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**STUDIES OF BIOLOGY, ECOLOGY AND SCHOOL
BEHAVIOUR OF SARDINELLA IN THE ANGOLAN FISHERY.**

DISSERTATION

Submitted in fulfillment

of the degree of

Master of Science

at the

University of Cape Town

by

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MARCH 2002

DECLARATION

I hereby declare that, unless otherwise stated, this thesis represents my own work, both in concept and execution. The data collected was carried out during cruises organized mainly to estimate the biomass of small pelagic fish. I participated in some of these cruises (from 1993-1998) as a researcher. All references have been accurately reported. Some of the paragraphs in chapter four are from an authored and co-authored papers submitted for the proceedings of the "International Council for the Exploration of the Sea" held in Lisbon-Portugal, 1998. In all other respects I lay claim to the ideas not cited, concepts, hypothesis or conclusions contained in this thesis.

Signed:

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Date:

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I am also indebted to the Marine and Coastal Management (M&CM) who provided me with a comfortable room and amenities on the 2nd floor (of the Oceanography Department) Cape Town. The “Nansen Programme” and R/V. *Dr. Fridtjof Nansen* are thanked for their cooperation throughout the surveys. Members of the Instituto de Investigação Marinha (IIM-Luanda) are acknowledged for their assistance in data collection as well as the processing of it on board the research vessels.

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ABSTRACT

Commercial fishing for small pelagic fish started in the early 1950s in Angola. Catches averaged around 100 000 tonnes, with a gradual increase from the mid-1960s to mid-1970s, but with much of annual variability. Following Angolan Independence in 1975, fishing agreements were made with Soviet vessels and the annual catch increased to between 300-500 000 tonnes p.a. After the mid-1980s the agreement fell away and the catches decreased to around 100 000 tonnes p.a. Estimates of abundance are not available for the period prior to the mid-1980s. Biomass estimates of two species in which *Sardinella maderensis* contributes about 80-95% and *S. aurita* about 5-20% to the catch showed an increasing trend by the late 1990s. The sardinella stock is a major fish resource off Angola, and is mainly managed on the basis of biomass estimates of the adult stock, obtained by standard hydroacoustic methods. The validity of the Total Allowable Catches (TACs) set for these species each year, is heavily dependent on the accuracy and precision of biomass estimates. The method used for sardinella has been acoustic surveys on a stratified random basis, covering known ranges of the species. These surveys have been designed according to the distribution of pelagic fish and the topography of the shelf. This study investigated the biological characteristics (linked with day-night and migration aspects) of the stock, the behavioural patterns of *sardinella spp* (school-behaviour and dynamics) that may lead to under-estimation as well as bias. Biological and acoustic data collected during 22 pelagic surveys (1985-1999), as well as schooling records of three cruises (1996-1998), were used to study the biology, distribution, behaviour of the school dynamics of sardinella. Between the two species, only *S. maderensis* showed here adequate results indicating that both males and females reach 50% maturity at sizes 23 and 24 cm total length, respectively. Sex ratios calculated on seasonal and geographical areas basis for the survey data seldom approached the expected 1:1 ratio for round sardinella. In contrast, for flat sardinella only few ratios slightly favoured females, whereas males were frequently dominant. Systematically higher estimates have been recorded in the northern region (Luanda-Cabinda) during the southern cold season and in the central-southern region (Benguela-Luanda) during the warm season. There is a southward displacement of the adults as far as Baia dos Tigres (16° 40'S) for *S. aurita* and to Lobito-Benguela for *S. maderensis* during the warm season. Northward displacement occurs during the cold season in connection with upwelling in the south.

Tests performed on the mean fish lengths of catches indicate that their distributions vary significantly according to the seasons. The results of surface school observations of sardinella in Angolan waters during *Dr Fridtjof Nansen* surveys between 1996 and 1998 revealed that sardinella shoals appeared at the surface in a bimodal pattern. Most schools are seen at the surface in large numbers between sunrise to 11 h 00, and again from about 13 h 00 to sunset. The number of sightings appears to be inversely related to the solar radiation, with the maximum number of sightings occurring at radiation levels of about 300 Wm^{-2} . Hydro-acoustic data collected during 1994 and 1997 were used to study diurnal changes in vertical distribution. A diurnal variation in sardinella densities per layer was found to be significant. Densities were lower at night (Layer 0-20 m, mean fish densities = 4.09 g.m^{-2} by day vs Layer 0-20 m, mean fish densities = 3.40 g.m^{-2} at night; Layer 40-60 m, mean fish densities = 1.41 g.m^{-2} by day vs Layer 40-60 m, mean fish densities = 1.05 g.m^{-2} at night). However, definite diel vertical migrations of sardinella were weak. Nevertheless, these results should be considered for the potential problem of under-estimation of sardinella biomass at night. These results suggest adaptive sampling is required along the Angolan coast and especially in the southern region in order to increase the precision and accuracy of biomass estimates.

Key words: Acoustics, sonar, *Sardinella aurita*, *Sardinella maderensis*, exploitation, length frequency, size at maturity, sex-ratio, biomass estimates, schooling behaviour, distribution and aggregation patterns.

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CHAPTER 1.

1.1 IMPORTANCE OF THE PELAGIC RESOURCE IN ANGOLA

INTRODUCTION

Angola has a coastline of 1 650 km, a continental shelf of 5 100 square km and its average width is about 30 km (Figure 1.1). At present the fisheries sector is the third main economic sector in Angola following the oil and mining industries (diamonds). Fish is the main source of animal protein available nowadays (Ca. 40 % overall and up to 90 % in the coastal areas), the consumption per capita is an average of 19 kg p.a with nearly 30 kg in the coastal zones of Angola (Alberts *et al.*, 1990).

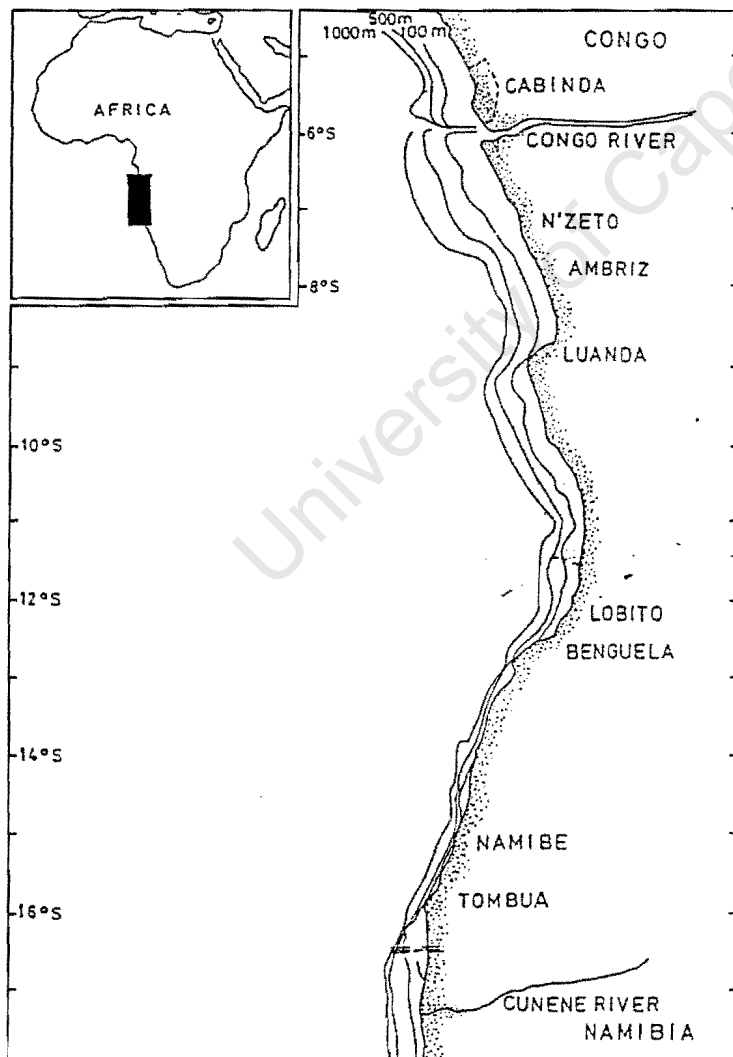


Figure 1.1 Location of the Angolan coast (Redrawn from Dias and Machado, 1973).

Pelagic stocks are a major fish resource off Angola and represent approximately 80 % of the total catches landed in the country (Anon, 1991; FAO, 1996). The most important pelagic fish stocks are sardinella (*Sardinella maderensis* and *S. aurita*) and horse mackerel (*Trachurus trecae* and *T. capensis*). The sardinella stocks in the area from the Congo to the southern border of Angola for many years supported fisheries of substantial importance. Total landings varying between more or less 60 000 and 250 000 tonnes were caught annually in the period 1961-1974 (Campos Rosado, 1974).

Commercial exploitation of small pelagic fish started for the purpose of the fish meal industry in the early fifties. During the fifties and sixties catch dynamics seemed to be dependent on stock fluctuations rather than on fishing effort (Campos Rosado, 1974). Prior to 1973, annual landings of sardinella did not exceed 160 000 tonnes and from 1974 to 1976, were apparently at very low levels when fishing was resumed by licensed USSR factory expeditions (FAO, 1976-88). Total landings exceeded 200 000 tonnes in the late 1970s and mid 1980s but then, partly as a result of management measures, declined to about 100 000 tonnes by the end of the 1980s.

The sardinella fishery was based, until the independence of Angola in 1975, on small wooden and well-equipped purse seiners with lengths of 20-25m with 100-200 HP engines supplying fish to small fish meal plants (Troadek and Garcia, 1980). No reliable catch data are available since the period of independence of Angola. However, due to the decline of fish meal production (in Lobito and Namibe), as well as the suspension of fishing operations by certain companies (mainly Portuguese), landings declined to about 20 000 tonnes in the years 1974-1976. In 1977, the Soviet purse seine fleet, consisting mostly of vessels with tonnage classes of 5 (100 – 149.9 GRT) and 6 (150- 249.9 GRT) as well as trawlers of class 10 (2 000 –3999.9 GRT), started intensively exploiting the stocks. Following independence and a period of a significant reduction in fishing effort, catch rates in the first years (1977-1979), were very good (Wysokinski, 1986).

During 1977, a record-breaking catch of 350 000 tonnes was made. In the years 1981-1983 however, total catches declined to a level of 150 000-180 000 tonnes (ICSEAF Stat. Bull. Nos. 7-12 and ICSEAF/1984). From 1989 catches declined, probably due to the retreat of the Soviet purse-seine fleet in 1990 (Figure 1.2). Comparisons of catch levels in mid 80s (declining) and biomass levels (constant) from the surveys carried out by the R/V "Dr. Fridtjof Nansen" indicate the intensive fishing, even when allowing for some under-estimations of biomass with the acoustic method. Observed trends of roughly constant biomass from 1985 to 1989 support the impression of the stock affected by the fishery (Figure 1.3). The statistics of the catch are unreliable and do not represent this fishery accurately (Figure 1.2). However, observed trends can illustrate some features of the resource.

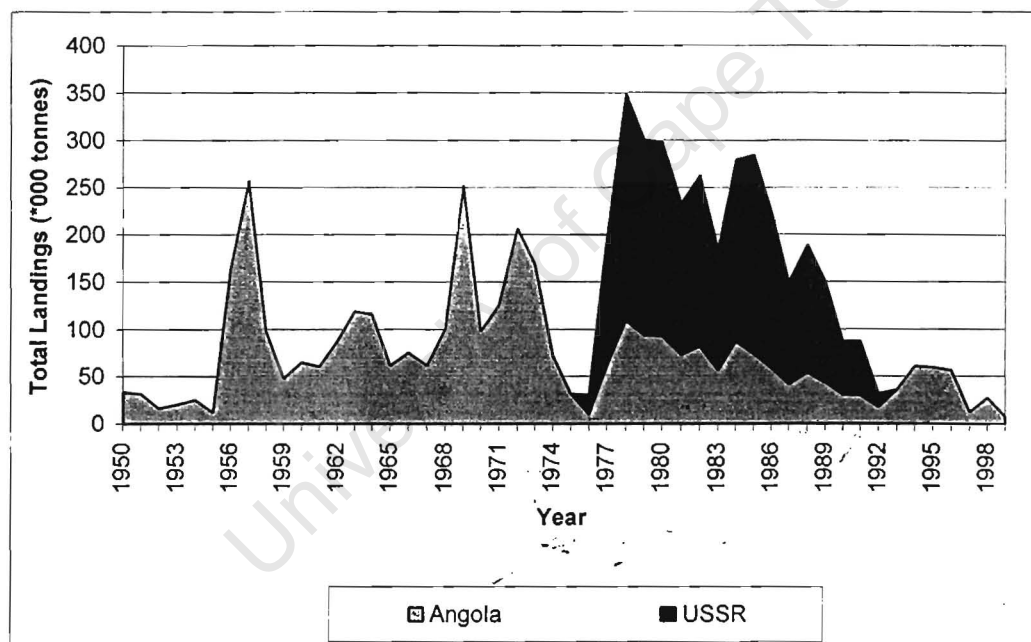


Figure 1.2. Annual catch of *Sardinella* spp landed in Angola (in thousand tonnes) from 1950 to 1999. [source: IIM-Luanda].

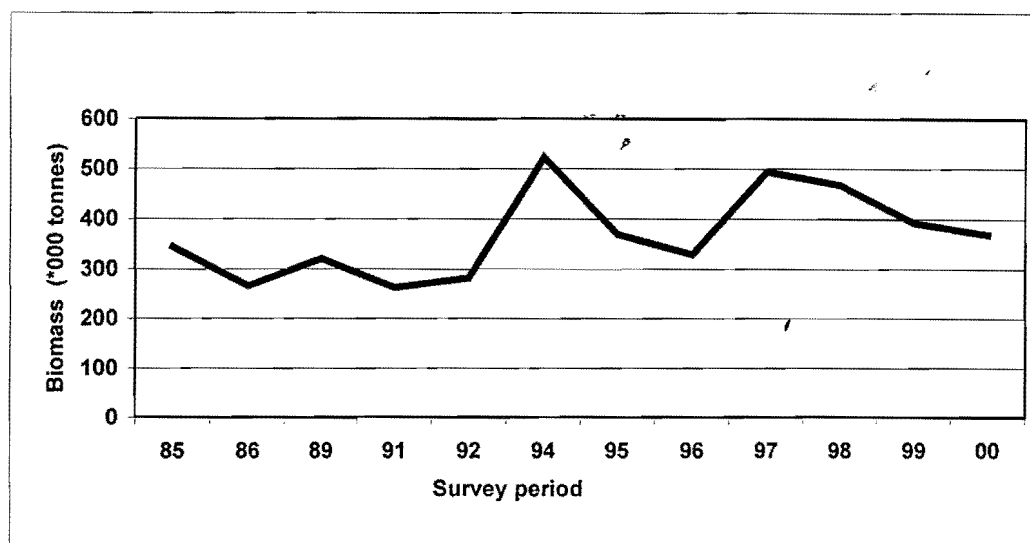


Figure 1.3. Acoustic biomass estimates of sardinella along the Angolan shelf, 1985 - 2000.
[source: R/V *Dr. Fridtjof Nansen* , IIM-Luanda, IMR-Bergen]

1.2 HYDROLOGICAL CONDITIONS AND CONSEQUENCES FOR THE BIOLOGY AND DISTRIBUTION OF THE SARDINELLA SPECIES IN ANGOLA

1.2.1 *Hydrological description*

The hydrographical regime off Angola is characterised by the cold northward-flowing Benguela current and the warm southward propagating waters of the Angolan current. These two currents meet (at about 15° S) at the Angola-Benguela front. The S.E.C current flows predominantly southward and is apparently formed by the South-East branch of the South Equatorial Counter current (SEC), and Southward-turning waters from the north branch of the Benguela current (Figure 1.4).

A characteristic of the Angolan current is that it is a generally southward moving stream from 9° to 16°S, which penetrates to depths of 250-300m and covers not only the shelf regions, but also the continental slope, with surface velocities exceeding 50 cm/sec.

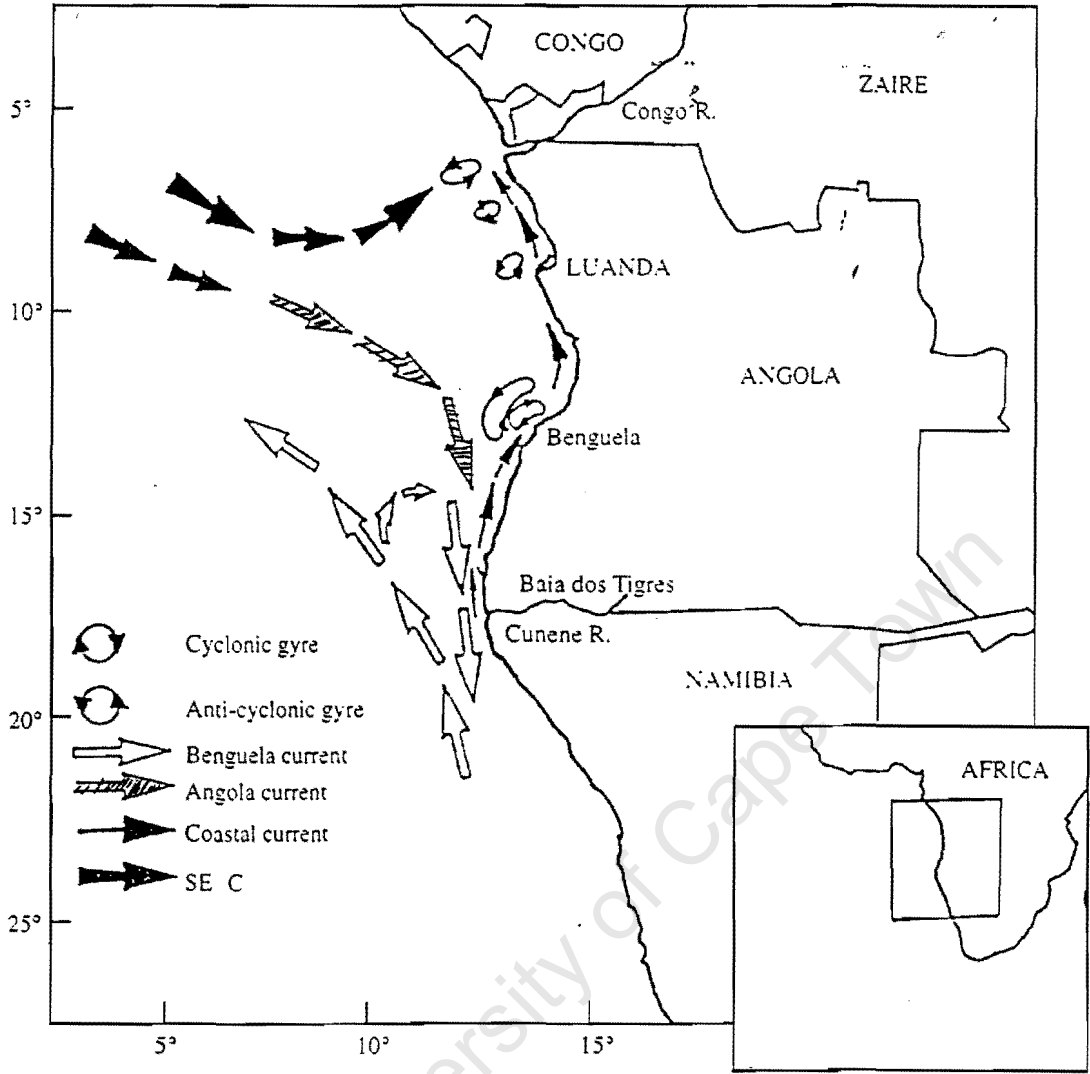


Figure 1.4. Map off the Angola coast with the main currents (after Pereira, 1991)
 S.E.C – South Equatorial Current

The hydro-climate of the Angolan coast north of 15° S is characterised by great variations of temperature and salinity, throughout the year (Pereira, 1991),

The Benguela current, forming the eastern boundary of the anticyclonic sub-tropical gyre of the South Atlantic flows parallel to the Southwest African coast in a north to north-westerly direction. Streams of the Benguela current proceed northward along the shore and reach 13-14°S and form a convergence zone along 11°E from 17° to 13°S, due to its interaction with the Angolan Current (Moroshkhin *et al.*, 1970).

There are two different ecological regimes along the Angolan coast, separated by the position of the Benguela-Angola frontal zone, which has a median position of about 15° S (Shannon *et al.*, 1987). The Benguela-Angola frontal zone is actually recorded as a time series of fronts between 14°S and 17°S throughout the year (Figure 1.5). This front is essentially produced by a convergence of surface waters in the upper 50-70m of the Benguela and Angolan currents as well as changes in the wind stress (Shannon *et al.*, 1987). The front is particularly well defined by a “tongue like” distribution of temperatures and salinity. Another important physical characteristic is the narrow shelf between Tombua and Namibia, which together with the front, could act as a barrier to the spreading of the northern species to the south and vice-versa (Strømme & Saetersdal, 1991).

In the warm season, along the central Angolan coast the flow of the Angolan current is towards the south, which is demonstrated by low salinity surface water originating from the Congo River, with discharges being found off N'Zeto and Pta.das Palmeirinhas and remnants even off Lobito. The Benguela Current influences the southernmost part of the Angolan coast, border with Namibia at more or less 17°S to approximately 13°-14° S. The hydrographical regime therefore differs significantly from this and further north along the coast, particularly in the low temperature of the inshore surface waters (Dias, 1983). This leads to a division of the coastal shelf region into two sub-areas. A northern area covering the region 6°S to 14°S and a southern area from 14°S to 17°S.

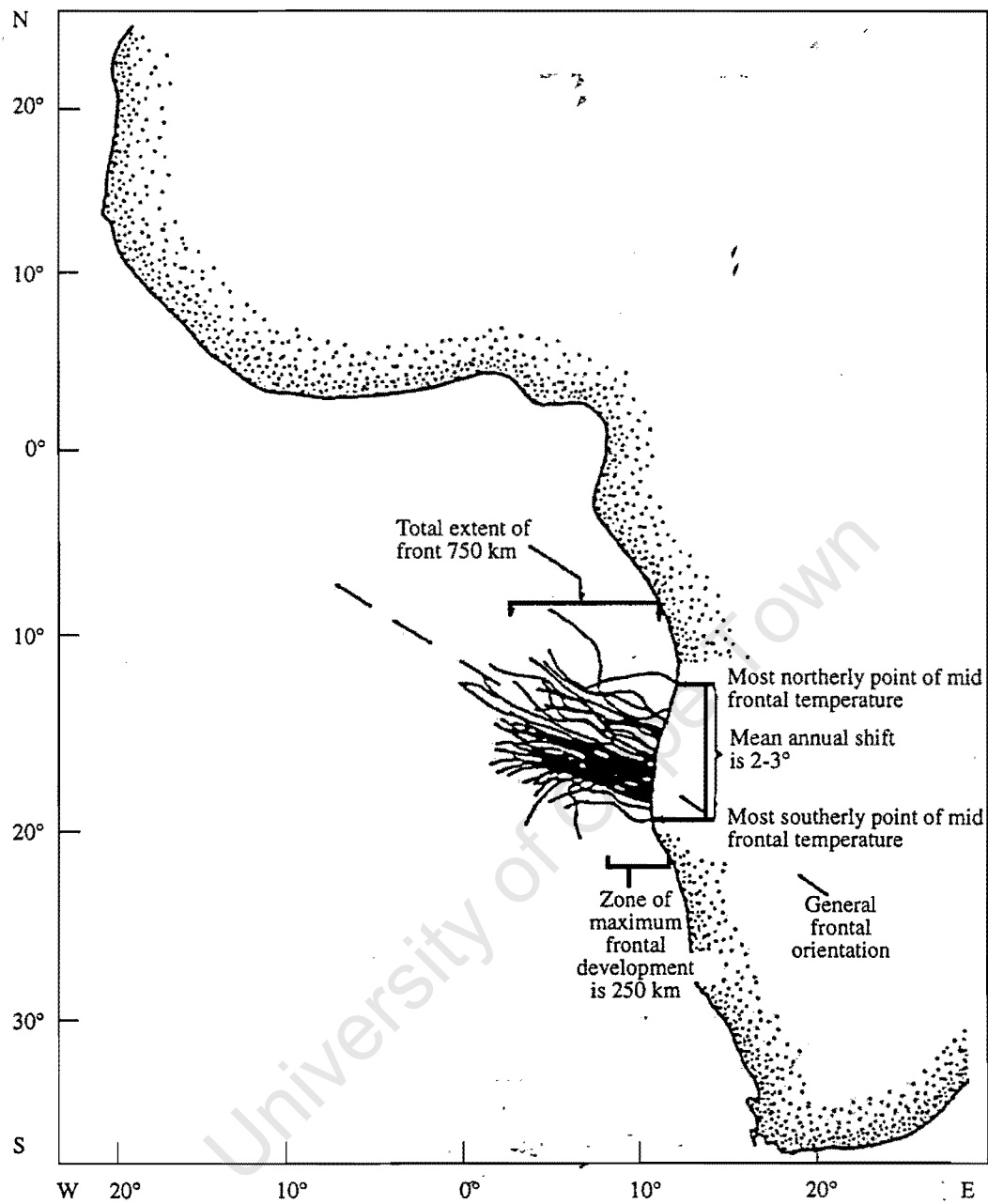


Figure 1.5. Superimposed positions for the mid-front isotherm of Benguela-Angola front, 1982-1985 (from Meeuwis and Lutjeharms, 1990).

1.2.2 *Influence of hydrological conditions (SST and S‰) on the biological cycle of the species*

A main feature of the hydrography of Southern Angola is the upwelling process with a maximum in August-September (Pereira, 1991). This results in intensified primary production, and the existence of a thermal front with an average position at 15° S, however it moves seasonally to 14° S in the cold season and 16° S in the warm season.

The warm Angola current is strong in the warm (summer) season, characterised by more stratified water masses, and higher temperatures in the water column. Seasonal variations of the hydrographical conditions cause temporal and spatial variables of the distribution of pelagic species (Dias, 1983). In the Angola system, coastal fauna is characteristic of a sub-tropical zone, with a number of important pelagic resources, such as the Clupeidae (**round sardinella**, *Sardinella aurita* and **flat sardinella**, *S. maderensis*) the Carangidae (Cunene horse mackerel, *Trachurus trecae*, false scad, *Decapterus ronchus*, and the Atlantic bumper, *Chloroscombrus crysurus*) species.

On the contrary, the Benguela current is strong in the cold season (August-September) causing upwelling and colder surface waters. The large abundance of a few species characterises the ichthyofauna of the pelagic zone in the southern region. The herring-like species, pilchard (*Sardinops sagax*), anchovy (*Engraulis encrasicolus*); and the Cunene horse mackerel (*T. trecae*) are found mainly in the inshore waters and dominate the main pelagic resources. Seasonal variations of hydro-climatical conditions induce temporal and spatial variable distributions of the pelagic species off Angola (Dias, 1983). Catches and surveys show that seasonal changes cause north-south movement of sardinella along the coast of Angola (Anon, 1995), with a southward displacement of the adults as far south as Baia dos Tigres (16° 40'S) for round sardinella and for the flat sardinella to Lobito (12° 30'S) during the warm season. The displacement north and south for both sardinella species is also linked to the feeding area as well as reproduction (Lukashev, 1976). It is known that the sardinella species feed on both phyto- and zooplankton. In different seasons, the two currents influence the movement of the phyto- and zooplankton north/south and consequently this leads to a redistribution of the sardinella species.

1.3 ASSESSMENT OF SMALL PELAGIC FISH STOCKS IN ANGOLA

1.3.1 *Acoustic Surveys*

Colonial era, 1482-1975

Assessment of pelagic fish started during the colonial period. When the former MEBPA (Missão de Estudos Bioceanológicos e de Pescas de Angola) carried out several acoustic surveys in 1972 with the R/V “Goa”, especially in the area south of 12° S. The research vessel was equipped with Simrad SR3 and EH2E echo sounders. As quoted by Campos Rosado (1974) “Maximum biomass of the pelagic fish was estimated at about 320 000 tonnes”.

Former Soviet Union, 1978-1982

During 1976, catches of pelagic fish declined dramatically. Due to this decrease, the AtlantNiro (Former USSR) as well as the Research center of Angola (CIP) carried out acoustic surveys on pelagic fish. The preliminary estimate of biomass by the Soviet institute was about 600 000 tonnes. From 1978 to 1982, the Soviet research institute carried out five surveys. Four surveys covered the entire coast and one covered only the southern area (12° 30' S- 17° 15'S in 1974). The R/V “ARGUS” had made three acoustic surveys making use of the echo sounder “Paltus-M” with integrator IC-1, between depths of 20 and 500m (in the southern part down to 2000m). In 1982 the R/V “EVRICA” carried out two acoustic surveys using the echo sounder FWGT-23 with a distance of 15 miles between transects. The species compositions of the shoals were estimated from trawl catches.

R/V “Dr. Fridtjof Nansen”, 1985-1999

From 1985 to 1999, the IIM (Instituto de Investigação Marinha) and IMR-Bergen jointly carried out twenty-two acoustic surveys with R/V”Dr. Fridtjof Nansen”. The most important fish stocks, sardinella and horse mackerel, were managed mainly on the basis of biomass estimates of the adult stock obtained through standard acoustic methods. Up to 1991, surveys were conducted using a 38 kHz Simrad EK 400 echo sounder connected to an echo integrator. Later surveys, from 1994, used a 38 kHz Simrad EK 500 echo sounder, which was connected to a Bergen Echo

Integration unit (BEI). Further details on the equipment and methods for this recent period are given in Chapter 4 as these data are used extensively in this thesis.

1.3.2 Indirect approaches (ICSEAF)

Various meetings of the ICSEAF Working Party Group on Resource Evaluation reviewed fisheries and biological data on the sardinella stocks in Congolese waters (FAO 1973, 1976). They noted that *Sardinella spp* belong to stocks distributed from southern Gabon to southern Angola, and felt that the exploitation of these stocks could be increased substantially. First attempts at evaluating stocks in the entire area was done at the meeting of the ICSEAF Working Group on Pelagic Species, held in Malaga, Spain, 6-9 December 1976 (ICSEAF, 1976). Simple production models of Schaefer and Gulland-Fox were used. However, the data available at the meeting did not allow for accurate stock assessments to be made but it was believed that the yield of the stocks could be substantially increased.

FAO, 1997

On 3-6 November 1997, a workshop was held in Luanda by the IIM (Instituto de Investigação Marinha, Angola), Congo, Gabon and FAO on the assessment of small pelagic fish. Due to the lack of reliable catch data and age at recruitment (which also requires estimates of fishing effort), the Maximum Sustainable Yield (MSY) could not be calculated. However, in an attempt to improve stock assessments, biomass was estimated with the limited data available at the workshop.

