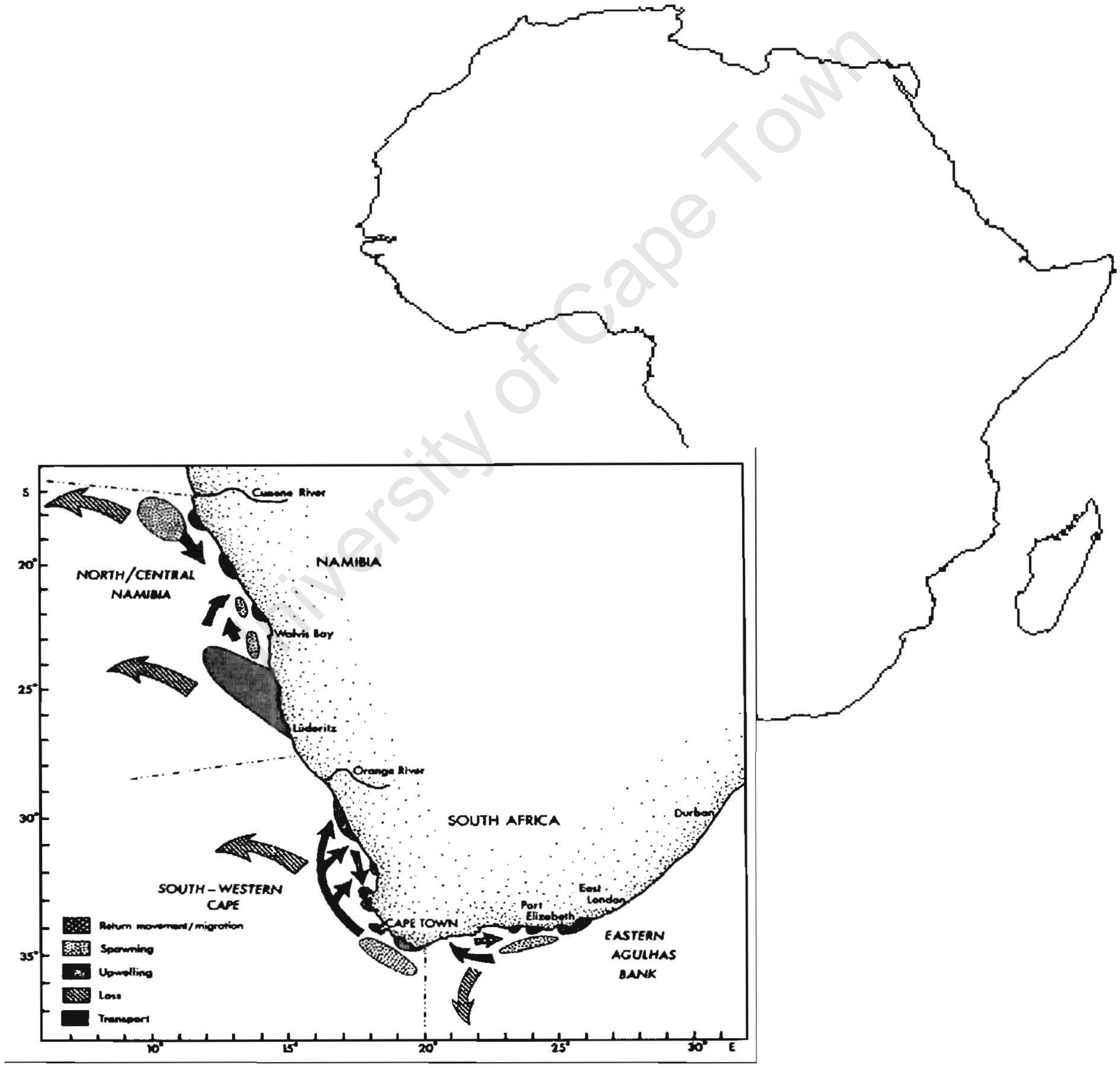

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Fig. 1.2: Schematic diagram of the life history of anchovy in the southern Benguela upwelling ecosystem (from Hutchings *et al.* 1992)

Previous studies have been conducted to characterize the spawning habitats of the two species in the southern Benguela upwelling ecosystem. Van der Lingen *et al.* (2001) used a time series of sea surface temperature data collected during annual spawner biomass surveys to characterize anchovy and sardine spawning habitats. Their results indicated that anchovy prefer to spawn in warm water between 17.4-21°C, whereas sardine spawn over a broader temperature range, but principally in cooler water (<16°C). Fowler (1998) used data collected during monthly surveys conducted over two spawning seasons, and observed that the anchovy spawn in a small range of temperature (16-19°C), whereas sardine show a larger range (14.5-21.5°C). These temperature ranges appeared to be related to feeding conditions for both species over their spawning seasons.

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The spawning range of anchovy (16-19°C) was positively correlated with the production of large copepods on the WAB. In addition, copepod biomass was most consistent in this temperature range on the WAB, including both small and large copepods, suggesting that this region may provide a better feeding environment for anchovy (Richardson 1998). The sardine range (14.5-21.5°C) was positively correlated with average chlorophyll *a* concentrations on the western Agulhas Bank, whereas there was no correlation between this parameter and anchovy spawning intensity. In addition, the peak spawning seasons of sardine (August/September & February/March) appeared to coincide with high densities of integrated chlorophyll *a* (Fowler 1998). Therefore, it appears that anchovy spawning habitat is characterized by zooplankton, whereas that of sardine is characterized by phytoplankton.

1.5: Aims of this dissertation

The broad objective of this dissertation is to characterize the spawning habitats of anchovy and sardine in the southern Benguela upwelling ecosystem in order to demarcate realized spawning habitats (i.e. where the eggs were found), and discover if they differ. The preferred areas of spawning will then be compared to examine any possible differences and/or similarities between them. This will be done using a time-series of data collected during Sardine and Anchovy Recruitment Programme (SARP) conducted along the South African coast between August 1993/March 1994 and September 1994/March 1995 and throughout the annual spawner biomass surveys (November 1984-1999). The data include both species' egg densities and environmental variables, and realized spawning habitats will be depicted by peaks of egg abundance within the range of each environmental variable. After the spawning habitats are characterized in terms of environmental variables, it will then be possible to evaluate which of these variables may be most likely to contribute to regime shifts in the southern Benguela ecosystem. Different analytical methods ranging from univariate to multivariate will be used during this study.

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Differences in spawning habitats between the two species will be tested statistically with the main hypothesis as follows:

H_0: Anchovy and sardine eggs co-occur within the same ranges of environmental variables.

H_A: Anchovy and sardine eggs do not co-occur and have different ranges of environmental variables.

If the spawning habitats of anchovy and sardine can be characterized, they may also be predicted in the absence of egg data through, for example, information from satellite images such as sea surface temperature, ocean colour and wind stress. This has obvious advantages in that satellite images can provide a better temporal and spatial coverage and hence more useful information than a single survey per year.

1.6: Structure of this dissertation

Data sources and methods of analysis are described in Chapter 2. A "quotient exception to the general rule" was followed to determine the preferred range of spawning habitats of anchovy and sardine. Geographic references for selected spawning habitats were determined using Surfer, Idrisi and ArcView GIS computer programs in order to discover where anchovy and sardine spawning is predicted to occur within the southern Benguela upwelling ecosystem. The relationships between eggs of the two species and environmental variables were also examined using a multivariate coinertia analysis in order to explain possible causes for changes and/or differences in spawning habitats of anchovy and sardine. Cluster analysis was used to assess whether the environmental variables were grouped together or the same at different stations.

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Chapter 3 consists of the presentation of SARP survey data results. Results for single variable quotient rule analyses are displayed in quotient curves and values, and only those indicating differences between the two species are presented. Probability images are used to illustrate where the spawning habitats of both species might be expected in the Southern Benguela upwelling ecosystem. Tables are used to illustrate the relationship between eggs and environmental variables. The correlations among the environmental variables are given in the form of dendrograms in hierarchical order. Results for the spawner biomass survey data are displayed in Chapter 4. The format of display is the same as in Chapter 3, except that all the results of the single quotient rule analysis on a yearly basis are shown to illustrate the interannual variability in spawning of the two species. Prediction of spawning habitat is then based on the ones indicating a consistent pattern through the 16-year time series. In Chapter 5, all the findings are discussed in relation to their implications for changes in spawning habitats and regime fluctuations of anchovy and sardine populations, and conclusions are drawn.

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CHAPTER 2:

DESCRIPTION OF DATA SOURCES AND METHODS OF ANALYSIS

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2.1: Introduction

The spawning habitats of anchovy and sardine were characterized by comparing egg abundance and environmental data collected during field sampling that was conducted through two different survey programs on board the South African research vessels FRS *Africana* and *Algoa,* and the Norwegian research vessel *Dr. Fridtjof Nansen.* The survey areas of both programs cover part of the coast where anchovy and sardine reproduction takes place, but the annual spawner biomass surveys covered a larger spatial extent than the SARP surveys. The SARP studies were conducted monthly between August 1993 and March 1994, and September 1994 and March 1995, and the spawner biomass surveys were conducted in November. All the data that are described below were collected by MCM research teams and made available for use in this study (see Appendices A-B). This chapter describes the methods of data collection, and provides summaries of the relevant data. It then goes on to describe the methods used to analyze the data to address the project objectives.

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2.2: Data sources

The first survey program was conducted by MCM on a monthly basis over two summer spawning seasons: between August 1993 & March 1994, and between September 1994 & March 1995. These surveys formed part of the South African Sardine and Anchovy Recruitment Programme (SARP) (Painting *et al.* 1998). The survey grid extended from the Olifant's River Mouth on the West Coast (18°E, 31°S) to Cape Agulhas (20°E, 35°S) on the South Coast (Fig. 2.1). The transects started as close as possible to the coast and extended to the 200m depth contour, with stations every ten nautical miles (Fowler & Boyd 1998).

For the purpose of data analysis this study area was divided into three strata: A, B and C (Fig. 2.1).

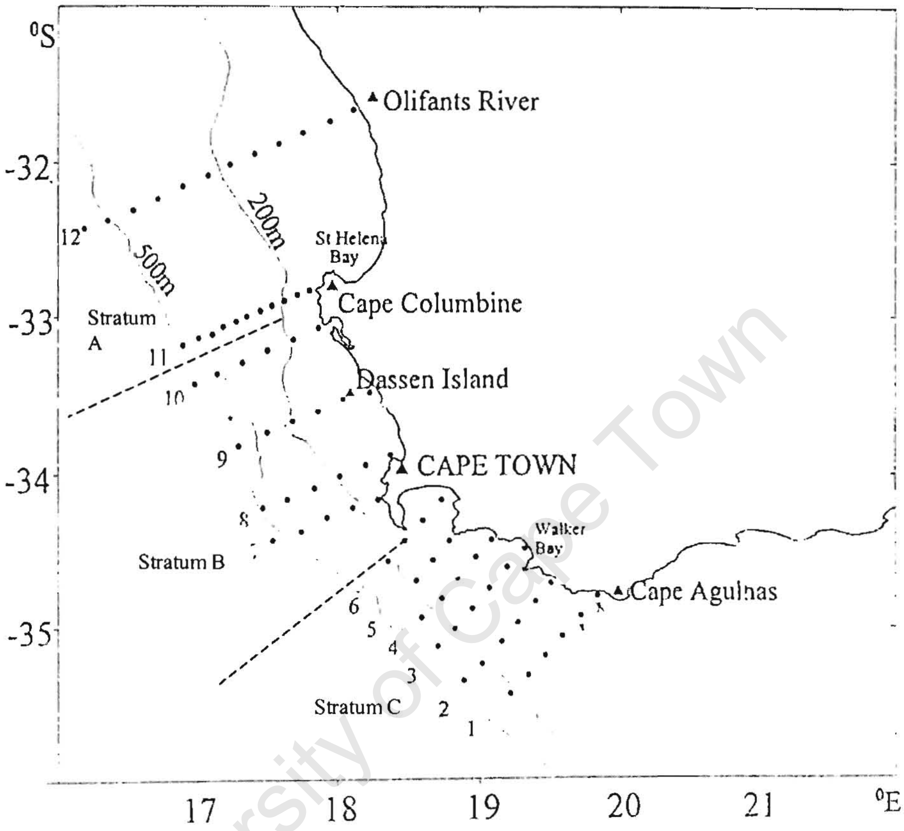

Fig. 2.1: A map showing the SARP study area and the sampling pattern followed during SARP surveys (Fowler 1998), with the three strata used.

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The second survey program is the annual pelagic spawner biomass survey conducted during November/December by Marine and Coastal Management. For this study I used data collected over a 16-year period (1984-1999). The spawner biomass surveys cover the continental shelf between Hondeklip Bay (18°E, 30°S) on the West Coast and Port Alfred on the South Coast (26°E, 35°S) (Fig. 2.2). The survey area is divided into five different shelf strata; stratum A extending north of Cape Columbine and representing the West Coast (WC), stratum B from Cape Columbine to Cape Point and representing the South West Coast (SWC), stratum C from Cape Point to Cape

Agulhas and is known as the Western Agulhas Bank (WAB), stratum D from Cape Agulhas to Cape St. Blaize and represents the Central Agulhas Bank (CAB), and stratum E is the Eastern Agulhas Bank (EAB), which extends eastwards from Cape St. Blaize. The survey grid consists of randomly spaced transects running more or less perpendicular to the coastline and extending to the edge of the continental shelf (about 200m-depth in most areas), with stations positioned 10 nautical miles apart (van der Lingen *et al.* 2001) (Fig. 2.2). Sampling at these stations is described later.

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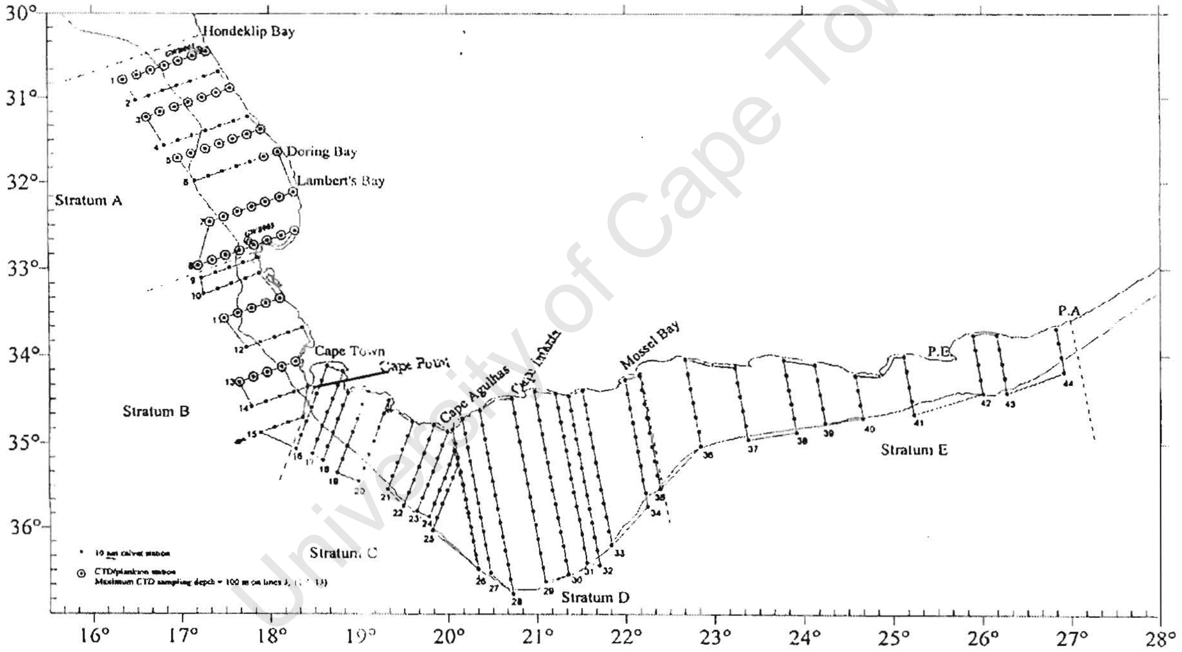

Fig. 2.2: The spatial coverage of annual spawner biomass surveys (this is from the Nov. 1998 survey) showing the five strata used

2.2.1: Anchovy and sardine eggs

Anchovy and sardine eggs were sampled by means of vertical hauls of a CalVET (CalCOFI Vertical Egg Tow) net deployed on station from 100 m (or 5 m off the bottom) to the surface. Stations were positioned at 5 or 10 nautical-mile intervals along survey lines (van der Lingen *et al.* 2001). The CalVET net, which has a 0.05m^2 mouth area and is fitted with 300 µm mesh net, is a very good fish egg sampling device under many conditions, and was designed for sampling anchovy eggs in California (Smith *et al.* 1985). Optimal sampling is achieved when the tow is vertical and the minimum volume of water is filtered per unit depth (Smith *et al.* 1985). Collected fish eggs samples were examined under a light microscope and preserved immediately in 5% buffered formalin. In the laboratory, eggs were identified and counted, and their densities at each station were standardized to numbers.m^{-2} (Fowler 1998). More CalVET stations were sampled during the November spawner biomass surveys (Table 2.2) than in the SARP surveys (Table 2.1). The data are expressed in terms of stations that had eggs of anchovy or sardine or both species.

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Table 2.1: Summary of CalVET stations where anchovy and sardine eggs were collected during the SARP survey

SARP Survey	Total No. of stations	% of positive stations		
		Anchovy	Sardine	Both species
Aug. 1993	17	41	53	35
Sept. 1993	21	43	29	29
Oct. 1993	34	26	21	15
Nov. 1993	177	56	28	24
Dec. 1993	41	27	30	20
Jan. 1994	23	9	26	9
Feb. 1994	35	14	23	14
Mar. 1994	25	0	20	0
Sept. 1994	51	14	43	8
Oct. 1994	85	25	38	14
Nov. 1994	170	47	27	22
Dec. 1994	40	30	25	15
Feb. 1995	76	7	26	1
Mar. 1995	70	3	11	0

Table 2.2: Summary table of CalVET samples from November pelagic spawner biomass surveys

Year	Total No. of stations	% of positive stations		
		Anchovy	Sardine	Both species
1984	307	61	12	10
1985	294	70	9	8
1986	271	73	23	20
1987	441	70	20	19
1988	480	51	23	16
1989	361	48	36	20
1990	338	50	28	22
1991	418	59	24	18
1992	425	51	16	11
1993	327	61	23	17
1994	305	55	24	18
1995	322	46	30	19
1996	473	26	29	11
1997	286	38	28	17
1998	373	29	19	8
1999	314	47	25	19

2.2.2: Physical variables

Sea surface temperature and vertical temperature profiles to 100m were obtained at each station by means of an electronic temperature/depth sensor suspended below the CalVET net. Continuous operation of a 150 kHz RDI narrow band acoustic doppler current profiler (ADCP), mounted in the hull of the vessel, was used to measure current speed at 32m while underway and on station (Fowler & Boyd 1998). Wind speed datum was obtained from anemometers on board the research vessels, and was used as a proxy for mixing. Surface salinity measurements were obtained from a thermosalinograph run continuously during surveys and calibrated against CTD data. Mixed layer depth, defined by Laevastu (1993) as the depth of the top of the seasonal thermocline where the difference in temperature from the surface is 0.5°C, was estimated from temperature profiles.

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Summaries of the physical variables collected over the two survey programs are given in Appendices A & B.

2.2.3: Biological variables

Water samples were collected at the surface and from the chlorophyll maximum layer by means of a Rosette sampler and were analyzed for chlorophyll and nitrate concentrations (Mitchell-Innes *et al.* 1999). The samples for chlorophyll analysis were filtered through GF/F filters, which were allowed to settle in 90% acetone in a centrifuge tube for 24 hours in the dark. The tubes were then centrifuged and extracted chlorophyll was measured fluorometrically using a Turner Designs fluorometer (Peterson & Hutchings 1992). Fluorescence profiles were calibrated in terms of chlorophyll equivalence and integrated chlorophyll concentrations were obtained for the upper 30m (Mitchell-Innes *et al.* 1999).

Zooplankton biomass was estimated from zooplankton abundance collected in the upper 200m or from 10m off the bottom using a vertically towed Bongo net fitted with 200-µm-mesh (Richardson *et al.* 1998), and equipped with flow, depth and temperature sensors (Peterson & Hutchings 1992). After collection, the samples were preserved in 5% buffered formalin before further laboratory analysis. Zooplankton were allowed to settle in graduated measuring cylinders for 24h and then diluted to 10 times the settled volume of copepods (Richardson *et al.* 1998). Copepods were identified to genus and species, and *Calanus agulhensis* were identified to stages. Counts were converted to dry mass.m^{-2} using literature-derived values of body mass (Richardson *et al.* 1998).

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Zooplankton egg production was estimated from on-board experiments using live copepods collected from the fluorescence maximum by drifting a 0.5m diameter, 300 µm mesh net for 5-10 minutes while on station. The copepods were gently transferred from the 2*l* codend to a 20*l* bucket filled with surface water. Female *Calanus agulhensis* were immediately sorted from the sample and placed into 1.1*l* plastic bottles, with two females per bottle and six replicates (Peterson & Hutchings 1995). Bottles were filled with seawater collected from the fluorescence maximum, which had been filtered through a 63µm mesh and were then incubated in shaded tubs cooled with a flow-through of seawater. After 24 hours, the contents of the bottles were filtered onto a 40µm screen and then rinsed into a sampling jar. Eggs were counted and fecundity was expressed as eggs per female per day (Peterson & Hutchings 1995). Daily zooplankton production was estimated as the product of zooplankton size-based growth rate and biomass for each species and/or stage of copepods in samples (Hutchings *et al.* 1995). Summaries of the available biological variables for the two survey programs are given in Appendices A & B.

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2.3: Data analysis

This section describes the analyses carried out to characterize anchovy and sardine spawning habitats in terms of a number of variables. For the purpose of analysis, the data collected during the SARP surveys were combined into a single dataset due to inconsistency in spatial coverage between surveys. As an example, the first survey was the smallest in terms of the area covered and hence the number of data points, whereas the fourth survey was larger, being part of a pelagic spawner biomass survey. In contrast, November survey data were analyzed separately for each survey.

Firstly, the selection of spawning habitat in terms of environmental variables was examined for anchovy and sardine, and these results were used to predict the location of spawning of anchovy and sardine in the southern Benguela upwelling ecosystem. Relationships between eggs and environmental variables were evaluated, and the relationships among environmental variables themselves were determined in order to understand possible confounding factors. The general structure of the water column was also examined.

2.3.1: Spawning habitat selection

A simple quotient rule analysis (van der Lingen *et al.* 2001) was carried out to assess the preferred ranges of physical and biological variables for anchovy and sardine spawning using Microsoft Excel® (1997). Each environmental variable was assigned a standard number of 30 classes (to ensure that the maximum occurrence per category never exceeded 10%), and their percentage frequencies of occurrence (% environmental variable) within each class (c) were calculated.

$$\%\ \text{environmental variable}_c = \frac{\text{env. var}_c}{\sum_{c=1}^{30} \text{env. var}_c} \times 100 \qquad (2.1)$$

Egg abundance data (e) were summed within each class (c) and expressed as percentages of the total number of eggs:

$$\%\ \text{eggs} = \frac{e_c}{\sum_{c=1}^{30} e_c} \times 100 \qquad (2.2)$$

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Quotients (Q) were then calculated for each variable class (c) by the percentage frequency of occurrence of the environmental variable:

$$Q_c = \frac{\%\ \text{eggs}_c}{\%\ \text{environmental variable}_c} \qquad (2.3)$$

The Q_c values essentially correct for over- or under - representation of eggs within certain classes of environmental measurements, giving a predicted trend if there are no preferences. Quotient values were smoothed using a 5-point running mean (for details see van der Lingen *et al.* 2001). Quotient curves were then generated from smoothed quotient values for better presentation of spawning selection. Only quotient values greater than one are considered to signify positive selection and those less than one indicate avoidance of the values for spawning (van der Lingen *et al.* 2001)

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A non-parametric Kolmogorov-Smirnov test for goodness of fit was used to compare frequency distribution curves of egg abundance per category of environmental variable against the distribution curves of that variable, i.e. the observed egg distribution against a random distribution. This test compares two groups and tests the null hypothesis that the two samples were drawn from the same cumulative frequency distribution. It was carried out manually in Microsoft Excel spreadsheets following the procedure given in Zar (1999). Frequencies of occurrence of individual environmental variables within categories of each particular variable were determined. The number of observed anchovy and sardine eggs (fi) according to each category were obtained by constructing pivot tables. Relative observed frequencies (Fi) were then determined (Zar 1999) using the formula:

$$\text{rel Fi} = \frac{\text{Fi}}{\text{n}} \qquad (2.4)$$

Expected frequencies of anchovy and sardine eggs ($\hat{\mathrm{f}}_{\mathrm{i}}$)were epxressed as :

FO = frequency of occurrence
f_i = observed number of eggs

Cumulative expected frequencies ($\hat{\mathrm{F}}_{\mathrm{i}}$) of anchovy and sardine eggs were obtianed as :

$$\text{rel } \hat{\mathrm{F}}_{\mathrm{i}} = \frac{\hat{\mathrm{F}}_{\mathrm{i}}}{\sum \text{fi}} \qquad (2.6)$$

The Kolmogorov-Smirnov goodness of fit statistics (D_i) for this test was obtained from the formula:

$$\mathrm{D}_{\mathrm{i}} = (\left|\text{rel } \mathrm{F}_{\mathrm{i-1}} - \text{rel } \hat{\mathrm{F}}_{\mathrm{i}}\right|) \qquad (2.7)$$

Critical statistics (D'_i) was calculated as the maximum difference between cumulative expected and cumulative observed frequencies of anchovy and sardine eggs:

$$(D'_i) = \max[(\max D_i), (\max D'_i)] \qquad (2.8)$$

Critical values for this test statistics are referred to as $\mathrm{D}_{\alpha,\mathrm{n}}$ were derived from the formula since the number of samples were greater than 160 (Zar 1999):

$$\mathrm{p} = \sqrt{\frac{(-\ln(\frac{\alpha}{2})}{2 * \mathrm{n}}} \qquad (2.9)$$

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n = number of observations

α = thel evel of significance

2.3.2:Predicting anchovy and sardine spawning in the southern Benguela ecosystem

The areas of occurrence of eggs were predicted from results of the quotient rule analysis through an overlay operation analysis. Surfer®(1999) was used for surface interpolation, IDRISI® (1998) for assigning environmental variables into membership functions and ArcView® (1998) for displaying the maps. Surface interpolation was conducted for each data set (eggs and environmental variables) followed by an overlay operation analysis. This analysis is based on the integration of two data sets based on a common key (Christen 1997). Overlay operation analysis is a function available in geographic information system (ArcView® 1999) program and Surfer® 1999), which involves a spatial referencing system that provides a geometric basis to connect two data sources.