The data described above were used to estimate the parameters of a Schaefer dynamic production model. The *Biodyn* package (Punt and Hilborn, 1996) was used to carry out the analyses. Best-fit parameters were estimated for both species using the "OBSLIK" spreadsheet, which fits a discrete Schaefer model using a dynamic observation-error analysis and a maximum likelihood estimator. It does this through projecting the simulated biomass forwards from the start of the catch time-series and estimating parameters using observed and estimated biomasses for the survey time-series (1985-1996). The confidence intervals were estimated using "OBSBOOT". OBSBOOT estimates the CVs of the key parameters by estimating values of r (the intrinsic growth rate of the stock), K (the mean carrying capacity of the stock) and q (the catchability coefficient or relative bias in the case of surveys) for 100 bootstrap sets, based on the fit of the model to the original data. In order to estimate the CVs, only the data from 1985-1996 were used and B_{init} (i.e. B_{1985}) was set as the proportion of K estimated from the OBSLIK estimation using

the full catch time-series. The MSY of *Sardinella spp* obtained in 1997 was 183 700 tonnes. The MSY estimates should not be viewed as reliable because recruitment was assumed to be constant.

1.4 BACKGROUND TO THE STUDY

The most important pelagic fish stocks, sardinella and horse mackerel are managed mainly by means of hydro-acoustic estimates of the adult stock biomass. It is however recognised that acoustic surveys are highly sensitive to errors caused by effects of fish behaviour, particularly those that may reduce the acoustic detectability of fish. Fish naturally exhibit a variety of behavioural patterns that are adaptations to biological and environmental conditions. Acoustic surveys in Angola were designed according to the known distribution and abundance of fish and to the topology of the shelf. It remains to be seen if these surveys are adequate to characterise the distribution of sardinella.

To acquire reliable accurate biomass estimates through this method, a vessel carrying a calibrated echo integrator must survey the stock. Regular sampling of the acoustic recordings must be conducted by trawling (mid-water trawl). The echo value originating from fish must then be allocated to species identified by trawling, and the echo intensity reflected from individual fish of the actual species must be known. If these criteria are fulfilled, biomass of fish stocks can be estimated by acoustic methods with an accuracy of more or less 25 % (Anon, 1994). There are however several sources of errors in acoustic abundance estimates of fish. These are usually classified as technical, methodological and behavioural.

During the last two decades several methodological and technical problems related to the methods have been investigated and solved by introduction of more reliable instruments, as well as of special procedures to calibrate the instruments.

Still, there are substantial concerns over the effects of fish behaviour on acoustic abundance estimates as under-estimations may occur, especially when pelagic fish school in near-surface layers or perform vessel avoidance. There is also the difficulty of dividing biomass between species and the classification of fish schools or acoustic populations (Rose and Leggett, 1988; Marchal and Petitgas, 1993; Fréon and Misund, 1999). Fish behaviour has a major impact on the accuracy at all stages of the estimation process. Fish that form dense schools may cause a

distortion of the school biomass within the beam, due to the absorption of the emitted and backscattered sound energy (Røttingen, 1976), instrument saturation or the misinterpretation of schools as a bottom feature. Surface schooling appears to be a serious problem, particularly for species like sardinella.

Along the ship's wake some fish may stay too close to the surface or bottom to be detected (dead zones of equipment) while some fish may avoid the vessel. Additionally, the distribution and migration pattern of fish introduces spatial and temporal sampling errors when observations along the track are used to estimate abundance within a stratum and when combining strata estimates.

There are important methodological problems related to the acoustic method. For example, due to the patchiness of fish distribution, substantial variations in the performance of the method arise both within and between surveys (Pennington *et al.*, 1977; Fréon *et al.* 1993). Consequently, inaccurate and possibly biased estimates are then produced which, strictly speaking, are not comparable from one year to the next, and associated errors of up to 50 % can occur (Aglen, 1989).

For many commercially significant pelagic fish stocks in tropical and subtropical regions, acoustic survey estimates are among the most valuable sources of data in standard assessment procedures for short-term predictions. In several developing countries, this information is directly used for taking management decisions, for example, the establishment of the annual Total Allowable Catch (TAC). The utilisation of other stock assessment methods, such as those based on catch and effort data, is often hampered by the difficulty in obtaining reliable fishery statistics.

Furthermore, the most productive areas in the world, especially those associated with the Eastern boundary currents (e.g. as off North West Africa, South West Africa, and West South America) are characterised by important year-to-year environmental changes often resulting in dramatic collapses or increases in fish biomass. These can be detected, and be integrated in the management process at an early stage, by means of acoustic surveys. Improved equipment and comprehensive experimental work have led to wide use of the acoustic method and to a gradual development from relative to absolute estimates.

Textbooks and review papers on the method reflect some of this development (Bazišos, 1975; Johannesson and Mitson, 1983, MacLennan and Simmonds, 1992; Misund and Floen, 1993; Fréon and Misund, 1999). The Norwegian Agency for Development Co-operation (NORAD) financed the operation of a research vessel (the R/V *Dr. Fridtjof Nanssen*) to carry out this type of work in developing countries. This vessel is presently working mainly off Angola, Namibia, South Africa, Mozambique, Morocco, Mauritania and Senegal, thus covering two of the main upwelling regions of the world.

In acoustic surveys, numerous behavioural patterns have long been known to lead to various problems when correctly evaluating fish biomass (Olsen, 1990; MacLennan and Simmonds, 1992; Fréon *et al.*, 1993). Fréon and Misund 1999 identified the advantages and disadvantages of various assessment methods (Table 1.1). The following examples of behavioural biases may be of importance when evaluating the biomass of sardinella:

- (i) **Shadowing effect** - Toresen (1991) quantified the absorption of acoustic energy in relation to fish density in herring schools and observed that increased fish density was associated with loss in bottom signal intensity, thereby providing indirect evidence of shadowing at high fish densities. Additionally, experimental comparisons of small (12cm) and large (35cm) fish revealed that shadowing effects increase at much higher densities of smaller fish (Røttingen, 1976).
- (ii) **Lateral avoidance** – Fish are often scared by the research vessel and try to avoid it; the density within the beam may therefore be diluted in comparison with the average density in the area. This dilution is likely to be most serious for fast-swimming fish in the upper layers. Studies summarized by Olsen (1990) show significant reductions in echo energy from scattering layers of fish just as a research vessel passes a stationary echo sounder.
- (iii) **Variation in tilt angle** (day/night, vertical avoidance) and also the **target strength estimate (TS)** - In addition to possible problems associated with shadowing in dense schools, the question arises whether the average target strength (TS) of fish remains constant when fish change their depth during

diel vertical movements. This is a behaviour commonly associated with changes in aggregation (Dembiski, 1971; Blaxter, 1975; Woodhead, 1966).

- (iv) **Species mixing in schools** – An accurate hydro-acoustic assessment of biomass of a particular species has been limited by the difficulty in objectively differentiating taxonomic groups of sound scatters. Identification methods most commonly used are based on trawl sampling in close proximity to the acoustic targets and on visual interpretation of the echograms based on previous knowledge of the species shoaling patterns. In many cases, however, these techniques have not enabled objective discrimination between co-occurring fish species (Rose and Leggett 1988). Species mixing in aggregations may also lead to errors in proportion to the measured acoustic energy being allocated to a particular species.
- (v) **Near surface shoaling** - Acoustic sampling in the water column is restricted to the volume below the transducer. Fish above the transducer are not assessed. This is a potential source of error whether the transducer is hull-mounted or mounted in a towed body. In this regard, diurnal variation in behaviour of pelagic organisms has been well documented (Hoar and Randall, 1978; Weston and Andrew, 1990). If extensive diurnal vertical movement does occur, the chances of not detecting fish close to the surface at night would lead to underestimation of the biomass.
- (vi) **Patchiness**- Schooling fish tend to aggregate in very high densities covering very small areas. This decreases the probability of encountering these high-density areas during a large-scale survey. Survey reliability therefore largely depends on sampling a sufficient number of these dense areas (Aglen, 1989).
- (vii) **Bottom or near bottom affinities** - The ability of the acoustic system to sample near the bottom is dependent on the extent of the “acoustic dead zone” (Ona and Godø, 1990), which is determined by parameters such as

pulse length, the transducer, beam-width and the distance between the transducer and the seabed. If fish were to migrate too close to the bottom, the biomass may only be partially estimated.

Table. 1.1. Comparison of the advantages and disadvantages of various assessment, adapted from Fréon and Misund 1999. Table 11.1

Behavioural pattern	Age structured analysis (ASA)	Surplus production models	Acoustic survey	Gear survey	Aerial survey
Habitat					
Selection					
Short term	0	0	++ or --	+ or -	+ or -
Circadian	0	0*	++ or --	++ or --	from - to ---
Seasonal	0	0*	+ or -	++ or --	from - to ---
Yearly	+ or -	+++ or ---	0	++ or --	from - to ---
Aggregation	0	+++ or ---	++ or --	++ or --	+ or -
Avoidance	0	0	--	---	0
Attraction/association	0	++	0	++	0
Learning	-	-	0	-	0

+ over-estimated, - under-estimated,

* except if, inter-annual changes in fishing patterns are not taken into account,

0 no results

1.5 AIM OF THE STUDY

Based on the above-mentioned shortfalls, the aim of this study is:

1. to investigate the hypothesis that fish behavioural aspects of *Sardinella spp* (schooling behaviour) may lead to under-estimation of fish abundance when assessed by acoustic methods. During the day, one of the factors of under-estimation is the lateral avoidance of the fish, which occurs when the fish are in schools. The density within the beam may therefore be diluted in comparison with the average density in the area. This dilution is likely to be most serious for fast swimmers in the upper layers.
2. to investigate the hypothesis that diel variability in behaviour affects acoustic estimates of sardinella. It is well known that during the day the spatial variability is higher, owing to the aggregation of fish in schools. The frequency distribution of acoustic density is therefore expected to be very different between day and night. This pattern has long been known to lead to various difficulties in correctly assessing fish abundance.
3. to investigate the stock characterisation: what are the biological characteristics (linked with day-night and migration aspects) of the stock? Better knowledge of stock characterisation and understanding of behavioural aspects of sardinella (e.g. schooling near the surface, migration, feeding behaviour) will represent an important scientific contribution and will improve management of important pelagic stocks of sardinella off Angola.
4. to improve pelagic assessment methodology that will contribute to sustainable management of *Sardinella spp.* off Angola. In the short to medium term sonar estimates of absolute abundance in the region (Angola, Namibia and South Africa) will tend to be very imprecise, and should be used more as indices of abundance (e.g. as relative estimates) to detect trends and support other data than as absolute estimates.

CHAPTER 2. REVIEW OF SOME ASPECTS OF THE BIOLOGY OF *Sardinella aurita* and *S. maderensis*.

2.1. INTRODUCTION

Sardinella spp are widely distributed on both sides of the Atlantic as well as in the Indo-Pacific and is one of the dominant genera in terms of the total world fishery landings (FAO, 1986). They are internationally traded as food for both human and animal consumption as well as industrial products such as fertiliser and paints (Blaxter and Hunter, 1982). Sardinellas and other clupeoids make a major contribution (80%) to marine protein resources (Blaxter and Hunter, 1982).

The highest catches of sardinellas are found in the Western Pacific (Figure 2.1). The Southeast Atlantic, where Angola is included is the area with the third largest reported catches of sardinella. In Angola, fish is the major source of animal protein available (about 40 % of the total nations protein and up to 90 % in the coastal areas) and the average consumption of fish per capita is 19 kg/year reaching nearly 30 kg/year in the coastal zones of Angola. The contribution of sardinellas as a source of animal protein is about 10% and up to 20% in the rural areas due to the affordable price for poor people (Alberts *et al.*, 1990).

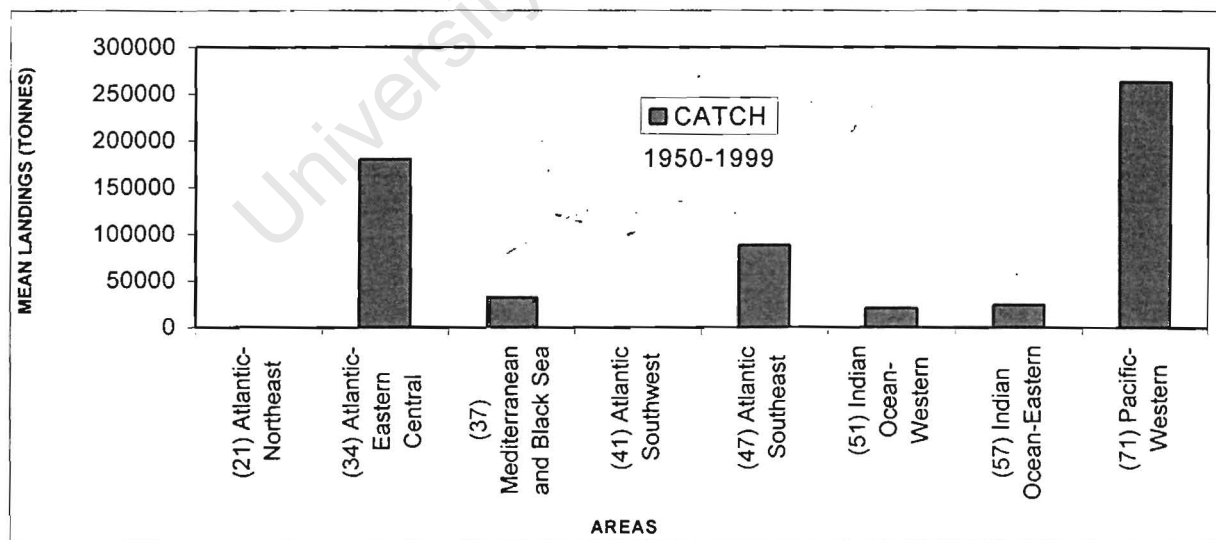


Figure 2.1. Yearly mean world landings of *Sardinella spp* in tonnes of the major fishing areas for statistical purposes. [Source: FAO Yearbook, 1999. Vol. 88/1].

2.1.1 *Sardinella aurita* (round sardinella)

Synonyms

These are regarded as separate species because they are located in the two major areas of distribution (Table 2.1):

Major area	
Eastern Atlantic	Western Atlantic
<i>Clupea allecia</i> Rafinesque, 1810	<i>Sardinella anchovia</i> Val., 1847
<i>Alosa senegalensis</i> Bennett, 1831	<i>Sardinia pseudohispanica</i> Poey, 1860
<i>Clupea aurovittata</i> Swainson, 1838	<i>Sardinella pinnula</i> Bean, 1912
<i>Meletta mediterranea</i> Valenciennes, 1847	<i>Sardinella aurita</i> Whitehead, 1973
<i>Clupea venulosa</i> Steinitz, 1927	
<i>Sardinella aurita terrasae</i> Lozano and Rey, 1950	
<i>Sardinella aurita</i> Svetovidov, 1952	
<i>Sardinella aurita</i> var. <i>mediterranea</i> Rossignol, 1959	

The scientific name used universally in the two major areas now is *Sardinella aurita* (See Table 2.1). The FAO common name is round sardinella.

Distribution and migrations

Pioneer studies in different areas on the geographical distribution of round sardinella were conducted by several authors (Furnestin, 1952; Devold, 1958; Ben-Tuvia, 1960; Regan, 1971; Ghéno and Campos Rosado, 1972; Ghéno, 1975, Boěly, 1980; Bebars, 1981; Boěly *et al.* 1982 and González, 1985). Round sardinella is found on the coastal areas of the Atlantic, in the Mediterranean area and the Indian ocean between the latitudes 40°N and 40°S as well as the longitudes 90°W-150°E, constituting a high population in coastal upwelling regions (Furnestin, 1952) (Figure 2.2). *S. aurita* is known to be associated with upwelling areas.

Round sardinella is found along the African coast, from the Mediterranean to Cape Frio (18° S).

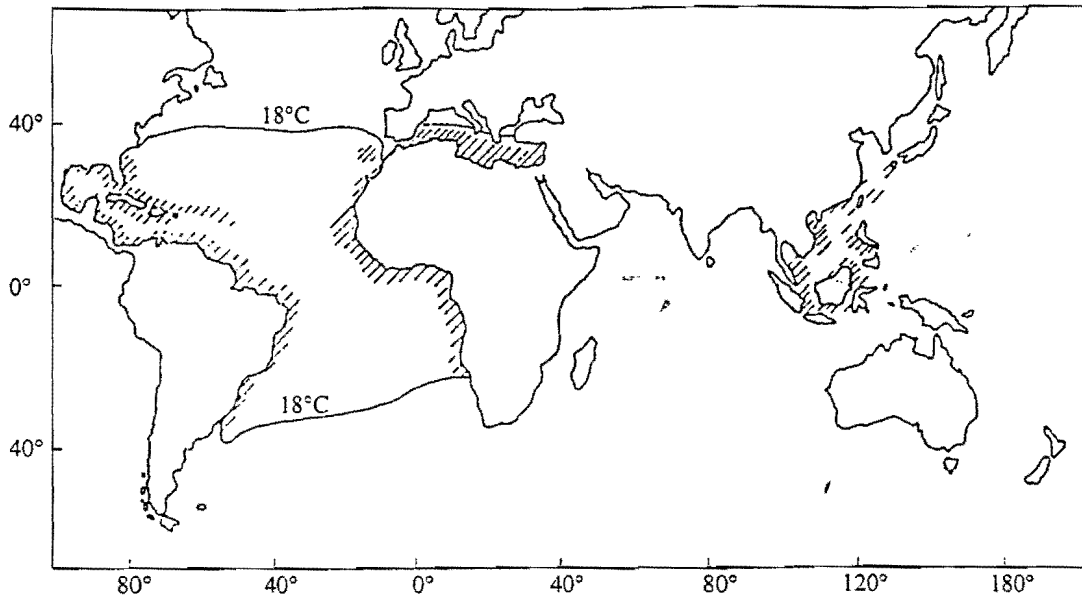


Figure 2.2. Distribution of round sardinella - *S. aurita* (after Ben-Tuvia, 1960 and Furnestin, 1952). Hatched areas indicate known distributions.

Little work has defined the distributions of sardinella stocks. Some studies (FAO, 1973; Conand, 1977; Boëly *et al.* 1978 and Boëly and Fréon, 1979) on the Eastern Atlantic indicated that round sardinella are concentrated in three sectors (Figure 2.3):

- a) Off north-west Africa from southern Morocco (from about 32°N) to Sierra Leone (about 8°N).
- b) In the Gulf of Guinea (8°N), mainly between Ivory Coast and Ghana.
- c) In the tropical southern region from Gabon (0°S) to Angola (17° 15'S).

Between the three sectors, there are not important fishing areas for sardinella. Each of these three important areas of concentration are probably occupied by distinct populations, as the current system does not favour species exchange (FAO, 1973). Variable genetic markers are a prerequisite for stock and population structure studies (Ryman *et al.*, 1984; Allendorf *et al.*, 1987; Carvalho, 1993). However, an unusually low level of genetic diversity was found by Chikhi *et al.*, 1998 from the samples collected in Venezuela (Isla Margherita) and in the three areas (Ghana, Ivory Coast and Congo) of the African coast. This makes the description of population structure difficult but is of fundamental interest because of the crucial role of genetic diversity as the basis of evolutionary change (Chikhi *et al.*, 1998).

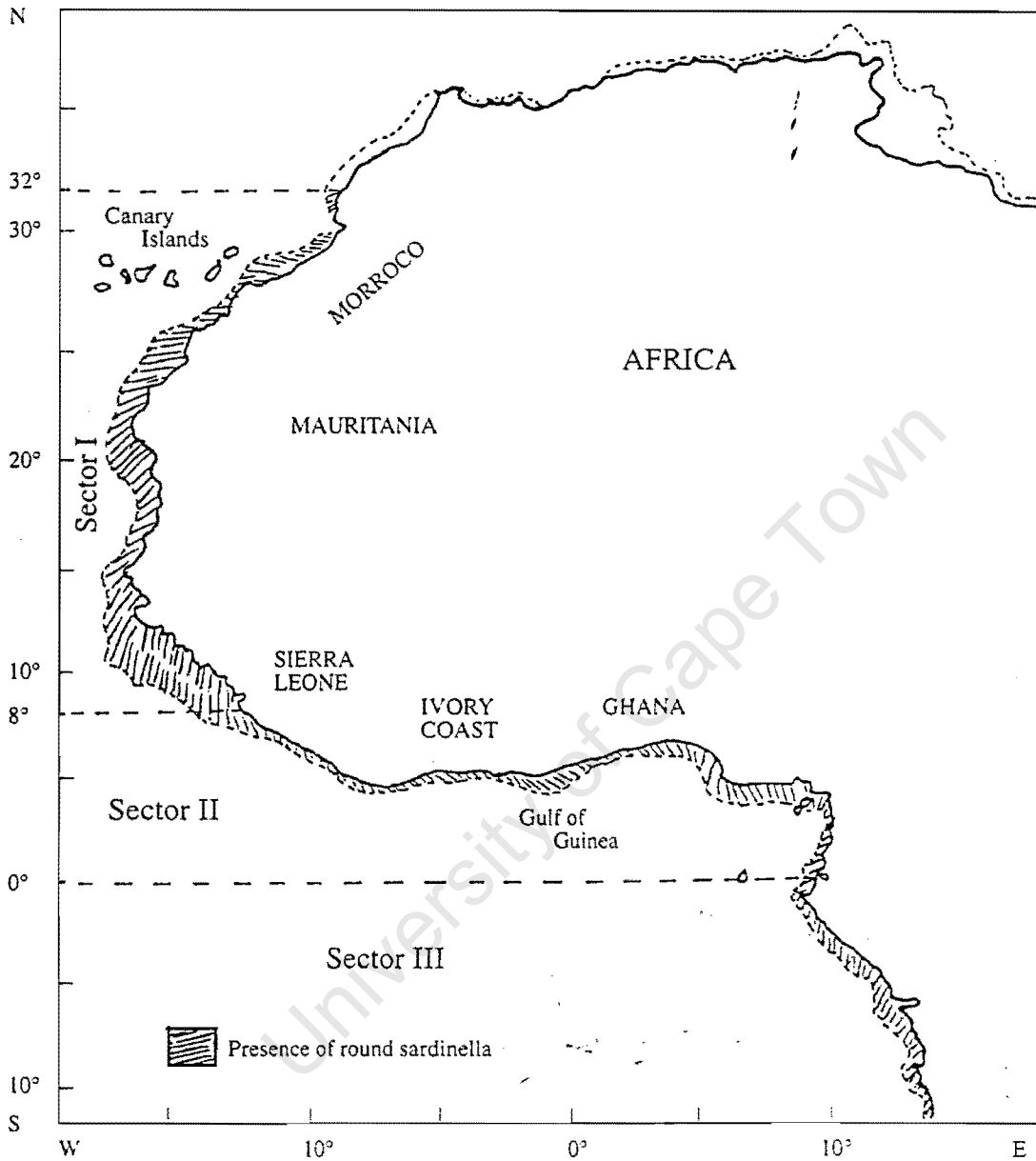


Figure 2.3. Spatial distribution of round sardinella along the African coast (after Conand, 1977). Broken lines indicate three studied sectors.

In the first (32°N) and second sector (8°N), the migratory cycle of adults may be summarised as follows:

- a) Period of widespread distribution in the open sea north of Morocco (from October to January),
- b) A phase of rapid migration toward the south in February,
- c) A pre-spawning concentration phase in March-April in the southernmost part of their habitat,
- d) Phase of northward migration as far as 24° N to 25° N, with spawning, from May to September (Böely *et al.*, 1978).

The last sub-region is the focus of this study. In this sub-region, the southernmost extension of *S. aurita* is normally the Cunene-River (17° 15'S), but in years with an anomalously large southern movement of the Angola front it has been observed as far south as central Namibia (23°S). From south of Gabon to south of Angola, there seems to be only one stock (Ghéno, 1975). In the last sector the adults move seasonally between Gabon and south of Angola following the oscillations of the southern inter-tropical front (Ghéno, 1975). Despite this, there is limited knowledge of the distance of the migrations of *S. aurita*.

The juveniles apparently colonise the entire coastal strip (down to 50 m depth), from the Bay of Tigres (Angola) to Cape Lopez (Gabon), (Ghéno and de Campos Rosado, 1972). Results of *Dr Fridtjof Nansen* surveys in the sub-region have indicated that adults are found at depths from 50-200 m and in some areas sardinella were found well offshore (over depths of 600 m) (Anon, 1994). Therefore, the stratification toward the open sea with age is not clear between the juveniles and adults of *S. aurita*.

The juveniles are mostly found in Congo-Gabon area, while the adults are located mostly along the Angolan coast with higher concentration from the south of Cabinda to the Bay of Tigres (Ghéno and de Campos Rosado, 1972). In Angola, the survey results have demonstrated clear along shore movements of the adults with seasonal changes (Anon, 1994). The distribution follows the movement of the Angola/Benguela front. In the warm season the adults are found to the south moving north in the cold season. The front is an approximate boundary of its southern limit.

Diet and feeding behaviour

Clupeoforms are usually divided into four groups (macrophagists, particulate-feeders, intermediate or mixed feeders and filter feeders) based on anatomical and behavioural adaptations (Table 2.2; James, 1988), which reflect an increase in specialisation towards microphagy. *S. aurita* is a filter feeder, its food is filtered through the gill rakers and it takes its food not by grabbing it, but by swimming with an open mouth (Probatov and Pupyshev, 1969). *S. aurita* is an active filter feeder on phytoplankton and zooplankton (Postel, 1955; Maiguy and Doutre, 1958; Komarovskiy, 1958; Prosvirov and Ryabikov, 1962; Pham-Tuoc and Szypula, 1973; Nieland, 1982 and Medina-Gaertner, 1985).

Many authors indicate that the most important prey items of *S. aurita* are mostly copepods (*Calanoides carinatus*, *Eucalanus spp* and *Arcartia spp*), dinoflagellates (*Ceratium*, *Peridinium 1*, *Peridinium 2*, *Prorocentrum* and *Dinophysis*), and diatoms (*Rhizosolenia*, *Chaetoceros*, *Navicula*, *Chaetoceros*, *Nitzschia*, *Melosira*, *Lauderia*, *Asteromphalus*, *Skeletonema*, *Lauderia* and *Thalassiosira*).

In Senegal, Nieland (1982) showed that in coastal waters (shallower than 10 m depth) the most important item found in the stomach was organic detritus (95%). The rest of the diet was composed of zoo- and phytoplankton. The role of detritus and its nutritive value (bacterial filter) remain unclear. However, toward the open sea (> 50 m depth) most of the diet was dominated by phytoplankton (96%) with small amounts (4%) of zooplankton.

Off the Ivory Coast, Dia (1972) in a detailed study of the stomach contents of *S. aurita* found the diet was dominated (50%) by copepods (*Calanoides carinatus*) and the rest by other species of zooplankton (e.g. ostracods, chaetognaths, and salps). Off the Congo coast, Ghéno (1975) reported that during the cold season the main food found in the stomach contents were copepods (e.g. *Calanoides carinatus*, *Arcartia spp*). Therefore the diet of *S. aurita* is varied and depends on the different plankton concentrations.

In Senegal, Nieland (1982) stated that the feeding behaviour of round sardinella depends mainly on the plankton composition in the specific area (the opportunistic theory). Medina (1985) partially refuted "the opportunistic" theory of Nieland (1982) on the feeding behaviour of *S.*

aurita. She showed that the feeding behaviour of round sardinella is relatively specialised. No studies have been made in Angola on the diet and feeding behaviour of the sardinellas.

Table 2.2. Trophic classification of clupeoids and their diets (James, 1988) [adapted to current knowledge].

Classification	Examples	Diet	Reference
Microphagists	<i>Megalops</i> and <i>Elops</i> <i>spp</i>	Planktonic and benthic diatoms	Manooch , 1973; Blaxter and Hunter, 1982
Particulate- feeders	<i>Clupea harengus</i> <i>Etrumeus whiteheadi</i> <i>Sardinops sagax</i>	Zooplankton	Wallace-Fincham, 1987; Vander der Lingen, 1994
Intermediate (mixed) feeders	<i>Sardinops caerulea</i> <i>Engraulis mordax</i> <i>Engraulis capensis</i>	Zooplankton	Anglescu, 1982; James, 1987
Filter-feeders	<i>Bevoortia tyrannus</i> <i>Sardinops sagax</i> <i>S. aurita</i> <i>S. maderensis</i>	Mainly diatoms, some detritus and copepods Phytoplankton and zooplankton Phytoplankton and zooplankton Phytoplankton and zooplankton	Pham-Thuoc, 1973; Nieland, 1982; Medina-Gaertner, 1985 and Vander der Lingen, 1994

Growth

For round sardinella several studies on growth were made relying both on length composition analysis and on the reading of growth marks on scales and otoliths. However, in different tropical and sub-tropical regions there are limitations when using these methods which rely on reading of growth marks on scales and otoliths (Boëly and Fréon, 1979). The growth studies of clupeoids in the tropical areas have been very difficult. Firstly, studies based on reading of growth marks from hard parts (e.g. scales, otoliths) have led to inconclusive results because not all the growth rings can be clearly distinguished. This has been attributed to the weak seasonal variations of the physical and biological environment, and often the presence of two marks per year. Secondly, interpretation of results based on length frequency distributions is also complex due to protracted reproduction periods.

Information is available on growth from length-frequency analysis between 22° S and 28° S along the Brazilian coast (Richardson and Sadowski, 1960; Vazzoler *et al.*, 1982). From Eastern Venezuela, the growth studies have been based on readings of the year rings in scales (Heald and Griffiths, 1967), and otoliths (González, 1985), and length frequencies (Mendoza *et al.*, 1994).

The growth studies along the African coast have been based on readings of the growth rings in scales (e.g. Pham Tuoc and Szypula, 1973; Ghéno, 1975; Scherbich, 1981 and Boëly *et al.* 1982). Tables 2.3, 2.4 and 2.5 show Von Bertalanffy growth parameter estimates (L_{∞} , K , ϕ' and t_0) for *S. aurita* from various regions of the world. There were marked differences between the growth studies based on hard structures and on length-frequency analysis in Eastern Venezuela. The growth estimates made by Heald and Griffiths (1967) and González (1985), were based on growth marks in hard structures and indicated that *S. aurita* has relatively slow growth ($L_{\infty} = 24.0$ cm and $K = 1.05 \text{ year}^{-1}$). In contrast, Mendoza *et al.* (1994) in Eastern Venezuela based their results on length-frequency analysis and found their results ($L_{\infty} = 26.6$ cm and $K = 1.26 \text{ year}^{-1}$) comparable with the study done off west Africa coast by Ghéno (1975).

The results indicate that the growth of this species is not homogeneous in the areas where exploitation occurs. Holt (1960) found that for the genera *Sardinella* the values estimated for the L_{∞} and K parameters of the best-fit growth equations increase with species that occur nearer the equator. The studies made along the African coast (e.g. Pham-Thuoc *et al.*, 1973; Ghéno, 1975; Boëly, 1975 and Scherbich, 1981) have not indicated significant differences in growth between

females and males. No study was done in Angola to examine differences in growth between females and males of sardinellas.

Table 2.3. Individual stock and average Von Bertalanffy growth parameter estimates for *Sardinella aurita* from the northern, central, eastern and southeastern Atlantic.

Stock	L_{∞} (TL, cm)	K (year ⁻¹)	t_0 (years)	ϕ'	References
Angola	43.3	0.28	- 0.5	2.72	*Scherbich (1981)
Off Congo	26.0	1.21	- 0.02	2.91	*Ghéno (1975)
Mauritania	40.7	0.33	NG	2.74	*Pham-Thuoc <i>et al.</i> , 1973
Tunisia	29.0	0.36	-0.92	2.48	*FAO, 1982: Rapp. Pêches (266):125 p., FAO, Rome
Senegal	30.6	1.21	- 0.06	3.05	Boëly <i>et al.</i> , 1982

* Values of ϕ' were calculated from $\phi' = \log K + 2 * \log L_{\infty}$ (Pauly and Munro 1984).

ϕ' = growth performance index

TL-Total length (cm), NG-Not given

* = based on reading of growth marks on scales

Table 2.4. Estimation of best growth parameters estimates for *S. aurita* (also called *S. brasiliensis*) from the South Eastern Brazilian coast, using length-composition analysis.

Author (s)	L_{∞}	K (year ⁻¹)	t_0 (years)	ϕ'
Richardson et al, 1960	25.4	0.31	-2.00	2.30
Santos & Frantzen, 1965	24.3	0.50	0.00	2.47
Matsuura, 1977	24.4	0.44	0.00	2.42
Rijavec <i>et al.</i> , 1977	33.5	0.87	0.00	4.98
Matsuura, 1983	26.0	0.62	-0.59	2.62
Average	26.7	0.55	- 0.52	

* Values of ϕ' were calculated from $\phi' = \log K + 2 * \log L_{\infty}$ (Pauly and Munro 1984).

Table 2.5. Growth parameter estimates for *Sardinella aurita* from eastern Venezuela (1967-1989, after Mendoza *et al.*, 1994). [derived from the reading of growth rings on scales and otoliths].

Year	L_{∞} (cm; TL)	K (year ⁻¹)	ϕ'
1967	24.0	1.05	2.78
1968	24.3	1.29	2.88
1971	27.5	1.20	2.96
1972	27.3	1.50	3.05
1973	26.6	1.40	3.00
1975	28.5	1.75	3.15
1976	26.2	1.45	3.00
1977	27.4	1.02	2.88
1978	24.0	1.40	2.91
1979	27.8	1.04	2.91
1981	23.8	1.04	2.77
1982	29.0	1.25	3.02
1983	25.2	1.20	2.88
1984	28.5	1.10	2.95
1985	28.8	1.10	2.96
1986	26.6	1.35	2.98
1987	26.0	1.40	2.98
1988	27.2	1.68	3.09
1989	26.0	1.10	2.87
Average	26.6	1.26	2.95

* Values of ϕ' were calculated from $\phi' = \log K + 2 * \log L_{\infty}$ (Pauly and Munro 1984).

Reproduction

Clupeoid pelagic fish are general highly fecund animals and often serial spawning occurs over protracted periods. Californian anchovy may spawn 20 times in a season (Hunter and Leong, 1981); Chilean sardine spawn every 6-7 days (Oliva *et al.*, 1989); while the Chesapeake Bay anchovy spawned 54 times in 1988 (Luo and Musick, 1991).

The spawning activity of *S. aurita* is reported to occur with the warming-up of the surface waters on the coastal waters of the Atlantic, Mediterranean area and Indian Ocean. Roy *et al.* (1992) reviewed the studies on spawnings of *S. aurita*, in several areas along the African coast. The spawning activity occurs in different months during the year with several minor and one major peak. Spawning occurs both during day and night, in places where the continental shelf broadens or in coastal indentations such as a bay or downstream of a cape, at water temperatures of 22°C-25°C and salinity of 32-38 psu (Roy *et al.*, 1992).

According to Conand and Fagetti (1971), *S. aurita* has two spawning peaks, which occur in periods of summer (May-June) and winter (October-November). In the Senegal-Mauritania region spawning of *S. aurita* occurs throughout the year with a peak between June and September (Boëly *et al.*, 1978). Those results are very similar to those found for sardinellas in Congo-Gabon region by Dessier and Pianet (1970). In Angola, the spawning of *S. aurita* is continuous throughout the year with a peak in May (Lukashev, 1976).

The size at first maturity seems to vary according to the populations of *S. aurita* in the different areas. Results reported in different areas are given in the Table 2.6. Fontana and Pianet (1973) found in the Congo area (3° 30' -5° 00' S) that females of *S. aurita* have started their sexual cycle (ovary stage III) at 21 cm (TL). Off Gabon, north of 2° 30' S, the same authors found that the size of females (TL) at maturity was much smaller (about 14 cm) than further south. In Angolan waters, the females of *S. aurita* have started their sexual cycle (ovary stage III) at 23 cm (TL). The differences between areas is linked to the difference in the maximum size of this species according to the area, with longer size in nutrient richer areas, as outlined by Fréon *et al.*, 1997.

Many authors (Korringa, 1947, Barnewell, 1976, Berry, 1986, Christy, 1986, Gibson 1992, Leatherland *et al.*, 1992 and Morgan, 1995) suggested that there is a link between spawning and feeding activities. The marine environment fluctuates physically on a variety of time scales, but principally within diurnal, tidal, lunar and seasonal cycles. These cycles often coordinate behavioural, physiological and reproductive activity within species. The pseudosynchrony between these cycles and the reproduction cycle ensure that sexual product release hatching, feeding activity can be accomplished at most appropriate times of day, month or year for the survival of the species.

Roy *et al.* (1992) suggested that the progressive shift in time of spawning along the African coast is the result of a seasonal *trade-off* between embryo survival and successful hatching during the periods of submergence. From the literature, food availability for larvae is related to biological dynamics (primary production) up to a point where the biological processes are disturbed by physical processes (turbulence generated by wind mixing). Roy *et al.* (1992) showed that along the whole African coast the timing of the spawning is associated to the wind intensity with an optimal reproductive windows at around 5-6 m.s⁻¹ which is the best trade off between vertical advection, enrichment by the upwelling and turbulence (wind mixing). As a result, this timing due to different wind regimes is different from Morocco to Angola.

Table 2.6. Size at first maturity of *S. aurita* from various areas, adapted from FishBase, 2002.

Length at first maturity	Sex of fish	Country	Locality
TL 12.0 cm	female	Tunisia	Tunisia
TL 13.0 cm	male	Tunisia	Tunisia
NG 21.0 cm	unsexed	Congo Rep.	Pointe Noire
FL 19.5 cm	unsexed	Ivory Coast	NG
FL 20.0 cm	unsexed	Senegal	Senegal
NG 16.0 cm	unsexed	Spain	Western Mediterranean
NG 17.0 cm	unsexed	Brazil	Brazil

TL- Total length, FL- Fork length and NG- Not given

Schooling behaviour

Clupeoid fish normally aggregate in dense schools during the daylight hours and reassemble in looser shoals during the dark hours at night (Blaxter and Hunter, 1982; Fréon and Misund, 1999). Structural and functional aspects of clupeoid schools have been investigated both in controlled conditions in aquaria and in the field. In nature, clupeoid schools are organised by similar sized individuals (Fréon, 1991), and Pitcher *et al.* (1985) also observed that individuals preferred neighbours of similar size.

Sardinellas are found dispersed in the surface layer during the night and in deep waters. Occasionally, under the influences of some factors (e.g. light threshold, bioluminescence) sardinellas school during the night to a definite limit of time, after which the schools begin to disperse (Probatov and Pupyshev, 1969).

Komarovsky (1958) suggested that during the day the schooling behaviour is associated with feeding along the Israeli coast. In contrast, Probatov (1959) near the west coast of Africa reported that the schooling behaviour occurs during moonlight nights and that sardinellas are frightened by the motion of the ship and the fish in the zone of the disturbance immediately form schools.

In tropical and subtropical areas, many species have been observed mixed in a single school or an assemblage of fish (review in Fréon and Misund, 1999). In some cases two or more species are mixed to a definite time, but most of the time they segregate either in the horizontal plane (Hobson, 1963) or in the vertical one (Parrish, 1989). Different species gather in a single school to benefit from the advantages of larger schools, especially in terms of reduced mortality by predation and increased food detection (Parrish, 1989). Less abundant species in a mixed school can be “trapped” because they could be forced to follow the migratory route and the habitat selection of the more abundant species in this school (Bakun and Cury, 1999). In Angola, surveys have revealed that the clupeids *Sardinella aurita* and *S. maderensis* form schools together in the coastal waters. *Sardinella* schools appear at surface during daytime between sunrise and sunset (06 h 00 -18 h 00 local time) and disperse at night, sometimes forming looser shoals (Misund *et al.*, 1998).

2.1.2 *Sardinella maderensis* (flat sardinella)

Synonyms

These are separated by country (Table 2.3):

Synonyms	Country
<i>Sardinella granigera</i> Valenciennes, 1847	Egypt
<i>Alausa eba</i> Valenciennes, 1847	Gorée, Senegal
<i>Pellonula modesta</i> Fischer, 1885	Elobey, Equatorial Guinea
<i>Sardinella cameronensis</i> Regan, 1917	Cameroon
<i>Sardinella maderensis</i> Ben-Tuvia, 1960; Whitehead, 1967	NG

NG-not given

The scientific name used universally from the Mediterranean area (southern and eastern parts, also penetrating Suez canal) to the south of Angola since two centuries is *Sardinella maderensis*. The FAO name is flat sardinella or Madeiran sardinella.

Distribution and migrations

Some well-documented literature is available on the general distribution of *S. maderensis* (Ben-Tuvia, 1960; Boëly and Fréon, 1979; Binet, 1988; Cury and Fontana, 1988; Marchal, 1991).

Along the African coast, *S. maderensis* is found only from the Mediterranean Sea to the Atlantic (Figure 2.4). It is found in areas similar to those of *S. aurita*, from Mauritania (26° N) to the Central area of the Angolan coast (12° 30' S). *S. maderensis* is a more coastal and euryhaline species, predominantly found closer to the coast and in estuarine habitats. It prefers warmer waters (> 25° C) and salinity below 35 psu. Its distribution is less influenced by the water temperature than that of *S. aurita* (Fontana and Pianet, 1973).

Several authors (Ben-Tuvia, 1960; Boëly and Fréon, 1979; Binet, 1988; Cury and Fontana, 1988; Marchal, 1991) have reported that there is no evidence of large migratory movements in either the young or the old fish from Mauritania to Congo. This species is coastal and displays limited migration (Cury and Fontana, 1988). Off Ivory Coast, Congo and Ghana the migrations are also not very extensive (Mendelsohn and Cury, 1987).

Similar to *S. aurita*, the juveniles are concentrated in the coastal waters from where they gradually move off toward the open sea, as they grow older. However, the stratification toward the open sea with age is clear (Anon, 1994). Along the African coast *S. aurita* and *S. maderensis* are often found together.

Diet and feeding behaviour

The diet and feeding behaviour of *S. maderensis* have been reported by earlier authors, who have made similar studies of *S. aurita* (Postel, 1955; Ben-Tuvia, 1960, Prosirov and Riabikov, 1962; Boëly and Fréon, 1979; Nieland, 1982 and Medina-Gaertner, 1985). They found that *S. maderensis* is also a filter feeder, feeding mostly on phytoplankton and zooplankton (copepods: *Calanoides carinatus*, *Eucalanus spp* and *Arcartia spp*), dinoflagellates (*Ceratium*, *Peridinium* and *Dinophysis*), and diatoms (*Rhizosolenia*, *Chaetoceros*, *Navicula* and *Thalassiosira*).

According to most authors (Postel, 1955; Ben-Tuvia, 1960, Prosirov and Riabikov, 1962; Boëly and Fréon, 1979; Nieland, 1982 and Medina-Gaertner, 1985), *S. maderensis* has the same diet and feeding behaviour as *S. aurita* along the African coast (Table 2.2). No studies have been made on the diet and feeding behaviour in Angola.

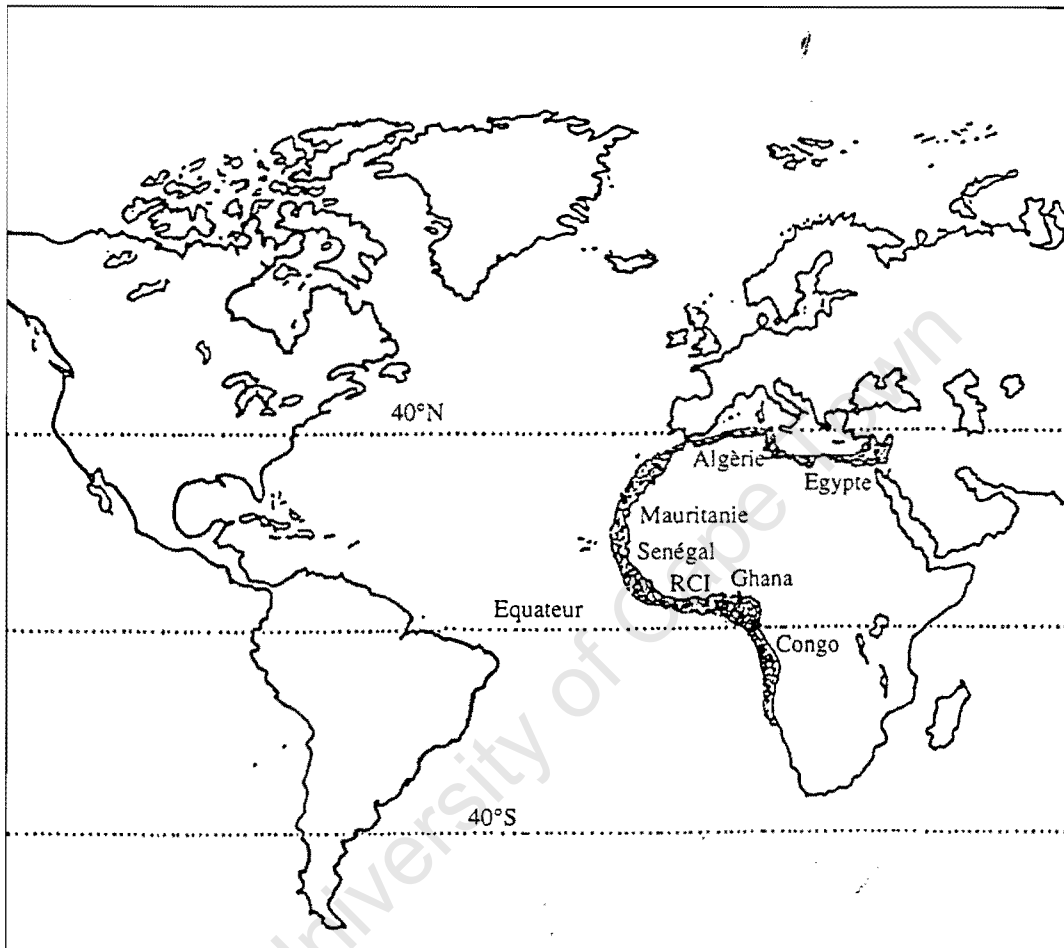


Figure 2.4. Distribution of flat sardinella, *S. maderensis* (after Whitehead, 1985). Hatched areas indicate known distributions.

Growth

Growth parameters of *S. maderensis* have been estimated in Congo (Ghéno, 1968), Nigeria (Marcus, 1984), Senegal (Postel, 1955; Samb, 1988), Cameroon (Djama *et al.*, 1989) and recently in Angolan waters (Fossen, 1998 unpublished). In the Congo area growth has been determined from reading growth marks on scales (Ghéno and Le Guen, 1968). For the rest of the areas, growth has been estimated from length frequency data (Table 2.7). Based on the results of growth parameters, the Angolan species has a larger L_{∞} (from 19 to 40 cm) than other areas. However, the growth performance index obtained in Angola waters appears to be quite similar to those found in other areas.

The studies made along the African coast have not indicated significant differences in size between females and males as *S. aurita* (Ghéno and Le Guen, 1968; Marcus, 1984 and Samb, 1988).

Table 2.7. Estimates of growth parameters of *S. maderensis* along the African coast.

Stock	L_{∞} (TL-cm)	K (year ⁻¹)	t_0 (years)	ϕ'	References
Angola	42.4	0.88	3.2	3.19	Fossen (1998)*
Cameroon	32.5	0.59	NG	2.79	Djama <i>et al.</i> (1989)
Congo	24.9	1.00	NG	2.79	Ghéno and LeGuen (1968)
Sénégal	39.5	0.45	NG	2.85	Samb (1988)
Nigeria	37.5	0.34	2.7	2.68	Marcus (1984)

*Unpublished

TL-Total length (cm), NG-not given

* Values of ϕ' were calculated from $\phi' = \log K + 2 * \log L_{\infty}$ (Pauly and Munro 1984).

Reproduction

From the Mediterranean Sea to the Atlantic, *S. maderensis* reproduces throughout the year, however this activity increases during the upwelling seasons. Three main spawning areas are found along the continental shelf of the Atlantic, namely:

- a) Off Morocco: south of Cap Spartel (36°-32° N), from Cap Ghir to Cap Juby (30°-27°N) and from Cap Bojador to Cap Barbas (26°-22° N) (Conand, 1975, Domanevsky and Barkova, 1976; Belvèze, 1991),
- b) Off Mauritania and Senegal: on the Arguin Bank south of Cap Blanc (18° 30'N-21° N) and from the Cap Vert peninsula to the coast of Sierra Leone (Conand and Fagetti, 1971; Boëly *et al.*, 1982),
- c) Off the Congo and Angolan coast (Ghéno and Campos Rosado, 1972; Fontana and Pianet, 1973; Lukashev, 1976), the main spawning area is located around Mayoumba (3°30' S).

On the Senegalese coast spawning occurs in coastal waters and the sexual cycle of reproduction is intense from February to October with a peak between May and July (Conand and Fagetti, 1971; Boëly *et al.* 1978).

In the Congo area, Fontana and Pianet (1973) concluded from the analysis of the data on the gonadosomatic index that spawning in this species takes place throughout the whole coastal area from Gabon to Cabinda (Angola), with a peak in winter (June to September). In Angolan waters spawning takes place throughout the year from South of Lobitô (13° S) to Cabinda (5° 00'S), with a maximum spawning in May (Lukashev, 1976). From these findings, it may be concluded that the spawning activity is continuous throughout the year with a maximum reproductive peak which occurs from May to September in three main spawning areas.

Little is known about the length at maturity of *S. maderensis* in two sectors (Morocco-Cap Barbas and Mauritania-Sierra Leone) due to the lower catch composition than *S. aurita* in these areas. However, Fontana and Pianet (1973) in the Congo area revealed that all females of *S. maderensis* of more than 20 cm have started their sexual cycle (ovary stage III).

Schooling behaviour

According to several authors (Blaxter and Hunter, 1982; Pitcher *et al.* 1985; Parrish, 1989; Fréon, 1991; Misund *et al.* 1998 and Fréon and Misund, 1999) as referred in the *S. aurita* section, both species are often found schooling together along the African coast. The studies made along the African coast have not indicated differences in schooling behaviour between both species (Probatov, 1959; Probatov and Pupyshev, 1969; Fréon *et al.* 1992 and Misund *et al.*, 1998). The analysis of echograms will provide detailed morphological descriptions of fish aggregating together with characteristics of their habitat (Petitgas and Levenez, 1996).

SUMMARY

The two species, round sardinella (*Sardinella aurita*) and flat sardinella (*S. maderensis*), are often found together. However, *S. aurita* has a broader distribution latitudinally and offshore than *S. maderensis*. Most round sardinella are found in upwelling regions due to the link between its life cycle and the process of upwelling. Flat sardinella is identified as a species of limited migration and no cases of wide scale migrations are known. However, the migratory cycle of adults of round sardinella is known along the Eastern Central Atlantic.

The two species of sardinellas are zoo- and phytoplankton filter feeders of which the main diet is zooplankton. Both species are relatively specialised in their diet. Growth studies based on reading of growth marks on scales and otoliths indicate that growth of round sardinella is rapid, reaching 90% of L_{∞} in about one year.

The spawning activity for the two species is continuous throughout the year with a maximum reproduction from May to September along the African coast. Many questions are still unanswered regarding the reproductive period in some areas and some of the strategies used by sardinellas.

CHAPTER 3. EXPLOITATION, ECOLOGY AND BIOLOGY IN ANGOLAN WATERS.

3.1 INTRODUCTION

History of the fishery in Angola

Commercial fishing for small pelagic fish started during the early 1950s, with the main objective of supplying raw material for the fish meal industry. Fishing was done with small boats of 20-30m in length, operating mainly in the area from Cunene to Namibe. The increase in catches of small pelagic fish, between the mid-60s and mid-70s, was mainly due to the introduction of sophisticated purse seines from the former Soviet Union consisting mostly of vessels in tonnage classes 5 (100 – 149.9 GRT) and 6 (150- 249.9 GRT) as well as trawlers in tonnage class of 10 (2 000 –3999.9 GRT) not found in the region before the mid-70s. From 1974 to 1975, there was a decline in total landings due to the departure of the Portuguese fleet (Figure 1.2).

Following Angola's independence (1976-1977), a significant increase of the Soviet purse seine fleet was observed, mostly in tonnage classes 5 and 6 (150-1000 GRT). The Soviet factory ships that processed fish onboard entered the fishery. With this fleet, catches in the years 1979 to 1985 were in the range of 350 000 tonnes. After 1992, there was a decrease in catches below 100 000 tonnes from the Soviet fleet (Figure 3.1).

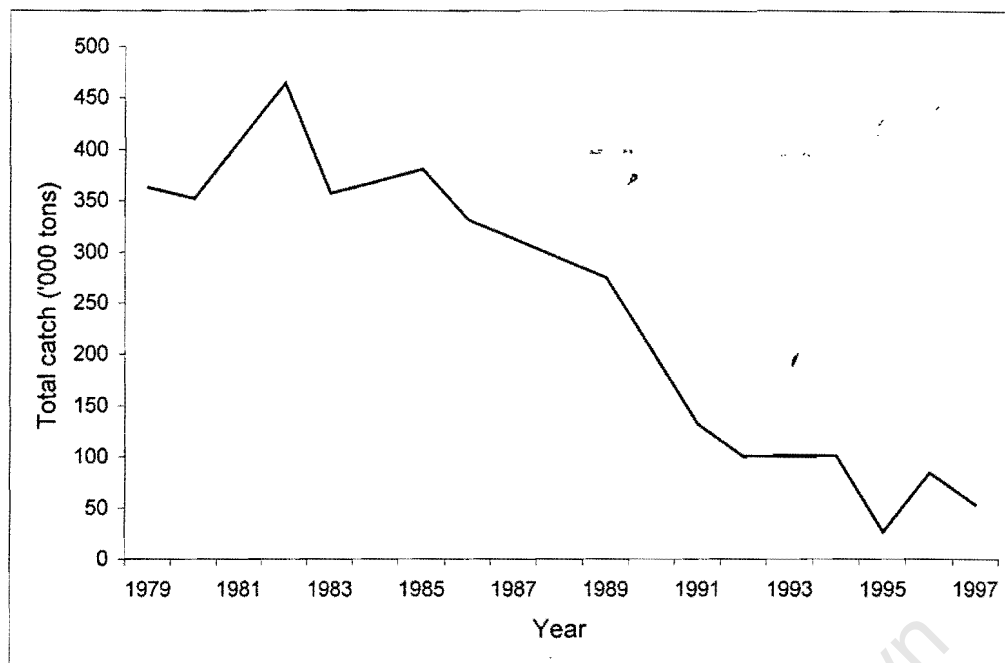


Figure 3.1: Total Soviet catch ('000 tonnes) of small pelagic species [source: Angolan Ministry of fishery].

Effort data are not reliable, but comparing the catch levels from 1985 with the estimates of biomass from the surveys indicates substantial rates of fishing mortality even when accepting some limitations of the acoustic method. A decrease in biomass as estimated from the surveys was observed in the period 1985 to 1989, the biomass decreasing from an average of 345 000 tonnes in 1985 to an average of 230 000 tonnes (see appendix II). The constant trend of biomass observed from 1985 to 1989 (Figure 1.3) also supports the impression of the stock being affected by intensive exploitation. Therefore, in 1989 the Ministry of Fisheries decided to introduce some management measures and to gradually decrease the number of boats, firstly foreign vessels and secondly, to introduce technical measurements like mesh size and hence minimum size of fish caught. The slight increases in national catches were mainly a result of Government Policy, which aimed to strengthen the capacity of national companies. During this period, the establishment of several companies, some national and others joint ventures, were made a priority by the Angolan government.

During the 1990s, a significant decrease in the foreign fleet was observed and catches were only at a level of 100 000 tonnes. The decrease in the foreign fleet was not completely compensated by an increase in the national fleet due to insufficient national capacity. In the period after 1992 there was an increase in the biomass of small pelagic fish, possibly indicating a recovery in the stock (Figure 1.3). Over 1995 and 1996 a decrease in biomass was observed, probably as a result of the “Benguela Niño” phenomenon which occurred on the Angolan coast, and which subsequently led to an abnormal distribution of the species for two years (1995-1996) (Gammelsrød *et al.*, 1998).

3.1.2 *Description of current fishery and statistical system*

Pelagic fish make up more or less 80% of the total fish landed in Angola (IIM, 1999). The main species are: the round sardinella (*Sardinella aurita*), the flat sardinella (*Sardinella maderensis*), Cunene horse mackerel (*Trachurus trecae*), Cape horse mackerel (*Trachurus capensis*). Four other species, the Atlantic bumper (*Chloroscombrus chrysurus*), African moonfish (*Selene dorsalis*), false scad (*Decapterus rhoncus*) and chub mackerel (*Scomber japonicus*) also contribute significantly to the total catch of small pelagic fish. However, it is not possible to estimate the proportion of individual species contributing to the industrial catch, because captains normally report only commercial groups to the national department of fisheries (Direcção Nacional de Pescas-DNP) and often regroup many species as “diverse”. According to the quality and the commercial value, captains merely report some species as “diverse”.

The fishing fleet in Angola is usually classified into artisanal, semi-industrial and industrial. These fishing sectors are identified by vessel size. The artisanal sector fish mainly from sailing canoes 4 to 10 m in length, however, to date more and more are becoming motorised. The semi-industrial sector uses vessels that range between 12 and 25 m, while the industrial sector includes vessels from about 25 m length overall.

In most cases the semi-industrial fishing sector is not well categorized. Along the Angolan coast, in some regions semi-industrial is classified as the artisanal sector.

The industrial fishery is the dominant sector, generally using seiners between 25 and 30 meters long. The three fishing sectors target the same aforementioned small pelagic species.

Since May 1996, the Artisanal Fisheries Institute (Instituto para o Desenvolvimento de Pesca Artesanal-IDPA), has in co-operation with the FAO and the French, been implementing a data collection programme for landings along the coast in which it is estimated that the total production from the artisanal fisheries currently reaches about 30 000 tonnes/year.

Artisanal catches may be assumed to consist largely of flat sardinella (Lartigue and Kingombo, 1996). However, catch statistics reported by the artisanal fishermen do not distinguish between the two species of sardinella. In the industrial fishery, from the end of 1990s when the Soviet Union fleet left the fisheries, the total catches decreased and have never reached previous levels.

The use of the Angolan catch data in the assessment models for the small pelagic fish is unreliable due to the problems associated with the collection of the data in the artisanal and industrial fisheries. The statistical system for data collection in two sectors of the fishery did not provide a full picture of the landings and species composition of the catches.

3.2 METHODS

3.2.1 Survey design

Surveys followed a systematic triangular transect pattern in areas where tight sardinella shoals were recorded, from shore (20 m) to the shelf edge at about 200 m depth, the endpoints of the transects being approximately 10 nautical miles apart. In areas of sparse fish concentrations, parallel transects separated about 7 to 10 nm were used (Figure 3.2a, b, c). Since 1994, fishing activities kept a distance from the coast of 20 nautical miles in the northern region (Cabinda) because of the extensive oil drilling activities in that region.

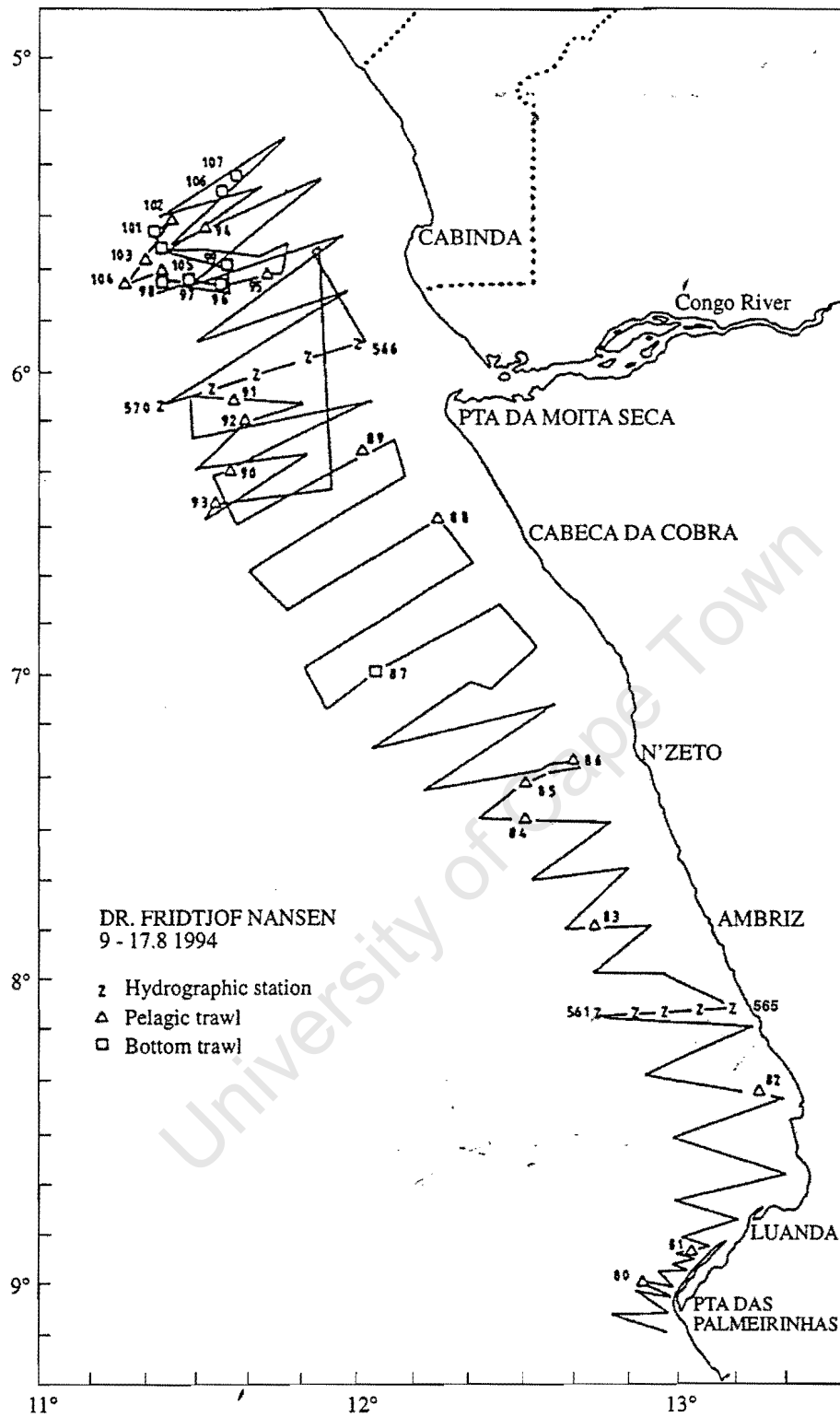


Figure 3.2a. Course track with fishing and hydrographic stations, Cabinda-Luanda.