A standard kriging method was followed for gridding data on egg abundance and environmental variables. Kriging is one of the more commonly used gridding methods. It is useful for gridding almost any type of data. The most important component of this method is the linear variogram, which needs to be constructed to ensure accuracy (Surfer® 1999). This method is very good in explaining the existence of a smooth phenomenon in the data. Contour maps were constructed for each data set; the two surfaces, one for each environmental variable and another one for fish eggs, were overlayed. Spatial relationships between the two data sets were examined using the spatial analysis tool in ArcView® (1999).

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Probability maps were generated based on the information provided by quotient curves by considering the environmental variable categories with quotient values that were greater than one. To perform more precise geographical referencing, fuzzy set theory was introduced as a way of dealing with uncertainty. The main aim was to determine a true or false possibility that spawning can be expected to take place within a particular range of each individual environmental variable. Fuzziness is an admission of the possibility that an individual measurement of the environmental variable is a member of a particular class (Burrough *et al.* 1998). It is also a way of creating approximate boundaries within environmental variables, at the same time assigning probability values (0-1) according to a user-defined membership function, which is bell-shaped following the shape of quotient curves. For example, a temperature at a certain range (e.g. 9.0-11.5°C) may be assigned to a class indicating 0% probability for sardine spawning, whereas the range of 15.5-19°C may indicate 100% probability. The way in which these temperature values are assigned to each class is through fuzzy membership functions. There are various kinds of membership functions that could have been used, but the one used was derived to maintain the shape of quotient curves (user-defined). A schematic representation of this membership function is given in Fig. 2.3.

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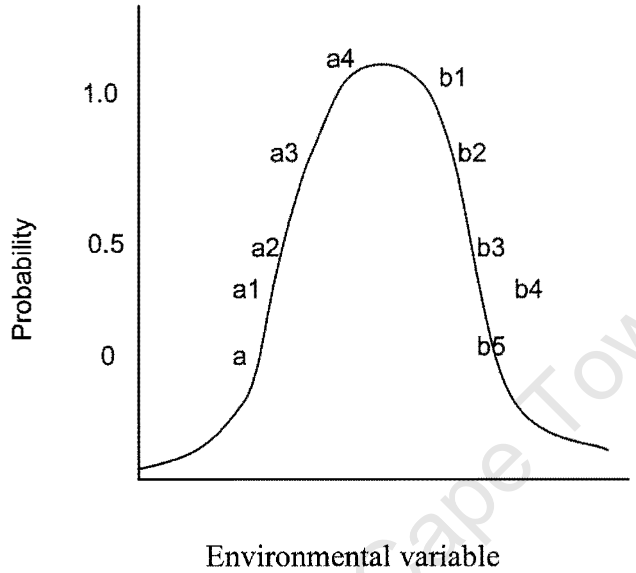

Fig. 2.3: A schematic representation of a fuzzy membership function. The probability scale is given on the y-axis and environmental variables categories are displayed on the x-axis. The control points for the curve are given as point a where the curve is still at 0, a1 where it starts leaving 0, at 0.5 is indicated by a2, when approaching 1 is indicated by a3 and when it reaches 1 its indicated by a4, and when it starts declining is illustrated by b1 and goes back to zero at point b5.

Although only few control points are shown, an unlimited number can be used to define the membership curve to obtain the best results. The fuzzy membership between any 2 control points is linearly interpolated (IDRISI® 1999). A fuzzy module was launched to create fuzzy sets (IDRISI® 1999), defined mathematically as follows:

$$A = (z, MF_A^Z(z)) \text{ for all } z \in Z \qquad (2.10)$$

where MF = a membership function

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z & A = constants

$z \epsilon Z$ = an ordered pair indicating that z belongs to Z.

That is, if Z denotes a space of objects, then the fuzzy set A in Z is the set of ordered pairs in the set. In fuzzy sets the grade of membership (also called a possibility) is expressed in terms of a scale that ranges from 0.0 to 1.0, indicating a continuous increase from nonmembership (0) to complete membership (1) (Burrough *et al.* 1998). The way in which the spawning of anchovy and sardine is predicted is illustrated on the scale, 0.0 indicating no probability to 1.0 for 100% probability.

In addition to single probability maps for spatial spawning predictions, multivariate maps were also constructed following a Multi-Criteria Evaluation (MCE) (IDRISI® 1999). The main aim was to assess the prediction of realized spawning habitats for anchovy and sardine with respect to more than one environmental variable. Sea surface temperature, wind speed, ocean color (indexed by phytoplankton biomass) and water column depth were chosen, since data on these parameters can be obtained from satellite. A number of modules were tried for this purpose, but were not successful due to insufficient information. For example, an attempt was made on the Bayesian Probability Theory, which evaluates the relationship between empirical evidence and one's beliefs about an investigated problem (IDRISI® 1999). This theory requires a prior knowledge leading to the probability that one hypothesis or the other is true with given evidence, i.e. *a posteriori* probability. The MCE tool serves in attempting to combine a set of criteria to

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achieve a single composite basis for a decision according to a specific objective (IDRISI® 1999). The specific objective in the current study is to form a single suitability map from which the recognized spawning habitat of anchovy and sardine can be predicted form egg occurrence. A MCE module was launched from IDRISI and the procedure involved specifying the aggregation method, creating factor images or criteria maps from standardized factors and aggregating all the information from factor images. The order weighted average (OWA) method was specified for the purpose of aggregating multiple criteria. This technique includes three criteria, i.e. factor weights, order weights and constraints (IDRISI® 1999).

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Factor weights apply to specific factors, i.e. all the pixels of a particular factor image receive the same factor weight. They also indicate the relative degree of importance each factor plays in determining the suitability for an objective. Order weights are a set of weights that apply to factors according to their rank order position. They serve to control the manner in which the factor weights are aggregated and can be assigned any combination of values that sum to 1. Constraints serve to exclude certain areas from consideration (IDRISI® 1999). Order weights were subjectively assigned as follows: SST (0.40), depth (0.26), wind speed (0.19) and phytoplankton biomass (0.15). This was based on an examination of quotient curves, their spread and overlap i.e. a big weight was given where quotient curves for both species are narrow and not overlapping and in cases of overlap a small weight was assigned. These weights were arranged in such a manner that they indicate the order of importance of each environmental variable based on information from the preceding analysis, using the quotient rule where spawning habitat selection with respect to SST was successful. They were then automatically adjusted by ranked order to minimize the risk that factor weights can influence the final result according to the relative dispersion of order weights. Sea surface temperature was placed at the highest level (0.46), wind speed followed (0.268), then phytoplankton biomass with 0.186 and lastly depth as 0.086. Factor images were created, a set of factor weights were developed that indicates the relative importance of each factor to the decision under consideration. Finally, the information from factor images was combined following the OWA technique and the final suitability map was created.

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2.3.3: Relationships between fish eggs and environmental variables

In addition to these analyses, a multivariate coinertia analysis was used to explore the common structure of the two data sets (egg abundance and environmental variables) and to test if there were statistically significant relationships between the two (Thioulouse 2000). This is a parametric analysis performed on standardized data, and regards the relationships between environmental variables and egg abundance as either positively or negatively linear, but not curvilinear. Coinertia analysis is unable to prove a direct relationship, but considers the third factor as the one influencing the resulting relationship. Two separate analyses were performed on eggs and environmental variables data. Firstly, a covariance principal component analysis (PCA) was performed on egg abundance data to determine if there is any uniformity between the eggs of the two species. Secondly, a correlation PCA was performed on environmental variables data to find out which ones are positively or negatively correlated with others either in a weak or strong way. Thereafter the information from the two analyses was combined by means of the coinertia analysis.

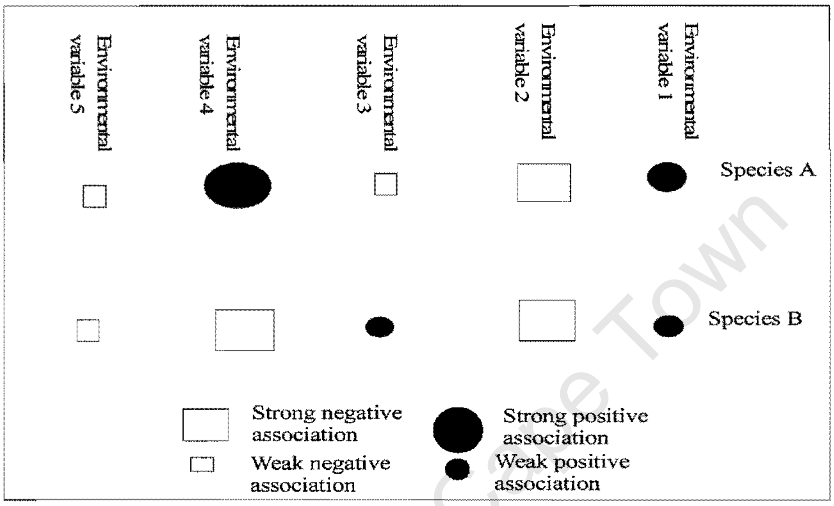

Fig. 2.4: A schematic representation of the output of a multivariate coinertia analysis showing a crossed matrix table (Thioulouse 2000)

Only if such a significant relationship ($p<0.05$) was identified was the coinertia analysis carried out (Thioulouse 2000). The outputs of this analysis are presented in the form of a table of factors. The relationships between anchovy and sardine eggs and environmental variables were displayed in a crossed matrix (see example Fig. 2.4), and are represented by circles and squares. Big circles indicate a strong positive association, whilst big squares indicate a strong negative association (Fig. 2.4). Small squares and circles indicate weak negative and positive association respectively (Thioulouse 2000).

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2.3.4: Anchovy and sardine egg abundance

Scrutiny of the frequency distributions of the egg data (Fig. 2.5) indicates a log-normal distribution for both species. Therefore, egg abundance was transformed using a logarithmic (log (x+1)) transformation to cater for zeros in the data.

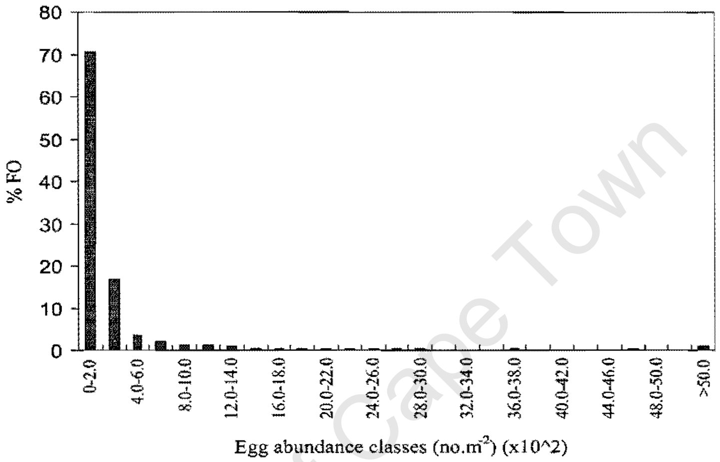

Fig. 2.5: Frequency distribution of anchovy and sardine eggs for both species combined

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2.3.5: Relationships among environmental variables

All the environmental variables were used to group the stations into ordered clusters using a cluster analysis package in Statistica® (1996). Grouping distances between variables were measured using the "power method" (Statistica® 1996), which allows one to increase or decrease the major differences between environmental variables. Ward's rule, which creates clusters of small size, was followed for the purpose of linking the clusters. This rule uses an analysis of variance (ANOVA) approach to evaluate the distances between clusters and attempts to minimize the sum of squares of any two clusters that can be formed at each step. Dendrograms in a form of rectangular branches were used to display these results (Statistica® 1996). PCA was used to standardize the environmental variables and to avoid variability caused by environmental variables being measured in different units.

Standardization involves the division of the difference between each observation and the mean ($\bar{x}$) by the standard deviation (s) of each variable.

$$\text{Standardized variable} = \frac{x - \bar{x}}{s} \tag{2.12}$$

At first, a correlation matrix module was created to measure the correlations among all 12 environmental variables. The number of variables used in this analysis was decreased e.g. going stepwise from 12 to 9 to see if different results were obtained. For example, when wind speed was included all the biological variables were positively associated with sardine eggs in the coinertia analysis. When this variable was not included, sardine eggs were only positively associated with phytoplankton biomass and negatively associated with the rest of biological variables. Various types of analyses, from univariate to multivariate, were performed to assess whether they give different pictures of the spawning habitats of anchovy and sardine. The results are displayed in Chapters 3 and 4 in the form of graphs, tables and maps.

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Chapter 3:

Anchovy and sardine spawning habitats during the SARP surveys

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3.1: Introduction

The main purpose of this chapter is to examine whether anchovy and sardine eggs occurred in specific habitats by examining data collected on a monthly basis between August 1993/March 1994 and September 1994/March 1995 as part of the Sardine and Anchovy Recruitment Programme (SARP). The first step is the presentation and description of anchovy and sardine spawning habitat with respect to environmental variables from information provided by quotient curves. Quotient curves are curves derived from quotient ratios of anchovy and sardine eggs within percentages of each environmental variable category (details on 2.3.1). The geographic references of expected areas of anchovy and sardine spawning are presented in maps. A multivariate probability diagram is also displayed to aid in mapping the potential area in which anchovy and sardine spawning can be expected with respect to four environmental variables (sea surface temperature, wind speed, phytoplankton biomass and depth). The relationships between the eggs of anchovy and sardine and environmental variables are verified, and the relationships among the variables that are involved in spawning habitats of anchovy and sardine are also examined.

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3.2: Spawning habitat selection during SARP surveys

This section describes the different ranges of environmental variables over which anchovy and sardine spawning occurred, and how suitable these variables may help to interpret successful spawning habitat of each species during monthly surveys. Quotient curves were used to reflect the selection of spawning habitat for each variable.

The indication that anchovy and sardine select certain spawning grounds was confirmed by the variation between the observed and expected frequencies of anchovy and sardine eggs within classes of each environmental variable. This is displayed in histograms, which were constructed using the percentage frequency of occurrence of eggs within different environmental variables categories based on those that have shown differences between anchovy and sardine spawning (Fig. 3.1).

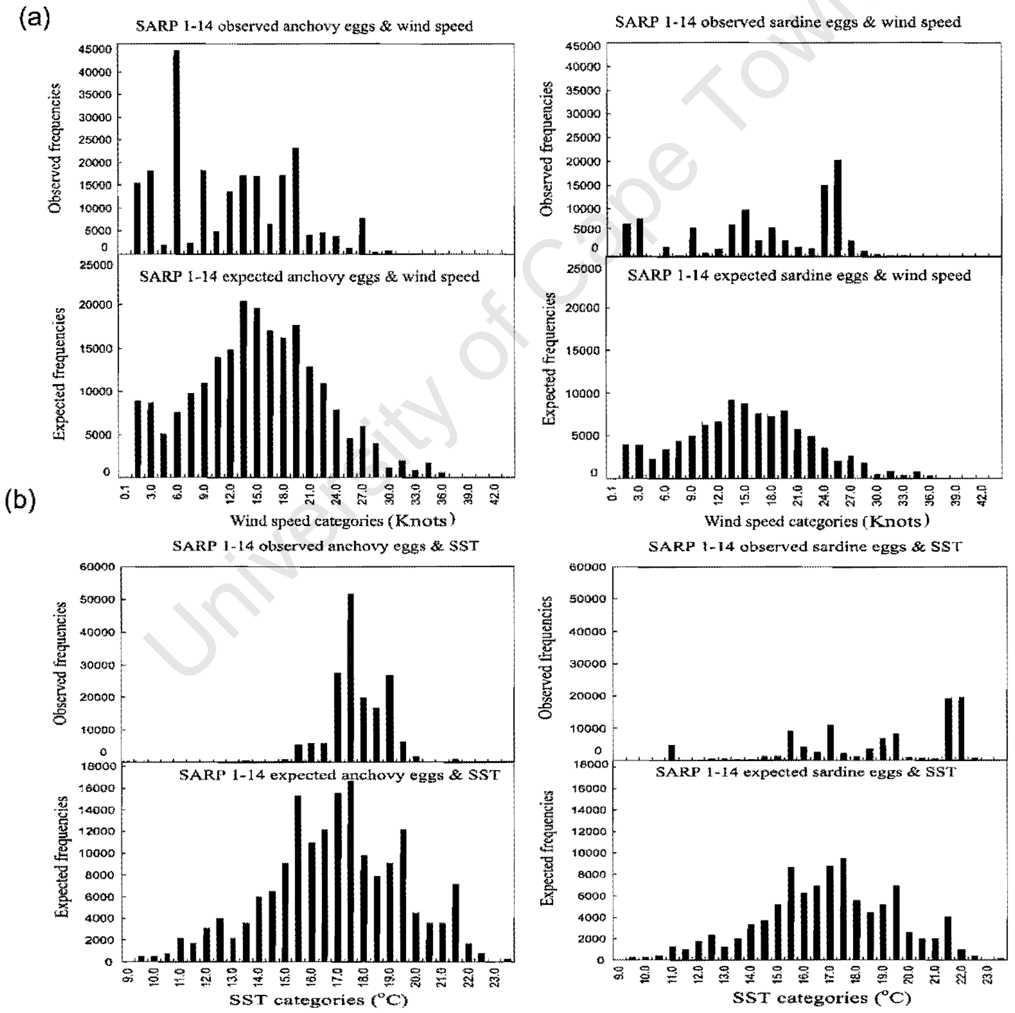

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Fig 3.1: Monthly surveys: Histograms displaying observed anchovy and sardine egg frequencies, and those expected if no habitat selection occurred for (a) wind speed and (b) SST

Only the spawning habitats characterised by sea surface temperature (SST), wind speed, zooplankton biomass and current speed are presented because they are the only ones where significant differences between anchovy and sardine spawning were observed. The observed differences in spawning habitats between the two species were confirmed statistically at a 5% level of significance, using a Kolmogorov-Smirnov goodness of fit test (Zar 1999) (Table 3.1).

Table 3.1: Monthly surveys: Results of Kolmogorov-Smirnov goodness of fit to test the null hypothesis: anchovy and sardine spawn randomly with respect to a particular environmental variable.

Calculated D_i (max[max D_i), (max D_i)] and critical $D = (|\text{rel } F_{i-1} - \text{rel } \hat{F}_i|)$ values for anchovy and sardine are displayed to describe significant differences between egg frequency distributions of each species and the 4 environmental variables, the number of observations (n) and levels of significance (p) are displayed.

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Environmental variable	D_i		D critical	n	P
	Anchovy	Sardine			
SST	0.359	0.383	0.048	716	<0.05
Wind speed	0.223	0.319	0.050	716	<0.05
Current speed	0.191	0.298	0.044	617	<0.05
Zooplankton biomass	0.252	0.435	0.068	391	<0.05

Anchovy appeared to spawn between 16 and 20°C, with the highest quotient value at 18°C (Fig. 3.2). In contrast, the sardine spawning range was broad and bimodal, with a minor peak between 15 and 17°C, and a major between 19.5 and 22.5°C (Fig. 3.2). Another wide range of sardine potential spawning habitat was identified by zooplankton biomass, with bimodal peaks between 0.6-0.8-1.2 and 2.0-3.0 g dry wt.m^{-2}.

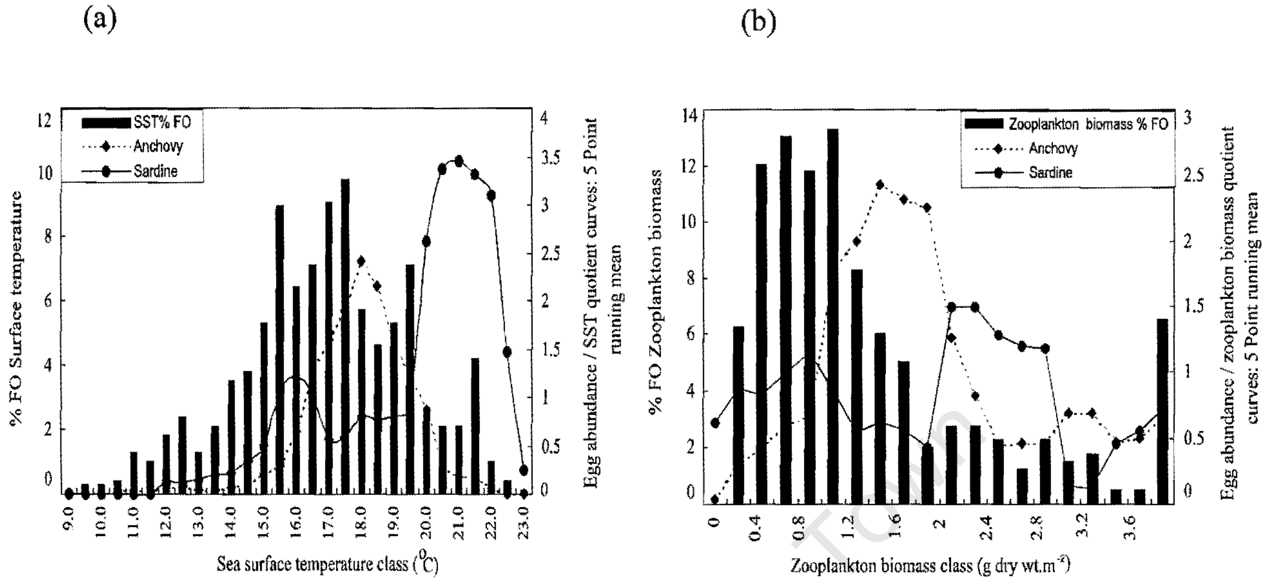

Fig. 3.2: Monthly surveys: Frequency distributions (histograms) of environmental variables and egg abundance / environmental variable quotient curves (the 5-point running means are shown) for anchovy (dotted lines) and sardine (continuous lines) eggs, generated from aggregated SARP survey data. Environmental variables are: (a) SST and (b) zooplankton biomass

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Anchovy spawning was associated with waters in which zooplankton was of moderate biomass (1.2-2 g dry wt.m^{-2}) that fell between the two peaks of the sardine range. The sardine spawning range appeared to be influenced by strong winds (21.1-30.1 knots), whereas anchovy spawning was associated with low winds (0.1-9.1 knots) (Fig. 3.3). Anchovy and sardine spawning ranges overlapped partially in areas with weak currents (19-30 cm.s^{-1}), and they appeared to be very different in areas with strong currents, with anchovy eggs showing a peak at 31-54 cm.s^{-1}, whereas sardine eggs were abundant at about 19-31 and 61-73 cm.s^{-1} indicating another bimodal spawning behaviour with respect to this environmental variable (Fig. 3.3).

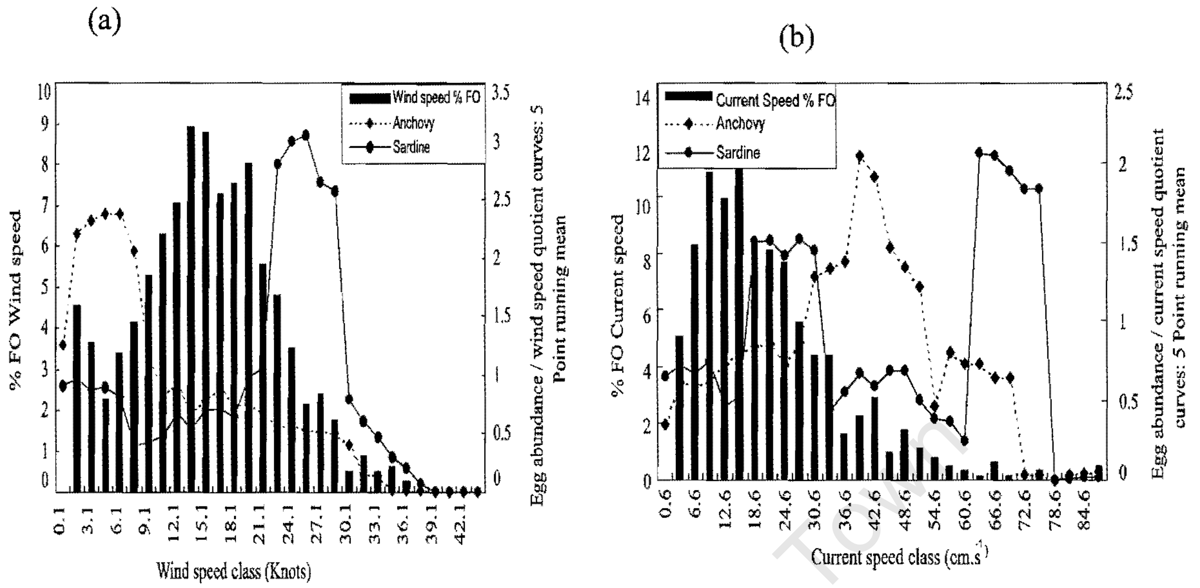

Fig. 3.3: Monthly surveys: Frequency distributions (histograms) of environmental variables and egg abundance / environmental variable quotient curves (the 5-point running means are shown) for anchovy (dotted lines) and sardine (continuous lines) eggs, generated from aggregated SARP survey data. Environmental variables are: (a) wind speed and (b) current speed at 32 m depth

This indicates that anchovy spawning habitats are stable and characterized by moderate currents, whereas sardine appear to spawn within moderate to strong currents. However the minor sardine peak is at lower current speeds than for anchovy (Fig. 3.3). Sardine spawning habitat was characterised by warm waters influenced by strong winds and currents and high zooplankton biomass. In contrast, anchovy spawning habitat was characterised by cooler waters, gentle wind and moderate current speeds, and average zooplankton biomass.

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3.3: Overlay Analysis: Spatial spawning predictions based on SARP surveys

This section demonstrates the probabilities of observing each of anchovy and sardine eggs within different areas according to the distribution of each environmental variable. This helps interpret where spawning is likely to occur. These results were obtained from the overlay operation analysis on aggregated SARP survey data. An overlay operation analysis is an analytical technique based on a geographical referencing system that provides a geometric basis to connect the two data sources (details in 2.3.2). The probability of spawning (based on either a single, or many environmental variables) is indicated by different colours and numbers in the scale, with red coloured areas regarded as having very high probability (100%) and the lowest probability (0%) symbolised by a dark colour (details on 2.3.2). Surface interpolation accounted for the problem of missing data points in areas where sampling did not take place due to bad weather conditions, and where sampled strata were small. An alternative way of finding the missing information between data points would be using another environmental variable with a complete coverage as a proxy.

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The probability of finding anchovy eggs was much higher in certain parts of the study area than for sardine, which had a predicted patchy spawning distribution. There were high probabilities of observing both anchovy and sardine eggs over most of the study site according to SST distribution, with reduced probability of finding both anchovy and sardine eggs in some inshore areas along the West Coast (WC), most likely due to low temperatures in these regions (Fig. 3.4 a-b).

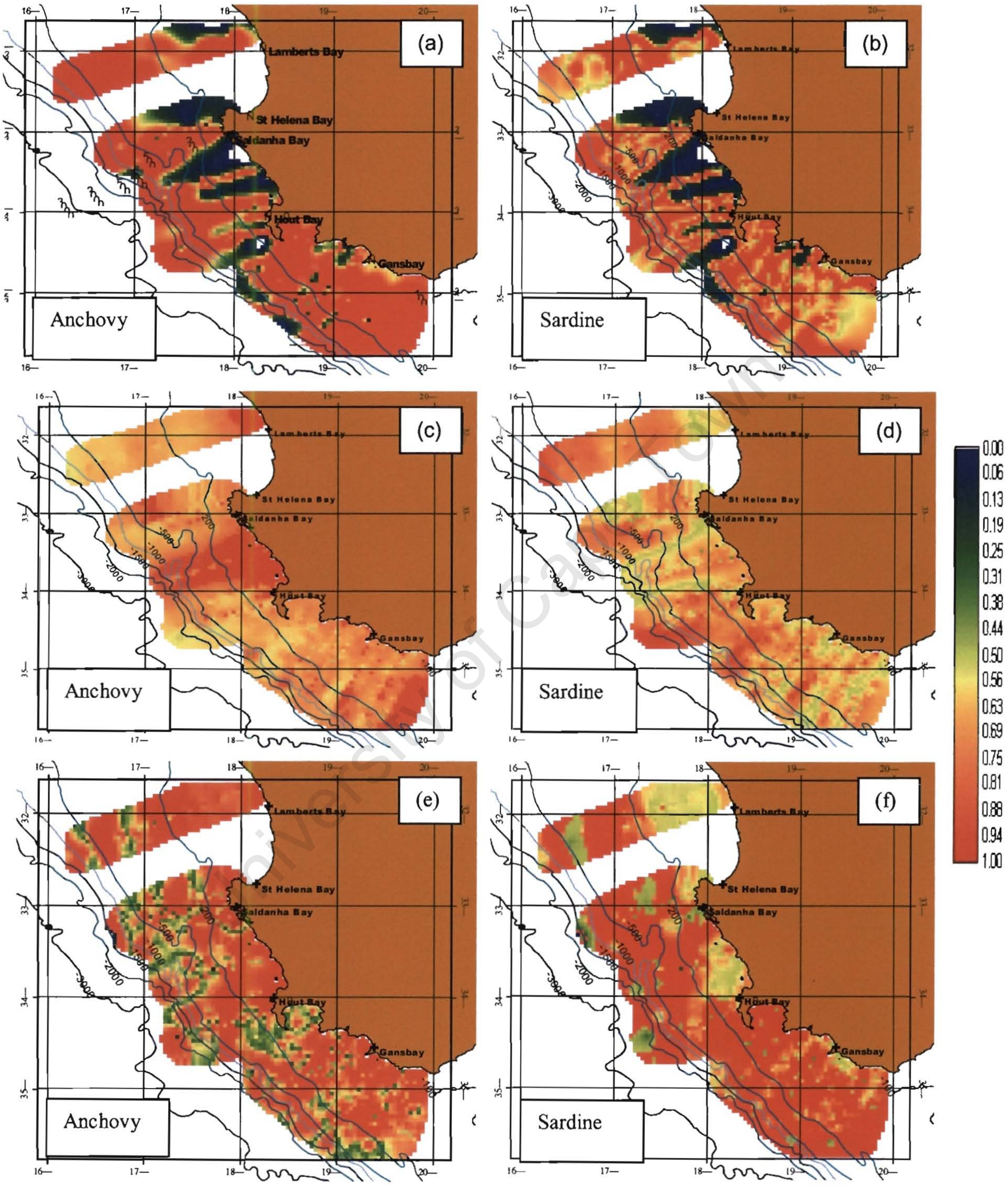

Fig. 3.4: Monthly surveys: Results of the overlay analysis showing spawning for anchovy and sardine estimated from SST (a - b), wind speed (c - d) and current speed (e - f) data, combined with egg distribution data

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There is a high probability that sardine and anchovy eggs would be expected in different strata according to varying wind speeds. In terms of wind speed, sardine eggs were predicted to be more offshore on the WC and South West Coast (SWC) where wind tends to be stronger, with very few high probability patches on the WAB. Anchovy spawning probability was highest in the southern tip of the WAB, throughout the area between Hout Bay and Saldanha Bay, and inshore close to Lambert's Bay. These results therefore show that the most favourable winds for anchovy spawning are found in the southern part of the WAB and inshore on the WC. On the other hand, sardine spawning is predicted to be intense where winds are offshore as the high number of eggs were found there (Fig. 3.4 c-d).

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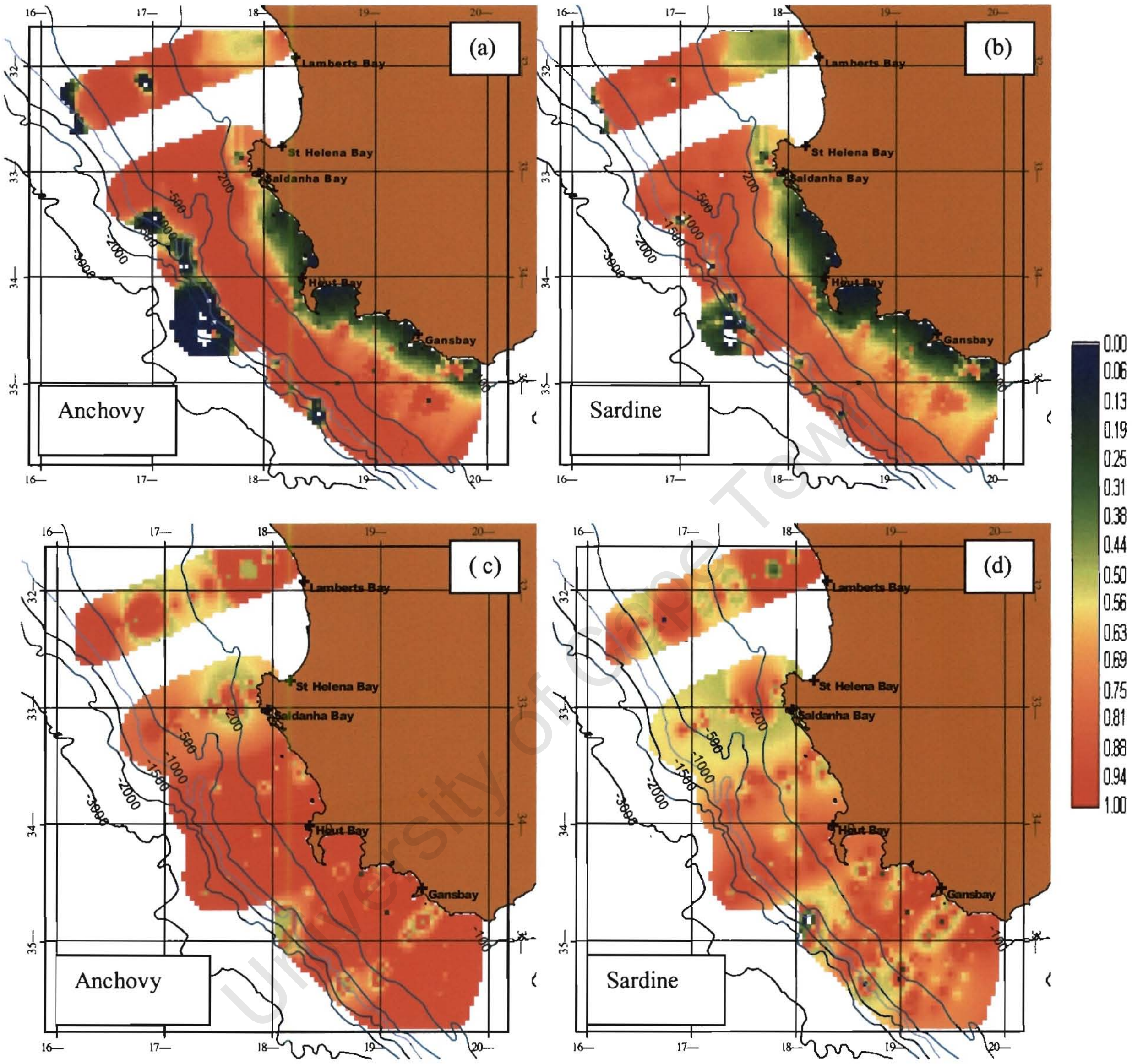

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Fig. 3.5: Monthly surveys: Results of the overlay analysis showing spawning for anchovy and sardine estimated from depth (a - b) and zooplankton biomass (c - d) data, combined with egg distribution data

With reference to current speed, anchovy eggs are predicted to be found where currents are 24-48cm.s^{-1}, mostly inshore along the SWC and WAB, except off the Cape Peninsula. Sardine might be expected to spawn where currents are 60-80 cm.s^{-1} over most of the WAB and along the shelf-edge, and offshore on the SWC. There is little chance of sardine eggs occurring inshore on the WC. This indicates that ideal currents for sardine were widespread all over the WAB and SWC, and offshore on the WC. Anchovy eggs are most likely to be found where the inshore waters of the WAB and WC are dominated by weak currents, and they would be expected to occur inshore close to Hout Bay when currents are too strong further offshore (Fig. 3.5 a-b). The probabilities of anchovy and sardine eggs occurrence were low in shallow waters, both on the SWC and WAB (Fig. 3.5 c-d). The greatest probability for eggs of both species occurred offshore of the 200m depth contour. The appearance of anchovy eggs in shallow areas indicate that this species were less likely to spawn in water of depth >1000m than sardine. However, according to zooplankton biomass distributions, the distribution of anchovy eggs was likely to take place across the entire shelf of the WAB and SWC, but being reduced inshore on the WC, especially between Saldanha Bay and St. Helena Bay (Fig. 3.5 c-d).

In contrast, the probability of finding sardine eggs according to zooplankton biomass was reduced compared to that of anchovy, and areas of high probability were very patchy over the study area (Fig. 3.5 c). These results suggest that, if only this factor was important anchovy spawning intensity might increase throughout the WAB and SWC, where zooplankton biomass is ideal (Fig. 3.5 c).

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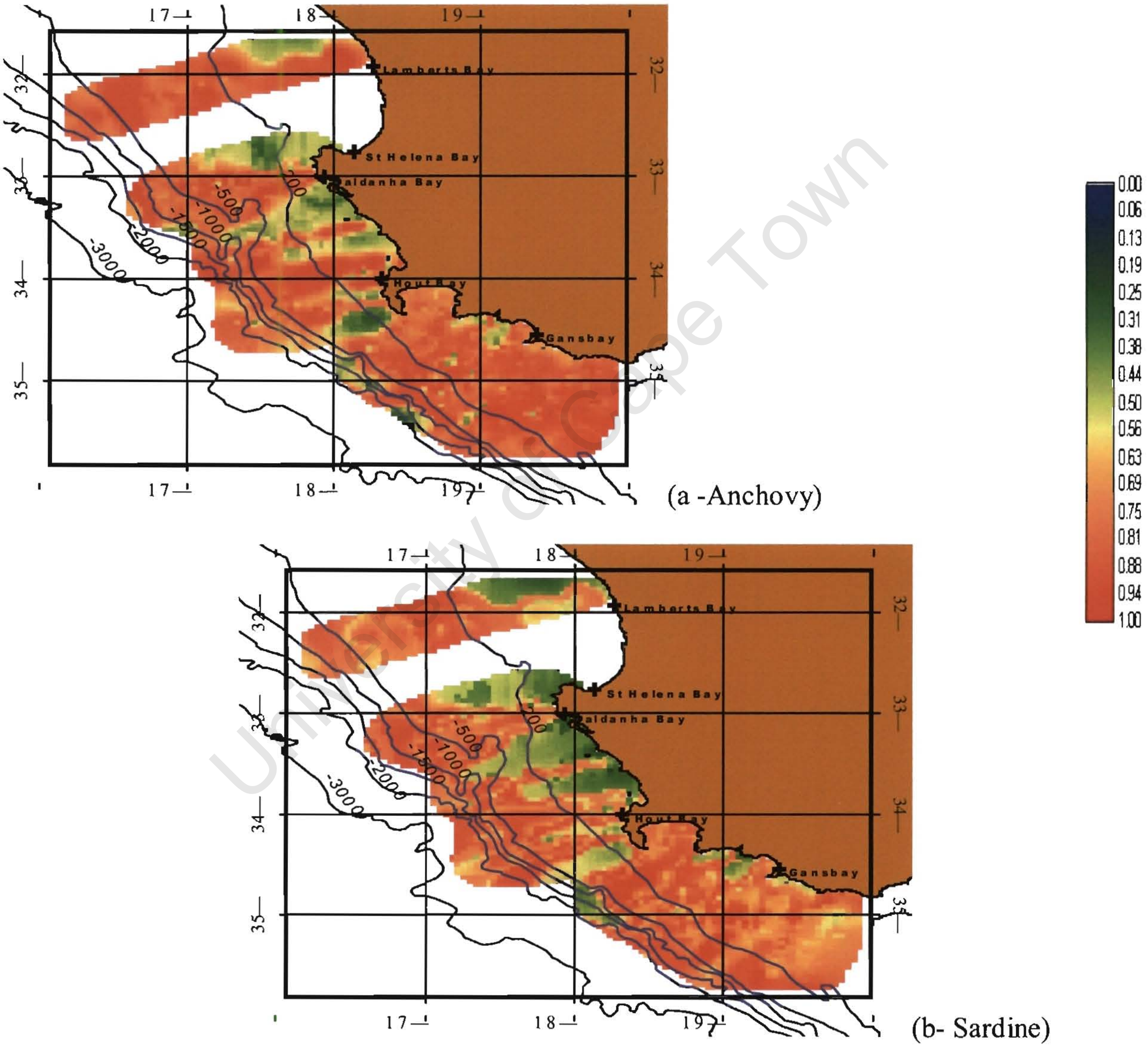
A multivariate probability map indicated that the potential spawning habitat of anchovy with respect to SST, depth, wind speed and phytoplankton biomass was not very different spatially, as is the case in annual surveys. Anchovy and sardine eggs were most likely to be found on the WAB, midshelf and offshore on the WC and SWC (Fig. 3.6 a - b).



(a -Anchovy)

(b- Sardine)

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Fig. 3.6: Monthly surveys: Results of the overlay analysis (multivariate) showing relative spawning for anchovy (a) and sardine (b) estimated from SST, depth, phytoplankton biomass and wind speed data from the quotient curves

The only difference in predicted areas where the eggs of the two species occur is that the ones for anchovy are more concentrated when compared to more or less patchy ones for sardine (Fig. 3.6 a-b)

3.4: Coinertia analysis: Relationships between eggs and environmental variables

This section focuses on how anchovy and sardine eggs are related to environmental variables and describes the results of a multivariate coinertia analysis. The strengths of the relationship between environmental variables and both anchovy and sardine eggs were highly significant at $p<0.000001$. Although all relationships are shown, only the ones that are stronger for one species over another are mentioned in to indicate differences in environmental variability between anchovy and sardine spawning (Fig. 3.7). Anchovy eggs were strongly negatively associated with water column depth, suggesting that anchovy eggs were not found far offshore. A strong positive association was observed between eggs of both species and SST, being stronger for anchovy eggs than for those of sardine; a strong positive relationship was found between salinity and anchovy eggs. This indicates that there was a high abundance of anchovy eggs in warm and saline waters (Fig. 3.7).

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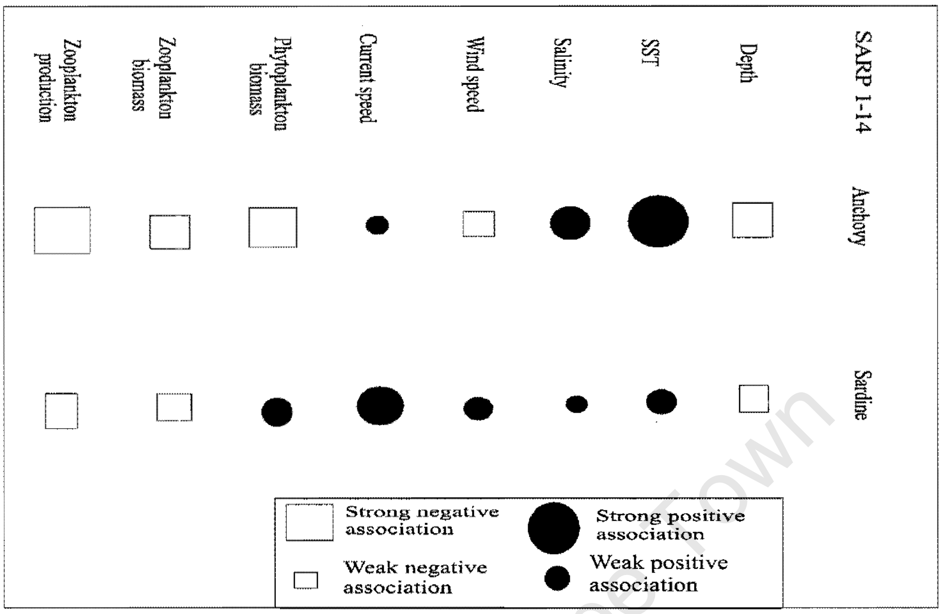

Fig. 3.7: Monthly surveys: Results of multivariate coinertia analyses showing relationships between fish eggs and environmental variables

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Eggs of anchovy were weakly, but negatively related with wind speed, indicating that anchovy eggs were less abundant in areas where there was strong wind and it is possible that they may occur only where there is reduced wind (Fig. 3.7). The relationship between eggs of anchovy and sardine, and current speed was positive and stronger for the latter, indicating that sardine eggs are found in waters of stronger current speed. Eggs of sardine were positively associated with phytoplankton biomass, whereas those of anchovy were negatively associated, therefore, eggs of sardine were abundant where phytoplankton biomass was high (Fig. 3.7). The negative relationship between anchovy and sardine eggs and zooplankton biomass and production indicates that there were few eggs where zooplankton biomass was low. This may also be explained by the possibility that zooplankton was reduced in places because adult spawners had grazed them down.

3.5: Cluster analysis: Relationships among the environmental variables

This section attempts to show relationships amongst some of the environmental variables. Environmental variables were clustered into two distinct groups, with one of the groups characterized by purely physical variables i.e. current speed, wind speed, SST, salinity and depth. The second group was characterized by biological variables such as zooplankton and phytoplankton biomass, and zooplankton production (Fig. 3.8).

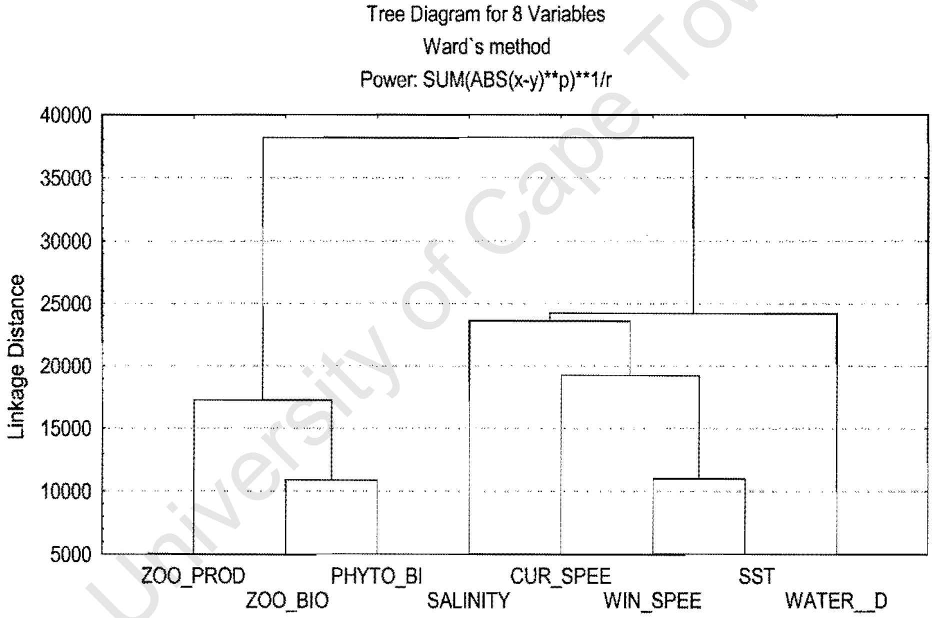

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Fig. 3.8: Results of cluster analysis showing the classification of environmental variable in ranked order during SARP surveys with a power distance as a measure of similarity, where p and r are user-defined parameters, p controls the progressive weight that is placed on differences on individual dimensions and r controls the progressive weight that is placed on larger differences between variables. Abbreviations on the x-axis are as follows: zoo_ prod = zooplankton production, zoo_ bio = zooplankton biomass, phyto_ bi = phytoplankton biomass, cur_ spee = current speed, win_ spee = wind speed, SST = sea surface temperature and water_ d = water depth

Although it is difficult to interpret the indication that physical variables were clustered separate from the biological ones at different sampled stations during monthly surveys, this may suggest a time-lag between these variables in a sense that the availability of biological variables depends on the period of the water to stabilize after physical processes like upwelling have taken place. The results presented above indicate that the spawning habitats of anchovy and sardine are different as they appear to be characterized by different environmental variables. Anchovy appeared to spawn in areas with cool waters (16-20°C), but mainly at 18°C, weak wind (0.1-9 knots) and moderate to high currents (31-54 $cm.s^{-1}$) speeds, and intermediate zooplankton biomass (1.2-2 g dry $wt.m^{-2}$), whereas sardine spawning was associated with warm waters (19-22°C), strong wind speed (21-30 knots), a range of current speeds (19-31 and 61-73 $cm.s^{-1}$), and zooplankton biomass ranging between 0.6-0.8 and 2-3 g dry $wt.m^{-2}$.

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CHAPTER 4:

Anchovy and sardine spawning habitat during 16 annual November pelagic spawner biomass surveys

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4.1: Introduction

The main aims of this chapter are to examine the interannual variability within the spawning habitat of anchovy and sardine, and whether the changes in environmental variables control the preferred spawning habitat of the two species from year to year.

4.2: Spawning habitat selection during spawner biomass surveys

This section shows results of the single parameter quotient analysis that reflect spawning habitat selection by anchovy and sardine. The selected spawning habitats of the two species with respect to different environmental variables are presented. The selection of spawning habitat is based on quotient curves that reflect the consistent spawning behavior of each species with respect to a particular environmental variable over time, but deviations are also mentioned.

Histograms illustrating differences between anchovy and sardine spawning within various environmental variable ranges are indicated. Only two diagrams are shown (current speed and sea surface temperature) (Fig. 4.1). The histograms were constructed using the percentage frequency of occurrence for the eggs of each species within different environmental variable categories based on those that have shown differences between anchovy and sardine spawning.

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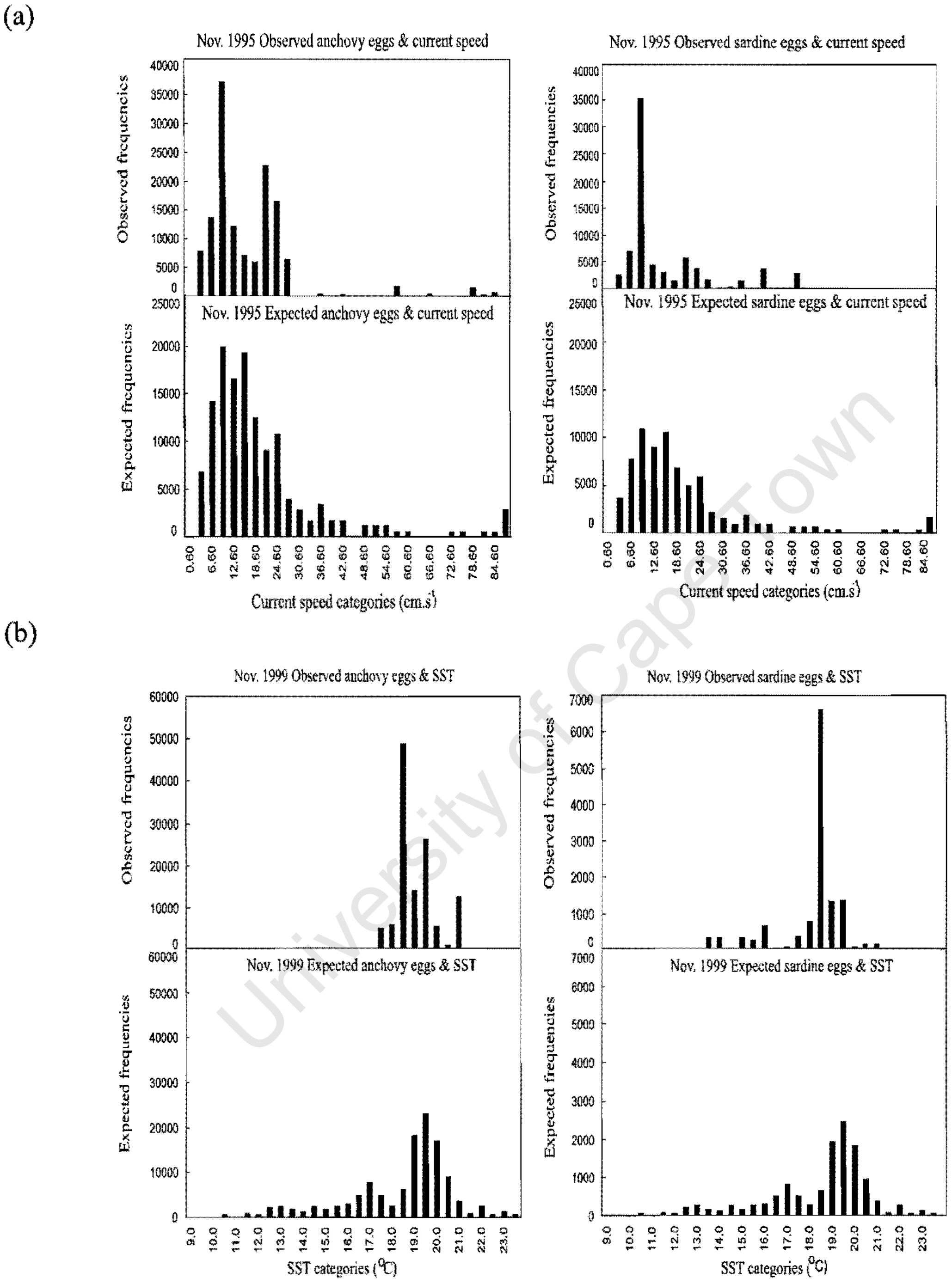

Fig 4.1: Annual surveys: Histograms displaying observed anchovy and sardine egg frequencies, and those expected if no habitat selection occurred, (a) for current speed and (b) sea surface temperature (SST)

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The observed differences in spawning habitats between the two species were confirmed statistically at a 5% level of significance, using a Kolmogorov-Smirnov goodness of fit test (Zar 1999) (Table 4.1). The greatest differences were obtained in spawning habitats characterized by sea surface temperature (SST), current speed, wind speed and depth.