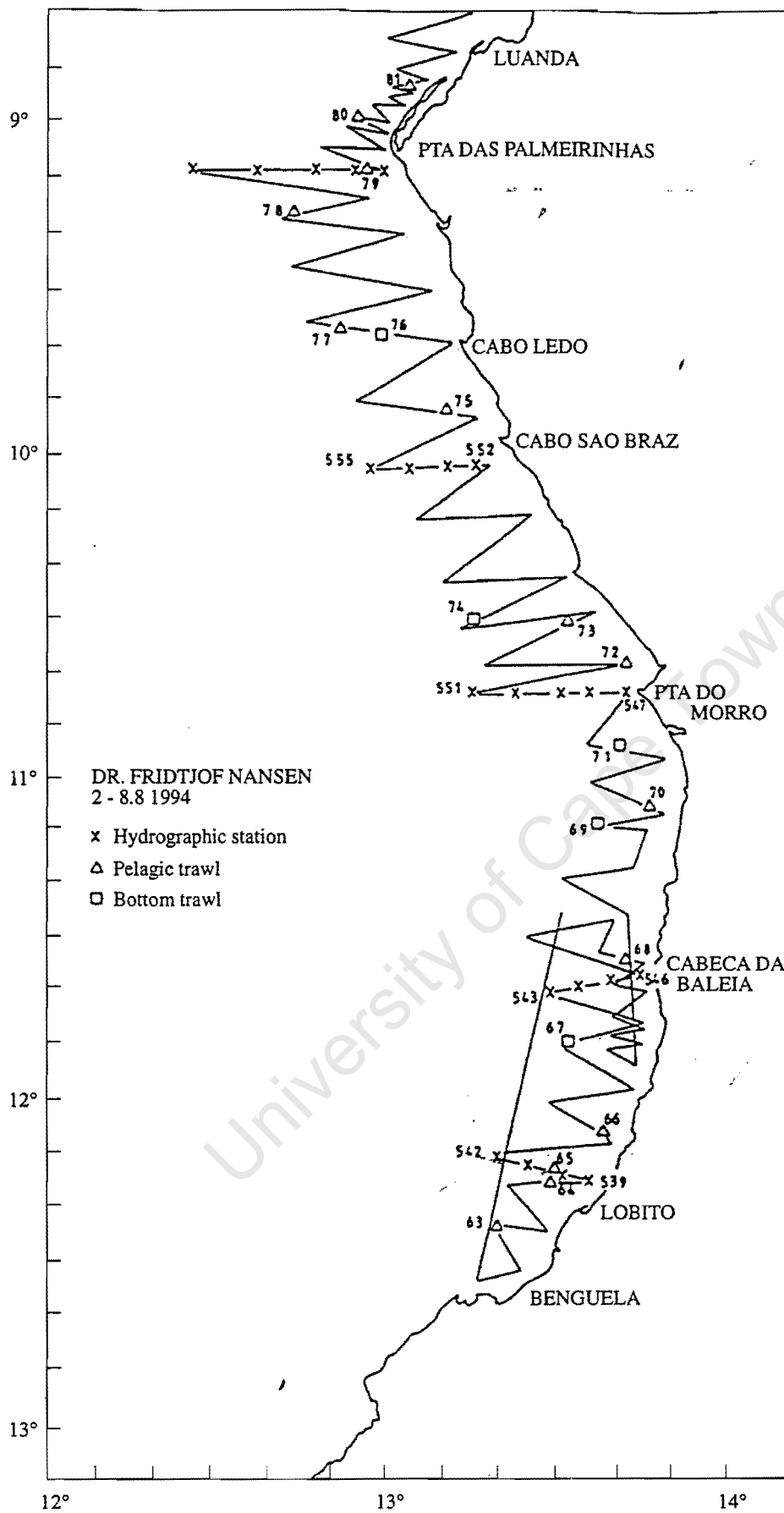


Figure 3.2b. Course track with fishing and hydrographic stations, Luanda-Benguela.

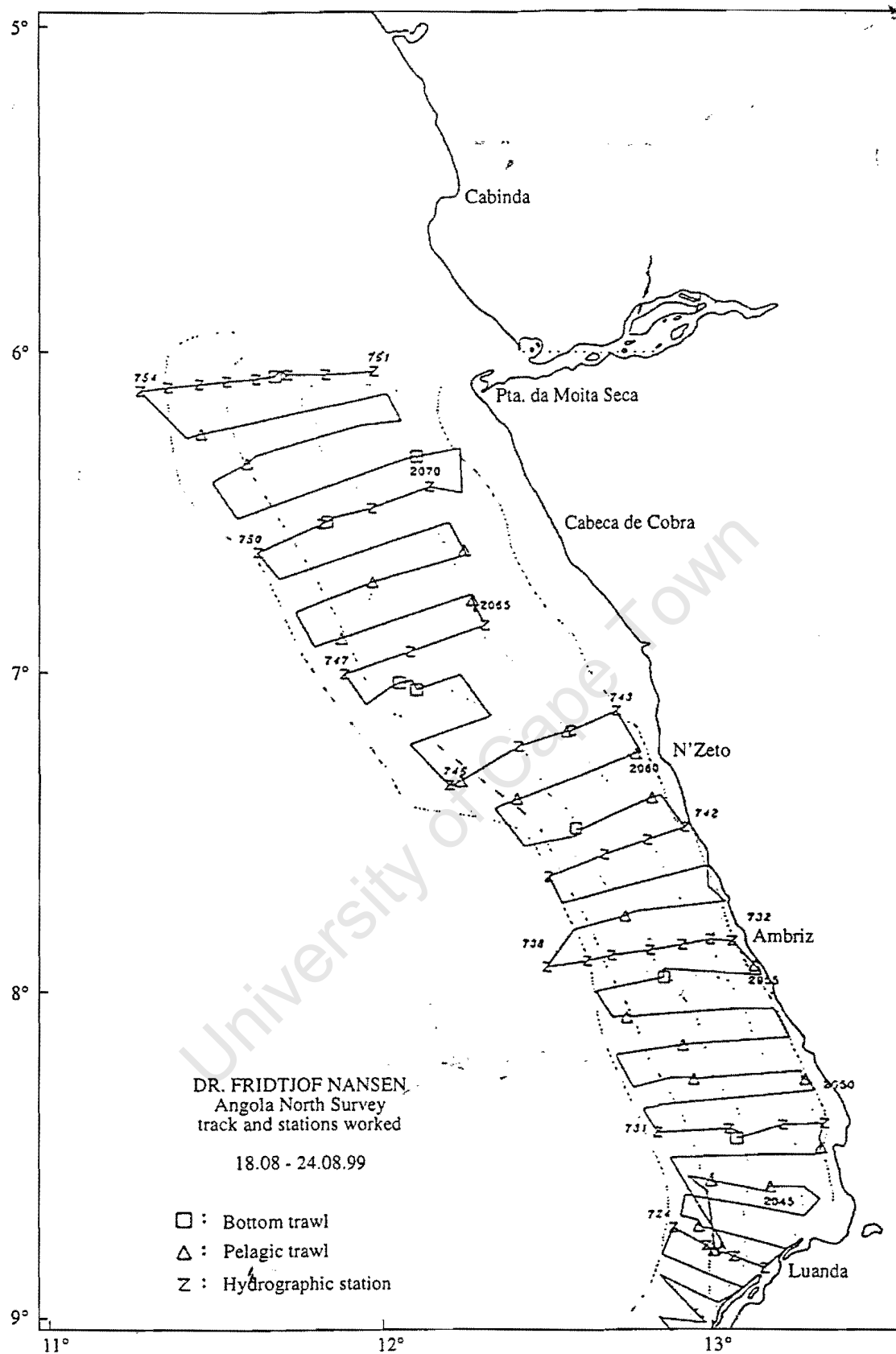


Figure 3.2c. Course track with fishing and hydrographic stations, Benguela-Cunene.

3.2.2 Collection of data

Trawl sampling

Trawls made during the surveys were not systematic. The catches were sampled for species composition by weight and number of the target species. Length distributions (total length) were taken for the main species. Biological samples (e.g. weight, sex and maturity stages) were taken for the target species.

Length-frequency

Total length (TL) and body weight (W) were recorded for sardinella to the nearest $\frac{1}{2}$ cm or 1 g below, respectively after each trawling. The species were measured in centimeters, from a random sample of more or less 100 fish. Length frequency data of *Sardinella aurita* and *S. maderensis* were extracted from the NAN-SIS database. The data extracted correspond to samples collected during surveys of the pelagic resources by the R/V “*Dr. Fridtjof Nansen*” in the period 1985 to 1999.

Biological sampling

Fifty fish from each of the target species were randomly collected in order to determine the sex and maturity stages. Sex and reproductive stages of sardinella were described by macroscopic examination, scoring each individually sampled fish according to the categories proposed by Holden and Raitt (1975). The empirical scale of the five maturity stages proposed by Holden and Raitt (1975) was applied. Stages 1 and 2 are the “immature state”, while stages 3 and 4 are the “pre-spawning state” and stage 5 is the “spawning and spent state”. Details of the different maturity stages are described in Table 3.1.

Table 3.1. Macroscopic scale of sexual maturity for male and female fish (after Holden and Raitt, 1975; adapted to current knowledge).

STAGE	STATE	EXTERNAL APPEARANCE
I	Immature (Immature state)	Gonads are very small, less than half the body cavity length, and flattened or tubular, i.e. thin and thread-like, the colour of the gonads is translucent. Gender is easy to distinguish. Approximately: 14-20 cm fish. Ovaries: Light orange gelatinous mass. Cannot see eggs with naked eye. Testis: Translucent-white, thin, elongate and balloon-like.
II	Inactive (Immature state)	Gonads are slightly larger than stage 1, approximately half of the body cavity length, but still generally flat. Colour more pronounced. Ovaries: Pale reddish tint back to orange colour. Testis: Creamy-white colour and very flat (lobe like) with sharp edges
III	Active (Pre-spawning state)	Gonads longer than half body cavity length and becoming cylindrical. Ovaries: Individual eggs clearly visible. Colour orange. Blood vessels marked. Spindle shaped. Testis: White to cream/testes more swollen. Spindle shaped.
IV	Ripe (Pre-spawning state)	Gonads very large, virtually filling body cavity, even causing distension of abdomen. Ovaries: Individual eggs almost 0.5 mm or larger and slightly elongated. Ovary sac breaks releasing eggs. Colour is dark orange. Testis: Cream, releases milt when punctured.
V	Running/Spent (Spawning and spent state)	Eggs or milt released through vent during handling i.e. running. Ovaries: Ovary is dark orange and greatly swollen. Could also be partly spent. Testis: External appearance changes from smooth structure to white and knob-like. Swollen to partly spent. Ovaries: Gonads flattened, but still elongated. Very blood-shot (dark red). Few eggs remaining appear grey/brown. Testis: Testis are deflated and grey in colour.

3.2.3 Analysis

Maturity ogives

Data from fish sampled between 1994 and 1999 were used during this study, fish in maturation stages 1 to 2 were considered as immature, while fish in stages 3 to 5 were mature. A logistic maturity ogive was fitted to the data on number of mature fish length-class using non-linear regression separately for males and females:

$$P_i = \frac{1}{1 + \exp(a - bTL)} \quad (3.1)$$

Where P_i is the proportion of fish sexually mature in size class i with total length (TL), while a and b are constants.

Sex-ratios

The sex ratios was determined from the equation $S = F/M$, where F is the frequency of female individuals and M is that of males. Generally, sex ratios were compared to unity and we studied how they varied over both time and space.

3.2.4 Statistical analysis

All statistical analyses were performed using the statistical package: "STATISTICA® V. 5.5".

Sex ratios

The sex frequencies in both seasons and the three zones were tested for deviations from unity, by applying the chi-square test. The statistic can be expressed as:

$$\chi^2 = \sum \sum \frac{(f_{ij} - \hat{f}_{ij})^2}{\hat{f}_{ij}} \quad \text{Zar, 1999} \quad (3.2)$$

Where, f_i is the observed frequency of males and females and \hat{f}_i is the expected frequency.

The ratio of female to male for flat sardinella and round sardinella was calculated for each season (warm: November to April and cold: May to October), as well as per zone for the period 1994 to 1999. Two Chi-square tests were performed:

- 1) Null hypothesis (H_0): The sex ratio is equal in both seasons.
- 2) Null hypothesis (H_0): The number of females is equal to males among the three zones ($\neq F = \neq M$).

Length distribution (average length)

The data used were not transformed, and the assumption of homogeneity was not tested due to the preliminary results of the surveys indicating the presence of bimodal length distribution in zone, depth and season. For this reason the statistical analysis was based on the Kruskal-Wallis nonparametric analysis of variance. The average fish lengths of round and flat sardinella were computed separately to verify the differences (H_0 : The mean fish lengths are the same; H_1 : The mean fish lengths are different) of two species according to season (warm/cold), time of day (day/night), zone (Northern, Central and Southern), bottom depth stratum (0-50m/>50m) and period. The period of study was grouped into two based on the period with intensive fishing by the Russian fleet (1985-1991) and the period with moderate fishing (1992-1999) due to the departure of the Russian fleet at the end of 1990.

An analysis of the variance for a single factor (Kruskal-Wallis Test) as indicated above is a technique by which each factor is tested separately. Generally, factors are linked in nature. Thus a simple analysis can lead to incorrect results. In such cases, the generalised linear model (McCullag and Nelder 1989) was applied as well as multivariate analysis (unbalanced ANOVA Type III, Dunn & Clark 1974), which include an apportioning of the total variance to the various factors considered (time of day, zone, depth and sampling periods). This method is relatively robust to the assumption of homogeneity of variance. The fitted generalised linear model with interactions (equation 3.4 and 3.5) allowed investigation in a single analysis how each factor contributes to the mean length (ML) taking into account the effects of other factors and their interactions. We used the two models for *Sardinella aurita* (round sardinella) and *S. maderensis* (flat sardinella) separately:

$$ML_{i,j,k,l,m} = \mu + S_i + T_j + Z_k + D_l + Y_m + \varepsilon_{m(ijkl)} \quad (3.4)$$

$$ML_{i,j,k,l,m} = \mu + S_i + T_j + Z_k + D_l + Y_m + (S*Y)_{im} + (S*D)_{il} + \varepsilon_{m(ijkl)} \quad (3.5)$$

Where μ is a constant, $S \dots Y$ are parameters depending on the main effects related to season effects (S_i -coded warm or cold season), time effect (T_j -coded night or day), zone effect (Z_k -coded north, center and south), depth effect (D_l -coded two depth levels, 0-50m and >50 m), sampling period effect (Y_m -coded two period levels, 1985-1991 and 1992-1999), while ε is the residual error expected to be normally distributed.

3.3 RESULTS

3.3.1 Dynamics of maturity

The number of females and males sampled by length in each zone and season varied between zones, resulting in an unbalanced sampling scheme (Table 3.2 and 3.3).

Table 3.2. Numbers of males and females of round sardinella sampled from 1994-1999 in each zone and season.

Season	Northern	Central	Southern	Total
Warm	M = 285	M = 285	M = 41	M = 611
	F = 357	F = 398	F = 39	F = 794
Cold	M = 247	M = 477	M = 59	M = 783
	F = 507	F = 478	F = 51	F = 1036
Total	M = 532	M = 762	M = 99	M = 1393
	F = 863	F = 875	F = 89	F = 1827

M = Male, F = Female

Table 3.3. Numbers of males and females of flat sardinella sampled from 1994-1999 in each zone and season.

Season	Northern	Central	Southern	Total
Warm	M = 1156	M = 1360	M = 237	M = 2753
	F = 1010	F = 980	F = 290	F = 2280
Cold	M = 2396	M = 2166	M = 258	M = 4820
	F = 1028	F = 1108	F = 278	F = 2414
Total	M = 3552	M = 3525	M = 495	M = 7572
	F = 2038	F = 2088	F = 568	F = 4694

M = Male, F = Female

Figure 3.3 shows maturity ogives for male and female round sardinella and indicates that there are many outliers in the data between 18 cm and 28 cm. Therefore it was not adequate to fit a proper maturity ogive ($r^2 = 0.65$ or 65% for females and $r^2 = 0.56$ or 56% for males, Figure 3.3). Pooled length data of flat sardinella for the entire coast are presented (Figure 3.4). One can see during this period that females and males of flat sardinella reach 50% of maturity at the size 24 and 23 cm total length, respectively. The quality of the fit of flat sardinella should be considered as satisfactory ($r^2 = 0.97$ for female and $r^2 = 0.94$ for male).

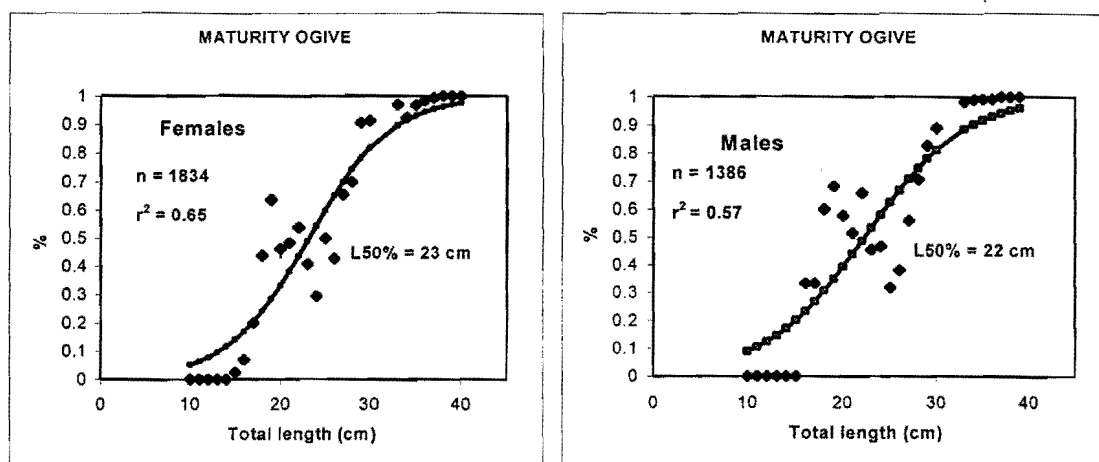


Figure 3.3. Maturity ogives for *S. aurita* from 1994-1999 (survey data of the R/V Dr. Fridtjof Nansen). The maturity stages were determined macroscopically using a five stage scale (Table 3.1).

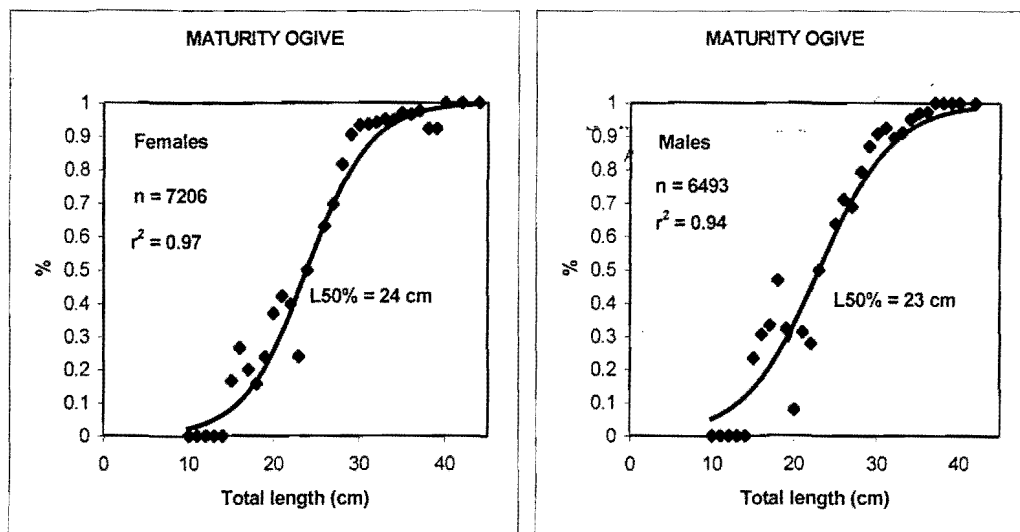


Figure 3.4. Maturity ogives of *S. maderensis* from 1994-1999 (survey data of R/V *Dr Fridtjof Nansen*). The maturity stages were determined macroscopically using a five stage scale (Table 3.1).

3.3.2 Sex ratios of *S. aurita*

It was observed that there are more females than males during both seasons. Females dominated ($S = 2.0$) only in the Northern zone and to a lesser extent in the Central zone (Table 3.4).

Table 3.4. Chi-square analysis for testing the independence of zone and season in frequencies of sexes of round sardinella (Data from Table 3.2). S = Sex ratio of females to males.

	Northern	Central	Southern	Total
Warm	S = 1.3 $\chi^2_{1df} = 8.08$ $P < 0.01^*$	S = 1.4 $\chi^2_{1df} = 18.69$ $P < 0.001^{**}$	S = 0.9 $\chi^2_{1df} = 0.05$ $P > 0.05$	S = 1.2 $\chi^2_{1df} = 23.84$ $P < 0.001^{**}$
Cold	S = 2.0 $\chi^2_{1df} = 89.66$ $P < 0.001^{**}$	S = 1.0 $\chi^2_{1df} = 0.01$ $P > 0.05$	S = 0.9 $\chi^2_{1df} = 0.58$ $P > 0.05$	S = 1.3 $\chi^2_{1df} = 35.19$ $P < 0.001^{**}$
Total	S = 1.6 $\chi^2_{1df} = 78.54$ $P < 0.001^{**}$	S = 1.1 $\chi^2_{1df} = 7.80$ $P < 0.01^*$	S = 0.9 $\chi^2_{1df} = 0.53$ $P > 0.05$	S = 1.3 $\chi^2_{1df} = 58.49$ $P < 0.001^{**}$

*= significant; **= highly significant

There is a significant difference in sex ratios between seasons ($\chi^2_{1df} = 59.03$, $P < 0.05$).

Also, the number of females is different to males amongst the three zones ($\chi^2_{2df} = 28.89$, $P < 0.05$) (Table 3.2).

3.3.3 Sex ratios of *S. maderensis*

The data of sex-ratios for *S. maderensis*, were analysed in the same manner as the round sardinella (Table 3.5). However, fewer females were found in both warm and cold. In contrast, females were dominant in the Southern zone (S = 1.1).

Table 3.5. Chi-square analysis for testing the independence of zone and season in frequencies of sexes of flat sardinella (Data from Table 3.3). S = Sex ratio of females to males.

	Northern	Central	Southern	Total
Warm	S = 0.7 $\chi^2_{1df} = 61.70$ $P < 0.001^{**}$	S = 0.9 $\chi^2_{1df} = 9.84$ $P < 0.01^*$	S = 1.2 $\chi^2_{1df} = 5.33$ $P < 0.05$	S = 0.8 $\chi^2_{1df} = 44.35$ $P < 0.001^{**}$
Cold	S = 0.5 $\chi^2_{1df} = 341.9$ $P < 0.001^{**}$	S = 0.4 $\chi^2_{1df} = 546.6$ $P < 0.001^{**}$	S = 1.0 $\chi^2_{1df} = 0.58$ $P > 0.05$	S = 0.5 $\chi^2_{1df} = 811.3$ $P < 0.001^{**}$
Total	S = 0.6 $\chi^2_{1df} = 367.9$ $P < 0.001^{**}$	S = 0.6 $\chi^2_{1df} = 410.0$ $P < 0.001^{**}$	S = 1.1 $\chi^2_{1df} = 5.01$ $P < 0.05$	S = 0.6 $\chi^2_{1df} = 675.3$ $P < 0.001^{**}$

*= significant; **= highly significant

Similar to the round sardinella, differences exist in the sex ratios between seasons ($\chi^2_{1df} = 855.6, P < 0.05$). The number of females is also different to males amongst the three zones ($\chi^2_{2df} = 113.9, P < 0.05$) (Table 3.3).

3.3.4 Average length of *S. aurita*

The average fish lengths (cm) (Figure 3.5) were significantly different (Kruskal-Wallis test: $H_c = 63.48$, $P < 0.0001$). As can be seen in Figure 3.5 there is a larger dispersion of fish lengths in the warm season.

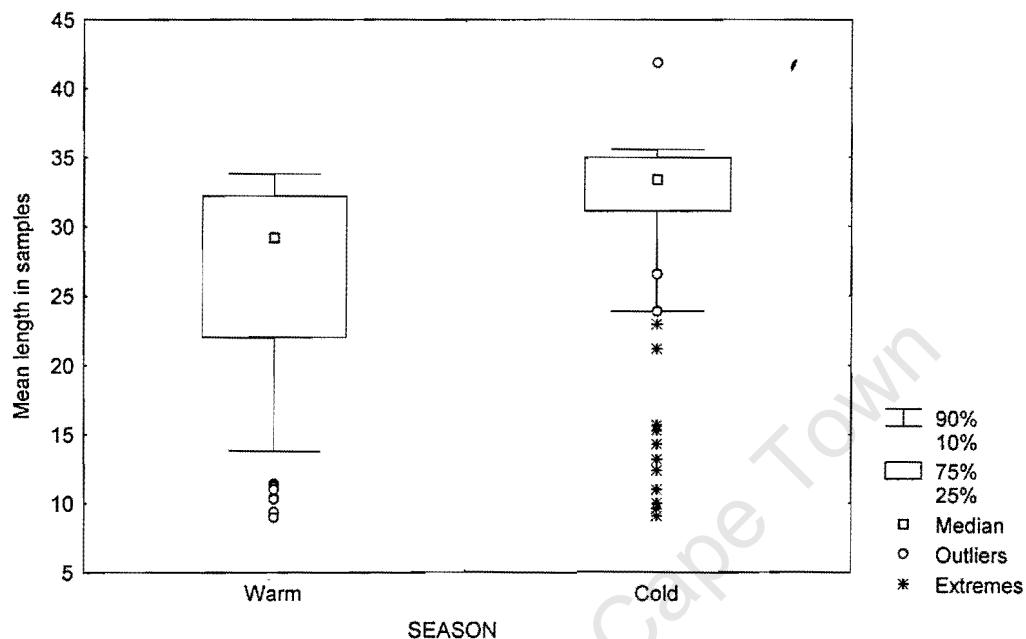


Figure 3.5. Comparison of the size distribution of mean fish lengths (cm) of round sardinella by season [$n_{\text{warm}} = 6457$ and $n_{\text{cold}} = 1450$].

Average lengths (cm) (Figure 3.6) of fish sampled during the day were not significantly different from those sampled during the night period (Kruskal-Wallis test: $H_c = 2.17$, $P = 0.14$). However, there is a larger dispersion of fish lengths by daytime.

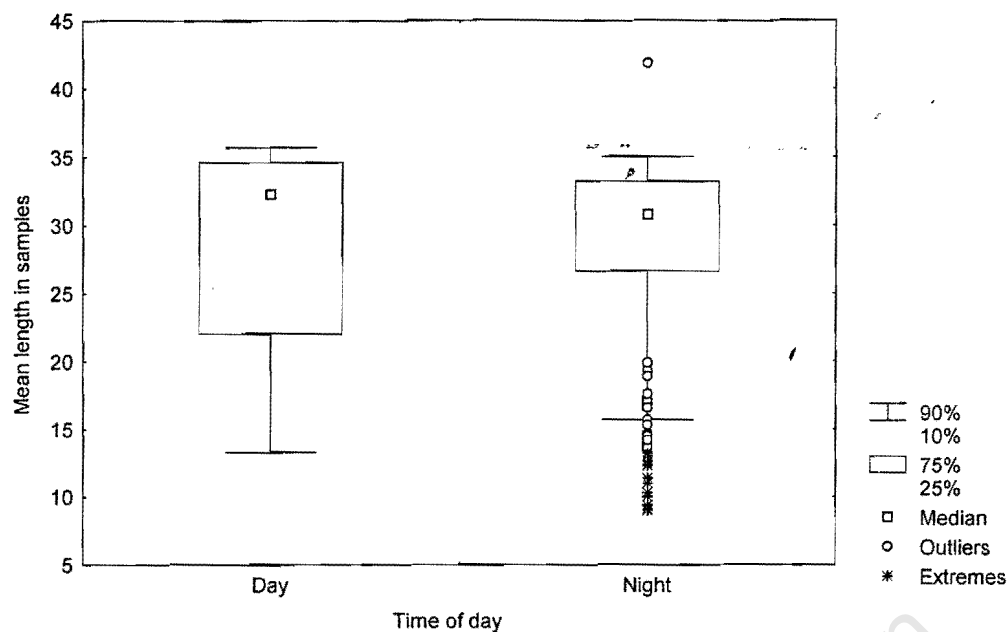


Figure 3.6. Comparison of the size distribution of mean fish lengths (cm) of round sardinella by time of day [$n_{\text{Day}} = 2521$ and $n_{\text{Night}} = 6741$].

The Kruskal-Wallis test showed a significant difference in average fish lengths (cm) among the three zones (Figure 3.7) ($H_c = 9.43$, $P = 0.009$).