Table 4.1: Annual surveys: Results of Kolmogorov-Smirnov goodness of fit to test the null hypothesis: anchovy and sardine spawn randomly with respect to a particular environmental variable.

Calculated D_i (max[max D_i), (max D_i)] and critical $D = (|\text{rel } F_{i-1} - \text{rel } \hat{F}_i|)$ values for anchovy and sardine are displayed to describe significant differences between egg frequency distributions of each species and the 4 environmental variables, the number of observations (n) and levels of significance (p) are displayed.

Environmental variable	D_i		D critical	n	p
	Anchovy	Sardine			
Current speed	0.145	0.302	0.084	262	<0.05
SST	0.293	0.390	0.078	297	<0.05
Wind speed	0.104	0.384	0.075	327	<0.05
Water depth	0.253	0.932	0.075	297	<0.05

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The selected spawning habitats by both anchovy and sardine indicated little variability with respect to SST throughout the time series. That is, sardine spawning was always associated with cooler waters than that of anchovy (Fig. 4.2 a), which is the opposite of what was found in Chapter 3. The first occurrence of sardine spawning started when SST values rose above 12°C and stopped at temperatures beyond 21.5°C (Fig. 4.2 a).

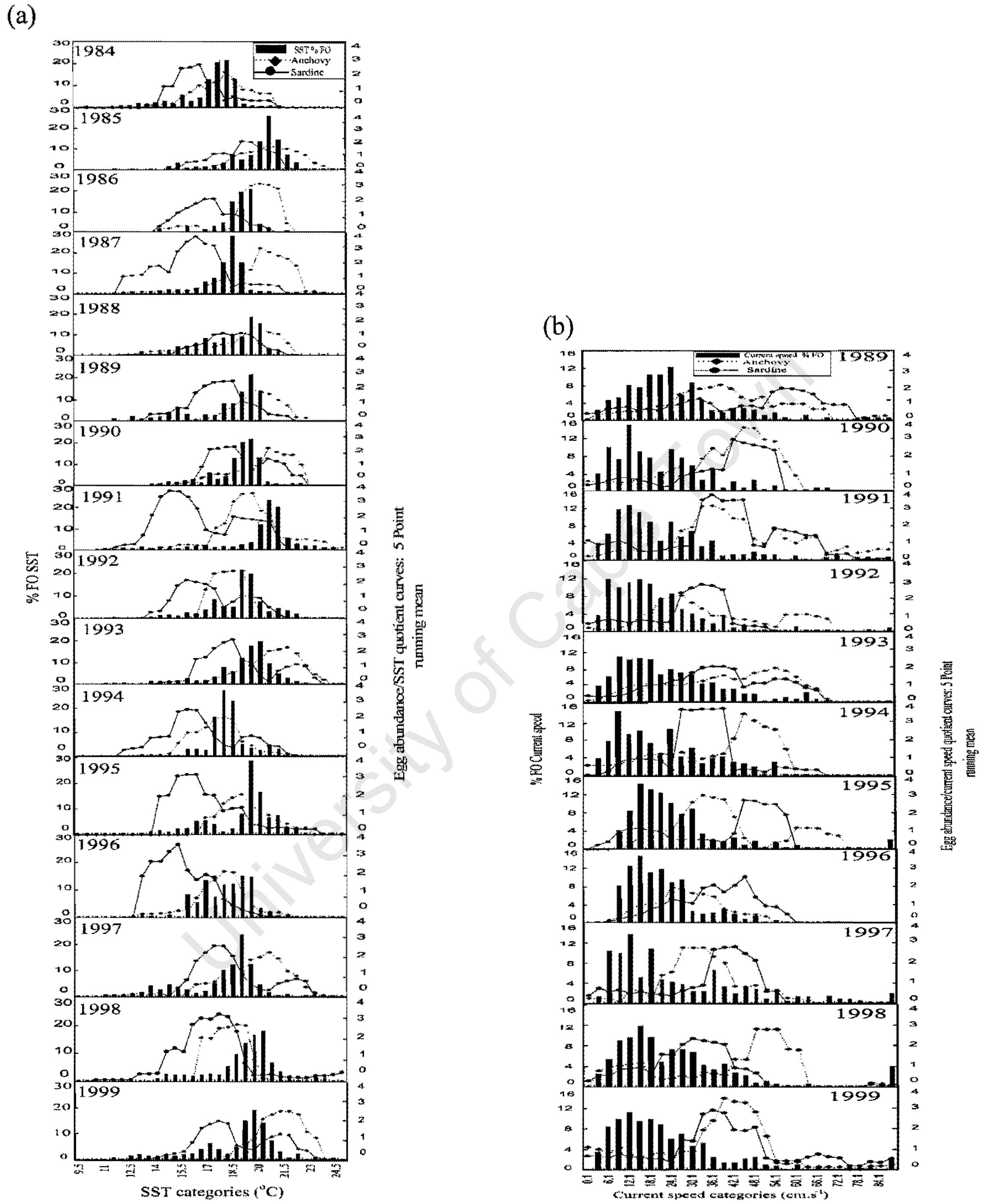

Fig. 4.2: Annual surveys: Frequency distributions (histograms) of environmental variables and egg abundance / environmental variable quotient curves (the 5-point running means are shown) for anchovy (dotted lines) and sardine (continuous lines) eggs and selected environmental variables used in this analysis, (a for SST 1984-1999 and b for current speed 1989-1999) during November spawner biomass surveys.

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Anchovy eggs were found at 16-23°C. A very wide separation in thermal conditions of spawning for the two species was observed in 1987. During this period, sardine appeared to spawn at 13-17°C, whereas anchovy spawned at 18-22°C waters. During parts of the time-series, anchovy and sardine appeared to spawn over a very narrow SST range (1985 and 1998). The sardine spawning behavior with respect to SST has been described by double peaks since 1990, whereas those of anchovy were narrow with respect to SST. Therefore, anchovy spawning is associated with warmer waters than sardine (Fig. 4.2 a).

Although a lot of variability was observed with respect to current speed, anchovy spawning appeared to be associated with weaker currents than that of sardine (Fig. 4.2 b), and at the same time anchovy spawning was associated with stronger currents than sardine in some years (1994 and 1998). The occurrence of anchovy eggs started at current speeds of 24 and 36 $cm.s^{-1}$, whilst sardine appeared to spawn at currents flowing between 36 and 72 $cm.s^{-1}$. Some overlaps and wide spawning of the two species were also observed and a very narrow and completely overlapping spawning environment was observed in 1999. The current strength tolerance of anchovy and sardine appeared to be very wide, displayed by double peaks between 1993 and 1995 (Fig. 4.2 b). This suggests that current speed changes through time and space in November, i.e. is highly variable.

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Anchovy and sardine spawning was more or less consistent over the years in relation to mixed layer depth, although anchovy spawning appeared to be associated with deeper-mixed layers than sardine on occasion (Fig. 4.3 a). There were periods (1990, 1993 and 1997) where anchovy spawning appeared to take place in shallow mixed-layers (9- 42 m), and the same applied to sardine in 1992, 1995 and 1996. Sardine spawning was not only associated with shallow mixed-layers, but also with deep ones at a range of 36-54 m in 1990, 1993 and 1997. Anchovy spawning appeared to occur at a wider range of mixed-layers in 1994 & 1998 (18-54 m) and being represented by two peaks in 1998 (Fig. 4.3 a). Therefore, anchovy and sardine spawning with respect to mixed layer-depth appeared to be very variable.

Between 1991 and 1994, anchovy spawned mainly in areas of low winds (9-23 knots), whereas peak sardine spawning habitat occurred at the range of 14-32 knots (Fig. 4.3 b). From 1996-1999, anchovy spawning shifted towards stronger winds than that of sardine. A continuous overlap in spawning of the two species with respect to winds was observed in 1995, whereas they tend to be widely separated in 1999 (Fig. 4.3 b).

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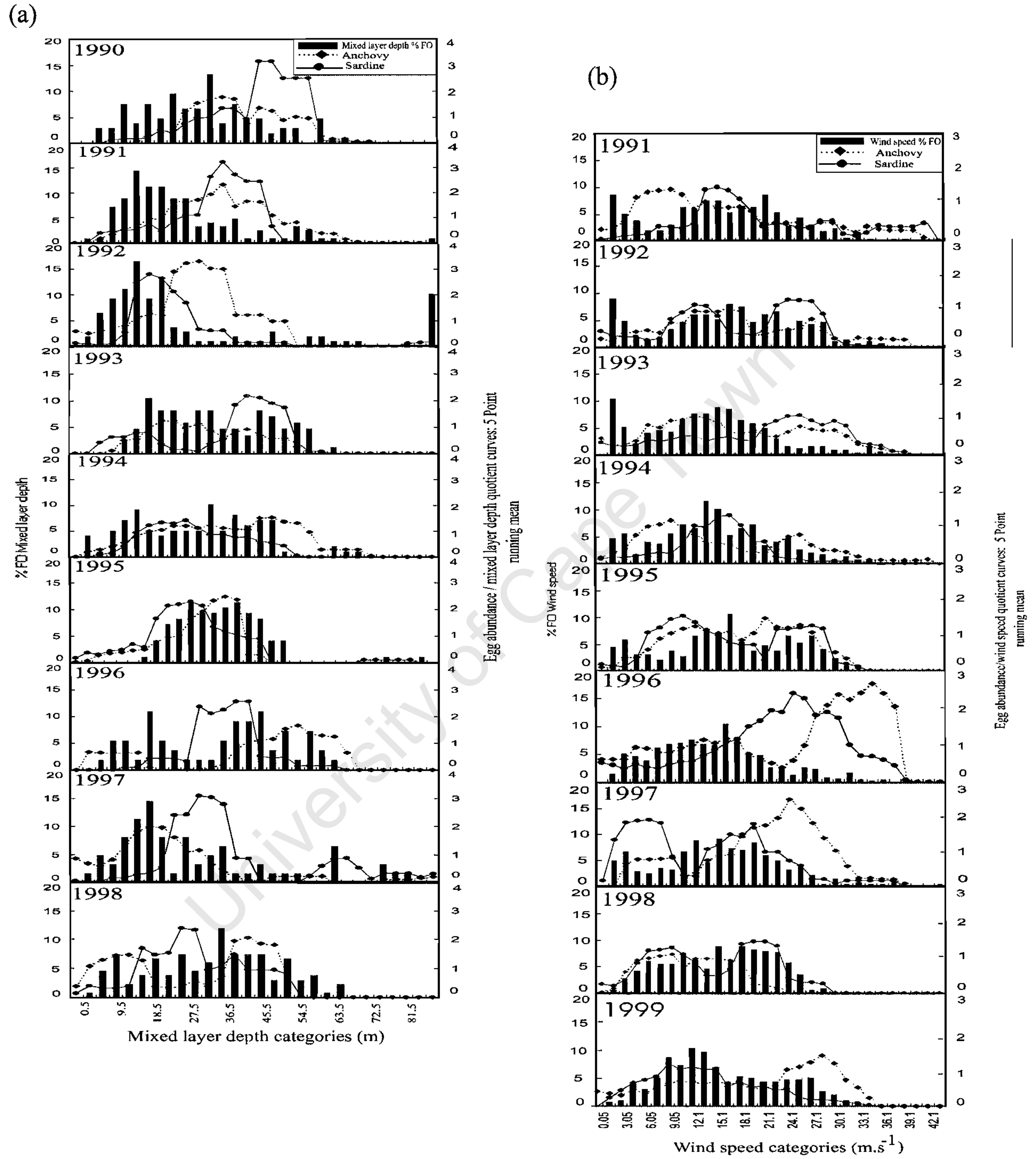

Fig. 4.3: Annual surveys: Frequency distributions (histograms) of environmental variables and egg abundance / environmental variable quotient curves (the 5-point running means are shown) for anchovy (dotted lines) and sardine (continuous lines) eggs and selected environmental variables used in this analysis, (a for mixed layer-depth 1990-1998 and b for wind speed 1991-1999) during November spawner biomass surveys.

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4.3: *Overlay analysis: Spatial spawning predictions based on spawner biomass surveys*

Maps indicating the possibility of predicting anchovy and sardine spawning throughout the time series were generated on a yearly basis and the ones presented are those that indicated a consistent spawning pattern for each species throughout the time series. Anchovy egg distribution in terms of SST was not predicted inshore along the West Coast (WC) and South West Coast (SWC), but it was indicated all over the Agulhas Bank (4.4 a). In contrast, sardine eggs were predicted to be found along the midshelf of the WC and SWC, with some patches all over the Agulhas Bank, (Fig. 4.4 b). In terms of current speed, sardine eggs were likely to occur everywhere within all strata, whereas those of anchovy were more likely on the Agulhas Bank, and to a lesser extent on the WC (Fig. 4.4 c - d). Anchovy spawning with reference to eggs occurrence was more likely than sardine to be successful on the WC, SWC and Central Agulhas Bank (CAB) in terms of wind speed whilst sardine spawning probability increased in most parts of the WC and patchily along the WAB and CAB (Fig. 4.4 e - f).

In terms of water depth, a very high probability of anchovy eggs to be found was indicated all over the Agulhas Bank and deeper shelf waters, and in the midshelf along the SWC and WC. The probability of finding sardine eggs was high in midshelf and offshore waters of the WC and SWC (Fig. 4.4 g - h), and was even higher along the southern tip of the Agulhas Bank. Optimum mixed layers in association with good probability of anchovy spawning were found over the WC, SWC, WAB and partly on the CAB (Fig. 4.4 g & h).

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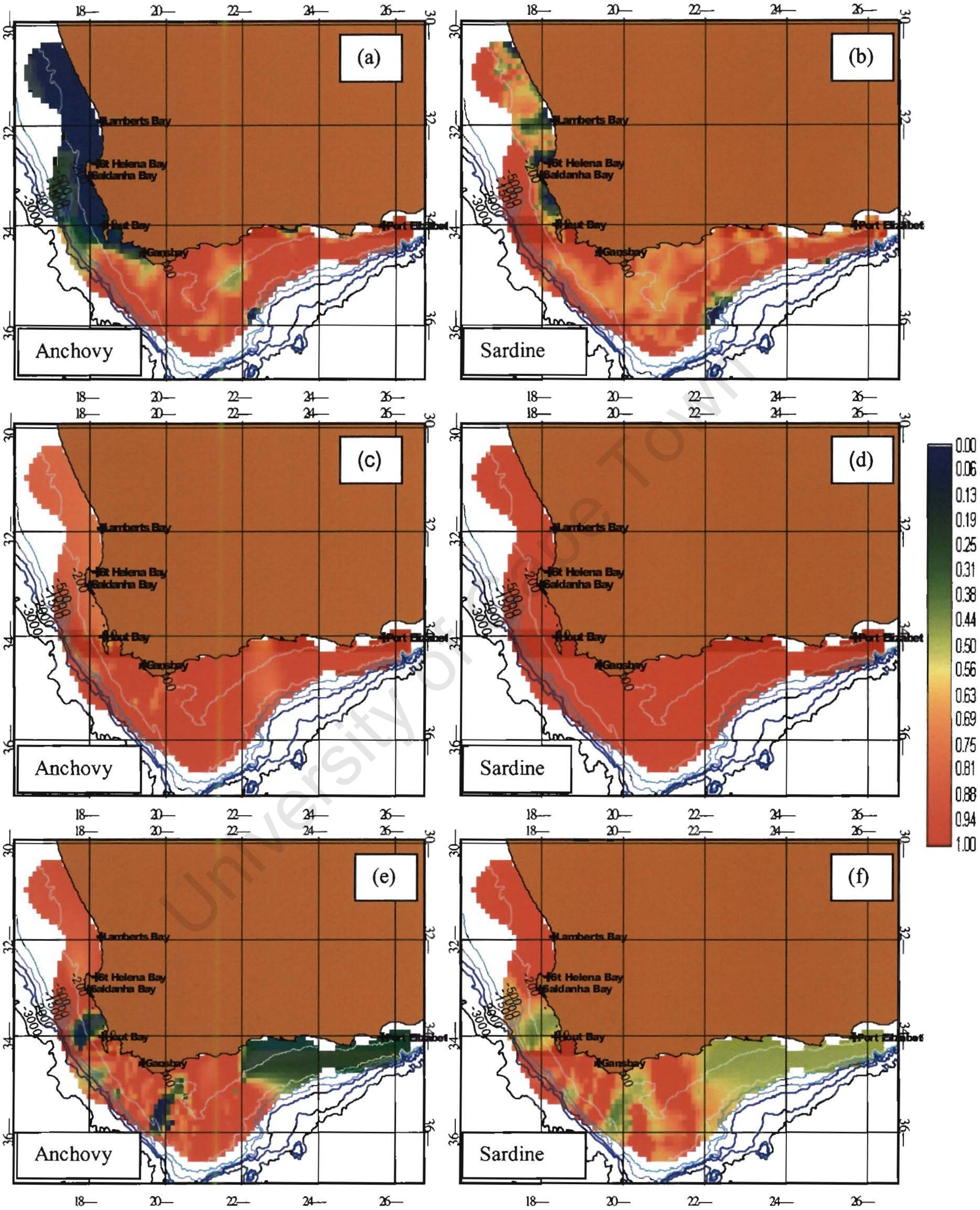

Fig. 4.4: Annual surveys: Results of the overlay analysis showing spawning for anchovy and sardine estimated from SST (a - b), wind speed (c - d) and current speed (e - f) data, combined with eggs distribution data

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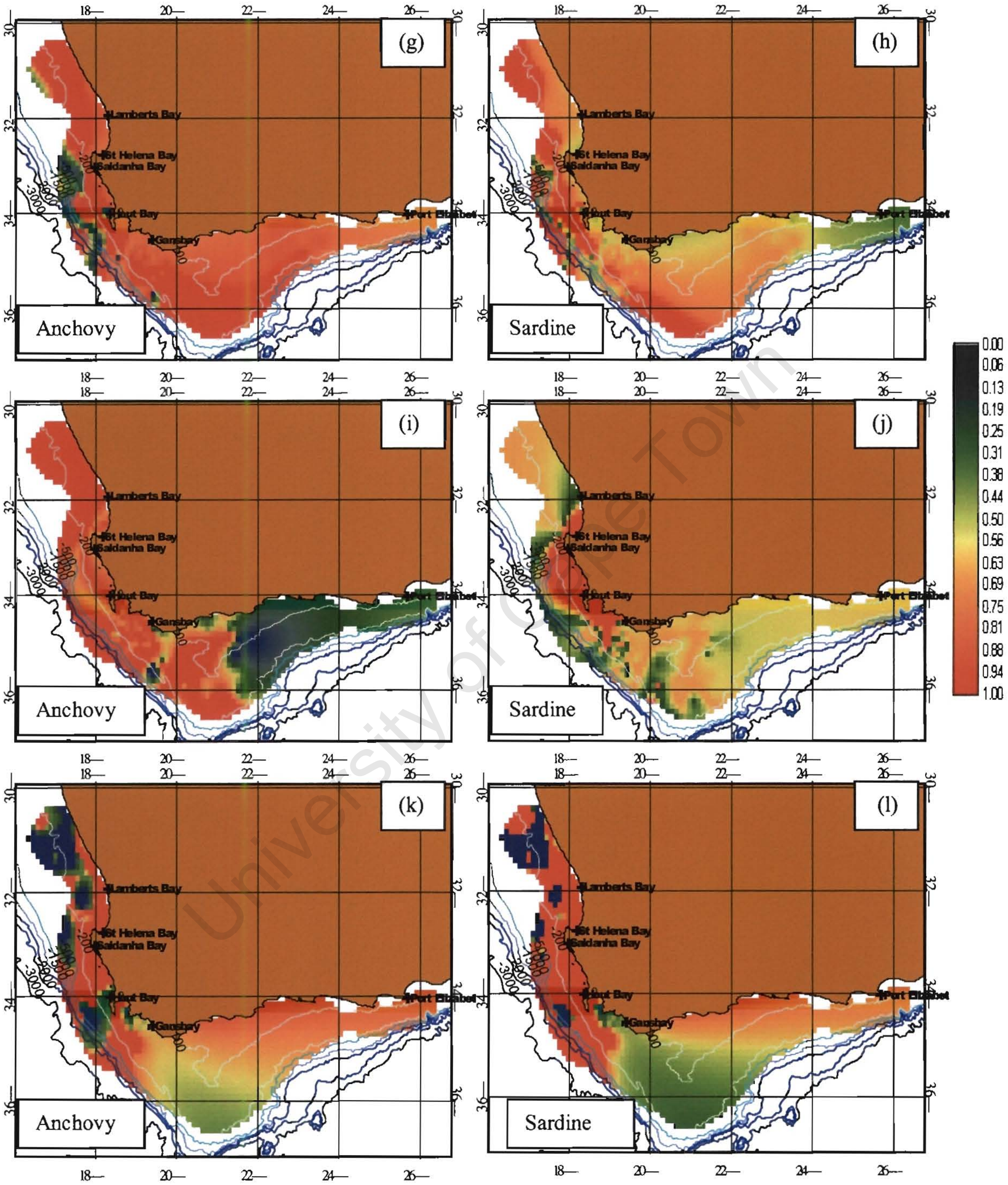

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Fig. 4.4: Annual surveys: Results of the overlay analysis showing spawning for anchovy and sardine estimated from depth (g - h), mixed layer depth (i - j) and zooplankton biomass (k - l) data, combined with egg distribution data

On the other hand inshore waters on the WC and SWC showed a high probability of sardine spawning with respect to mixed layer depth (Fig. 4.4 i & j). With respect to zooplankton biomass, anchovy and sardine spawning probability was low over the Agulhas Bank except for the western half of the WAB, and even lower offshore in this region. There is a good possibility that anchovy and sardine spawning would be expected in some parts of the WC, SWC and WAB. Anchovy and sardine spawning was not predicted in some areas of the WC and SWC (Fig. 4.4 k & l).

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A multivariate probability map indicated that the probability of finding anchovy eggs as a proxy of spawning was much reduced on the WC and EC, whereas increased on the WAB and to the lesser extent on the CAB (Fig. 4.5 a). The realised spawning habitat for anchovy with respect to SST, wind speed, phytoplankton biomass and depth was more localised and confined to the smaller area. This can be associated with the great influence of SST due to the fact that it was given a high priority during this analysis. In addition, SST happened to be the most favourable variable to indicate significant differences between anchovy and sardine spawning with all other analyses. Sardine eggs were most likely found in small continuous patches in midshelf waters of the entire WC and WAB, and less likely occurred on the SC and EC (Fig. 4.5 b). This indicates that sardine spawning habitat predicted from these four environmental variables can be much wider compared to that of anchovy, with SST, wind speed and depth seemed to have played a big role.

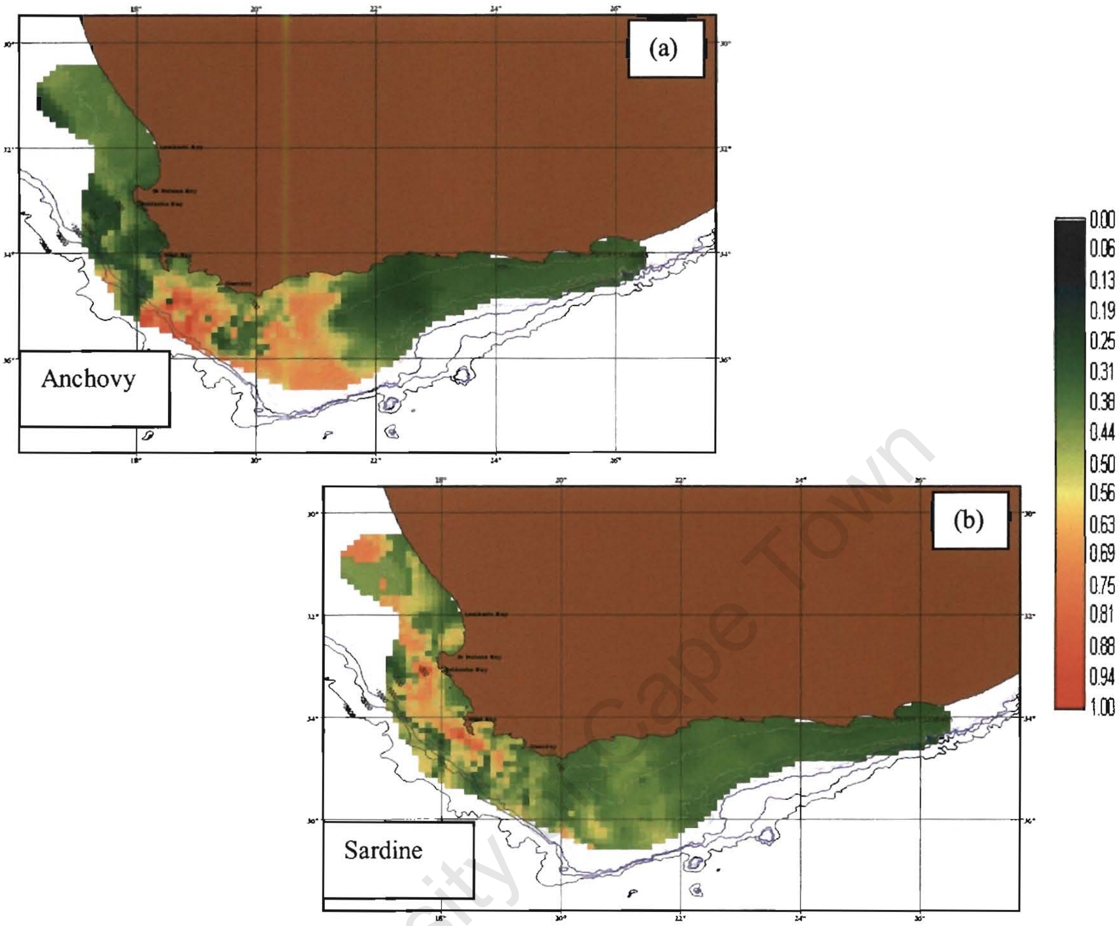

Fig. 4.5: Annual surveys: Results of the overlay analysis (multivariate) showing relative spawning for (a) anchovy and (b) sardine estimated from SST, depth, wind speed and phytoplankton biomass data from the quotient curves

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4.4: Coinertia analysis: Relationships between eggs and environmental variables

This section illustrates how the environmental variables were related to eggs of anchovy and sardine; and how these relationships changed between and within years. This analysis was only performed on the data between Nov. 1989-1999 due to many missing data for earlier years. These results are presented by considering the consistent relationship between eggs of the two species, and each environmental variable, and the summary of overall results was constructed and presented in Fig 4.6 for simplicity.

Further results on a yearly basis are given in Appendix C. All the relationships with respect to each environmental variable are presented, but much attention is given to those that appear to be stronger towards one species over another. Although the relationships between eggs of the two species and SST were positive (Fig 4.6), anchovy eggs were even more strongly positively associated with SST for several times between 1989-1998 than sardine eggs (Appendix C).

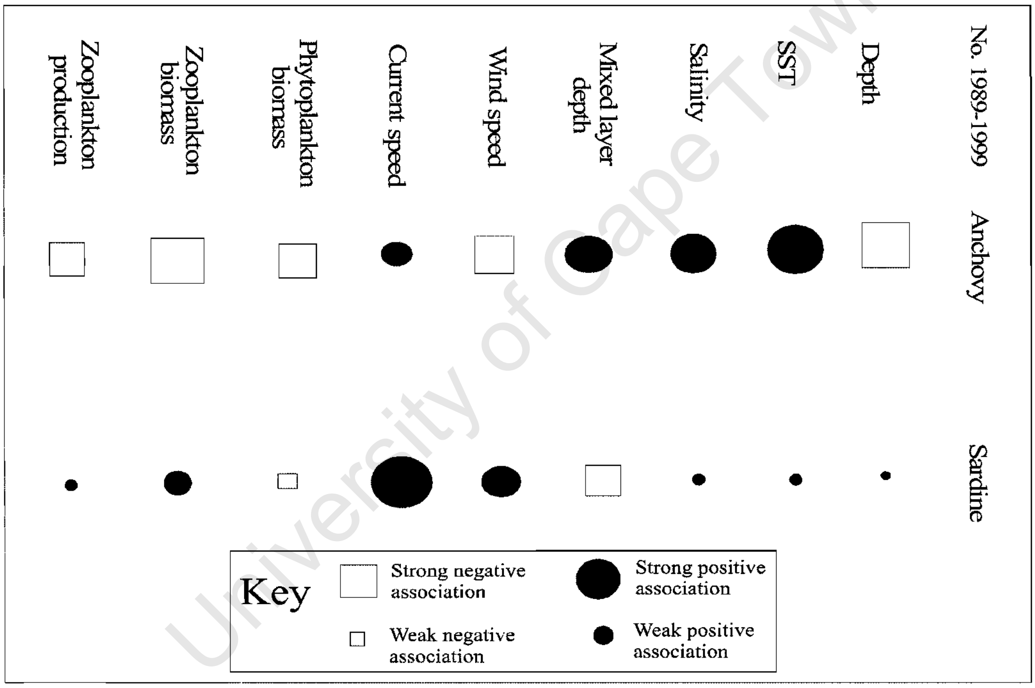

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Fig. 4.6: Annual surveys: Results of multivariate coinertia analysis illustrating linear relationships between the environmental variables and eggs of anchovy and sardine

This suggests that the higher the temperatures, the greater the abundance of anchovy eggs. Anchovy eggs were strongly negatively associated with depth, whilst sardine eggs showed a weak positive association (Fig. 4.6). The exception was observed in 1992 and 1999 where the eggs of anchovy and sardine were weakly positively associated with water depth (Appendix C). This indicates that unlike sardine, adult anchovy do not inhabit deep waters, and so they spawn eggs at the same depth of distribution. With respect to the distribution of salinity, anchovy eggs were more strongly positively associated with this environmental variable than were sardine eggs over most of the time-series (Nov 1989-1999) (Fig. 4.6). This indicates that one was most likely to get an abundance of anchovy eggs in more saline waters. In Nov. 1996 a strong positive association was observed between sardine eggs and this variable (Appendix C). There was a strong negative association between anchovy eggs and wind speed (Fig. 4.6), except in Nov. 1995 and 1999 where eggs of anchovy were strongly positively associated with this variable (Appendix C). Sardine eggs were strongly positively associated with wind speed between 1995 and 1999 (Appendix C). There was generally a strong positive association between anchovy eggs and mixed layer depth than sardine eggs and a moderate negative association for anchovy eggs in 1996 (Appendix C). This suggests that the deeper the mixed layer becomes, the more anchovy eggs are found.

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Sardine eggs were more strongly positively associated with current speed than anchovy eggs (Fig. 4.6), indicating that adult sardine tend to spawn in areas where the currents are more stronger (Appendix C). One was likely to find anchovy eggs occurring in a reduced phytoplankton biomass, as their eggs were frequently negatively correlated with this variable (Fig. 4.6). Anchovy eggs were also strongly negatively associated with phytoplankton biomass over most part of the time series, except in 1996 when a positive association was observed (Appendix C). Zooplankton biomass was strongly negatively associated with anchovy eggs for part of the time series, 1989, 1990, 1992, 1993, and 1994, whereas it was strongly positively associated with sardine eggs in 1991, 1996, 1997, 1998 and 1999 (Appendix C). This indicates that there was a consistent strongly negative relationship between eggs of the anchovy and zooplankton biomass during the early part of the time series, whereas sardine eggs were strongly positively associated with this variable at a later period (Fig. 4.6). This indicates that, where zooplankton biomass was greater, there were few anchovy eggs and where there was more zooplankton biomass, sardine eggs were found. Eggs of anchovy were found strongly negatively associated with zooplankton production than sardine eggs during most instances, except in 1995, 1996 and 1998 where the eggs of this species were strongly positively associated with this variable (Appendix C).

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4.5: Relationships among the environmental variables

Results of cluster analysis indicate that the water masses during spawner biomass surveys had two distinct groups. One was for biological variables (zooplankton and phytoplankton biomass, and zooplankton production interestingly joined by mixed layer depth) and another one for physical variables was formed by current speed, wind speed, salinity, SST, and depth were clustered together (Fig. 4.7). It is also difficult to interpret the indication that physical variables were clustered separate from the biological ones at different sampled stations during annual surveys as it is the case with monthly surveys.

This may suggest a time-lag between these variables in a sense that the availability of biological variables depends on the period for the water to stabilize after the physical processes like upwelling have taken place.

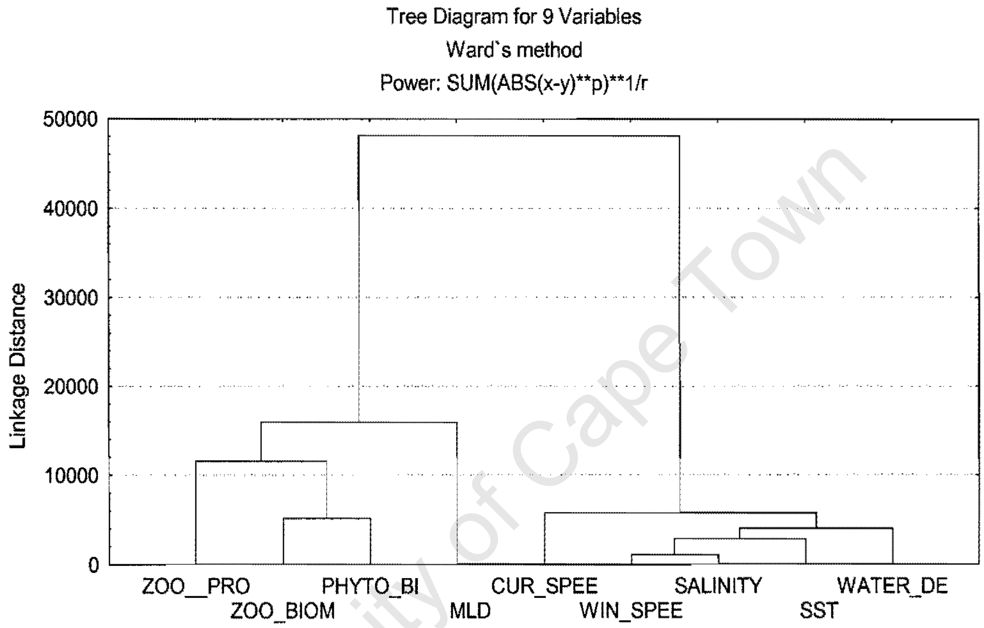

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Fig. 4.7: Results of cluster analysis showing the classification of environmental variable in ranked order during SARP surveys, where p and r are user-defined parameters, p controls the progressive weight that is placed on differences on individual dimensions and r controls the progressive weight that is placed on larger differences between variables. Abbreviations on the x-axis are as follows: zoo_ pro = zooplankton production, zoo_ biom = zooplankton biomass, phyto_ bi = phytoplankton biomass, mld = mixed layer depth, cur_ spee = current speed, win_ spee = wind speed, SST = sea surface temperature and water_ de = water depth

The results presented above indicate that the spawning habitat of anchovy is different from that of sardine, and that they change with space and time. The spawning habitat of the two species appeared to differ with respect to SST, current speed, mixed layer depth and wind speed throughout time. Discussions on strong points about the characteristics of realised spawning habitats of anchovy and sardine are discussed; and together with conclusions are in Chapter 5.

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Chapter 5:

Discussion and conclusions

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Data on the abundance and distribution of anchovy and sardine eggs collected during monthly Sardine and Anchovy Recruitment Programme (SARP) surveys between August 1993/March 1994 and September 1994/March 1995 and annual spawner biomass surveys over 16 years (1984-1999), together with the environmental variables measured at stations where egg samples were collected, were used to characterize and compare the spawning habitats of the two species. The SARP surveys were spatially limited but temporally extensive and covered the peak spawning seasons of both anchovy and sardine. In contrast the November surveys are temporally limited, and only coincide with the assumed peak spawning season of anchovy, but are spatially extensive and cover 16 years data.

The spawning habitats selected by anchovy and sardine were identified by constructing quotient curves derived from egg abundance data and individual environmental variables. The probability of spawning by each species with reference to the distribution of environmental variables measured during surveys was examined using overlay operation analysis. Relationships between eggs of the two species and the environmental variables were verified using a multivariate coinertia analysis. The way in which the environmental variables were related among themselves was examined through cluster analysis.

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5.1: Spawning habitat selection

The "univariate quotient rule" analysis (Van der Lingen *et al.* 2001) successfully identified and characterized anchovy and sardine spawning habitat. Sea surface temperature (SST), wind speed, current speed, mixed layer depth and zooplankton biomass and production were found to be very important in distinguishing between spawning habitats of the two species.

5.1.1: Characterizing sardine spawning habitat

The SARP data indicated that sardine spawned in waters with warm temperatures (19-22°C), strong wind (21-30 knots) and low (19-31 $cm.s^{-1}$) and high (61-73 $cm.s^{-1}$) current speeds, and low (0.6-0.8 g dry $wt.m^{-2}$) and high zooplankton biomass (2-3 g dry $wt.m^{-2}$) (Fig. 3.2 a-b & 3.3 a-b). Sardine, therefore appear to spawn in relatively unstable environments influenced by strong winds and currents.

The data obtained from November spawner biomass surveys indicated that sardine spawning habitat during this part of the summer season was characterized by cooler waters (12-21.5°C) compared to anchovy (16-23°C), which are believed to be influenced by strong currents and winds. From spawner biomass survey data, sardine spawning habitat appeared to be represented by double peaks in the quotient curves with respect to SST and current speed. These results, together with those from the SARP data indicate that sardine select their spawning habitats over a broad range of environmental variables. This suggest that they are fairly unspecific with respect to spawning habitat

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selection. From the results it appears that sardine spawn over a wide range of environmental variables may be explained by the patchy distribution of their eggs, which have been found in previous studies. Fowler (1998) reported that sardine eggs were never found predominantly and constantly occupying a defined area. This indicates that the sardine spawning strategy is flexible and is capable of taking advantage of wide ranges of environmental variables that will support their spawning success.

Interestingly, the bimodal peaks representing sardine selected spawning habitat with reference to the distribution of some environmental variables have never attained the same magnitude, there always being a minor and a major peak. Another factor that might be considered in spawning habitat expansion is the population size. The spatial distribution of the Japanese sardine (*Sardinops melanostictus*) contracts with decreasing population and expands when the population increases (Watanabe *et al.* 1996). A similar pattern has been observed for the Californian sardine; this stock also has an extended spawning range with respect to SST, and it was noticed that the two peaks in sardine spawning activity occur under totally different thermal conditions (Alheit 1989). This author reported that the secondary peak could become the major peak if unfavorable conditions persist.

The relationship between SST effects in sardine spawning with regard to wind intensity is indicated by the high probability of spawning in mid-shelf and towards the shelf-edge along the West Coast (WC) (Fig. 3.4 a - b), which was predicted according to SST

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distributions during SARP surveys. The fact that sardine spawning was never predicted inshore along the WC during SARP study is a result of the wind-driven upwelling being more stronger inshore and resulting in cold waters. On that note, sardine spawning had a moderate probability of occurring throughout the WC during the November surveys. This gives a clear indication that sardine can shift towards offshore areas of the WC and South West Coast (SWC) during November with respect to SST.

A similar study comparing spawning habitats of anchovy and sardine was conducted using November spawner biomass survey data from 1984-1999, but using aggregated quotient rule analysis (van der Lingen *et al.* 2001). In that study the association between sardine and cool waters, and anchovy and warm waters was evident, and the major peak of sardine eggs occurred between 15.5-17.5°C. The results from the November data analyzed in the present study identified the major peak between 15.5-18.5°C. The spawning range of sardine during the SARP study reflected the association of sardine with warm water, and is similar to findings of studies conducted by Richardson (1998). The wide spawning SST range for the southern Benguela sardine happened to be similar to that of California sardine in that peak California sardine spawning was associated with cool waters (15°C) but occurs over a range of 13.5-25°C (Lluch-Belda *et al.* 1991).

Off California, Lluch-Belda *et al.* (1991) regarded both SST and upwelling as important in determining the time and location of sardine spawning. The gap between the two spawning peaks corresponds to intermediate upwelling values and a temperature range

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between 15 and 18°C (Lluch-Belda *et al.* 1991). King (1977) reported that the two peaks of spawning of sardine in South West African (Namibian) waters would appear separated on the basis of time and locality, based on successful full-term incubation of blastodisc eggs that was achieved at temperatures at 11-22°C. In Peru, SST seems to be an important factor influencing the annual fecundity of sardine in various ways (Blaxter & Hunter 1982). Increased temperatures increase growth rates and could also potentially increase fecundity as larger sardine females have higher batch fecundity and a longer spawning season. Evidence of the influence of SST on the Namibian sardine was also provided by laboratory studies (King 1977), and it was reported that sardine egg survival was maximal within ranges of 16-21°C, and successful development was achieved at 13-22 °C. Eggs that were kept at temperatures beyond this range did not develop normally and this reduced their survival considerably (King 1977).

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The suggestion that sardine spawning was influenced by strong winds and currents in both surveys indicates the association of sardine spawning with an unstable water masses. Strong winds that are assumed to influence sardine spawning occurred along the WC and SWC during the SARP surveys (Fig. 3.4 c - d), whereas strong winds occurred along the WC during November surveys (Fig. 4.4 c - d). As winds are considered to be the main driving force of surface currents, this environmental variable is also regarded (Laevastu 1993) as directly or indirectly the main cause of temperature fluctuations. Strong winds have a positive impact in terms of mixing the water column, driving strong upwelling and promoting a high primary production leading to increased phytoplankton biomass for feeding of adult spawners (Mitchell-Innes *et al.* 1999).

5.1.2: Characterizing anchovy spawning habitat

The data presented from SARP and spawner biomass surveys indicate that anchovy spawn in waters influenced by weak winds and moderate to high currents (Fig. 3.3a-b; 4.2b & 4.3b). However, different results were indicated with respect to SST, zooplankton biomass and mixed-layer depth for both surveys, with anchovy spawning habitat associated with warm waters (16-23°C) during the spawner biomass surveys (Fig. 4.2a) and cool waters (16-20°C) during SARP surveys (Fig. 3.2a). In contrast to sardine, anchovy spawning habitat was not frequently represented by more than one peak in quotient curves. Therefore, anchovy appear to be more specific than sardine when selecting their spawning areas with respect to a number of environmental variables, and can be considered to spawn in narrow areas with stable conditions in the southern Benguela upwelling ecosystem.

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Shelton & Hutchings (1989) reported that a stable environment is usually needed to allow the formation and maintenance of food aggregations. Areas with weak winds are regarded as reducing the primary productivity because they disrupt the upwelling process and the renewal of nutrients in the surface layers (Shelton & Hutchings 1989). Another stable and predictable environment for anchovy was found on the South-Eastern Bay of Biscay for *Engraulis encrasicolus* (Motos *et al.* 1996), which appeared to prefer spawning at sea surface temperatures in the range of 14-18°C. With respect to temperature, anchovy spawning habitat in the southern Benguela ecosystem was indicated by warm temperatures (19.5-23.5°C) during November surveys (Fig. 4.2a). A strong correlation between the area of anchovy spawning environment and highly stratified and thermally constant waters was reported to occur on the WAB throughout the spawning season (Shelton & Hutchings 1989). These authors stated that the warm surface layer over the Agulhas Bank in summer provides conditions that are conductive to rapid anchovy egg development. The indication that anchovy spawning with respect to SST was predicted along the Western Agulhas Bank (WAB) during the November spawner biomass surveys (Fig. 4.4 a) suggest that the spawning of this species can shift towards that region.

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The current findings corroborate previous suggestions by Richardson (1998) that anchovy spawn in water temperatures from 16-19°C. From laboratory studies, King *et al.* (1978) reported that development of anchovy eggs was optimal over a temperature range 16-18°C, which approximates the average summer temperatures in the midshelf region of the WAB. Their studies further revealed that anchovy eggs died at temperatures below 14°C, therefore the WAB may appear as the primary spawning habitat of anchovy because of the thermal stability of the region that is conducive to rapid egg development (King *et al.* 1978). It is also be possible that since November surveys coincide with peak spawning season for anchovy, anchovy inhabited warm waters such that sardine ended up spawning outside this warm range. Considering the fact that differences in spawning habitat selection with reference to SST may be associated with feeding conditions, Richardson *et al.* (1998) found that the food environment on the WAB was more stable in the 16-19°C range than the WC, and the production of large copepods was greater than in cooler waters. Thus, the area of 16-19°C water during SARP can be considered as a food-rich environment. A relatively low batch fecundity of Peruvian anchovy females less than 30g during the 1976 *El Nino* was probably related to a combined action of high temperatures and low food availability (Blaxter *et al.* 1991). The specific and narrow range of anchovy spawning confirms with similar findings with the anchovy stocks in California (Lluch-Belda *et al.* 1991). These findings together with the current ones support those of Shelton (1986), who regarded anchovy, and to a lesser extent sardine, as selecting specific environmental opportunities for spawning in order to make the best of reproductive output and survival through to recruitment.

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5.2: Comparing spawning habitats

The indication that the spawning environments of anchovy and sardine were characterized by different environmental variables shows that the spawning habitats of the two species differ spatially and temporally. In addition to significant different spawning habitats between the two species shown by the Kolmogorov-Smirnov test, a correlation could have been calculated between the quotient ratios of anchovy and sardine for all environmental variables. A strong positive correlation could have been found in cases where quotient curves for both species overlapped and a negative correlation when the curves did not overlap. This will be taken further in the publication being prepared.

During SARP, the probability of finding the two species spawning was not very distant geographically, but it was different in intensity; anchovy spawning was predicted to be more intense compared to the patchy spawning for sardine. The appearance of localized spawning grounds of anchovy and the expansion of sardine spawning areas in the southern Benguela upwelling ecosystem may be related to the size of the adult spawning population, as has been described for this region (Barange *et al.* 1999). Considering sardine and anchovy populations in the southern Benguela upwelling ecosystem, Barange *et al.* (1999) reported that anchovy spawning biomass has been fluctuating between 1990-1997, whereas sardine was steadily recovering.

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Although sardine spawning biomass has been recovering, the relationship between its spatial distribution and stock size was unclear (Barange *et al.* 1999). Also during the same period of study, the anchovy population was distributed over the Agulhas Bank, whereas peak densities of sardine spawners were close to the shore, mostly on the WAB (Barange *et al.* 1999). The indication that the anchovy spawning strategy was narrow and more selective supports the density-dependent concept in selecting spawning habitats, as has been reported for the Bay of Biscay anchovy (Motos *et al.* 1996). According to those authors, as the abundance declines in that particular environment, the spatial range also shrinks. These authors also added that narrow spawning was practically restricted to the more favorable spawning sites, which maintain minimal sustaining conditions for that anchovy population (Motos *et al.* 1996). For example, the selection of the 16-19°C temperature range may indicate that if there is an increased population of anchovy within a small spatial range, they will all compete for the most suitable conditions in that particular habitat. According to Blaxter & Hunter (1982), evidence of density-dependent effects is scarce and the large variation in stock size of clupeoid testifies to the weak density-dependence in these species. It was also noticed that biological variables were unsuccessful in indicating differences between spawning habitats of the two species during the spawner biomass surveys. This may be because of difficulty of measuring appropriate variables.

5.3: Relationships between eggs and environmental variables

The examination of relationships between eggs of the two species and environmental variables using coinertia analysis makes the assumption that fish select spawning habitats according to all the environmental variables that were used. There were stronger correlations between anchovy eggs and the environmental variables than was the case for sardine eggs. Because anchovy are more specific with regard to their selection of spawning habitat, their spawning behaviour is more affected by environmental variability than that of sardine. Therefore, anchovy spawning follows the distribution of optimal values of environmental variables.

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5.3.1: SARP surveys

Anchovy eggs were strongly positively associated with salinity and SST, and strongly negatively associated with phytoplankton biomass, zooplankton biomass and zooplankton production (Fig. 3.7). There was a strong positive association between sardine eggs and phytoplankton biomass, whereas anchovy eggs were strongly negatively associated with this variable. This gives an impression that there are differences in feeding conditions of the two species according to the areas they inhabit, with sardine being more associated with phytoplankton biomass than anchovy. Therefore sardine eggs were spawned according to feeding conditions of adults so as to benefit from their feeding conditions. This work corroborates the findings of Lluch-Belda *et al.* (1991) that sardine spawning is more strongly associated with upwelling than that of anchovy. In supporting this statement, Mitchell-Innes *et al.* (1999) reported an abundance of sardine eggs during both peak spawning seasons (September/October and February/March) on the WAB, but noted that eggs of this species were always abundant on the WC where intensive upwelling occurs. The production and abundance of phytoplankton is greater on the WC than on the WAB (Brown *et al.* 1991), and phytoplankton biomass would appear to influence sardine spawning both in terms of area and period.

Sardine spawning may increase on the WC between February/March being influenced by increased phytoplankton densities. Although the spawning pattern of South African sardine is similar to Californian sardine in terms of SST, Lluch-Belda *et al.* (1991) considered the relationship between the latter species and upwelling as controversial due

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to increased water turbulence. Sardine spawning in California as a function of upwelling indicates peak spawning intensity during moderate upwelling, suggesting that there must be some way for sardine to select appropriate upwelling conditions for spawning (Lluch-Belda *et al.* 1991). Similar findings about sardine spawning and upwelling were reported in the Galatian coast, which is the major upwelling system in Spain. The distribution of sardine (*Sardina pilchardus*) in this ecosystem was not only generally associated with areas of strongest coastal upwelling, but they also reside within these areas (Edward & Alonso-Naval 1989).

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5.3.2: Spawner biomass surveys

Anchovy eggs were strongly positively associated with SST, salinity, mixed layer depth and zooplankton production, and strongly negatively associated with water depth (Fig. 4.6). Sardine eggs were strongly positively associated with current speed and zooplankton biomass. The indication that sardine eggs were positively associated with zooplankton biomass, whereas anchovy eggs were negatively associated with this environmental variable suggest that zooplankton biomass decreased or never co-occurred with anchovy eggs, but did with eggs of sardine. According to van der Lingen *et al.* (2001) sardine eggs were more patchily distributed both in the WC and SC, and were found on the East Coast (EC) through the time-series. Adult sardine spawners might have positioned themselves on the EC during spawner biomass surveys to utilize the large copepod biomass that is known to occur in that region (Richardson 1998).

5.3.3: Comparing the two surveys

The most interesting findings are those indicating that anchovy spawning was associated with cooler waters (16-20°C) during monthly SARP surveys, but with warm waters (16-23°C) during annual spawner biomass surveys. In addition, sardine eggs were associated with warm waters (19-22°C) during monthly SARP surveys, but with cooler waters (12-21.5°C) annually. Although it is difficult to compare these results and interpret them because one survey is based on an annual time series and the other one on months. Therefore, main point revolves around the time basis and distribution of sea surface temperature during different periods. Another important point to be considered in relation to the shift in temperature between the two species and surveys is the sampling bias during both surveys, the Spawner Biomass survey having a very good spatial coverage and therefore over-sampled compared to SARP. For example, during SARP surveys much effort of sampling is put into the WC, SWC and WAB, excluding the CAB and EAB. This is based on the known fact that the Agulhas Bank, much of which is under-sampled during SARP, is generally warmer than the West Coast (Shelton & Hutchings 1990). This might therefore be the main reason why the optimum temperature for anchovy during SARP surveys was 16-20°C and 16-23°C during Spawner Biomass Surveys. An increase of 3°C for anchovy is therefore noticed during Spawner Biomass Surveys, which cover a warmer part of the environment.

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The indication that the relationship between anchovy eggs and SST and salinity remained strongly positive for both survey programs indicates that anchovy spawning was more intense at high temperatures and salinities. Most of the work previously done on effects of SST on spawning support the current findings. Lluch-Belda *et al.* (1991) confirmed the importance of SST and regarded it as affecting the metabolic rate processes such as regulating the hatching success and larval growth. Since there is a very wide range of appropriate temperatures, SST is regarded as a good spawning indicator (Lluch-Belda *et al.* 1991). Successful development of anchovy eggs and the subsequent survival of their larvae in nature are partly dependent upon their remaining within an appropriate temperature range (King *et al.* 1978).