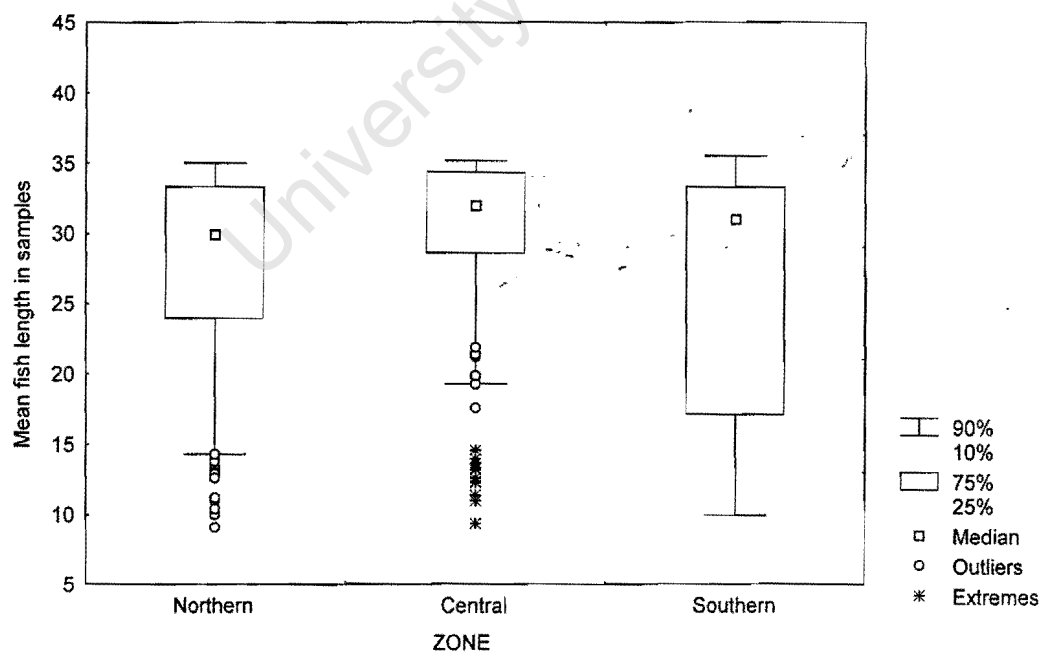


Figure 3.7. Comparison of the size distribution of mean fish lengths (cm) of round sardinella by zone [$n_{\text{Northern}} = 5715$, $n_{\text{Central}} = 3510$ and $n_{\text{Southern}} = 519$].

No significant difference was found in mean fish lengths (cm) between the two depth strata (m) (Figure 3.8) (Kruskal-Wallis test: $H_c = 5.49$, $P = 0.01$). However, there is larger dispersion of fish lengths at the depth stratum $<50\text{m}$.

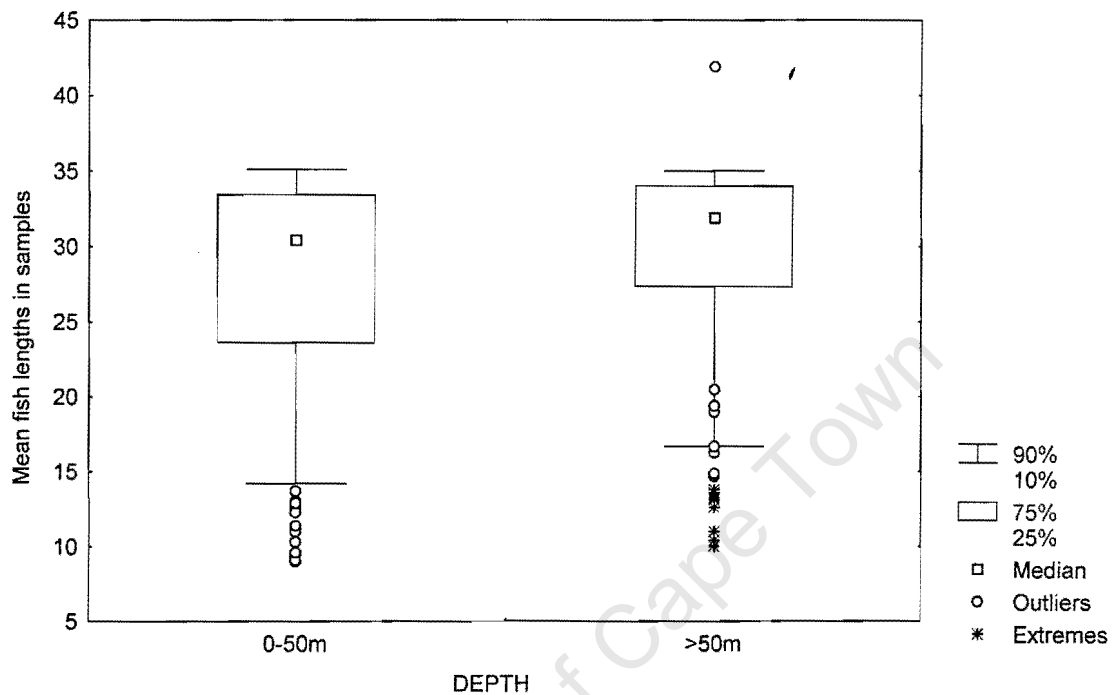


Figure 3.8. Comparison of the size distribution of mean fish lengths (cm) of round sardinella by depth stratum [$n_{0-50\text{m}} = 1806$ and $n_{>50\text{m}} = 972$].

Average fish lengths (cm) in the period with intensive fishing are significantly smaller than that of fish sampled after 1992 (Kruskal-Wallis test: $H_c = 37.49$, $P < 0.0001$, Figure 3.9).

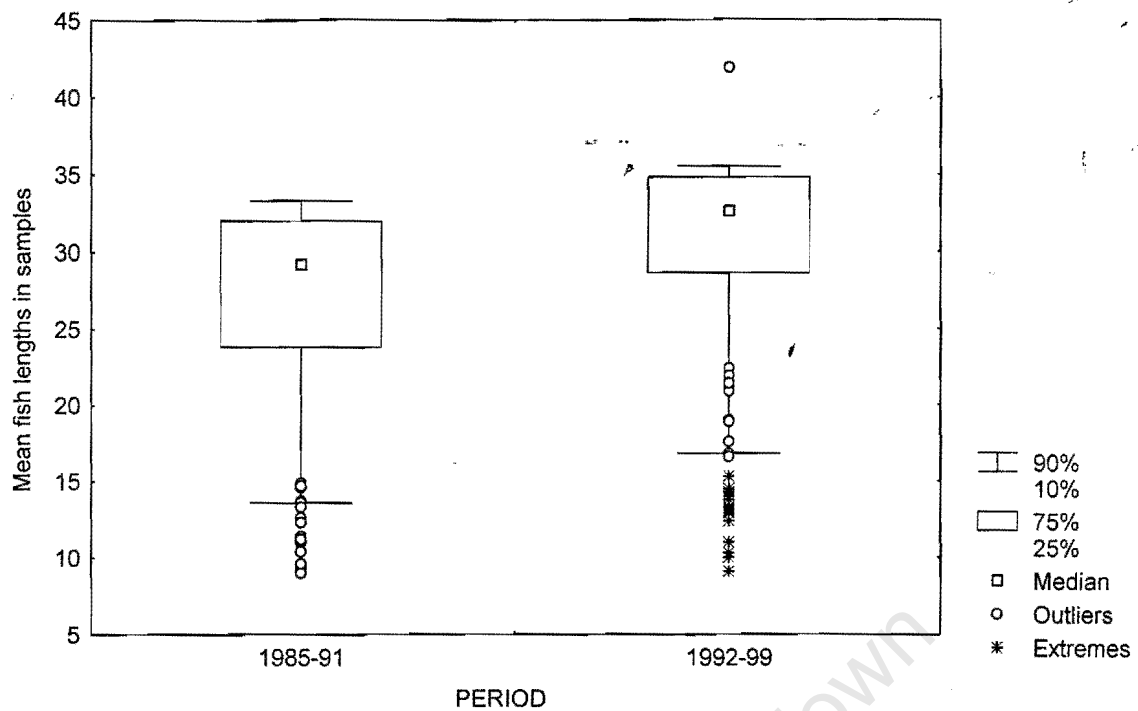


Figure 3.9. Comparison of the size distribution of the mean fish lengths (cm) of round sardinella by period [$n_{1985-91} = 3520$ and $n_{1992-99} = 5741$].

The sampling scheme was too unbalanced to estimate the parameters of all interactions simultaneously. Therefore to estimate the unbiased mean fish lengths for all time/space strata, we first adjusted the following models without interactions, enabling us to estimate average lengths per season, time, zone, depth and sampling period separately ($r^2 = 0.170$ or 17%, Table 3.5). Time of day and zone have no significant effect on the mean fish length variability of round sardjnella (Table 3.5). The season had a highly significant effect on the mean fish length variability, but it is not important (explains <4% of the variance).

We tested for interactions between the significant variables (season x depth, and season x period) (Table 3.6). There were no significant (season x depth and season x period) level interactions ($P > 0.05$). The model explained 15% of the total variance. The highest mean square (MS) and the sum of square (SS) in the second model (model with interactions) was found in the sampling period effect (Table 3.6).

Table 3.5. *Sardinella aurita*. Sources of variability in mean length of fish amongst season, time, zone, depth and period, resulting from the general linear model (df, degrees of freedom, SS-sum of squares; MS-mean square; *F* Fisher test; $r^2 = 0.152$

Source of variation	(df)	SS	MS	F-values	P-values
Model	6	2957.4	492.9	10.92**	<0.0001
Error	318	14348.2	45.1		
Corrected Total	324	17305.6			
Season	1	732.5	732.5	16.23**	<0.0001
Time	1	78.5	78.5	1.74NS	0.1880
Zone	2	306.8	153.4	3.40 NS	0.0346
Depth	1	372.3	372.3	8.25*	0.0043
Period	1	490.5	490.5	10.87**	0.0011

NS- not significant, *- significant ($P < 0.05$), **- highly significant ($P < 0.01$)

Table 3.6. *Sardinella aurita*. Sources of variability in mean length of fish amongst season, time, zone, depth and period as well as the interactions (season x depth and season x period) resulting from the general linear model (df, degrees of freedom, SS-sum of squares; MS-mean square; *F* Fisher test; $r^2 = 0.197$

Source of variation	(df)	SS	MS	F-values	P-values
Model	5	2624.5	524.9	11.41**	<0.0001
Error	319	14681.1	46.0		
Corrected Total	324	17305.6			
Season	1	333.2	333.2	7.24 **	0.0075
Depth	1	287.2	287.2	6.24*	0.0130
Period	1	465.0	465.0	10.10**	0.0016
Season x depth	1	0.24	0.24	0.01NS	0.9423
Season x Period	1	24.46	24.46	0.53 NS	0.4665

NS- not significant, *- significant ($P < 0.05$), **- highly significant ($P < 0.01$)

3.3.5 Average length of *S. maderensis*

Similar to the round sardinella, the analysis of the variance for a single factor shows that there is a very significant difference in average fish lengths (cm) between the two seasons for all surveys (Kruskal-Wallis test: $H_c = 34.73$, $P < 0.0001$, Figure 3.10).

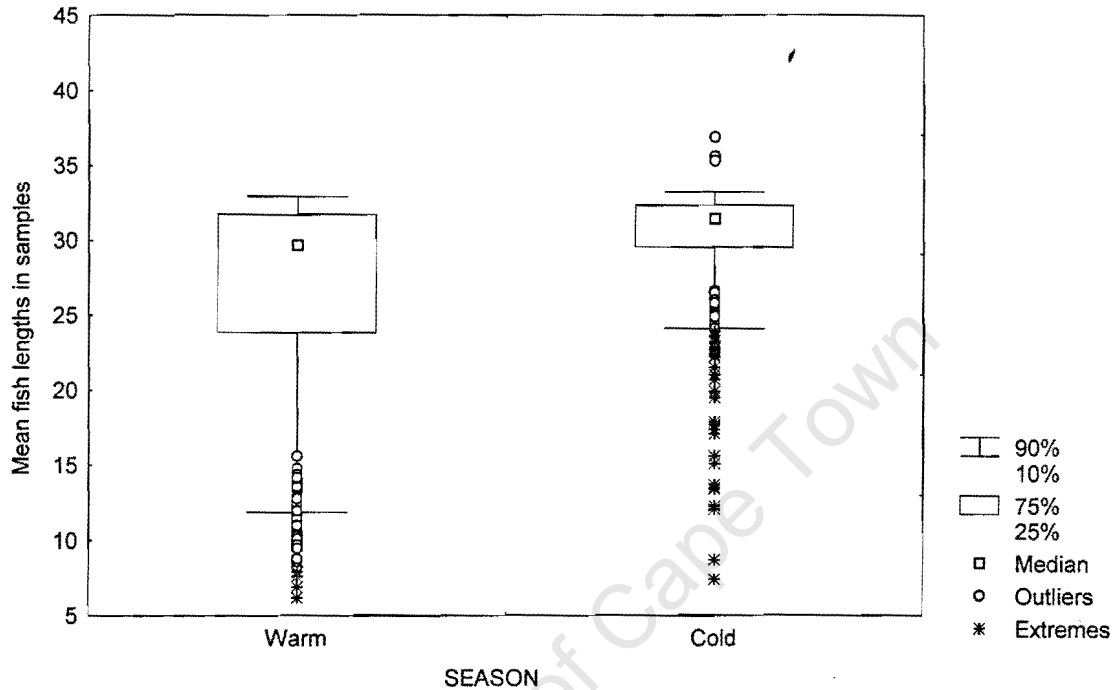


Figure 3.10. Comparison of the size distribution of mean fish lengths (cm) of flat sardinella by season [$n_{\text{Warm}} = 13454$ and $n_{\text{Cold}} = 17008$].

In contrast to round sardinella, there is significant difference in lengths of fish sampled during the day from those sampled during the night period (Kruskal-Wallis test: $H_c = 7.60$, $P = 0.006$). As can be seen in Figure 3.11 there is larger dispersion of mean fish length during the night.

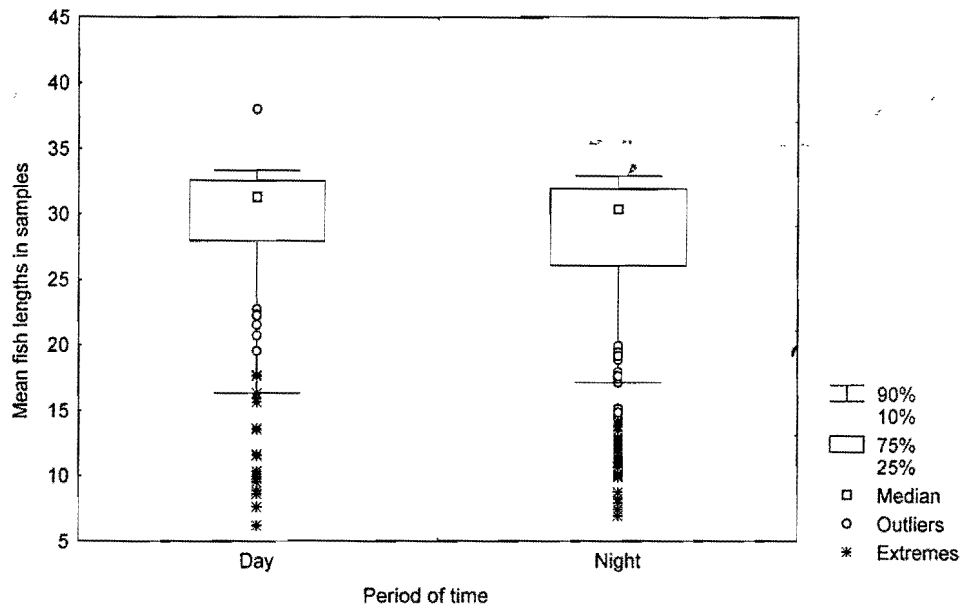


Figure 3.11. Comparison of the size distribution of mean fish lengths (cm) of flat sardinella by time of day [$n_{\text{Day}} = 4924$ and $n_{\text{Night}} = 12379$].

The Kruskal-Wallis test showed a very significant difference in mean fish lengths among the three zones (Figure 3.12) ($H_c = 83.88$, $P < 0.0001$). The largest dispersion of fish lengths is found in the Northern zone.

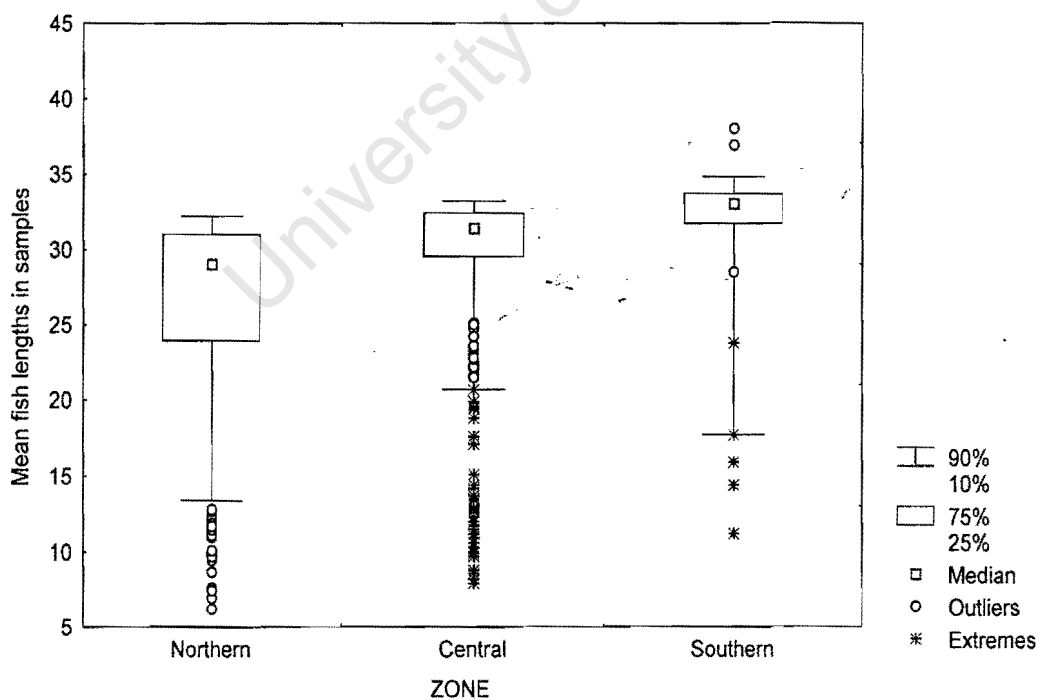


Figure 3.12. Comparison of the size distribution of mean fish lengths (cm) of flat sardinella by zone [$n_{\text{Northern}} = 6629$, $n_{\text{Central}} = 9599$ and $n_{\text{Southern}} = 1074$].

The mean fish lengths of flat sardinella (Figure 3.13) were significantly different (Kruskal-Wallis test: $H_c = 83.88$, $P < 0.0001$) between the two depth strata. The largest dispersion of fish lengths is observed at the depth stratum 0-50m.

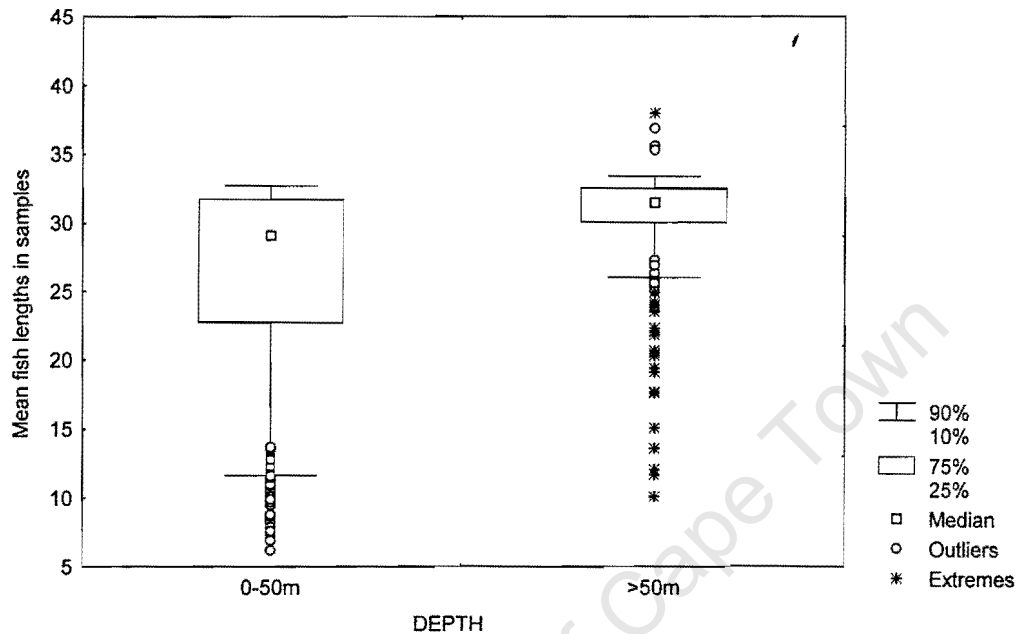


Figure 3.13. Comparison of the size distribution of mean fish lengths (cm) of flat sardinella by depth stratum [$n_{0-50m} = 8257$ and $n_{>50m} = 9046$].

Similar to round sardinella, average lengths (cm) in the period with intensive fishing are significantly smaller than that of fish sampled after 1992 (Kruskal-Wallis test: $H_c = 28.18$, $P < 0.0001$, Figure 3.14). Figure 3.14 indicates larger dispersion fish lengths in the period before 1992.

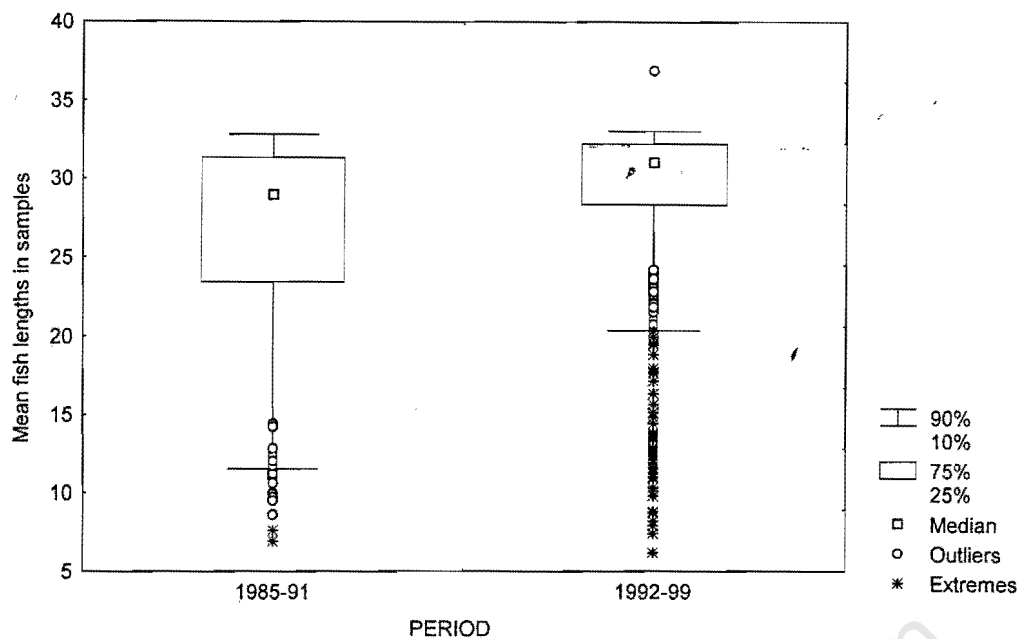


Figure 3.14. Comparison of the size distribution of mean fish lengths (cm) of flat sardinella by period [$n_{1985-91} = 4442$ and $n_{1992-99} = 12860$].

There was a highly significant effect of the depth on mean fish length of flat sardinella for the GLM model without interactions (Table 3.8), although not important (<10% of the variance explained). Interactions were then incorporated between the three most significant variables (season x zone and season x depth, $P < 0.0001$) (Table 3.9). There were no highly significant interactions at the 5% level, for this model. However, the interaction between season and zone is significant, but not important (explained <1% of the variance). The model explained 25% of the total variance. The highest mean square (MS) and the sum of squares were found in the depth effect (Table 3.9) in the model with interactions.

Table 3.8. *Sardinella maderensis*. Sources of mean length fish variability between season, time, zone, depth and period, resulting from the main effects of the general linear model (df- degrees of freedom, SS-sum of squares; MS-mean square; *F* Fisher test; $r^2 = 0.238$ for the whole model).

Source of variation	(df)	SS	MS	F-values	P-values
Model	6	6293.5	1048.9	31.81**	<0.0001
Error	610	20116.4	32.97		
Corrected Total	616	26409.9			
Season	1	1304.05	1304.05	39.54**	<0.0001
Time	1	32.45	32.45	0.98 NS	0.3216
Zone	2	1718.2	859.1	26.05**	<0.0001
Depth	1	2598.4	2598.4	78.79**	<0.0001
Period	1	2.42	2.42	0.07 NS	0.7867

NS- not significant, *- significant ($P < 0.05$), **- highly significant ($P < 0.01$)

Table 3.9. *Sardinella maderensis*. Sources of mean length fish variability amongst season, time, zone, depth and period and the interactions (season x zone and season x depth) for a general linear model (df- degrees of freedom, SS-sum of squares; MS-mean square; *F* Fisher test; $r^2 = 0.249$ for the whole model).

Source of variation	(df)	SS	MS	F-values	P-values
Model	7	6589.2	941.3	28.92**	<0.0001
Error	609	19820.7	32.55		
Corrected Total	616	26409.9			
Season	1	155.5	155.5	4.78*	0.0292
Zone	2	1397.1	698.6	21.46**	<0.0001
Depth	1	2513.9	2513.9	77.24**	<0.0001
Season x zone	2	282.6	141.3	4.34*	0.0134
Season x depth	1	42.48	42.48	1.31 NS	0.2537

NS- not significant, *- significant ($P < 0.05$), **- highly significant ($P < 0.01$)

3.3.6 Comparison of General Linear Model (GLM) results

The two models with different interactions explained 15% and 25% of the total variance for round sardinella and flat sardinella respectively. The interaction between season x depth for round sardinella and the interaction between season x depth for flat sardinella do not make significant contributions to the mean square (MS) and the sum of squares (SS) (Table 3.6 and 3.9). However, for flat sardinella it was found that the interaction between season x zone is significant (Table 3.9). In summary, the general linear model without interactions revealed that season as an independent class variable had little (<4% and <5%) contributions to the total variance in the GLM for round and flat sardinella respectively, despite its high significance level. Similar to the season, the zone and depth as the independent class variables had low (<7% and <10%) contributions to the total variance in the GLM. This is due to the difference in mean fish lengths between season, depth and among zones, which appears in figures 3.5, 3.10, 3.12 and 3.13 where outlier points are observed.

3.4 DISCUSSION

Size at 50% maturity is very important in fisheries management, as this is one of the main criteria for decisions on minimum size limits (Booth, 1984). However, for pelagic fish species having a high natural mortality, size-based management is not necessarily relevant. The results on length at 50% maturity of *S. maderensis* in the Angola area are 23 and 24 cm (TL) for male and female respectively (Figure 3.4). However, for *S. aurita* it was not possible to create an accurate ogive due to the presence of outliers in the data between 18-26 cm (Figure 3.3). However, the numbers sampled seem to be adequate. This inconclusive result might be due to the use of a macroscopic scale of maturity used during the surveys, which may be not realistic enough. This has been observed in several studies in Senegal (Boëly and Fréon, 1979), in Brazil by Isaac-Nahum *et al.*, 1988, in Nigeria by Marcus (1989) and on the west coast of Cameroon by Youmbi *et al.*, 1991. Off Angola, south of Congo, the size of *S. maderensis* is much bigger than further north, where 50% of the males and females may reach maturity at about 20-24 cm (ovary stage III). This suggests the existence of a separate stock of *S. maderensis* in that area.

Off Congo, north of 5° 00'S, Fontana and Pianet (1973) record the lengths at first maturity from 1967 until 1969. They found that all females of *S. aurita* of more than 21 cm have started their sexual cycle (ovary stage III). From their graphs it can be noted that 50% of females of *S. aurita* have started stage III at 19 cm (TL), which is closer to the lower range of maturity observed in Angola (Figure 3.3). While 50% maturity of female *S. maderensis* is observed at slightly over 18 cm (Fontana and Pianet, 1973). Fontana and Pianet (1973) mentioned that in *S. maderensis* there is evidence of a difference in size at 50% maturity in different seasons. In other regions of the world (e.g. off California) it was observed that the length at 50% maturity changes with time (Knaggs and Parish, 1973). It may be a response of a population towards disturbance of various kinds (Oliva *et al.*, 1989) like density-dependent effects at large population sizes which result in less food for each individual, which may delay maturity.

No obvious biological conclusions can be drawn from the small differences observed in the sex ratios, even when some differences in space or time are significant from a statistical point of view. However, an overall dominance of *S. aurita* females over males are observed in this study (Figure 3.15) and is also recorded in studies by Boëly and Fréon (1979) in Senegal. For the large *S. aurita* in the Congo area (Fontana and Pianet, 1973) and off Ivory Coast (Anon, 1976) it was pointed out that the females are also dominant. In contrast, the dominance of males over females for *S. maderensis* (Figure 3.16) was recorded by Youmbi *et al.* (1991) in the western Cameroon, while no significant difference was observed in Venezuela (Fréon *et al.*, 1997). The preponderance of females *S. maderensis* increases with size off the Ivory Coast (Marchal, 1965) and off the Congo (Fontana and Pianet, 1973).