The negative relationship between anchovy eggs and food availability (phytoplankton biomass and zooplankton biomass) during SARP and spawner biomass surveys may imply that the eggs of anchovy were not concurrently found in areas with those variables during both surveys for reasons related to the food web. These results are similar to those of the single parameter quotient analysis in which there was no difference between spawning habitats of the two species with respect to food availability during spawner biomass surveys. No figure was provided due to lack of differences between anchovy and sardine spawning ranges. It is also possible that there were very few anchovy eggs in areas where most zooplankton and phytoplankton biomass samples were collected or vice versa. The possible reduction in zooplankton may be associated with high predation

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pressure by adult spawners, since copepods form the major food source for anchovy (James 1987). Many authors provide evidence from different studies on the role played by food availability in anchovy spawning. Food limitation can lead to adult spawners resorbing their developing oocytes, a condition known as atresia, and this results in decreasing spawning frequency and a reduction or cessation of egg production for the rest of the season (Richardson *et al.* 1998). Laevastu (1993) reported that the presence of food can make a huge difference within an otherwise tolerable and featureless hydrographic area.

Blaxter *et al.* (1991) showed that anchovies can react very quickly to adverse feeding conditions and recover rapidly when again supplied with sufficient food. By looking at variables affecting zooplankton availability, for example phytoplankton biomass, Mitchell-Innes *et al.* (1999) reported that there was enough phytoplankton biomass throughout the SARP surveys to support zooplankton production and biomass, therefore there is little chance that this variable was a limiting factor. Therefore, it is possible that increased zooplankton populations started feeding on phytoplankton, increasing secondary production and supporting adult anchovy spawner biomass during the spawning season. The relationship between copepod (*Calanus*) and phytoplankton biomass was indicated by *Calanus finmarchicus* in the Gulf of St. Lawrence (Runge & de Lafontaine 1996). The life cycle of this *Calanus* species has been traditionally considered as one in which spawning is tied to periods of phytoplankton growth or diatom increase. This *Calanus* species apparently requires higher phytoplankton concentrations to achieve

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maximum egg production rates than many smaller copepod species, creating a strong foodweb link, and promoting survivorship of fish larvae (Runge & de Lafontaine 1996). The indication that the realised spawning habitat for anchovy was very small compared to that of sardine from the multicriteria evaluation is also important (Fig. 4.5a- b). SST, wind speed, phytoplankton biomass and depth were arranged in such a manner that they indicate the order of importance of each variable based on information from the quotient rule (2.3.1). The results (Fig. 3.2a & 4.2a); (Fig. 3.5a-b & 4.4a-b) strongly indicated that SST is the strongest signal in demarcating spawning habitats of anchovy and sardine (Fig 4.5 a). Depth and phytoplankton biomass may not appear very important in indicating a sharp selection of spawning habitats by the two species, possibility due to insufficient data, but they seem to have influenced the wide and patchy spawning habitat of sardine (Fig. 4.5 b). SST was the only environmental variable that indicated a very close picture to the real spawning habitat of anchovy and sardine from the probability maps (Fig. 4.4 a-b).

The overall results on characterizing the spawning habitats of anchovy and sardine in the southern Benguela upwelling ecosystem are listed in Table 5.1.

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Table 5.1: Summary table for overall results obtained from different analyses (quotient curves, overlay and coinertia) during the two survey programs, monthly SARP and annual spawner biomass surveys

Analyses	Monthly SARP surveys		Annual Spawner Biomass surveys
Optimum spawning conditions, From quotient Rule analysis	Anchovy	Cool water temperatures (16-20°C) Weak wind speeds (0.1-9.0 knots) Moderate to high current speed (31-54 cm.s^{-1}) Moderate zooplankton biomass (1.2-2.0 g dry wt.m^{-2})	Warm water temperatures (16-23°C) Moderate to low wind speed (9-23 knots) Weak current speeds (24-36 cm.s^{-1}) Variable mixed layer depth (9-42 & 18-54m)
	Sardine	Warm water temperatures (19-22°C) Strong wind speeds (21-30 knots) Low and high current speed (19-31 & 61-73 cm.s^{-1}) low and high zooplankton biomass (0.6-0.8 & 2-3 g dry wt.m^{-2})	Cooler water temperature (12-21.5°C) Moderate wind speeds (14-32 knots) Variable current speed (36-72 cm.s^{-1}) Variable mixed layer depth (36-54m)
Overlay analysis (SST, depth, wind speed & phytoplankton biomass)	Anchovy	Eggs were most likely to be found on the entire WAB, midshelf to offshore waters of the WC and SWC, this applies to both species.	High probability of finding eggs on the WAB and CAB, and low on WC, EC and SC.
	Sardine		High probability of egg occurrence on the entire midshelf of the WC and WAB ,and less on the SC and EC
Coinertia analysis	Anchovy	Strongly positively associated with: SST and salinity. Strongly negatively associated with: water column depth, phytoplankton biomass, zooplankton biomass and production	Strongly positively associated with: SST, salinity and mixed layer depth. Strongly negatively associated with water column depth, wind speed, phytoplankton biomass, zooplankton biomass and production
	Sardine	Strongly positively associated with current speed.	Strongly positively associated with current speed

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The next step is to follow the approach that was introduced by Lluch-Cota *et al.* (2001) in the Gulf of California sardine fishery. These authors derived double logistic functions relating spawning probability to SST and an upwelling index. The upwelling index was used considering the fact that weak winds result in reduced upwelling-related enrichment and weak circulation, whereas strong winds result in extremely fast dynamics and poor retention. On the other hand temperature was used because it directly affects growth rates and other specific metabolic activities. It was found that upwelling index-dependent spawning preceded the catch with variable time lags but with the best fit (linear correlation) at a time lag of 1 year, whereas there was no time lag with regard to temperature-dependent time series of spawning probability indicating poor sensitivity. Therefore, spawning was found to be better described by the upwelling index, while the SST series only provided information relating to changes in spawner distributions during extreme SST events (Lluch-Cota *et al.* 2001). This approach may be applied to the November 2000 spawner biomass survey data, which resulted in a large anchovy and sardine recruitment the following year. If the suggested approach of double logistic functions can be successfully implemented in the southern Benguela upwelling ecosystem it can be adapted to aid the monitoring and analysis of pelagic fisheries in other eastern boundary current ecosystems.

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5.4: CONCLUSIONS

1. The results suggest that anchovy and sardine spawning habitat can be characterized in terms of environmental variables through simple quotient curves, and indicate that these two species show substantial differences in selection of their spawning habitat. The quotient analysis is simple and based on single parameters, non-parametric and non-linear, unlike the multivariate coinertia analysis in which many environmental variables were assessed.

2. Sardine spawning habitat is characterized by warm water temperatures (19-22°C), strong winds (21-30 knots) and low (19-31 cm.s^{-1}) and high (61-73 cm.s^{-1}) current speeds, and low (0.6-0.8 g dry wt.m^{-2}) and high zooplankton biomass (2-3 g dry wt.m^{-2}) during two spawning seasons of SARP surveys, whereas they are characterized by cool waters (12-21.5°C), variable, but frequently strong currents (36-72 cm.s^{-1}) and moderate wind speeds (14-32 knots) during November spawner biomass surveys over 16 years.

3. Anchovy spawning habitat is characterized by cool waters (16-20°C), weak winds (0.1-9 knots) and moderate-high current (31-54 cm.s^{-1}) speeds, and average zooplankton biomass (1.2-2 g dry wt.m^{-2}) during SARP surveys, whereas they are characterized by warm waters (16-23°C), weak currents (24-36 cm.s^{-1}) and moderate- low wind (9-23 knots) speeds during spawner biomass surveys.

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4. The spawning behaviour of the two species differs with respect to SST and current speed, water column depth and mixed layer depth.

5. The spawning behavior of the two species was similar in terms of salinity and current direction, phytoplankton biomass and zooplankton production.

6. Anchovy are more specific in their selection of spawning habitats than sardine and they appear to spawn under moderate wind and current speeds.

7. Sardines are flexible in their selection of spawning habitat and they appear to spawn in turbulent environments. Their spawning habitats are described by double peaks and associated with strong winds and currents.

8. Spawning habitat characterizations may be used to predict potential spawning habitat when information on egg abundance is not available, through, for example, satellite-derived data on SST, depth, chlorophyll and wind speed. This has been partly achieved through the GIS overlay analysis (Fig. 3.6a-b & 4.5a-b). Anchovy habitat appeared to be smaller and concentrated on the WAB and to the lesser extent on the CAB, that of sardine appeared on the WC extending down to the SWC. This will be further applied on November 2002 spawner biomass survey.

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9. This study will be useful in monitoring space-time variability in the dimensions and location of the spawning habitats of these two ecologically and commercially important species.

10. Spawning habitats of anchovy and sardine differ in terms of space and various environmental variables, with anchovy being more specific than sardine in selecting their spawning habitats (see paragraphs 2, 3 above). Therefore, the null hypothesis: anchovy and sardine eggs co-occur within the same ranges of environmental variables is rejected by the results of this study.

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APPENDIX A

Environmental variables related to egg abundance data during monthly SARP surveys. For each of the environmental variables, the cruise name, date of collection, area covered and the number of samples (n) collected are given. The number of samples (n) includes pairs of eggs and environmental variables. Relationships between eggs and individual environmental variables are presented in scattergrams after each data description. Egg data was transformed $(\log_{10} x+1)$ to stabilize variances and account for zeros. SARP 10 is not included in this Appendix because it was conducted on the Norwegian vessel, Dr. Fridtjof Nansen and data were not available, see Fig. 2.1-2.2 for place names.

Environmental variable
1.Sea surface temperature (SST)

Cruise	Date	Area	n
SARP 1:	Aug. 1993	Cape Agulhas-Cape Town	17
SARP 2:	Sept. 1993	Cape Infanta-Cape Columbine	21
SARP3:	Oct. 1993	Cape Agulhas-Olifant's River:	34
SARP 4:	Nov. 1993	Cape Columbine-Port Alfred	177
SARP 5:	Dec. 1993	Cape Agulhas-Olifant's River	47
SARP 6:	Jan. 1994	Cape Agulhas-Cape Columbine	29
SARP 7:	Feb. 1994	Cape Agulhas-Olifant's River	36
SARP 8:	Mar. 1994	Cape Agulhas-Olifant's River	26
SARP 9:	Sept. 1994	Cape Ahulhas-Cape Columbine.	51
SARP 11:	Nov. 1994	North of Lambert's Bay-Port Elizabeth	170
SARP 12:	Dec. 1994	Cape Agulhas-Olifant's River	41
SARP 13:	Feb. 1995	Cape Agulhas-Cape Town	76
SARP14:	Mar. 1995	Cape Agulhas-Olifant's River	70
			Total = 708

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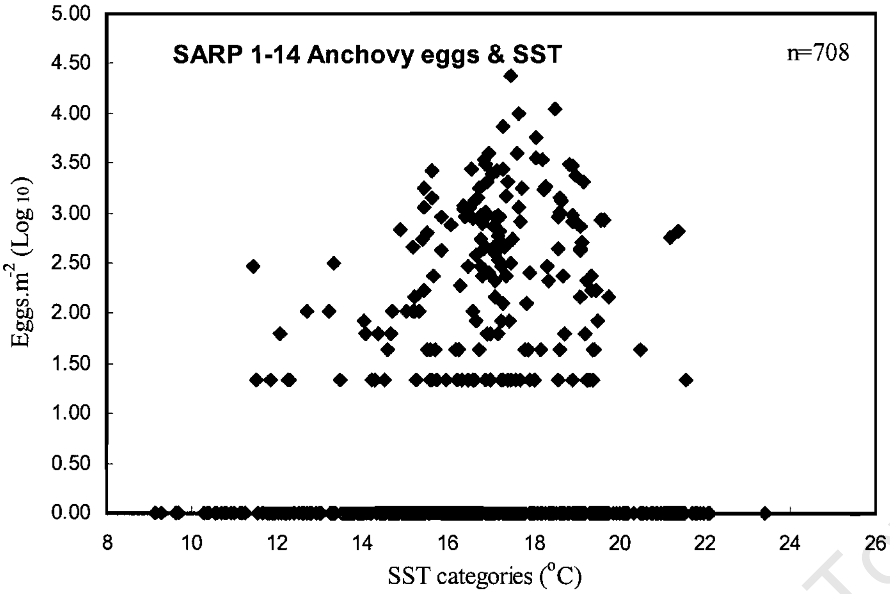

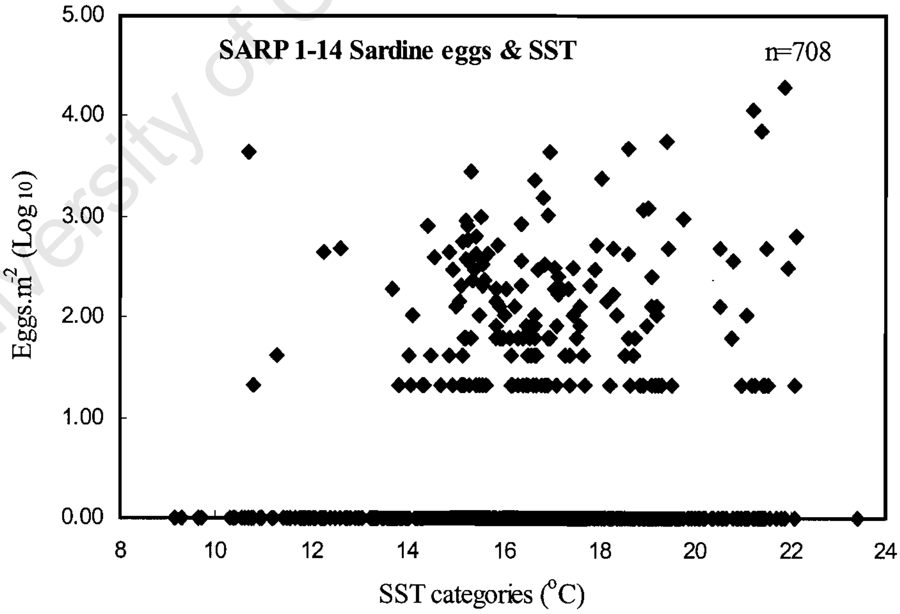

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Fig. A 1: Scattergrams showing the relationship between anchovy and sardine eggs and sea surface temperature

2. Water column depth

SARP 1	17
SARP 2	12
SARP 3	13
SARP 4	142
SARP 5	29
SARP 6	19
SARP 7	18
SARP 8	14
SARP 9	50
SARP 11	161
SARP 12	34
SARP 13	17
SARP 14	63

Total = 526

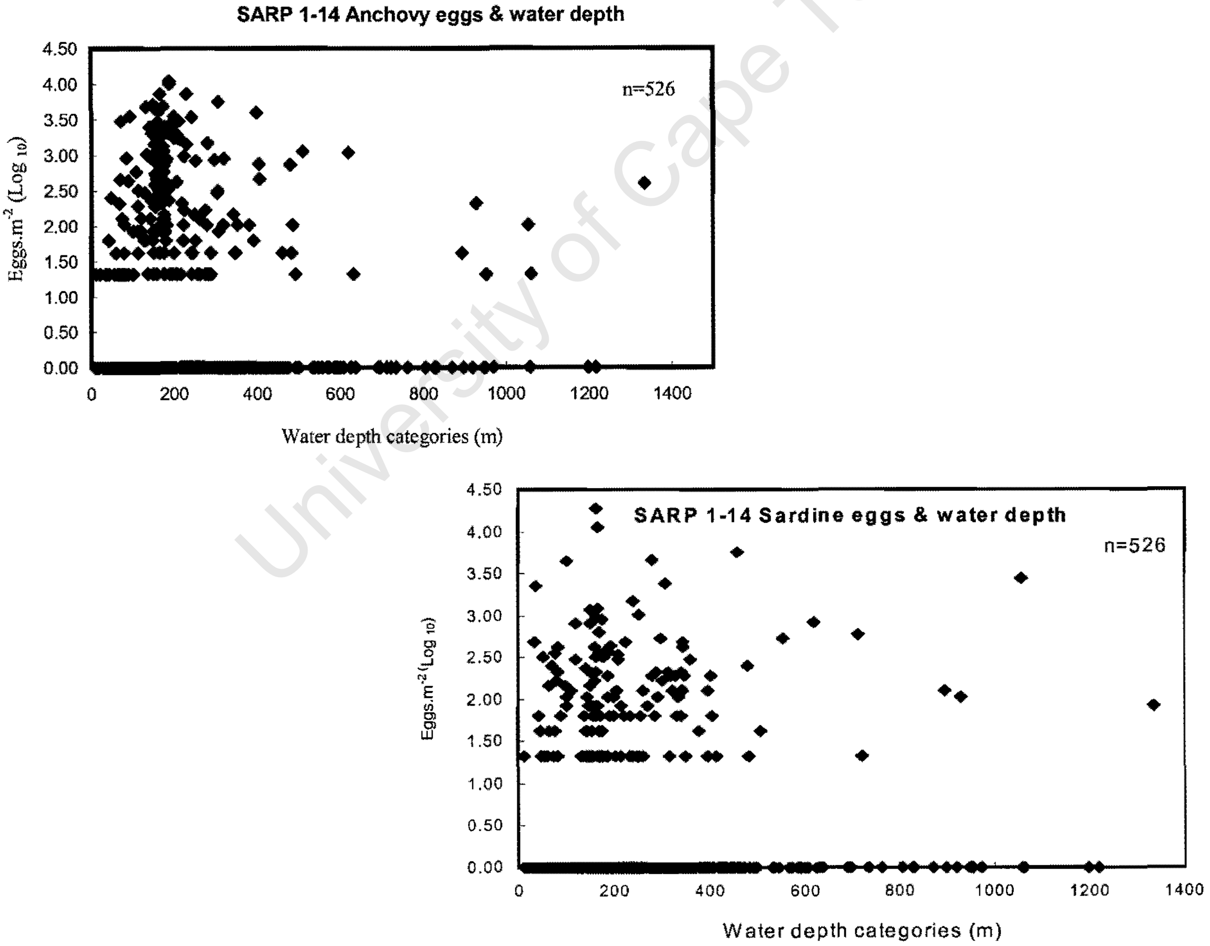

Fig. A 2: Scattergrams showing the relationship between anchovy and sardine eggs and water column depth

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3. Salinity

SARP 1	4
SARP 2	6
SARP 3	9
SARP 4	158
SARP 5	11
SARP 6	4
SARP 7	6
SARP 8	13
SARP 9	50
SARP 11	79
SARP 12	14
SARP 13	8
SARP 14	35
	Total = 362

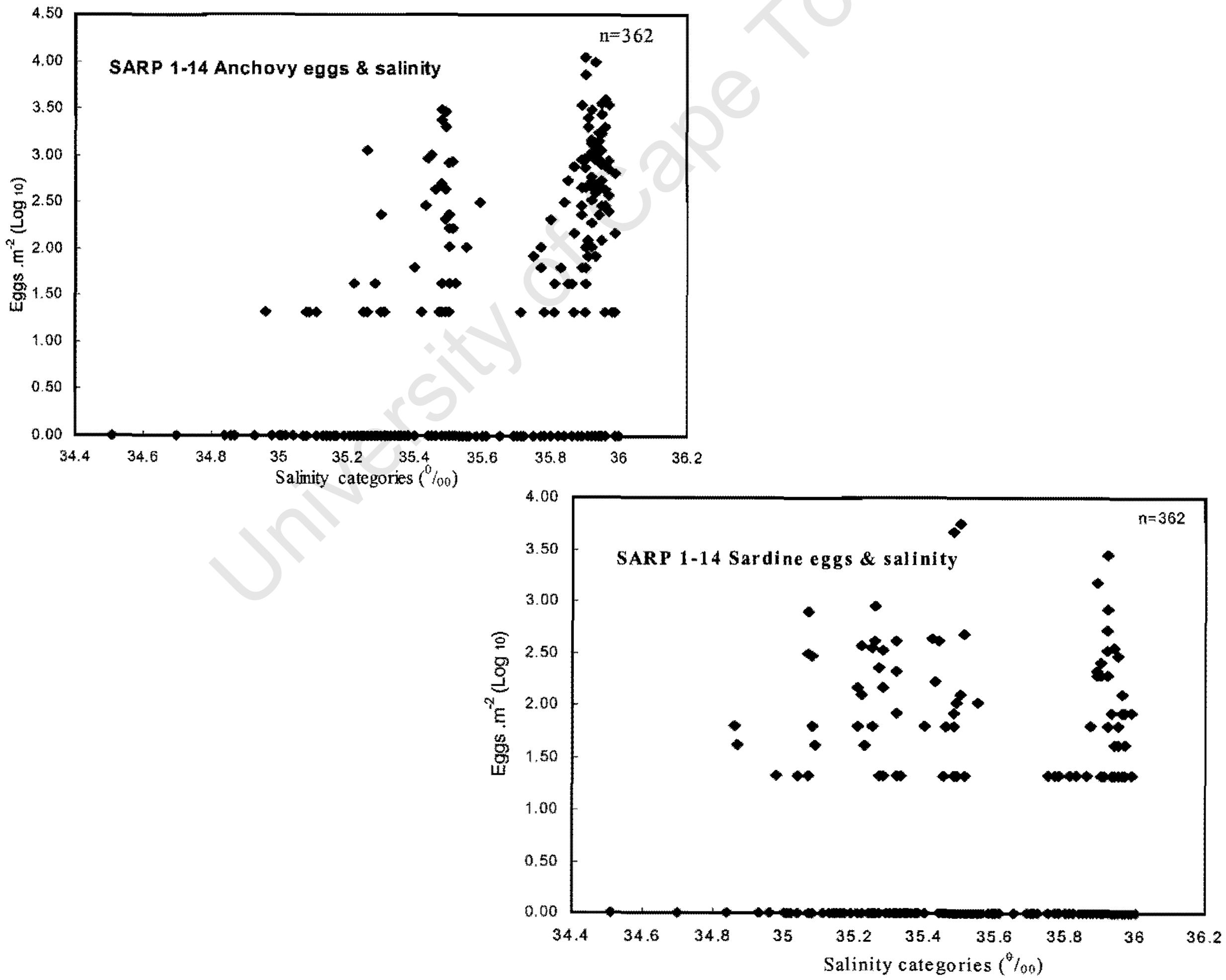

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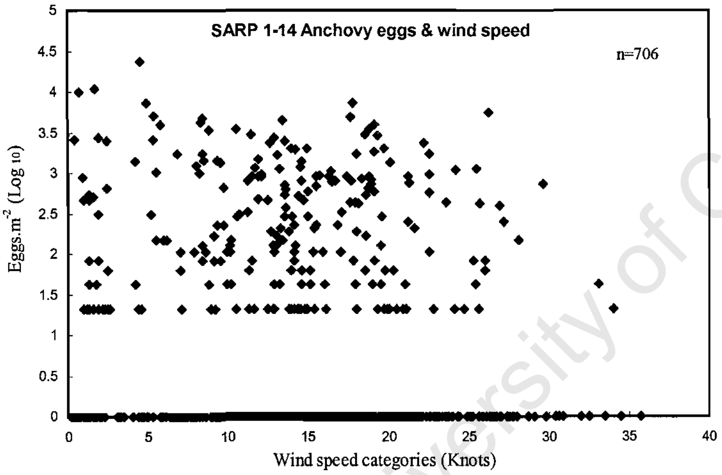
Fig. A 3: Scattergrams showing the relationship between anchovy and sardine eggs and salinity

4. Wind speed

SARP 1	17
SARP	21
SARP 3	34
SARP 4	158
SARP 5	48
SARP 6	30
SARP 7	37
SARP 8	28
SARP 9	50
SARP 11	161
SARP 12	39
SARP 13	83
SARP 14	71
	Total = 706



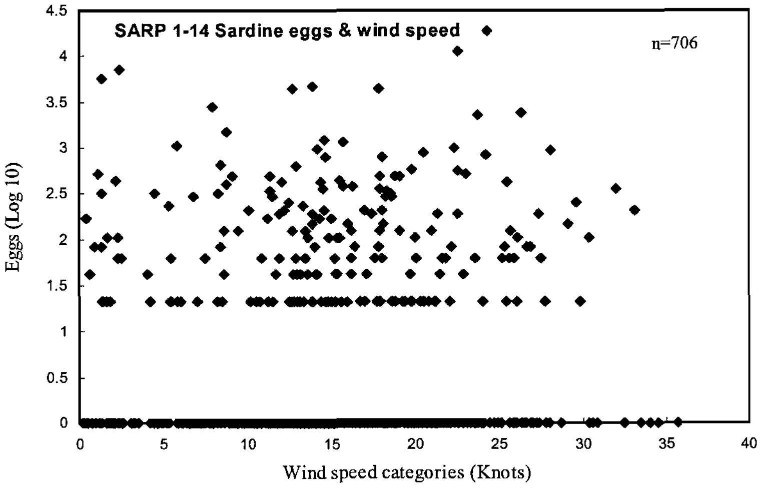


Fig. A 4: Scattergrams showing the relationship between anchovy and sardine eggs and wind speed

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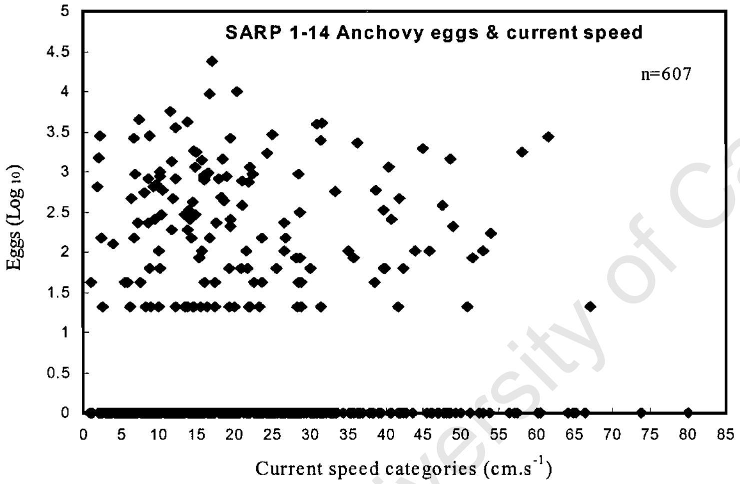
5. Current speed	
SARP 1	8
SARP 2	77
SARP 3	45
SARP 4	113
SARP 5	33
SARP 6	51
SARP 7	35
SARP 8	41
SARP 9	60
SARP 11	50
SARP 12	29
SARP 13	65
SARP 14	88
	Total = 607



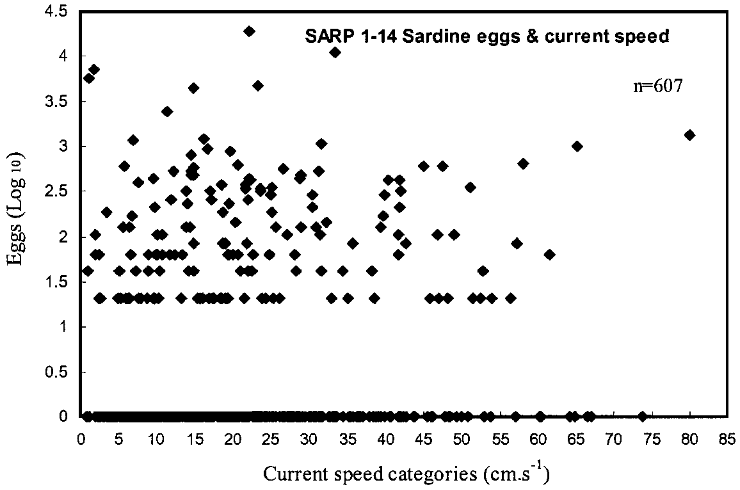


Fig. A 5: Scattergrams showing the relationship between anchovy and sardine eggs and current speed

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6. Nitrate concentration

SARP 1	16
SARP 2	51
SARP 3	35
SARP 4	37
SARP 5	24
SARP 6	18
SARP 7	30
SARP 8	21
SARP 9	22
SARP 11	44
SARP 12	27
SARP 13	70
SARP 14	20
	Total =415

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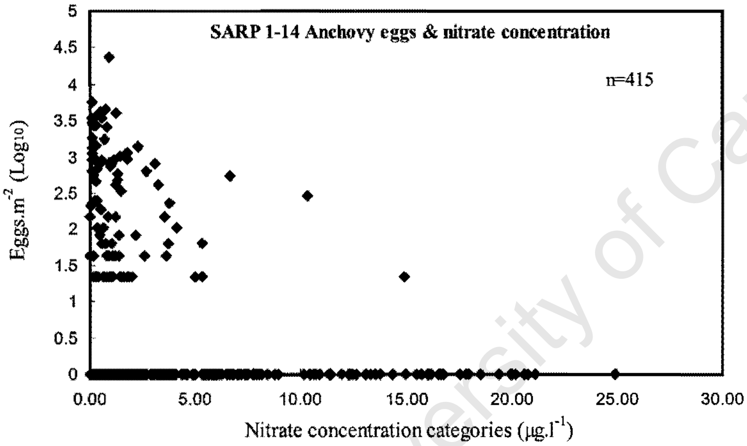


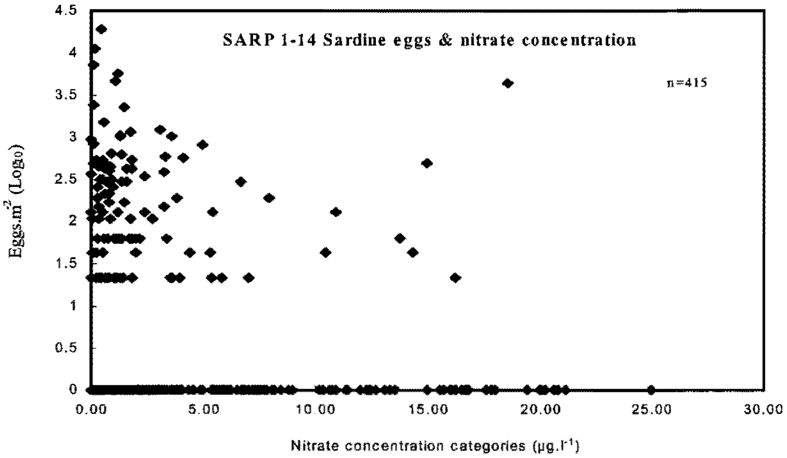
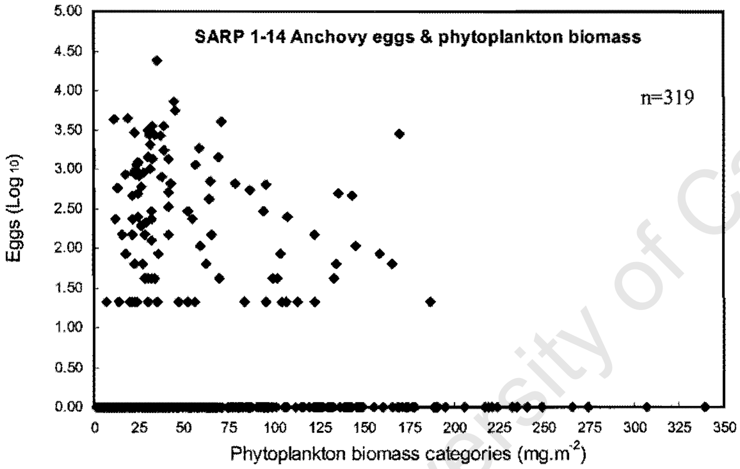


Fig. A 6: Scattergrams showing the relationship between anchovy and sardine eggs and nitrate concentration

7. Phytoplankton biomass

SARP 1	17
SARP 2	17
SARP 3	33
SARP 4	40
SARP 5	29
SARP 6	22
SARP 7	29
SARP 8	23
SARP 9	26
SARP 11	46
SARP 12	15
SARP 13	22
SARP 14	71
	Total = 319



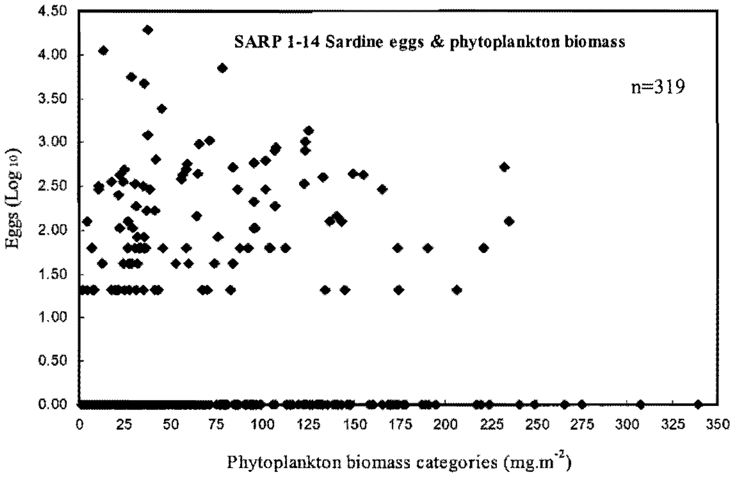


Fig. A 7: Scattergrams showing the relationship between anchovy and sardine eggs and phytoplankton biomass

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8. Zooplankton biomass

SARP 1	11
SARP 2	12
SARP 3	34
SARP 4	53
SARP 5	29
SARP 6	22
SARP 7	24
SARP 8	23
SARP 9	23
SARP 11	47
SARP 12	15
SARP 13	41
SARP 14	70
	Total = 334

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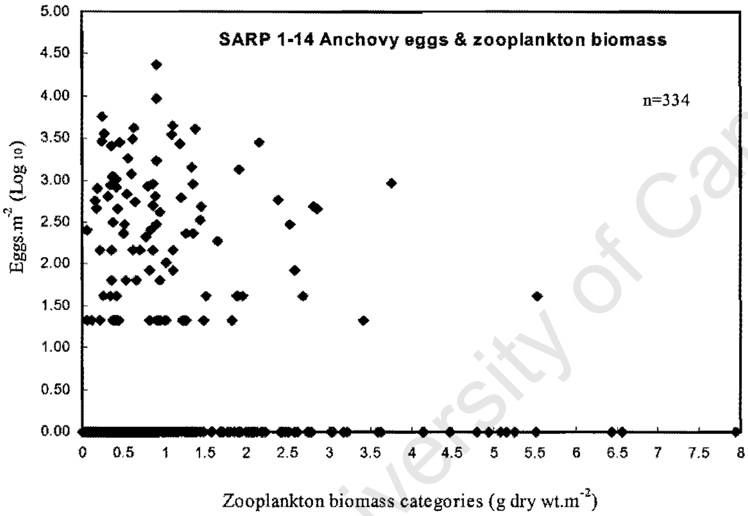

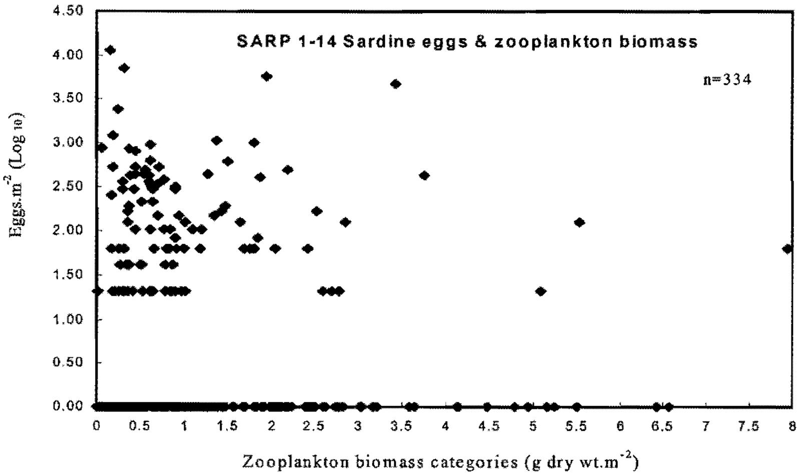

Fig. A 8: Scattergrams showing the relationship between anchovy and sardine eggs and zooplankton biomass

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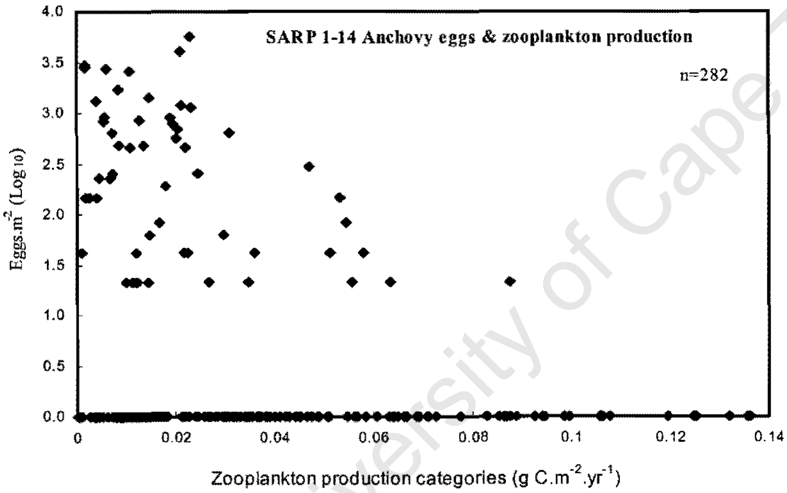
9. Zooplankton production

SARP 1	16
SARP 2	10
SARP 3	19
SARP 4	52
SARP 5	19
SARP 6	16
SARP 7	18
SARP 8	26
SARP 9	18
SARP 11	28
SARP 12	41
SARP 13	19
SARP 14	19
	Total = 282



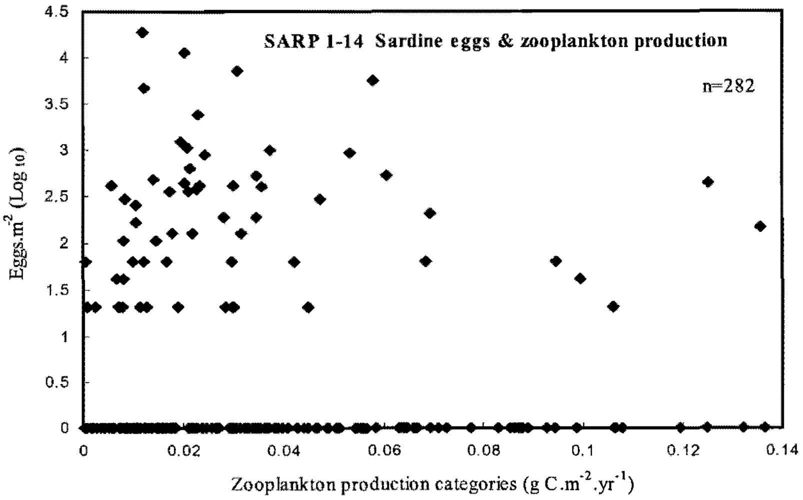


Fig. A 9: Scattergrams showing the relationship between anchovy and sardine eggs and zooplankton production

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APPENDIX B

Environmental variables related to egg abundance data during November spawner biomass surveys. For each of the environmental variables, the cruise name, date of collection, area covered and the number of samples (n) collected are given. The number of samples (n) includes pairs of eggs and environmental variables. Relationships between eggs and individual environmental variables are presented in scattergrams after each data description. Egg data was transformed to ($\log_{10} x+1$) to stabilize variances and account for zeros, see Fig. 2.1-2.2 for places names.

Environmental variable
1.Sea surface temperature (SST)

Cruise	Date	Area	n
Spawner biomass I:	Nov. 1984	St. Helena Bay-Port Elizabeth	304
Spawner biomass II:	Nov. 1985	Cape Columbine-Port Elizabeth	294
Spawner biomass III:	Nov. 1986	Cape Columbine-Port Elizabeth..	271
Spawner biomass IV:	Nov. 1987	Hondeklip Bay-Port Elizabeth	441
Spawner biomass V:	Nov. 1988	Hondeklip Bay-Port Alfred	480
Spawner biomass VI:	Nov. 1989	West Coast 31°North of Port Alfred	361
Spawner bioamss VII:	Nov. 1990	West Coast-Port Alfred..	338
Spawner biomass VIII:	Nov. 1991	Cape Town-Port Elizabeth..	418
Spawner biomass IX:	Nov. 1992	Hondeklip Bay-Port Elizabeth	425
Spawner biomass X:	Nov. 1993	Cape Columbine-Port Elizabeth..	327
Spawner biomass XI:	Nov. 1994	North of Lambert's Bay-Port Elizabeth..	305
Spawner biomass XII:	Nov. 1995	Between Hondeklip Bay & Port Alfred..	322
Spawner biomass XIII:	Nov. 1996	Cape Point-Mossel Bay	437
Spawner biomass XV:	Nov. 1997	Hondeklip Bay-Port Alfred..	285
Spawner biomass XV:	Nov. 1998	Hondeklip Bay-East London	373
Spawner biomass XVI:	Nov. 1999	Hondeklip Bay-Port Alfred	314
			Total = 5731

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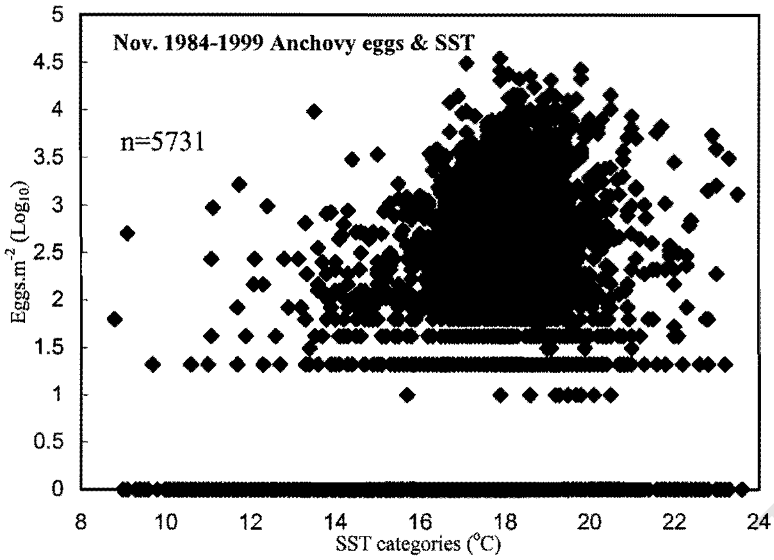

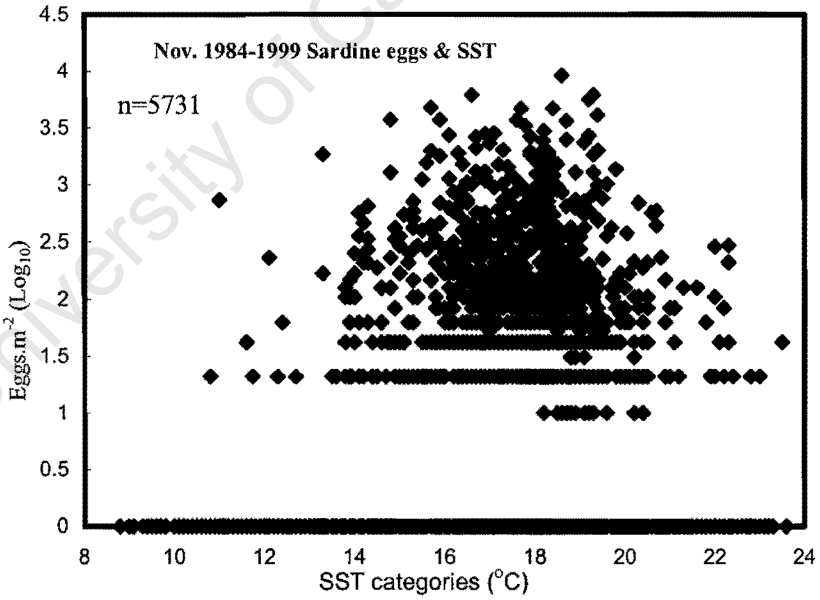

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Fig. B 1: Scattergrams showing the relationship between anchovy and sardine eggs and sea surface temperature

2. Water column depth

Spawner biomass I	304
Spawner biomass II	294
Spawner biomass III	271
Spawner biomass VI	441
Spawner biomass V	480
Spawner biomass VI	361
Spawner biomass VII	338
Spawner biomass VIII	418
Spawner biomass IX	425
Spawner biomass X	327
Spawner biomass XI	305
Spawner biomass XII	322
Spawner biomass XIII	473
Spawner biomass XIV	285
Spawner biomass XV	373
Spawner biomass XVI	314
	Total=5731

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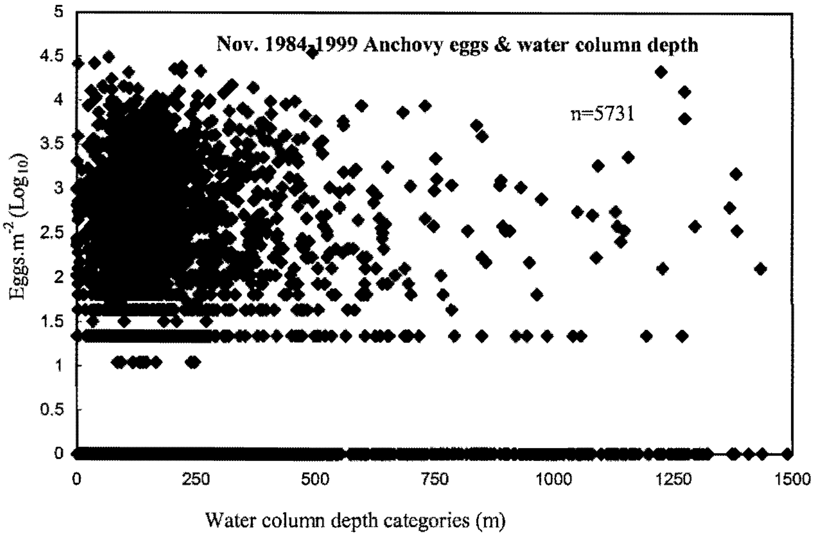

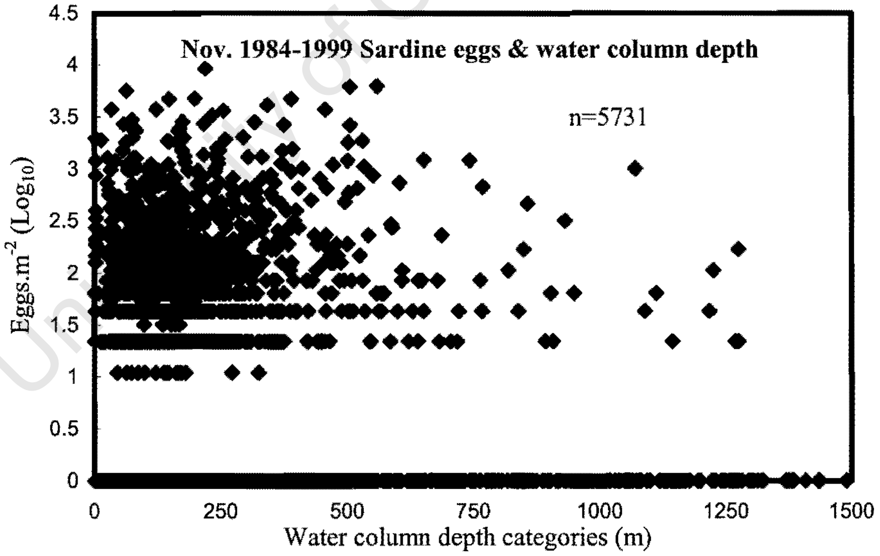

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Fig. B 2: Scattergrams showing the relationship between anchovy and sardine eggs and water column depth

3. Salinity

Spawner biomass I	50
Spawner biomass II	71
Spawner biomass III	63
Spawner biomass VI	25
Spawner biomass V	24
Spawner biomass VI	28
Spawner biomass VII	16
Spawner biomass VIII	419
Spawner biomass IX	425
Spawner biomass X	232
Spawner biomass XI	178
Spawner biomass XII	291
Spawner biomass XIII	274
Spawner biomass XIV	131
Spawner biomass XV	373
Spawner biomass XVI	301
	Total=2901

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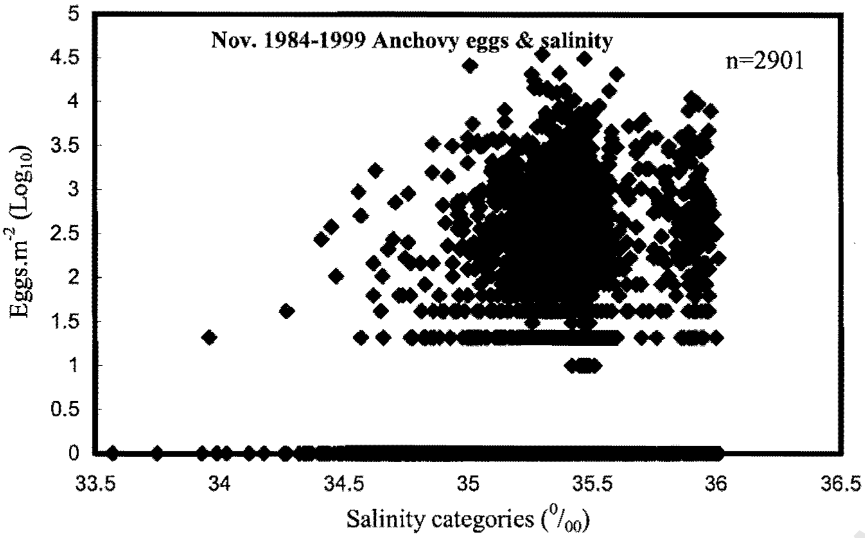

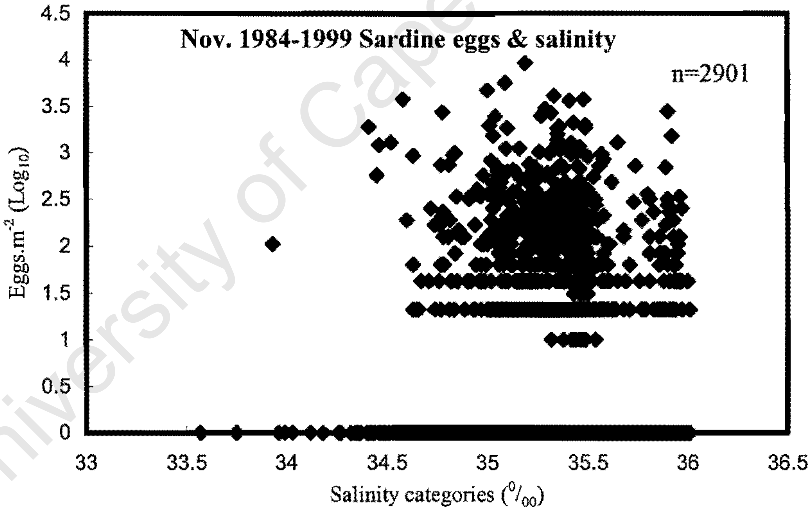

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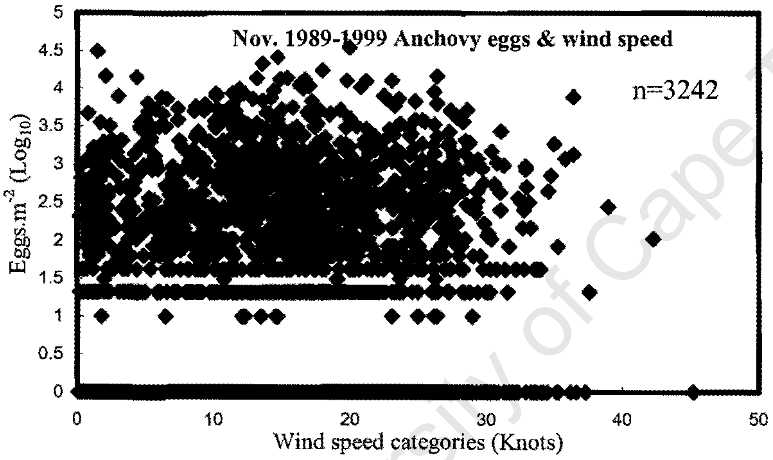
Fig. B 3: Scattergrams showing the relationship between anchovy and sardine eggs and salinity

4. Wind speed	
Spawner biomass VI	0
Spawner biomass VII	48
Spawner biomass VIII	408
Spawner biomass IX	423
Spawner biomass X	327
Spawner biomass XI	300
Spawner biomass XII	290
Spawner biomass XIII	474
Spawner biomass XIV	285
Spawner biomass XV	373
Spawner biomass XVI	314
	Total=3242