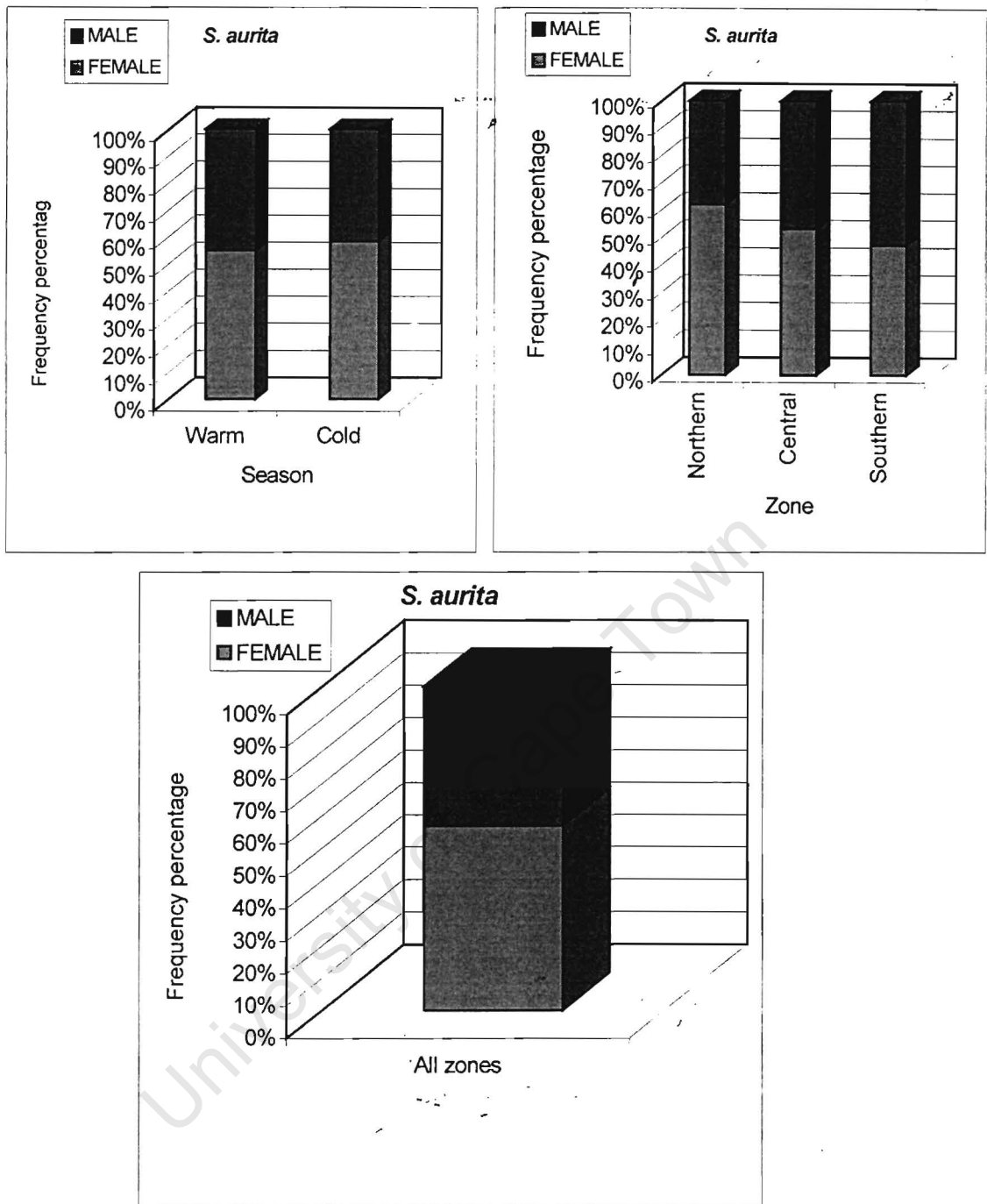


Figure 3. 15. Sex ratios of *Sardinella aurita* computed by season, zone and all zones from samples obtained during the Angolan surveys from 1994 - 1999 .
 [source: RV Dr. Fridtjof Nansen].

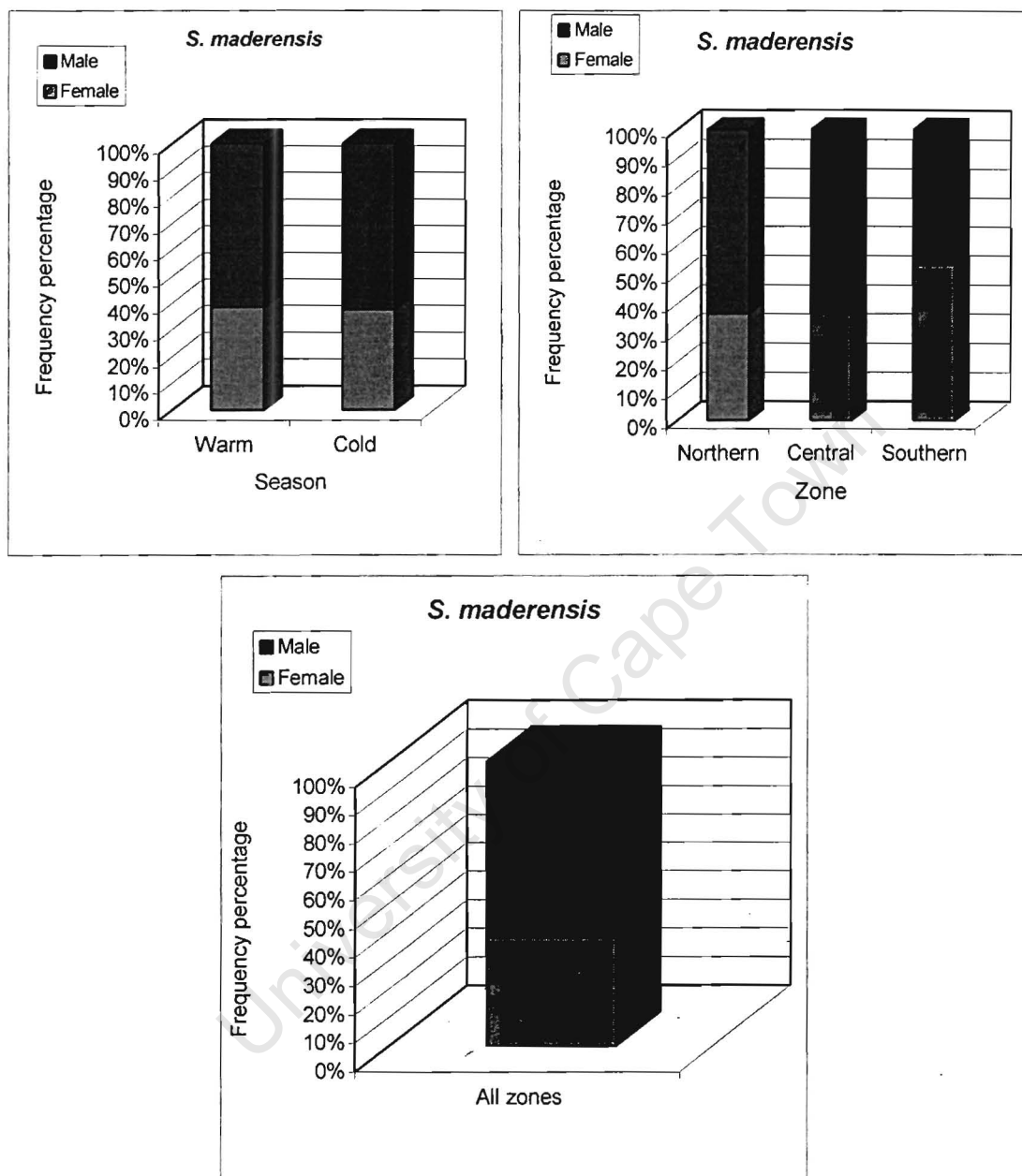


Figure 3.16. Sex ratios of *S. maderensis* computed by season, zone and all zones from samples obtained during the Angolan surveys in the 1994 - 1999 period. [source: RV Dr. Fridtjof Nansen].

The length distribution is one of the most important parameters in fish populations, reflecting the environmental conditions in different areas, migration patterns and relative abundance of different stock components. Changes in size composition have direct implications for the biology of the stock (e.g. fecundity, migration pattern etc.) as well as into the fishery and marketing success. Mean fish length was different between warm and cold seasons for *S. aurita*. However, the study done by M'fina (1985) off the Congo coast in 1982 did not show any differences between seasons in the mean length of *S. aurita*. Similar findings were observed previously from 1969 to 1972 off the Congo coast (Gh no and Fontana, 1973). In contrast, differences in mean lengths of *S. maderensis* were observed off the Congo coast by Gh no and Poinard (1969), as well as in 1982 by M'fina (1985). The same finding is observed in this study along the Angolan coast (Figure 3.10).

Differences in mean fish lengths for flat sardinella were significantly higher among the three zones (Kruskal-Wallis test: $H_c = 83.88$, $P < 0.0001$, Figure 3.12). This indicates that the length distributions as a function of geographical sector followed a north-south gradient. Large differences in the average fish lengths (Kruskal-Wallis test: $H_c = 70.60$, $P < 0.0001$, Figure 3.13) were found between the two depth strata for flat sardinella indicating that juveniles tend to occur inshore of adults. This suggests that the two species may not have the same behaviour in some respects. However, no specific studies were made for the differentiation between the behaviour of the two species. Results show that the size frequency distributions of sardinella have bimodal patterns (Figs 3.17 and 3.18). This pattern may be attributed either to seasonal north-south, south-north migrations or to inshore/offshore migrations.

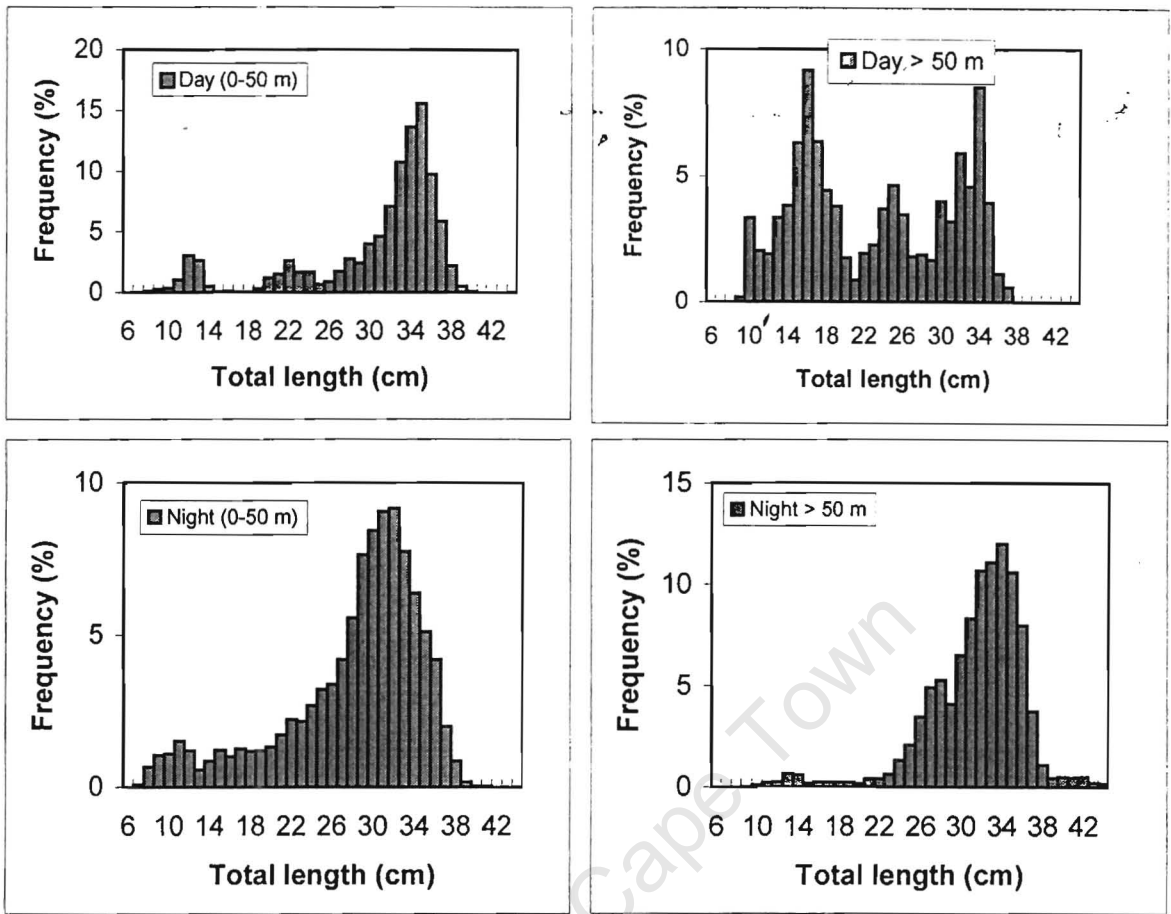


Figure 3.17. *Sardinella aurita* : Size frequency distributions (cm) for two depth strata (m) (combined data from 1985 to 1999, Nansis-database). Note differing vertical scales.

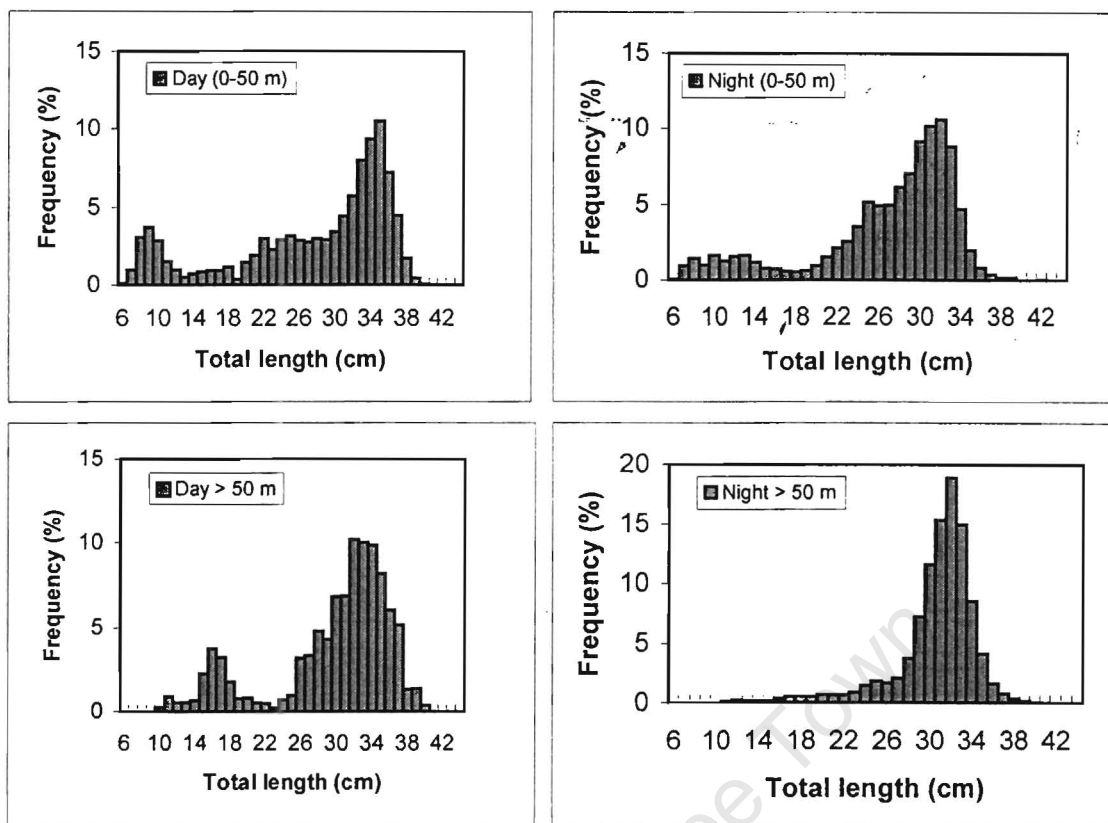


Figure 3.18. *S. maderensis*: Size frequency distributions (cm) for two depth strata (m) (Combined data for 1985 to 1999, from Nansis-database). Note differing vertical scales.

The observed increase in average fish lengths during the period of study (Kruskal-Wallis test, $P < 0.0001$, Figs 3.9 and 3.14) for two species from the survey data suggests that there was intensive exploitation by the Russian fleet during 1985 and 1991.

The explanatory variables that account for most of the total variance in the mean fish length were season and depth with 15% and 25% for round sardinella and flat sardinella respectively in the GLM analysis. The full model with the interactions for both species does not show values of the explanatory variables as high as the single model, emphasizing the importance of interactions. These seem to demonstrate that the interactions used in the above models do not account for much of the total variance in the mean fish lengths, except for flat sardinella (season x zone). A highly significant p value and a low r^2 -value can occur when there are many degrees of

freedom (df) in the model. The highly significant values of P are mainly due to non-independence between observations (high correlation in time and space) that artificially increases the number of degrees of freedom in the model.

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CHAPTER 4.

4.1 ACOUSTIC ANALYSIS OF ANGOLAN SARDINELLA: DISTRIBUTION, ABUNDANCE AND AGGREGATION PATTERNS

4.1.1 Introduction

Hydro acoustic methods are being used increasingly in freshwater and marine systems to quantify fish abundance and biomass. Mapping is a relatively new activity in this field, even though it is a traditional one in oceanography. The accuracy of acoustically estimated abundance data depends largely on established empirical relationships between echo strength and units of fish size and fish biomass (Love 1971, 1977; Foote, 1987). The echo integration approach to abundance assessment has been proposed as the standard method (Johannesson and Mitson, 1983; MacLennan, 1990; MacLennan and Simmonds, 1992), as it can be applied in situations where single fish, or aggregations, are being measured. During acoustic surveys, data was obtained by accumulating measurements from individual schools and dispersed fish. In the process of generating the data, the data were separated into different components (e.g. plankton, pelagic fish and demersal fish).

4.2 MATERIAL AND METHODS

4.2.1 Acoustic instruments

Data used for this study are acoustic data gathered from trawl sampling of small pelagic fish during twenty-two *ad hoc* acoustic surveys (Table 4.1, see appendix I for more details), by means of standard echo integration methodology (MacLennan and Simmonds, 1992). The equipment used is standard acoustic equipment and was used during all the Nansen acoustic surveys in Angola. These include a Simrad 38-kHz EK400 echo integrator (from 1985-1991) or a 38 kHz Simrad EK500 echo integrator

(On the new R/V *Dr. Fridtjof Nansen*, from 1994). The vessel has two different sized “Åkrahamn” pelagic trawls and one Gisund super bottom trawl. Often the bottom trawl was used during the surveys. The bottom trawl has a headline of 31 m, footrope 47 m and 20mm mesh size in the codend with an innernet of 10mm mesh size. The estimated headline height is 5m and distance between wings during towing about 18m. The two echo integrators used here (EK400 and EK500) have different capacities in terms of saturation effect (less or no saturation).

Table 4.1. Detailed survey information on the pelagic fish stocks in Angola (1985-199). R/V "Dr Fridtjof Nansen".

Year	Project cod	Survey no	Dir. Nam	Trawl stations		Length sample		CTD	
				First	Last	First	Last	First	Last
1985/1	AN	851		1	116	1	141	1	28
1985/2	AN	852		117	247	1	103	38	74
1985/3	AN	853		248	401	1	179	96	135
1985/4	AN	854		402	533	1	182	146	178
1986/1	AN	861		534	777	1	629	1	51
1986/2	AN	862		778	992	1	331	52	72
1989/1	A2	981		1	187	1	444	15	43
1989/2	A2	892		188	418	1	403	44	72
1989/3	A2	893		419	531	1	245	87	112
1991/1	A3	911	ANG1	1	231	1	653	120	144
1991/2	A3	912	ANG2	232	457	1	481	145	185
1992/1	A3		NAM1	1276	1297	547	582		
1994/1	A4		ANG1	1	62	1	125	153	245
1994/2	A4		ANG2	63	107	126	186	539	570
1995/1	A4		ANG1	283	512	610	1255	1	202
1995/2	A4		ANG2	609	788	1485	1723	622	759
1996/1	A4		ANG1	789	878	1731	1786	250	433
1996/2	A4		ANG2	1073	1152	2412	2562	705	740
1997/1	A4		ANG1	1153	1256	2563	2784	246	366
1998/1	A4		ANG1	1539	1636	3632	3785	236	423
1998/2	A4		ANG3	1709	1811	4170	4292	759	923
1999/1	A4		ANG2	1993	2068	4651			

4.2.2 Mapping of fish stocks

Biological information was collected during 22 surveys conducted in Angolan waters for the years 1985,1986,1989,1991, 1994, 1995, 1996, 1997, 1998 and 1999. R/V “*Dr. Fridtjof Nansen*” conducted the conventional acoustic surveys off Angola to map

the distribution as well as to estimate the biomass of pelagic fish (see Figs 3.2a, 3.2b, 3.2c).

Prior to each survey the echo integration unit was calibrated according to a standard procedure (Foote *et al.*, 1987). During the surveys echo recordings were scrutinised manually, echo intensities were then allocated to species based on catch compositions of trawl catches or the appearance on the echogram. Distribution charts categorised into scattered, dense, and very dense recordings for dominant pelagic species were then drawn for each survey according to the density in a given area. The filter used to eliminate plankton echoes from the integration is an average density per ESDU (Elementary Sampling Distance Unit) and the threshold ranged between – 60 dB and – 80 dB.

4.2.3 Distribution and abundance

Data used in this study was obtained from acoustic surveys on the R/V “*Dr. Fridtjof Nansen*” during 1985 to 1999. After 1994, sampling of the northern zone corresponding to Cabinda-Luanda was restricted due to oil industry activities. This means that most fishing occurs from the mouth of the Congo River to the Cunene River (Figure 4.1).

Three main zones are distinguished: Cunene to Benguela (17° 15 S-12° 30 S), Benguela to Luanda (12° 30 S-8° 50 S) and Luanda to Cabinda (8° 50 S-5° 00 S). These zones do not correspond to areas distinguished by their fauna or on any other ecological basis. The main pelagic fish are distributed according to two systems in Angolan waters: the Benguela and the Angolan system; in the Benguela system, the Cape horse mackerel and sardine are dominant, while the Cunene horse mackerel and two sardinella types are dominant in the Angolan system. The species of round sardinella (*Sardinella aurita*) occurs along the entire coast, from Cunene to Cabinda, while the flat sardinella (*S. maderensis*) is only found in the north from Benguela to Cabinda (Baptista, 1977) (Figure 4.2).

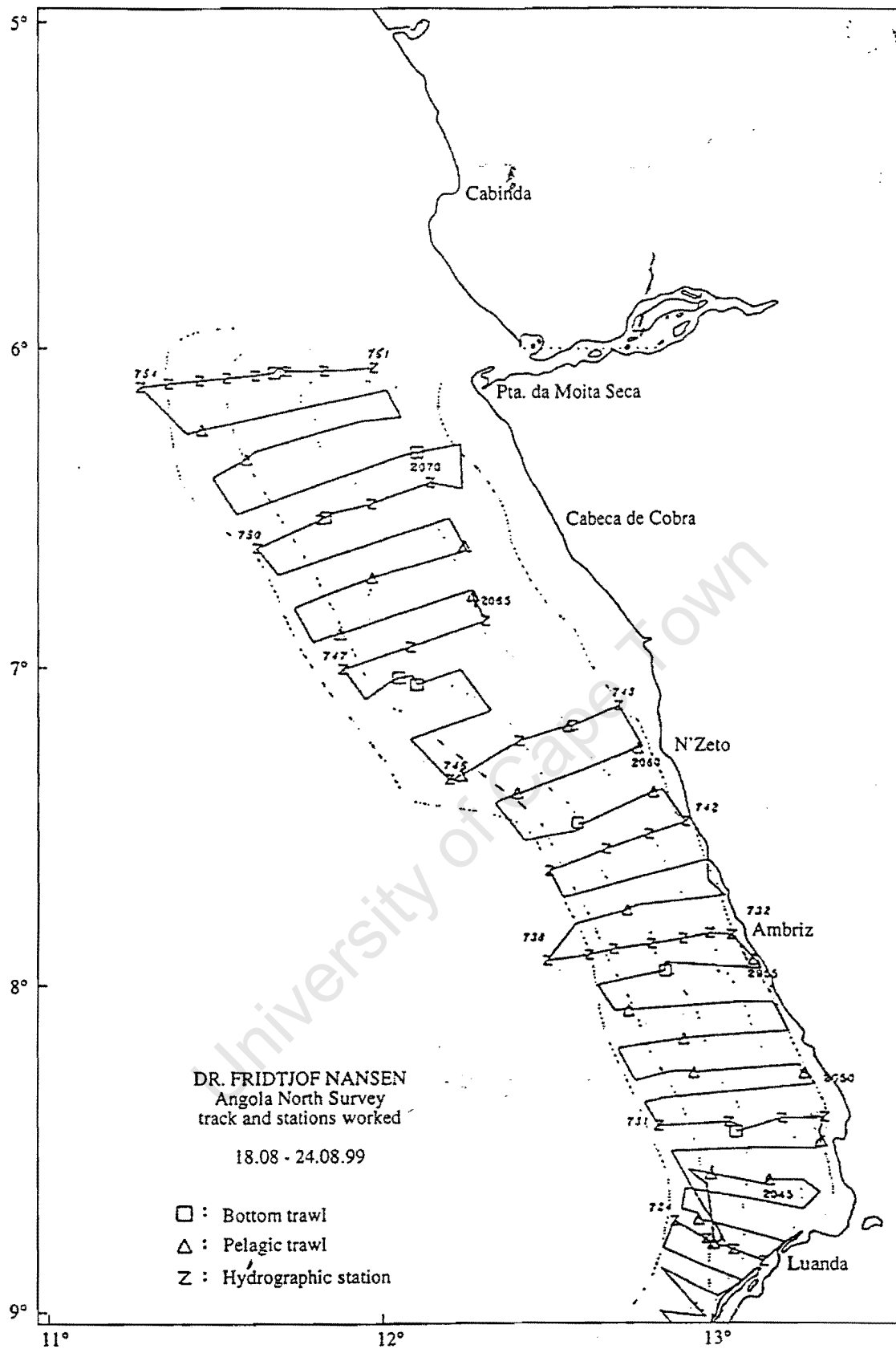


Figure 4.1. Course track with fishing and hydrographic stations, Congo River - Pta Das Palmerinhas.

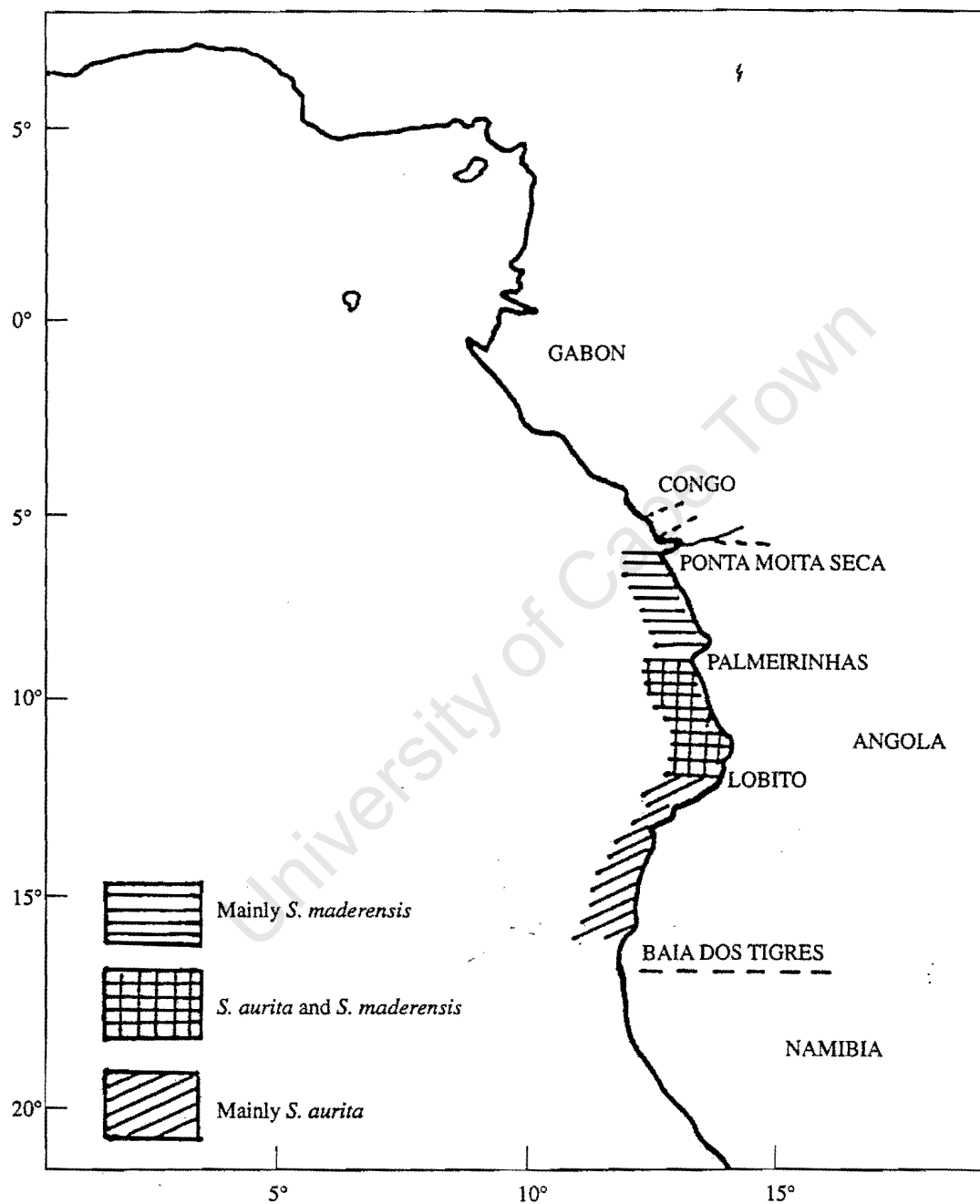


Figure 4.2. Distribution of sardinellas in Angolan waters between February and April (after Baptista, 1977).

4.2.4 Biomass estimates

Due to the absence of other reliable target strength values, the following target strength function for the North Sea Herring was applied to convert acoustic density values ($S_{A\text{-values}}$, mean integration value for a given area). The biomasses of these species were then estimated (see appendix II) by assuming a single target strength (TS, in dB) relationship:

$$TS = 20 \log L - 72 \text{ [dB]} \quad (4.1)$$

where L is the total length of the fish, expressed in centimetres. Then, using backscattering strength, distribution area, and species total weight recorded for each survey, the standard method of calculation was applied (Dalen and Nakken, 1983). All data was collected on a continuous basis, along transects throughout the survey. Further scrutiny of the data and the omission of unwanted echoes (noise, plankton) were performed using the Bergen Echo Integrator (BEI). The data was split into daytime and nighttime, starting at least 1 hour after sunset and finishing not later than 1 hour before sunrise. This procedure was followed because fish are more dispersed at night, and differences between day and night hydro acoustics have been reported (e.g. Aglen, 1983; Unger and Brandt, 1989; Amin and Nugroho, 1990; Schalk *et al.*, 1990; Fréon *et al.* 1993). The data were transformed into estimates of fish abundance, assuming that the size distributions were derived from hydro acoustic recordings in the area. Alternatively an average length of each species or species group was calculated and used to convert the acoustic density values ($S_{A\text{-values}}$) to the total number in a given area of fish through the following formulae (Dalen and Nakken, 1983):

$$C_{Fi} = 1.26 * 10^6 * L^{-2} \quad (4.2)$$

where L is the average length of fish, and C_{Fi} is fish conversion factor for length group i

$$N_i = A * S_A * \frac{p_i}{\sum_{i=1}^n \frac{p_i}{C_{Fi}}} \quad (4.3)$$

where N = number of fish in length group i

A = area of fish concentration in nm²

S_A = average integrator value in area A

p_i = proportion of fish in length group i from samples in area A

The number of fish for each local fish distribution was added together for each species or species group to obtain a total number of fish per species or group for the entire survey area. The total number of fish per species or group was then multiplied by the average weight (\bar{W}) of each species or group to obtain biomass (B) in tonnes:

$$B = \sum_{i=1}^n N_i \bar{W}_i \quad (4.4)$$

These calculations were performed by the scientific staff from the Institute of Marine Research (IMR), Bergen- Norway as well as by the staff from the Instituto de Investigação Marinha (IIM), Luanda-Angola.