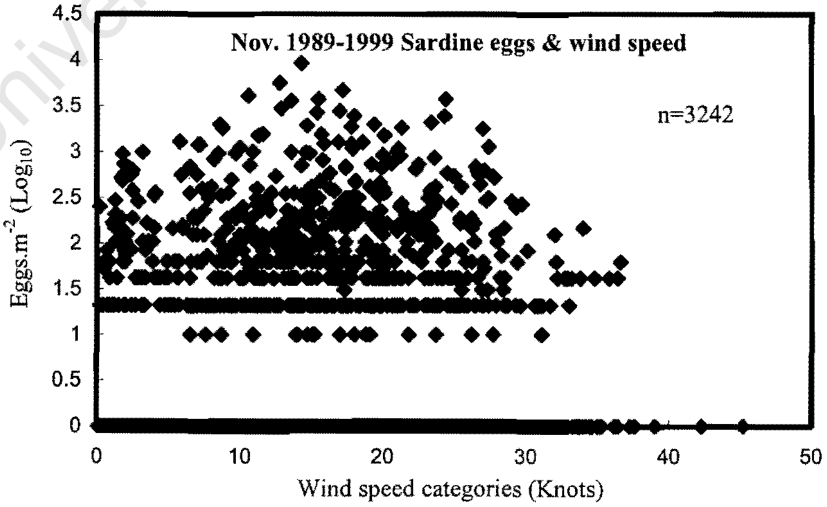


Fig. B 4: Scattergrams showing the relationship between anchovy and sardine eggs and wind speed

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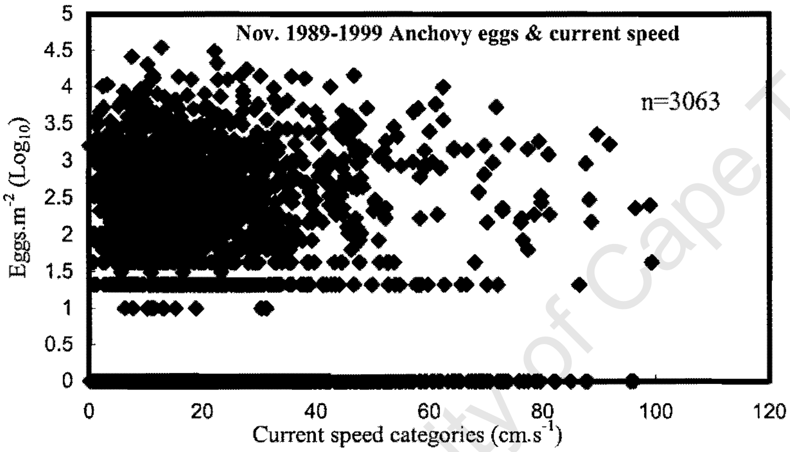
5. Current speed

Spawner biomass VI	173
Spawner biomass VII	220
Spawner biomass VIII	325
Spawner biomass IX	124
Spawner biomass X	272
Spawner biomass XI	305
Spawner biomass XII	290
Spawner biomass XIII	474
Spawner biomass XIV	211
Spawner biomass XV	355
Spawner biomass XVI	314
	Total=3063



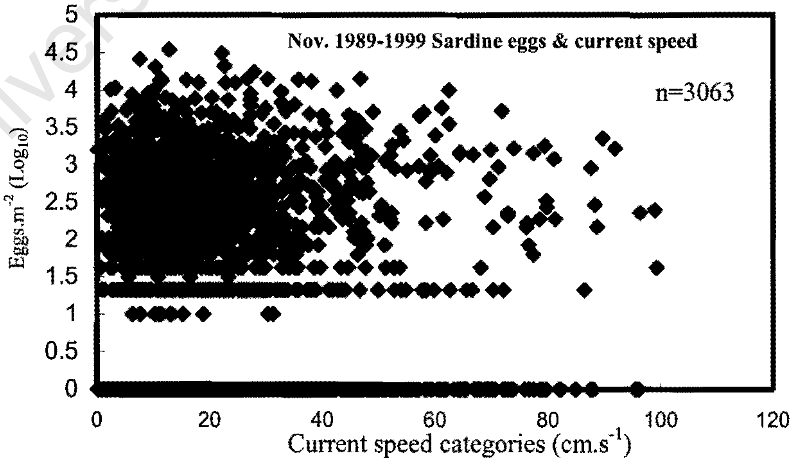


Fig. B 5: Scattergrams showing the relationship between anchovy and sardine eggs and current speed

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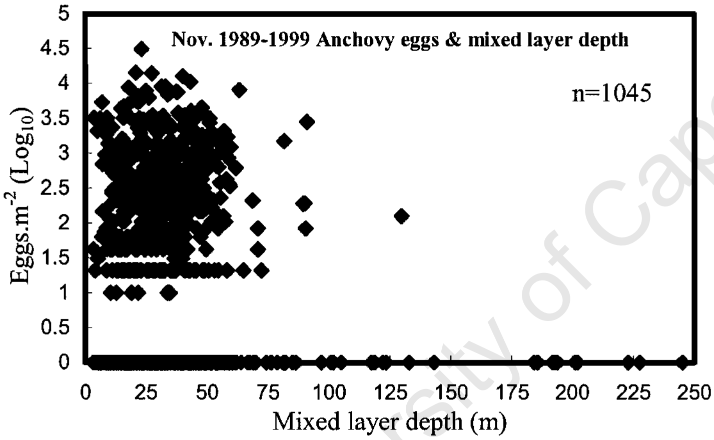
6. Mixed layer depth

Spawner biomass VI	103
Spawner biomass VII	106
Spawner biomass VIII	125
Spawner biomass IX	108
Spawner biomass X	85
Spawner biomass XI	98
Spawner biomass XII	97
Spawner biomass XIII	62
Spawner biomass XIV	55
Spawner biomass XV	135
Spawner biomass XVI	71
	Total=1045



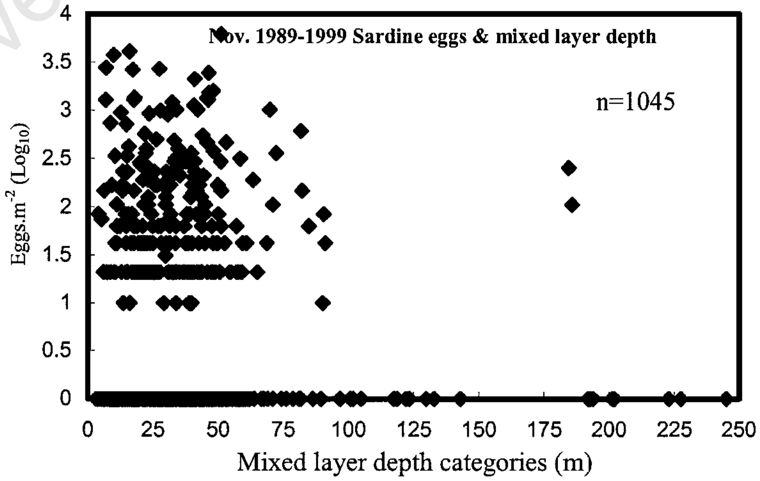


Fig. B 6: Scattergrams showing the relationship between anchovy and sardine eggs and mixed layer depth

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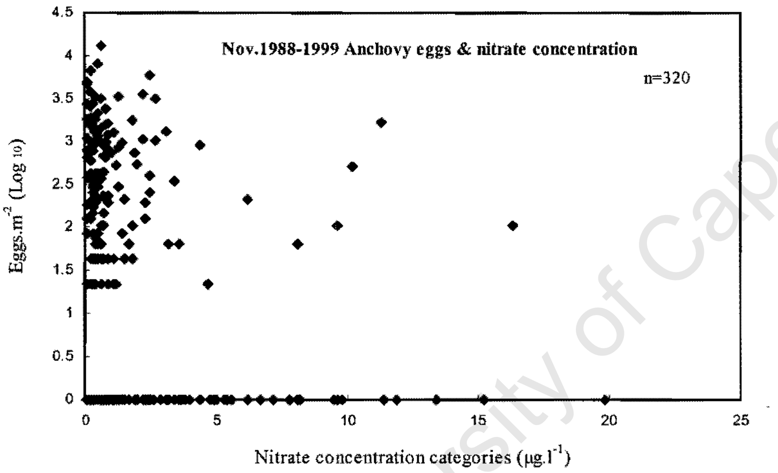
7. Nitrate concentration

Spawner biomass VI	13
Spawner biomass VII	28
Spawner biomass VIII	36
Spawner biomass IX	70
Spawner biomass X	17
Spawner biomass XI	30
Spawner biomass XII	24
Spawner biomass XIII	26
Spawner biomass XIV	21
Spawner biomass XV	27
Spawner biomass XVI	28
	Total = 320



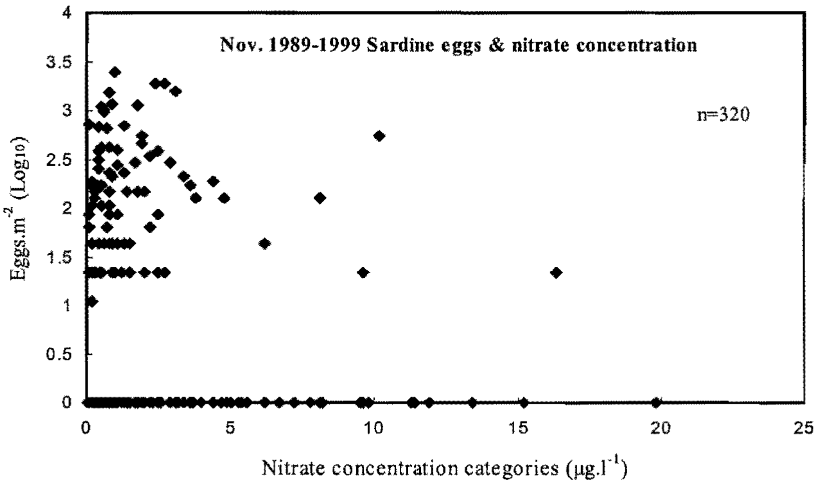


Fig. B 7: Scattergrams showing the relationship between anchovy and sardine eggs and nitrate concentration

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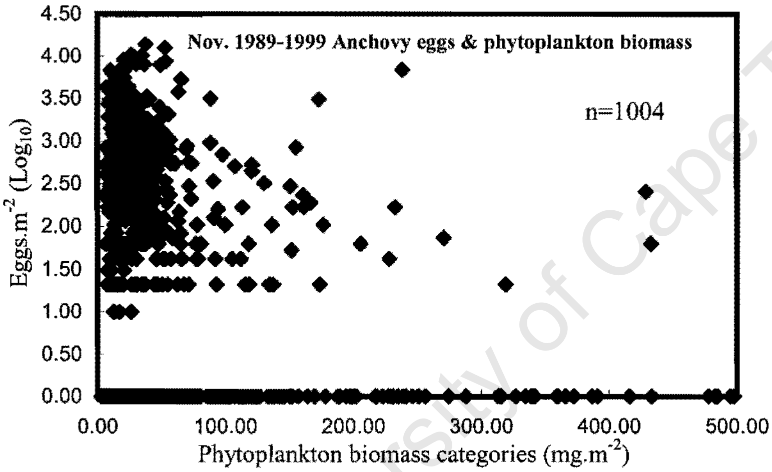
8. Phytoplankton biomass

Spawner biomass VI	103
Spawner biomass VII	107
Spawner biomass VIII	124
Spawner biomass IX	108
Spawner biomass X	85
Spawner biomass XI	99
Spawner biomass XII	73
Spawner biomass XIII	62
Spawner biomass XIV	47
Spawner biomass XV	139
Spawner biomass XVI	57
	Total=1004



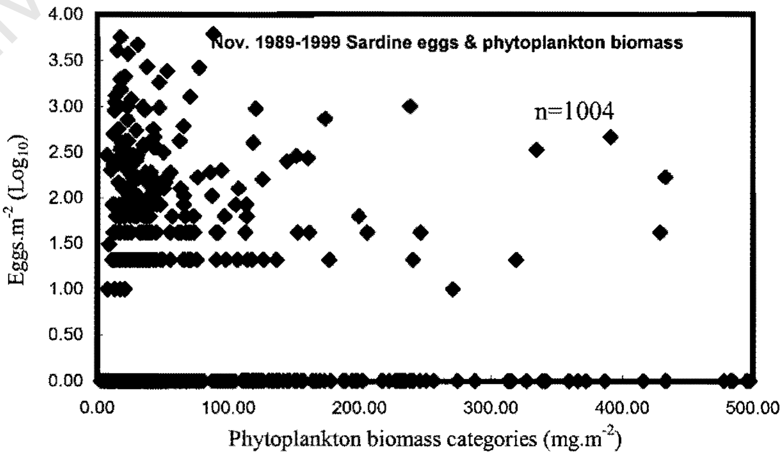


Fig. B 8: Scattergrams showing the relationship between anchovy and sardine eggs and phytoplankton biomass

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9. Zooplankton biomass

Spawner biomass VI	96
Spawner biomass VII	114
Spawner biomass VIII	110
Spawner biomass IX	121
Spawner biomass X	57
Spawner biomass XI	57
Spawner biomass XII	72
Spawner biomass XIII	98
Spawner biomass XIV	65
Spawner biomass XV	123
Spawner biomass XVI	132
	Total=1045

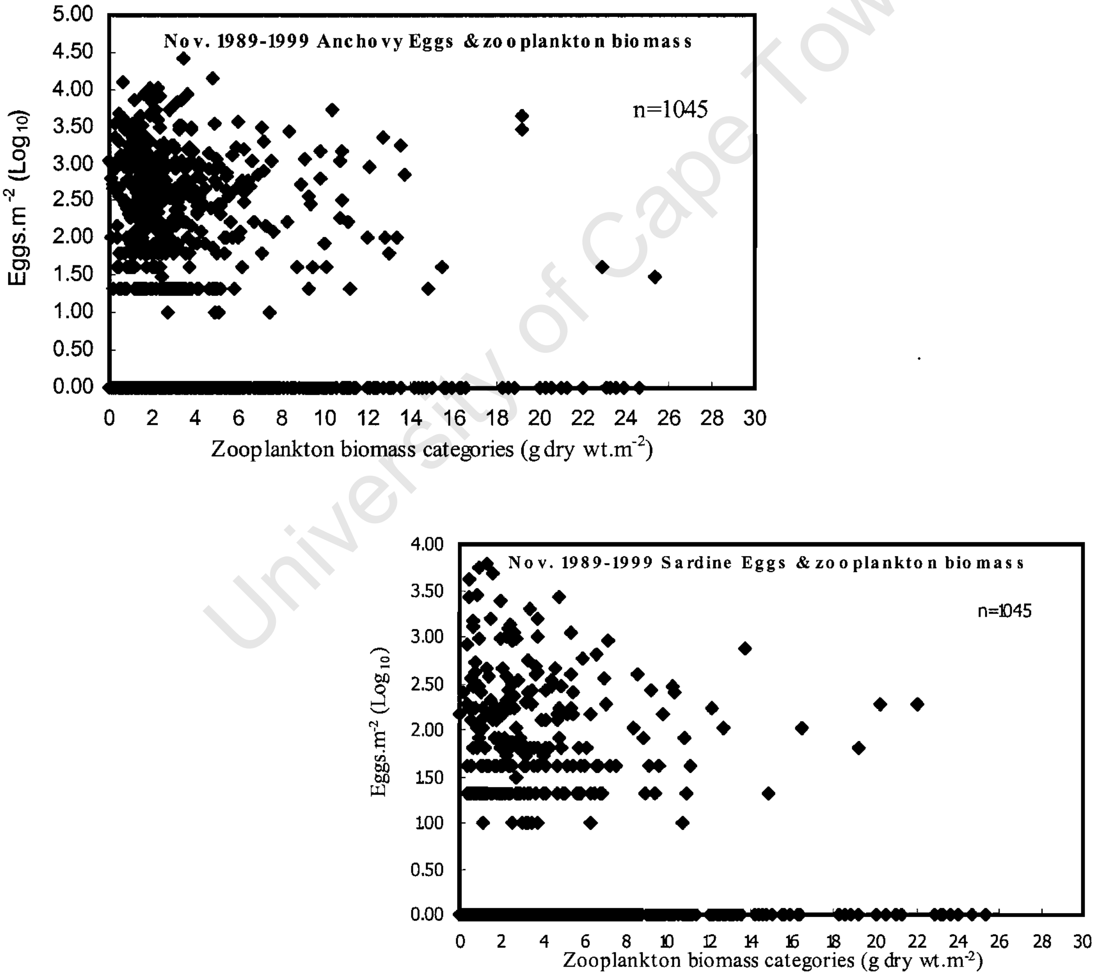

Fig. B 9: Scattergrams showing the relationship between anchovy and sardine eggs and zooplankton biomass

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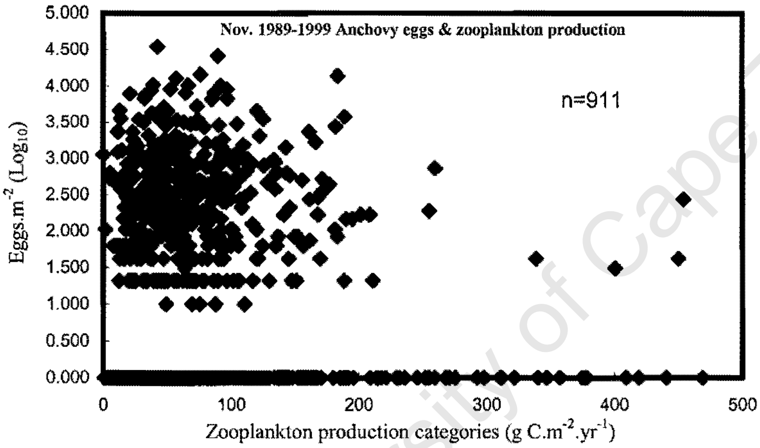
10. Zooplankton production

Spawner biomass VI	38
Spawner biomass VII	114
Spawner biomass VIII	110
Spawner biomass IX	118
Spawner biomass X	10
Spawner biomass XI	98
Spawner biomass XII	67
Spawner biomass XIII	99
Spawner biomass XIV	39
Spawner biomass XV	87
Spawner biomass XVI	131
	Total=911



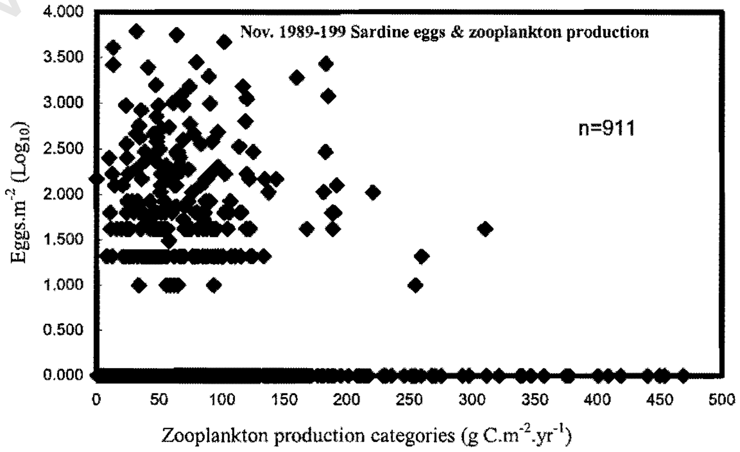


Fig. B 10: Scattergrams showing the relationship between anchovy and sardine eggs and zooplankton production

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APPENDIX C

Results of multivariate coinertia analyses for spawner biomass surveys on a yearly basis between 1989-1999 showing relationships between eggs and environmental variables.

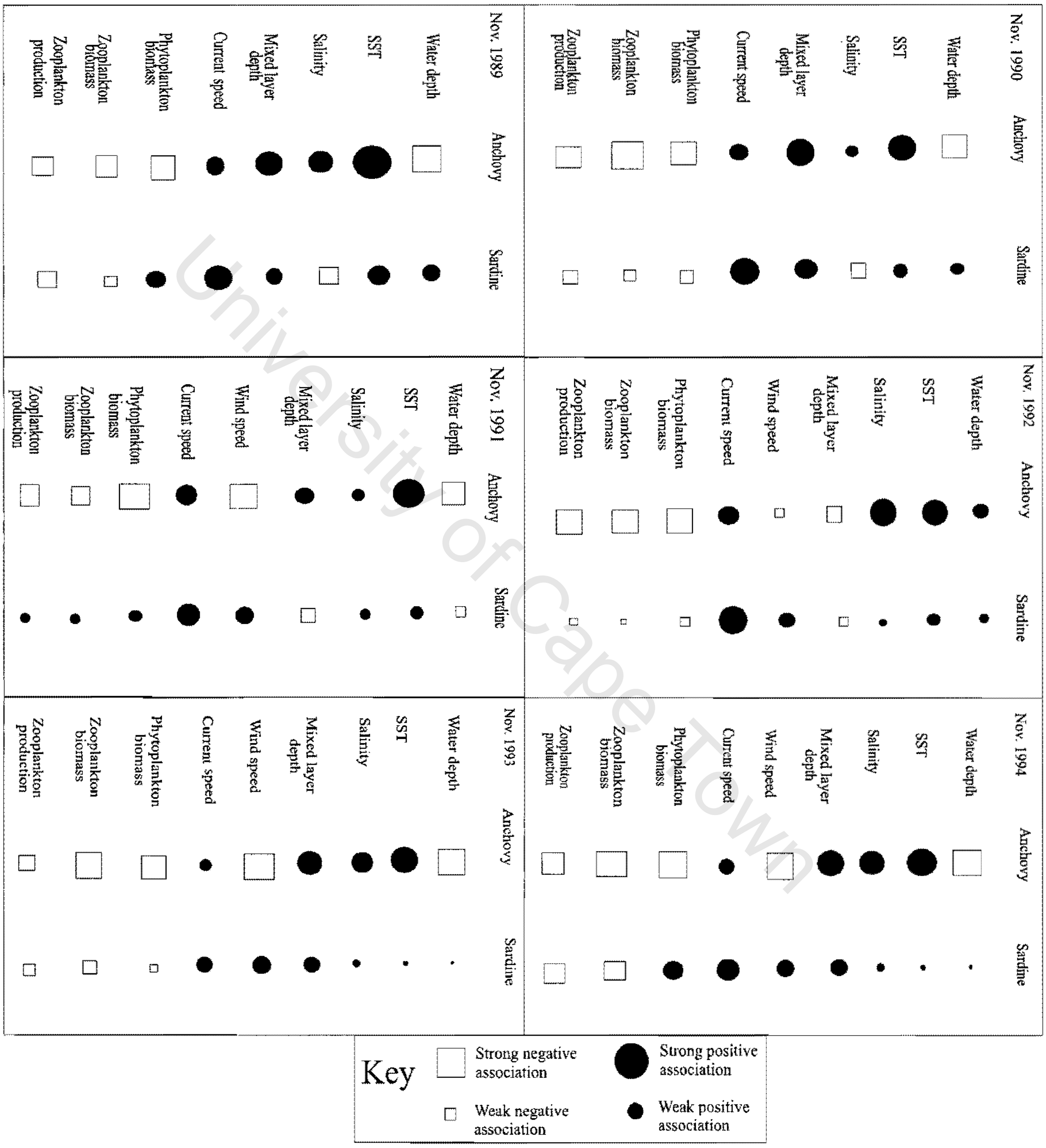

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Fig. C1: Relationships between eggs of anchovy and sardine and environmental variables, November surveys, 1989-1994.

Appendix C (continued)

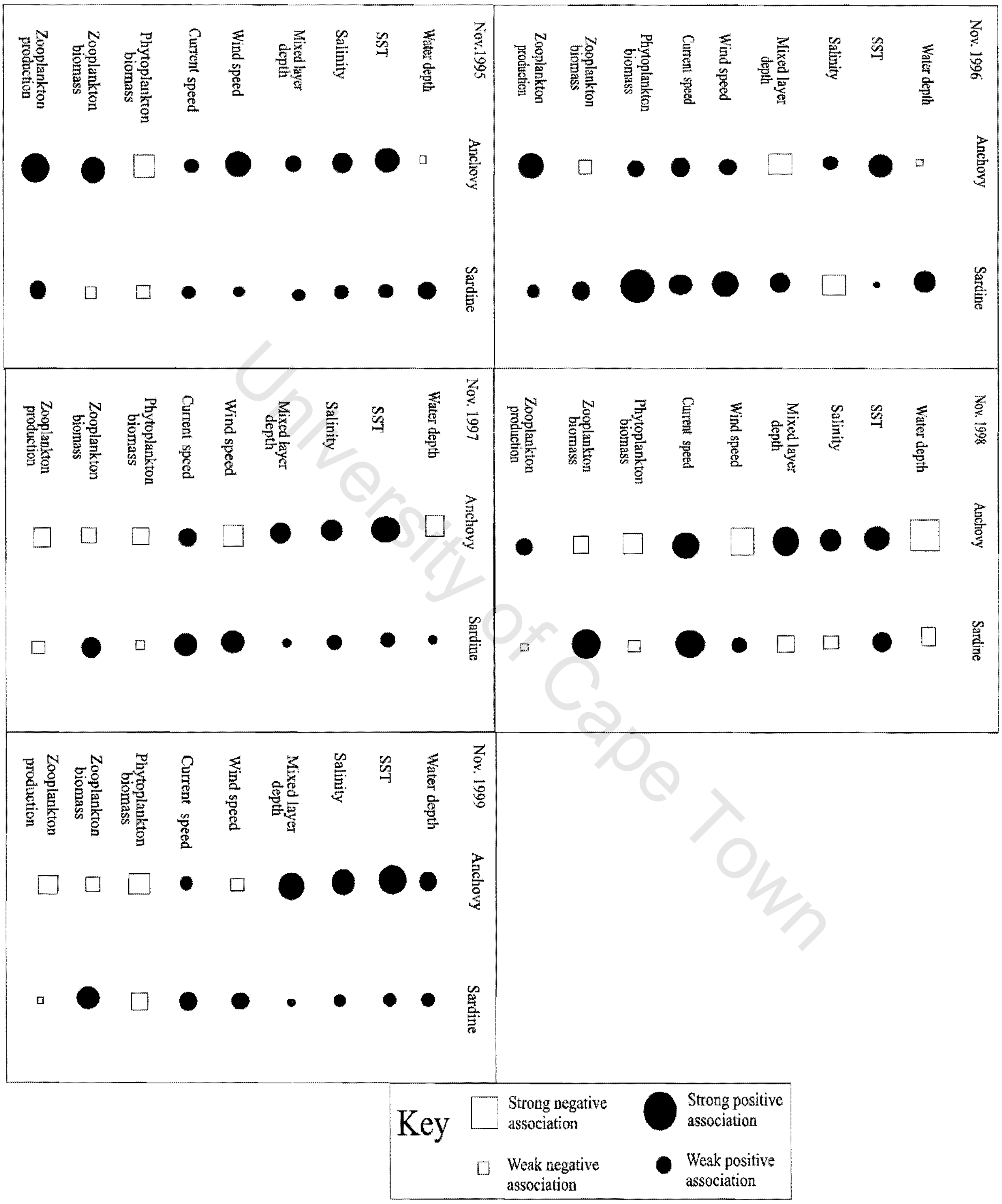

Fig. C 2: Relationships between eggs of anchovy and sardine and environmental variables, November surveys, 1995-1999.

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