4.2.5 *Fish school measurements by sonar* (after Misund *et al.* 1998)

In many surveys, a large portion of a school is visually observed near the surface but not recorded or partially recorded by acoustic equipment due to their location above the transducer and/or to avoidance reaction. In order to establish a representative quantification of the structure of near surface schools of fish off Angola, the following strategies were applied during the 1996 exercise. A regular survey making use of sonar, and conventional echo integration was performed with east/west transects, covering the coast out to 200m depth from Luanda to Lobito. Once areas with frequent recordings of schools were encountered either with the sonar or echo sounder, the regular survey discontinued in order to conduct special acoustic measurements of schools in the area. The speed of the vessel was reduced to 5- 8 knots. When the sonar detected distinct schools in front of the vessel it was

manoeuvred as accurately as possible to pass directly over the school. The school detection program connected to the sonar operated continuously, while both the sonar as well as the school detection program was operating within the same settings as during regular surveys. Once the school detection program recorded a specific school, the school number given by the detection program was noted on the sonar echogram in order to identify the school during the post-processing of the sonar data. Should the vessel be successfully manoeuvred over the school in order for it to be recorded on the echo sounder, the same school number was then noted on the echo sounder echogram. Sonar recordings were analysed by a program written in SAS software to determine the maximum area (A) of selected schools by eliminating schools through the school box option when post-processing the echo sounder recordings through a BEI-system. The vertical extent (H), average depth (D) and recorded transect length (TL') of the selected schools recorded by the echo sounder, were then measured by a ruler on the echogram and scaled to real dimensions. The transect length (TL) was then corrected for beam pattern by the equation (Misund *et al.*, 1990):

$$TL = TL' - 2 * D * (\tan (\beta/2)) \quad (\text{m}) \quad (4.5)$$

Where β is the beam width (-3 dB points) of the echo sounder. TL is the real transect length, TL' is the transect length measured, D is the beam width (- 3dB) and H is the height of school.

The fish density (ρ) of the school was calculated from the equation (Misund *et al.*, 1990):

$$\rho = s_A / (4\pi * \sigma * 1852 * TL * H) \quad (\text{nm}^{-3}) \quad (4.6)$$

Where $\sigma = 10^{(20 \log L - 72)/10}$, and L is the average length of fish in the school. The volume (V) of the school was estimated by assuming an ellipsoid shape and using the equation (Misund *et al.*, 1990):

$$V = 4/3 * \pi * A * H/2 \quad (\text{m}^3) \quad (4.7)$$

Finally, biomass of the school was then determined by multiplying the volume, density, and average weight of one fish in the school.

4.2.6 School tracking by sonar (after Misund *et al.* 1998)

To study the swimming behaviour of pelagic schooling fish off Angola, the Simrad SA950 sonar was used during all three surveys, tracking selected sardinella schools to record the dynamics, swimming behaviour as well as direction of movement. The vessel approached a selected school as slowly as possible until the latter was at a distance of more or less 200m and the vessel was stopped. The vessel was then manoeuvred gradually to keep the school within a distance of 100 to 250m. Should the school approach the vessel, it would stop. During tracking, the sonar was trained and tilted to obtain an optimal recording of the school. Once the tracking situation was established with a school in a fairly stable distance from the vessel, the position of the vessel, range, bearing and depth of the school was then recorded at 2 minute intervals for as long as possible. Tracking was stopped once the school disappeared. Any observations lasting less than two minutes (2 records) were disregarded; the longest period of observation was 72 minutes. Approaches and coalescing with other schools, or splitting of the target school changed the shape significantly. The sonar recordings of tracked schools were analysed by programs written in SAS software visualising the swimming behaviour of the schools, and quantifying the swimming speed and direction of the schools.

4.2.7 Surface school observations (after Misund *et al.* 1998)

It is known that during the day sardinella tend to be found near the surface. In an attempt to determine frequency and the time of this behaviour, appearances of sardinella schools at the surface were recorded visually from the bridge between sunrise and sunset (06:00-18:00 local time). This was done for 4 days during the 1996 and 1998 surveys, and for 13 days during the 1997 survey. Numbers of shoals sighted were pooled into 15-minute intervals. The presence of sea birds and their feeding or feeding attempts on accumulated sardinella was also noted. The ship-based Anderaa meteorological station automatically recorded solar radiation intensity at 10-minute intervals. This data was used to investigate the relationship between surface occurrence of shoals as well as light intensity.

4.2.8 Statistical analysis

The densities per layer (20 cm) of both sardinella species were analysed, using a one-way ANOVA, based on a significance level (α) of 0.05 (Zar, 1999). However irregular sampling over space and time, limits the use of the analysis. In such instances, unbiased estimates of average density per season, time, zone or year may be obtained by using a full general linear model (McCullag and Nelder 1989). To test for differences in average densities between the surveys, time of day and layer, as well as interactions among time of day and layer, survey and layer, an unbalanced ANOVA Type III model was used on all the average densities (*AVD*) (1985-1999, "Dr. Fridtjof Nansen" surveys). The general linear model can be summarized as follows (McCullag and Nelder 1989):

$$AVD = b_0 + b_1 (S) + b_2 (T) + b_3 (L) + b_4 (L*T) + b_5 (S*T) + \varepsilon \quad (4.8)$$

where:

AVD is an average density (g.m²),

S is survey effect (2 year level, 1994, 1997),

T is time effect (night or day),

L is layer effect (4 depth levels),

*b*₀ is the intercept,

*b*₁ to *b*₄ are parameters

ε is the error term.

The survey, time and layer are independent discrete variables.

4.3 RESULTS

4.3.1 Distribution and abundance

The relative proportion of the two species was assessed by their occurrence and catch composition in trawl samples during the “Nansen” surveys. These data indicated that in the area, Cunene-Benguela the round sardinella might be more common compared to flat sardinella (more or less 70% for the former species versus 30% for the latter). The main resource, in terms of biomass in Angolan waters, is represented by the two-sardinella species (60% in the acoustic surveys). The main area of stock distribution is the area of Benguela-Luanda (Figure 3.2b). For all the years of the surveys, the catch composition frequencies for both species during warm and cold seasons indicates a significant difference ($\chi^2_{1df} = 543.0, p < 0.001$) with a higher occurrence of flat sardinella (64-95%) and 5% -36% of round sardinella (Figure 4.3, for more detail see appendix III). Figure 4.4 shows the biomass estimates of sardinella species during warm and cold seasons. During the warm season, higher biomass estimates are found in the central region (Benguela-Luanda). In contrast, during the southern cold season the highest biomass estimates are found in the northern region (Luanda-Cabinda). This pattern is most likely due to north-south migrations, possibly applicable to both species.

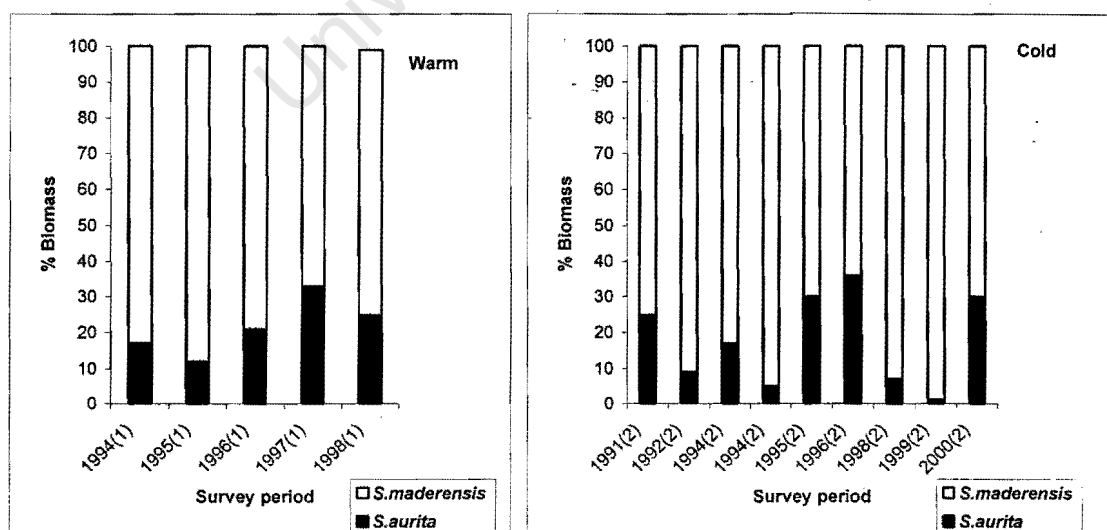


Figure 4.3. Seasonal catch composition of sardinellas from the overall estimates of biomass. Each column represents the % of the seasonal catch composition of two species. In some years only one survey was performed [source: *R/V Dr. Fridtjof Nansen*]. [warm: *S. aurita* = 22%, *S. maderensis* = 78% in average for all years; cold: *S. aurita* = 18%, *S. maderensis* = 82% in average for all years].

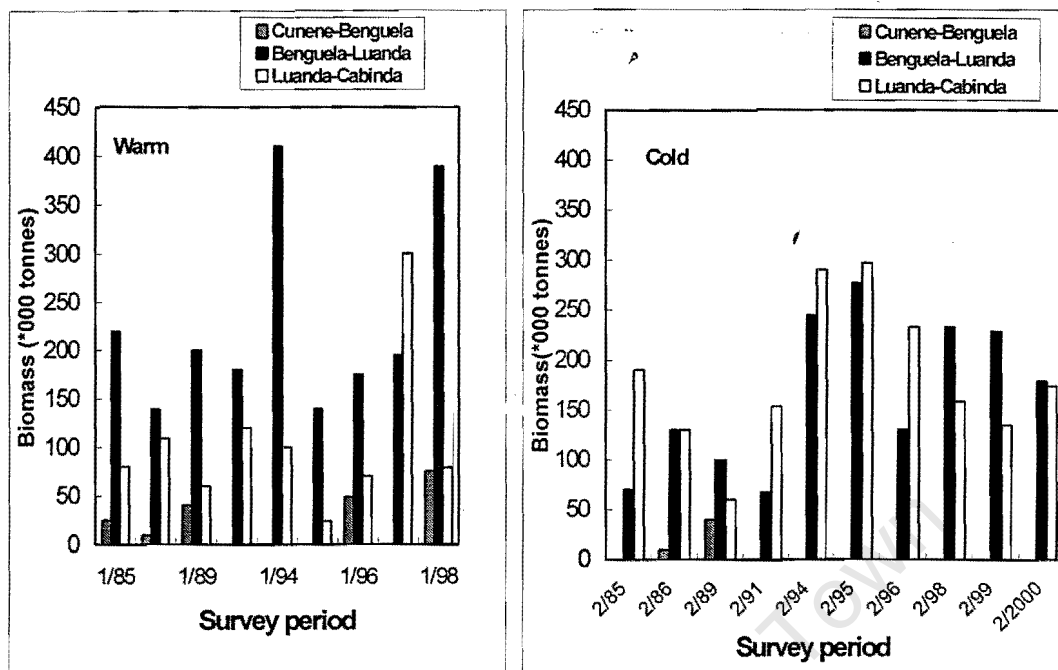


Figure 4.4. Acoustic biomass estimates of two sardinellas in Angolan waters during the warm and cold season. Each bar represents the acoustic biomass estimates. [source: survey data].

4.3.2 Seasonal changes in distribution and aggregation characteristics

Along the entire shelf of Angola, both sardinella species are found near the coast (Figures 4.5– 4.7), over bottom depths ranging from 20-200m. In 1985 during the warm season the sardinella species were concentrated in the Benguela - Luanda region, however a clear northward shift is noted in the distribution during the cold season. During 1986 the distribution of sardinella was more similar both in the warm and cold seasons. In later years, especially in 1996, a clear northward shift of the distribution of sardinella was observed from warm to cold seasons.

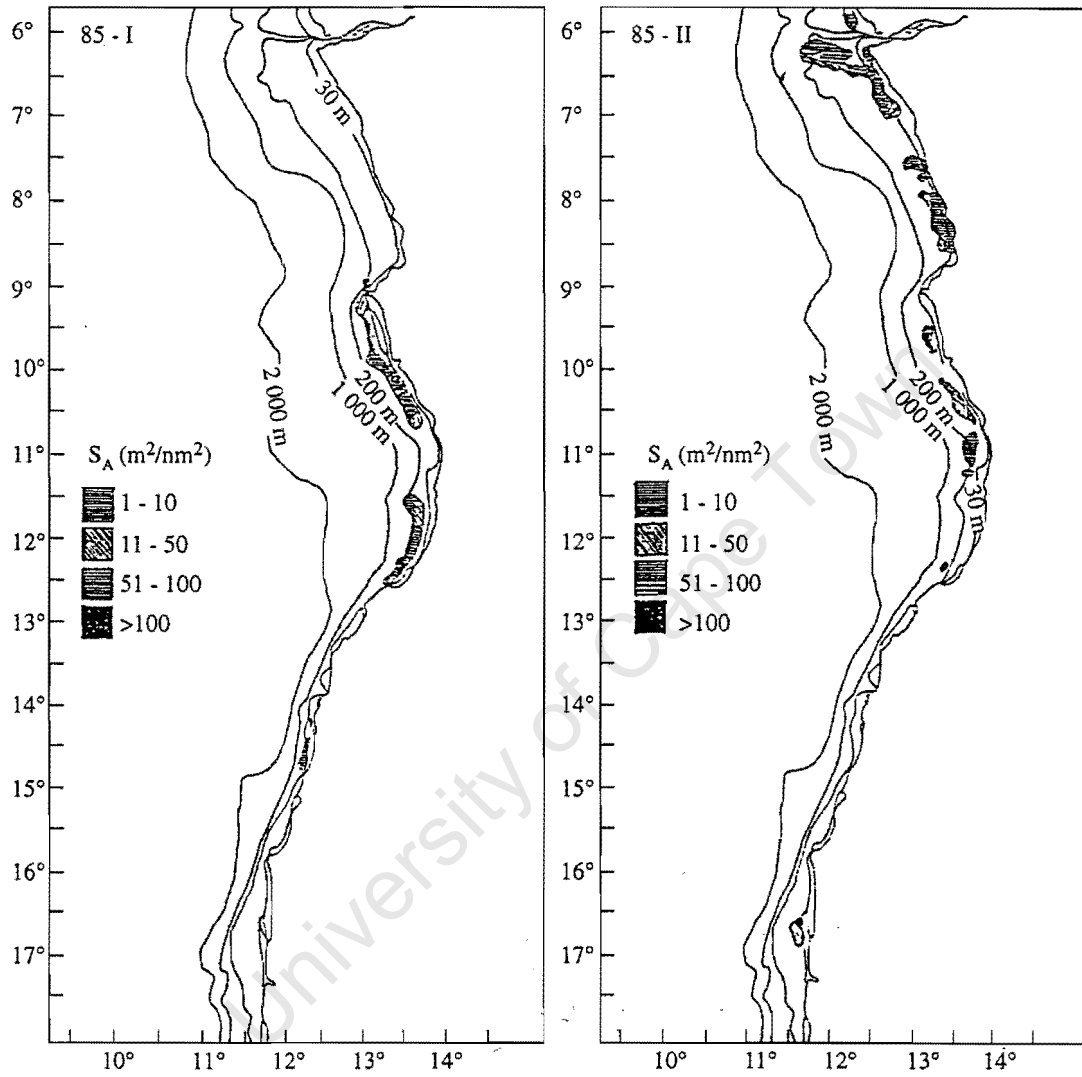


Figure 4.5. Distribution of acoustic recordings of sardinella in warm (I) and cold season (II) in 1985. [Source: survey data].

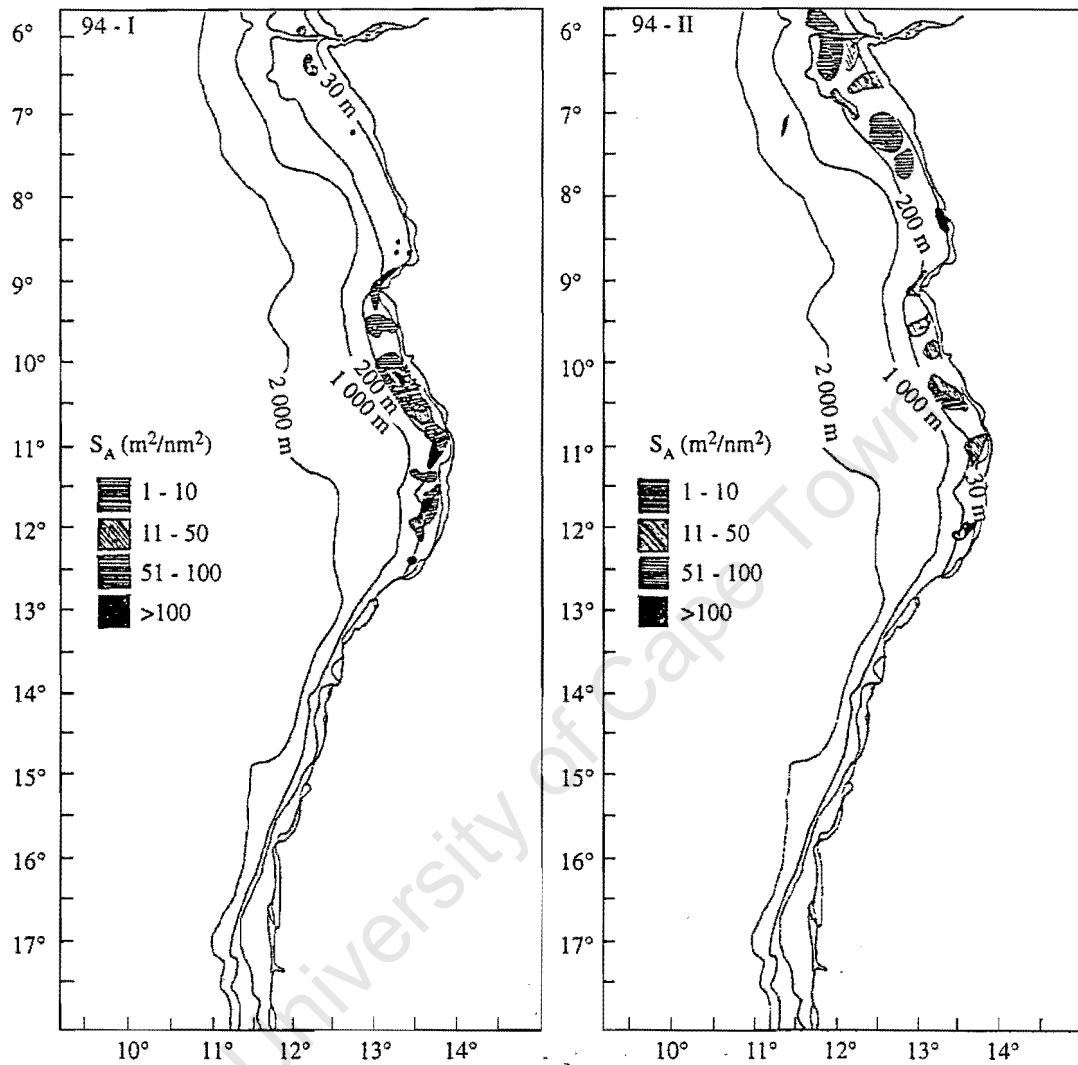


Figure 4.6. Distribution of acoustic recordings of sardinella in warm (I) and cold season (II) in 1994. [Source: survey data].

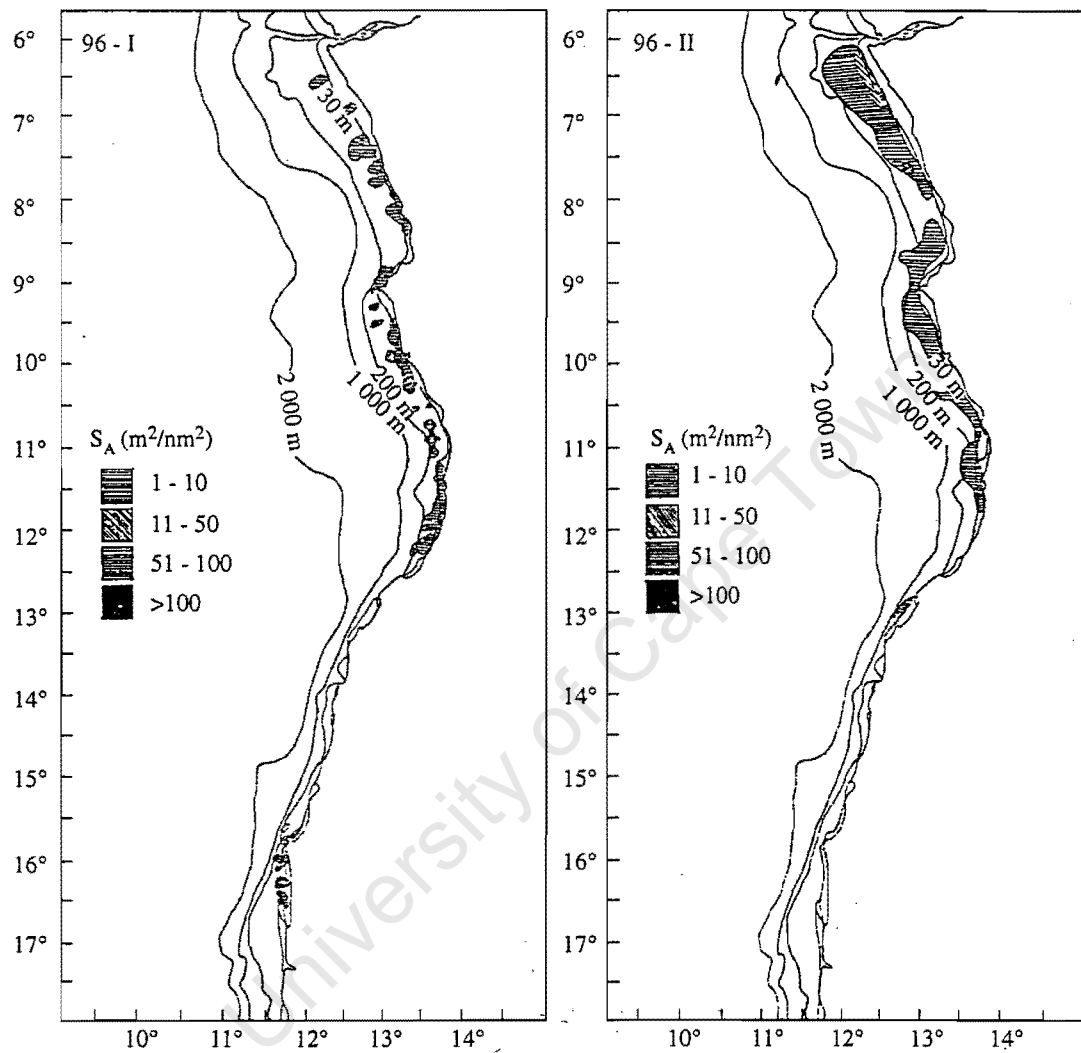


Figure 4.7. Distribution of acoustic recordings of sardinella in warm (I) and cold season (II) in 1996. [Source: survey data].

Generally, the biomass fraction (portion of area between 11°E and the coast, covered by sardinella stock and estimated acoustically, see Figs. 4.5-4.7) (from 1985, 86, 89, 91 and 94) in the Cabinda region varied from 14 – 42% during the warm to 30 – 73% in the cold season. Both absolute biomass and biomass fraction recorded for the sardinella species in the Cabinda region were significantly higher in the cold than in warm season ($P < 0.05$, Wilcoxon 2-sample test). Averaged biomass fractions in this region increased from a minimum of 6 to 48% from warm to cold seasons, indicating that there has been a movement of the sardinella into the Cabinda region. The Luanda region biomass fractions varied from 54 – 85% in the warm, to 27 – 50% in the cold season. In the Luanda region, there was no significant difference between the absolute biomass in the warm and cold season ($P > 0.05$, Wilcoxon 2-sample test), however the biomass fraction was significantly higher in the warm compared to the cold season ($P < 0.05$, Wilcoxon 2-sample test). This discrepancy could be attributed to the differences in the abundance of the resource from one season to the other and also to the fact that there were not surveys during both seasons in every year. Over the entire period of acoustic observations, the biomass fraction increased in the Luanda region by a minimum of 5% (1986) to a maximum of 42% (1985) from warm to cold seasons. This indicates that there has been a movement of sardinella out of the Luanda region from warm to cold seasons.

Together, these results illustrate seasonal shifts in the biomass distribution of sardinella along the Angolan coast with a northward movement during the initial part of the year (from warm to cold seasons), and a southward movement in the latter part of the year (from cold to warm seasons). Once the total biomass of sardinella increased (Table 4.2), the scattered aggregations of sardinella in the distribution area increased accordingly ($r = 0.55$, $P < 0.05$, $n = 28$). However the correlations between the dense and very dense aggregations and the total biomass are not significant ($r = 0.22$, $P > 0.05$, $n = 26$; $r = 0.39$, $P > 0.05$, $n = 21$, respectively). There was a seasonal dependence in the relationship between the distribution area of scattered recordings and the total biomass of sardinella since the relationship is maintained only during the cold season (Tables 4.2a, 4.2b). The distribution areas of sardinella in dense as well as very dense recordings were not linked to a total biomass for any season.

Table 4.2a. Overall correlations found in the areas of acoustic recorded categories and the biomass of sardinella [Data from Figs. 4.5-4.7] (r = correlation coefficient, n = number of observations, *: $P < 0.05$).

Biomass vs Total area	Correlations
Scattered aggregation	$r = 0.55^*$, $P < 0.05$, $n = 28$
Dense aggregation	$r = 0.22$, $P > 0.05$, $n = 26$
Very dense aggregation	$r = 0.39$, $P > 0.05$, $n = 21$
All aggregations	$r = 0.38$, $P > 0.05$, $n = 75$

* = Correlation

Table 4.2b. Overall correlations found in the areas of acoustic recorded categories and the biomass of sardinella [Data from Figs. 4.5-4.7] (r = correlation coefficient, n = number of observations, *: $p < 0.05$).

Biomass vs area		
Correlations	Warm season	Cold season
Scattered area	$r = 0.25$, $n = 15$	$r = 0.79^*$, $n = 13$
Dense area	$r = 0.31$, $n = 14$	$r = 0.08$, $n = 12$
Very dense area	$r = 0.48$, $n = 14$	$r = 0.22$, $n = 8$
Scattered fraction area	$r = -0.15$, $n = 13$	$r = 0.01$, $n = 7$
Dense fraction area	$r = 0.20$, $n = 13$	$r = 0.01$, $n = 7$
Very dense fraction area	$r = -0.01$, $n = 13$	$r = -0.12$, $n = 7$

* = Correlation

4.3.3 School biomass estimates (Misund *et al.* 1998)

During the 1996 survey in Angola the relationship between the school area and biomass for sardinella was determined. Altogether 96 schools were measured by sonar as well as by echo sounder, most schools were measured off Pta. das Palmeirinhas, however schools were also observed off Cabo Ledo and between Ponta Do Morro and Cabeça Da Baleia. The schools measured were distributed at depths varying from 11 to 35 m (average depth 17 m), while the area of the schools ranged from 33 to 1777 m² (average area 504 m²).

Vertical extents of the schools averaged 6.5 m, and varied from only 1m up to 25m. Assuming that all the schools measured were sardinella, with an average length of 29.5cm and weight of 0.295kg (average length and weight of sardinella in 17 of the trawl samples in 1996), fish densities in the schools ranged from a minimum of 0.1 fish m⁻³ to a maximum of 11.8 fish m⁻³ (Figure 4.8). The average density of the schools was 2.8 fish m⁻³, remarkably similar to average fish densities in herring schools in the northern hemisphere (Misund *et al.*, 1990). The estimated biomass of the schools varied from ± 10kg to more or less 20 000kg. The biomass and the area of the schools are related (Figure 4.8). This relationship is expressed through a borderline regression ($r^2 = 0.60$) between the area and biomass of schools, which follows the equation:

$$\text{School biomass} = 4.6 * (\text{School area}) \quad (\text{kg})$$

The relationships between school areas and biomass were developed by regressing echo-integration estimates of biomass on sonar estimates of selected schools.

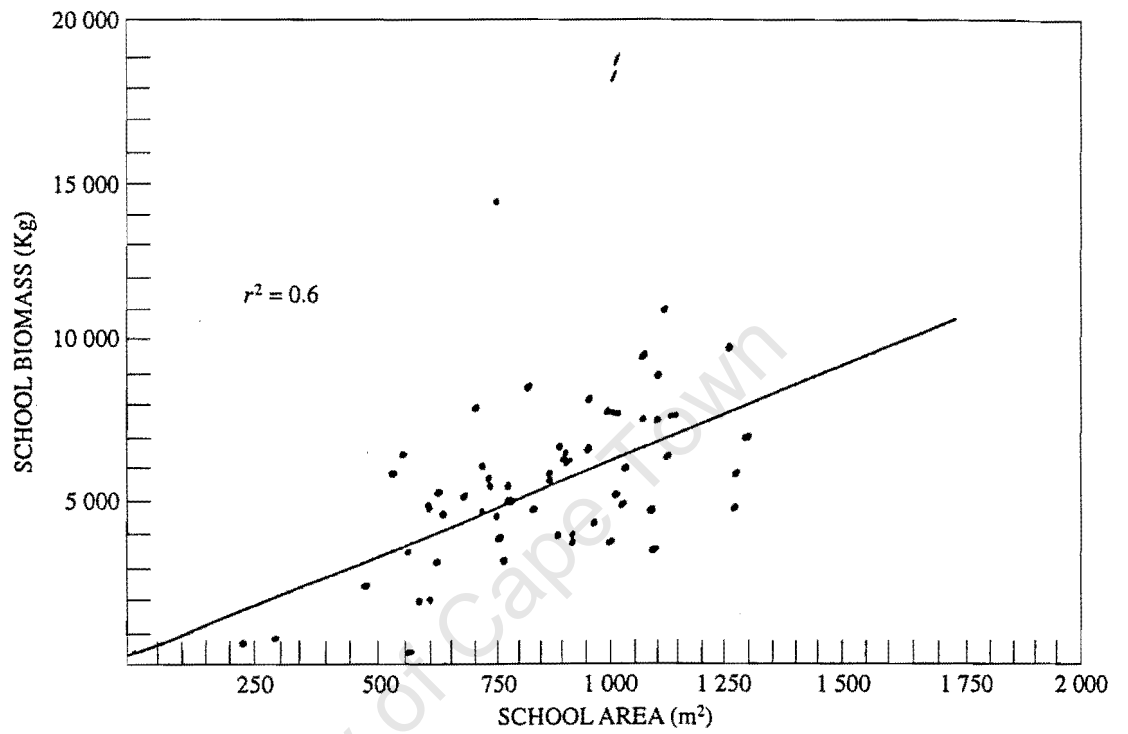


Figure 4.8 Relationship between school area and school biomass for sardinella schools off Angola. June 1997, [after Misund *et al.*, 1998]

4.3.4 School dynamics (Misund *et al.* 1998)

During cruises, 17 - 27 schools were tracked for 2 - 72 minutes respectively, mainly off Pta.das Palmeirinhas (area A in Figure 4.10), off Cabo Ledo (area B in Figure 4.9) and near Lobito (area C in Figure 4.9). In many cases tracking was initiated on schools that appeared at the surface, which could also be recorded by the sonar. Some schools appeared in mid-water, therefore the recorded schools were distributed from average depths ranging from 1-33 m. An example of the swimming- direction and speed of a tracked school is illustrated in Figure 4.10. Schools swam at horizontal speeds of 0.42 - 3.37 m/s, and moved at migration speeds of 0.09 - 2.27 m/s. Distributions of migration- direction and speed for schools are illustrated in Figure 4.9. In all three the areas, most schools headed east, towards the coast (26 cases), and less westwards (16 cases) or southwards (13 cases), while only nine schools were heading northwards.




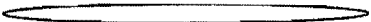

Sardinella schools were rather dynamic, in many cases the duration of the tracking was short, mainly caused by the fragmented or dispersed appearance of the schools causing the echo to fade from the sonar display, making further tracking impossible.

Intraschool (within schools) occurrence was observed at average rates of 0.63 events min^{-1} during 1996, indicating an activity within the school, every 1.6 min. In 1997 and 1998 average intraschool occurrence rates were more or less 50 % lower (Figure 4.11). A similar reduction in activity was found in the interschool (between schools) occurrence rates (Figure 4.11) which averaged 0.097 events min^{-1} in 1996, 0.064 events min^{-1} in 1997 and 0.058 events min^{-1} in 1998. Therefore interschool events occurred every 10.3 min during 1996, but only every 17.2 min in 1998. Amongst the interschool occurrence categories, change of shape dominated (Figure 4.12) with an average frequency of 0.35 events min^{-1} , indicating that the shape of schools changed every 3rd minute. For other interschool occurrences, average frequencies varied from 0.01 - 0.06 events min^{-1} only. Visible schools observed during sonar surveys were categorized as circular, elliptical, rod, crescent or ring-shaped, amorphous or fragmented (Table 4.3). The fragmented forms had the longest duration (5 minutes), while the ring-shaped were the least stable, typically persisting in this form for less

than a minute. Fragmented appearances were most common among schools, however distinct shapes such as a circle, an oval, rod and crescent were also quite common. Ring structures as well as amorphous appearances were rather rare (Figure 4.13).

Schools did not seem disturbed by approaching predators. Seabirds were remarkably absent, especially considering the large number of surface schools. A few gannets (*Sula spp*) were observed in the Lobito area, this however was only observed once, to attack the sardinella schools. Fish predators like barracuda (*Sphyraena guanchancho*) were caught during targeted trawling on sardinella schools, especially in the Palmeirinhas area. Sharks (*Sphyrna spp.*) were also observed on the surface, both off Cabo Ledo and Lobito. However, it was not observed that fish predators hunted schools during the tracking. Several seals (*Arctocephalus pusillus pusillus*) were also observed in the Lobito region. Nevertheless, distinct noisy, as well as water splashing “flashes” could occasionally be seen that were being performed in sardinella schools on the surface. These “flashes” are most likely a predator deterrent manoeuvre, probably effective to scare and confuse both bird and fish predators.

Table 4.3. A brief summary showing the different shapes of schools observed during the sonar surveys along the Angolan shelf (1996-1998).

Shape	Category
	Circular
	Crescent or ring-shaped
	Elliptical or oval
	Rod
	Amorphous or fragmented

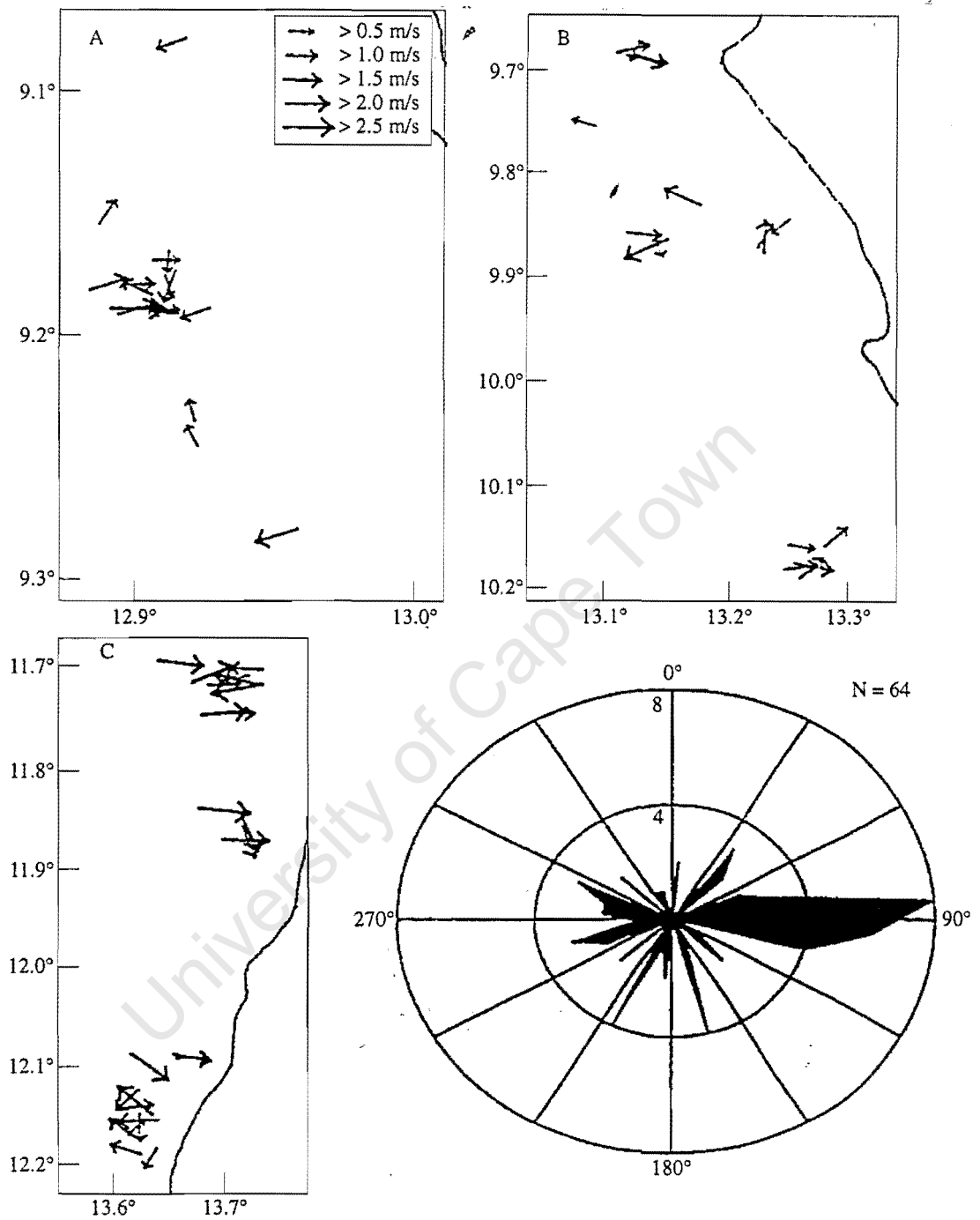


Figure 4.9 Distribution of average migration direction and migration speed for sardinella schools recorded off Pta. Das Palmeirinhas (A), off Cabo-Ledo (B), and north of Lobito (C). Lower right: distribution of migration Direction of all sardinella school tracked off Angola, 1996-1998. [after Misund *et al.*, 1998]

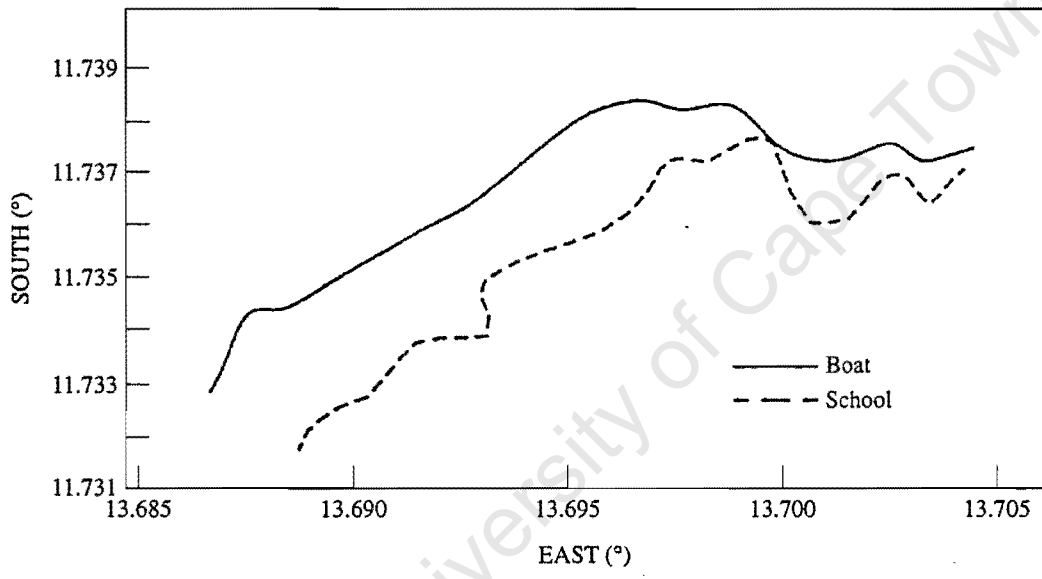
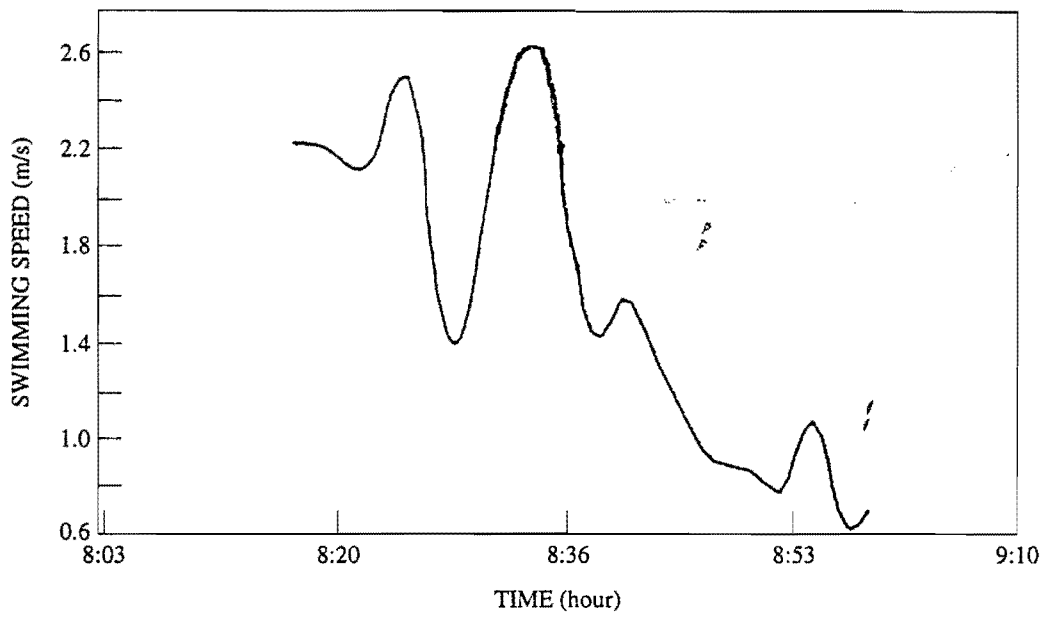


Figure 4.10 Tracking of single sardinella school off Angola. [after Misund et al., 1998].

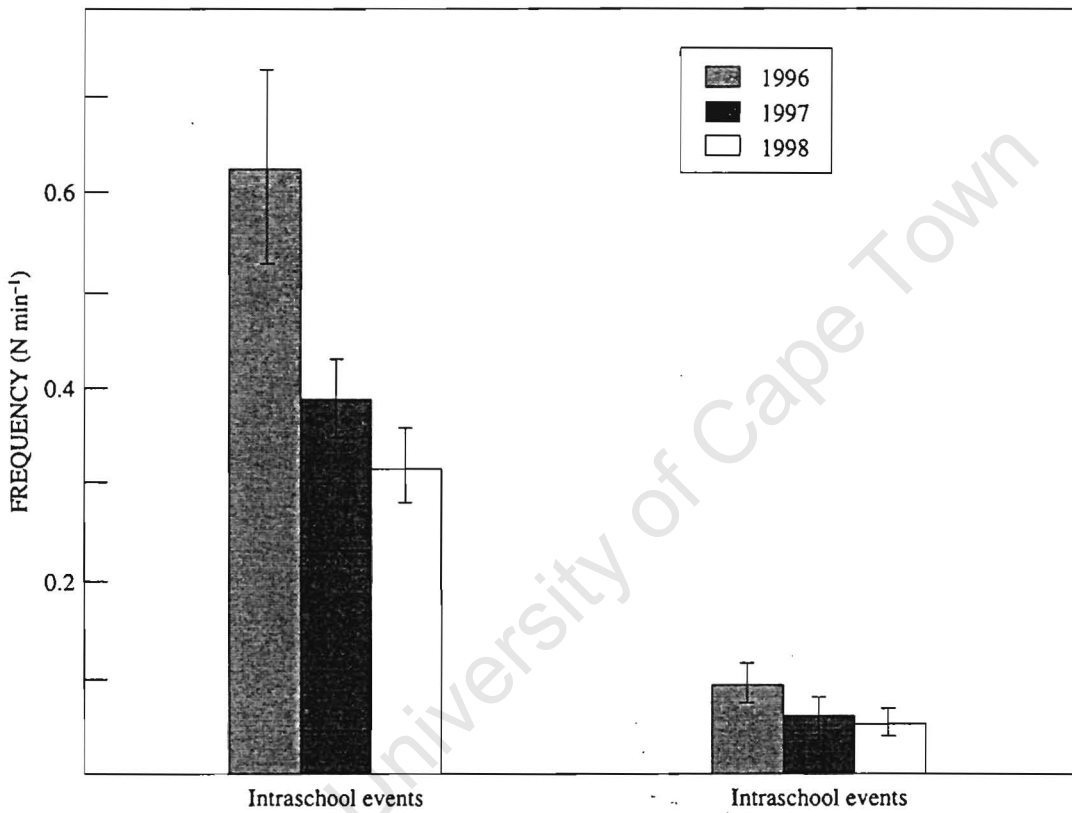


Figure 4.11 Intra and interschool event rates for sardinella schools tracked off Angola, 1996 (bars = SD). [after Misund *et al.*, 1998]

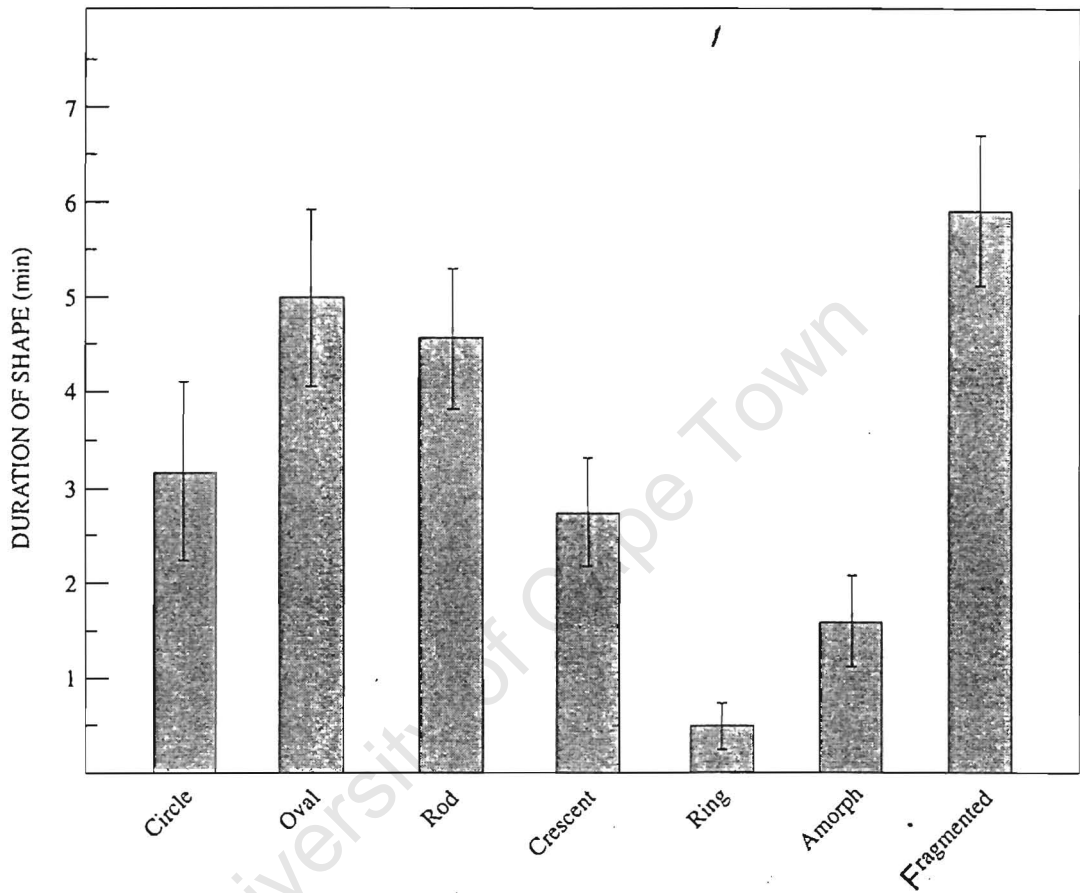


Figure 4.13 Distribution of duration of school shape categories (circle, oval, rod, ring, amorph) for sardinella schools tracked off Angloa, 1996–1998. (bars = SD). [after Misund *et al.*, 1998].

4.3.5 Influence of the solar radiation and time of day (Misund *et al.* 1998)

Visual observations from the bridge revealed that sardinella shoals appeared at the surface in a bimodal pattern (Figure 4.14). Shoals were seen at the surface in large numbers from 06:00 in the morning (sunrise) to 11:00. During midday, from 11:00 to 14:00, shoals seemed to be diving, eventually returning to the surface from 14:00 to 18:00, although with a lower frequency than in the morning (Figure 4.14). Maximum number of schools at the surface occurred at a radiation of more or less 300 Wm^{-2} , while numbers of schools on the surface leveled off at a lower radiation as well as a higher radiation. The number of sightings appears to be inversely related to the solar radiation with the maximum number of sightings occurring at radiation levels of about 300 Wm^{-2} .

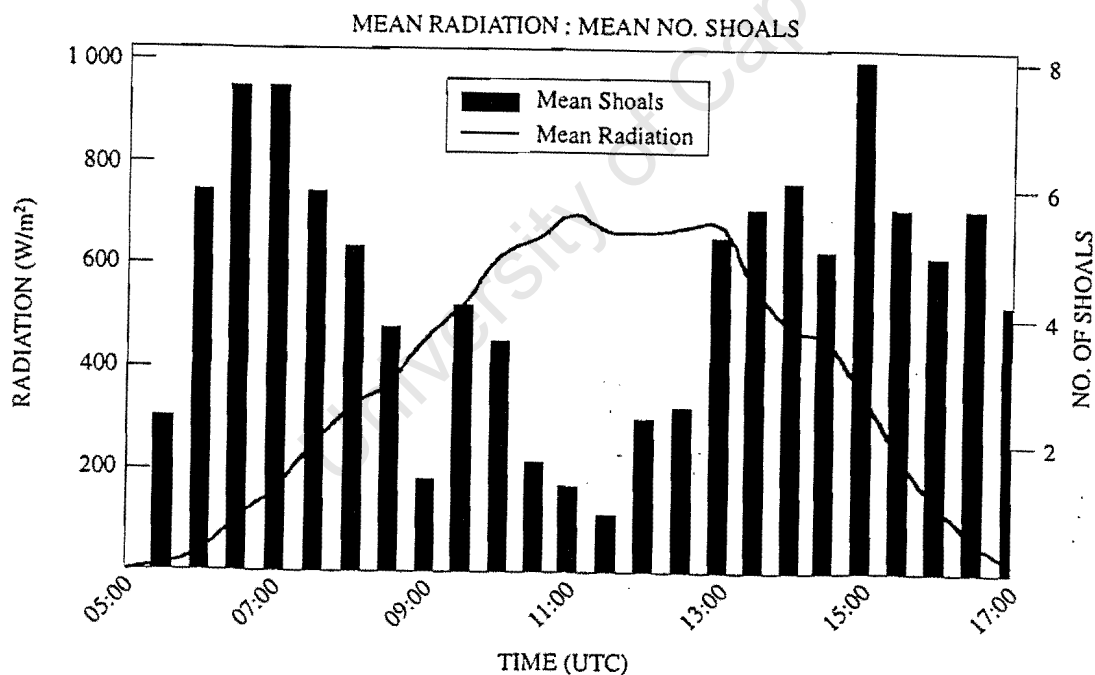


Figure 4.14. Counts of visible sardinella schools as a function of time of day for the 1997 *Nansen* survey off Angola, in relation to temporal changes in mean solar radiation during the day [after Misund *et al.*, 1998].

4.3.6 Diurnal variation in density

Standard statistics (\bar{X} , SD, CV) were calculated making use of the untransformed data for the day and night coverage of each survey during 1994 and 1997 (Table 4.5). In two of the surveys, the average recorded density is higher during the day, however the largest coefficient of variation was found at night. The density function of fish density data is often overdispersed, and frequently a log transformation is required to obtain a normal or Gaussian distribution. Therefore a one-way ANOVA analysis of the variance on acoustic densities was applied to the log-transformed density data. A comparison of day/night variations for the two surveys for all layers indicated a significant difference in diurnal variation patterns between day and night (one-way ANOVA, $F = 4.56$; df 1,1373 ; $P = 0.0329$) (Table 4.5). Average densities are found to be higher during the daytime. Nevertheless, due to a high variability in the data, the percentage of variance accounted for the model of day/night differences is low ($r^2 = 0.33$ or 33 %).

Table 4.5. Basic statistics calculated for fish densities $\log(g \cdot m^{-2})$ for time of day as well as results of a single factor analysis of variances between day/night averages (1994/97 surveys).

Time of day	\bar{X}	SD	CV	n	Min.	Max.
Day	194.8	768.7	3.95	692	0	12276
Night	112.2	660.9	5.89	679	0	12807
ANOVA						
Source of variation	SS	df	MS	F-value	P-value	Fcrit
Day/Night	22.7	1	22.7	4.56	0.0329	3.85
Error	6836.9	1372	4.9			
Total	6859.6	1373				

4.3.7 Temporal dynamics

Vertical patterns of dispersion

A pattern of diurnal vertical migration was explored during two of the surveys (1994 and 1997). This pattern illustrating the difference in vertical distribution is observed during day and night on the average layers (Figure 4.15). Error bars indicate standard errors for the averages. The fish densities estimated for each class layer for all the surveys (0-20 m, 20-40 m, 40-60 m, 60-80 m, Tables 4.6, 4.7, 4.8 and 4.9), show a pattern with the higher densities during the day and lower densities at night (Figure 4.15), except in the layers 20-40 m and 60-80 m where the layer effect was not significant ($P>0.05$) (Tables 4.7 and 4.9).

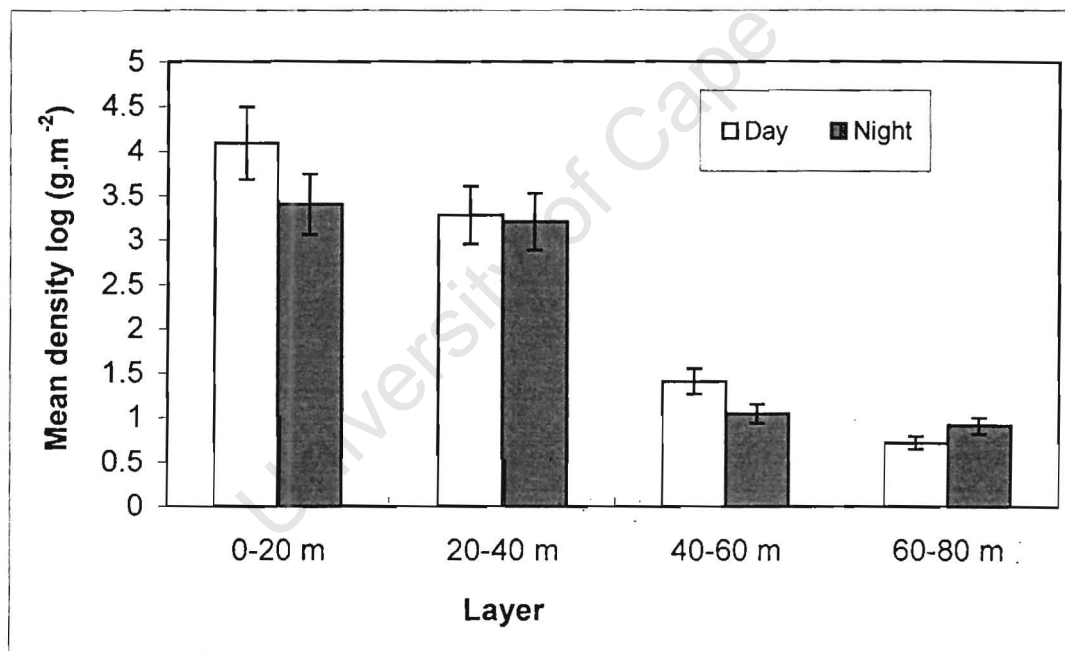


Figure 4. 15. Differences in mean density estimated by day and night for two surveys (1994 and 1997, error bars = $\pm 1SE$). [survey data of R/V *Dr. Fridtjof Nansen*]

Nevertheless, the percentages of variance explained by the model was very low ($r^2 = 3\%$ and 1% for layers 0-20 m and 40-60 m, respectively) (Tables 4.6, 4.8). Other depths show non significant day-night differences in density. Notwithstanding, the multi-factorial analysis (an unbalanced ANOVA Type-III model) also shows that the layer effect was highly significant ($*P < 0.0001$) (Table 4.10). The total variance explained by the model is very low, $r^2 = 4\%$. From this model, it is clear that layer (depth) contributes to the interpretation of acoustic density values ($S_{A\text{-values}}$). But obviously the survey variable contributes the most, while interactions of day/night and layer (depth) explain the smallest proportion of the variability of acoustic density values ($S_{A\text{-values}}$) with all the factors included in the model. This means that with a full model more or less 96% of the variance in acoustic density values ($S_{A\text{-values}}$) is not explained.

Table 4.6. Basic statistics calculated of fish densities $\log(g \cdot m^{-2})$ for the layer (0-20 m) as well as results of a single factor analysis of variances between day/night averages. $r^2 = 0.028$

Layer (0-20 m)	\bar{X}	SD	CV	Min.	Max.	
Day	4.09	2.17	0.53	0	7.9	
Night	3.40	1.90	0.55	0	8.9	
ANOVA						
Source of variation	SS	Df	MS	F-value	P-value	Fcrit
(0-20 m) Day/Night	41.7	1	41.7	10.01**	0.0017	3.87
Error	1469.8	353	4.2			
Total	1511.5	354				

** - Highly significant ($P < 0.01$)

Table 4.7. Basic statistics calculated of fish densities log (g. m⁻²) for the layer (20-40 m) as well as results of a single factor analysis of variances between day/night averages. $r^2 = 0.0003$

Layer (20-40 m)	\bar{X}	SD	CV	Min.	Max.
Day	3.28	2.46	0.75	0	9.4
Night	3.20	1.84	0.58	0	9.5

ANOVA						
Source of variation	SS	Df	MS	F-value	P-value	Fcrit
(20-40 m) Day/Night	0.5	1	0.5	0.10 NS	0.752	3.87
Error	1671.3	353	4.7			
Total	1671.8	354				

NS- Not significant

Table 4.8. Basic statistics calculated for fish densities log (g. m⁻²) of the layer (40-60 m) as well as results of a single factor analysis of variances between day/night averages. $r^2 = 0.012$

Layer (40-60 m)	\bar{X}	SD	CV	Min.	Max.
Day	1.41	2.00	1.42	0	8.8
Night	1.05	1.35	1.29	0	6.3

ANOVA						
Source of variation	SS	df	MS	F-value	p-value	Fcrit
(40-60 m) Day/Night	11.8	1	11.8	4.05*	0.0449	3.87
Error	1011.3	347	2.9			
Total	1023.1	348				

*- Significant ($P < 0.05$)

Table 4.9. Basic statistics calculated for fish densities log (g. m⁻²) of the layer (60-80 m) as well as results of a single factor analysis of variances between day/night averages. $r^2 = 0.006$

Layer (60-80 m)	\bar{X}	SD	CV	Min.	Max.
Day	0.72	1.19	1.65	0	4.3
Night	0.91	1.30	1.43	0	6.9

ANOVA						
Source of variation	SS	df	MS	F-value	p-value	Fcrit
(60-80 m) Day/Night	2.98	1	2.98	1.90 NS	0.17	3.87
Error	490.0	313	1.57			
Total	492.9	314				

NS- Not significant

Table 4.10. Results of a multifactorial analysis done on variance of main effects plus 1 interaction on acoustic density. $r^2 = 0.042$

Source of Error	SS	df	MS	F-value	p-value
Model	29955516	8	3744439	7.53	<0.0001*
Error	676844239	1362	496948		
Corrected Total	706799755	1370			
Survey	6696207	1	6696207	13.47	<0.0003**
Day / Night	2325340	1	2325340	4.68	<0.0307*
Layer	18743601	3	6247867	12.57	<0.0001**
Day/Night*Layer	998044	3	332681	0.67	0.5708 NS

*= significant, **= highly significant, NS = not significant

Multi-factorial analysis of variance on acoustic density

Fish densities estimated for each class layer for all surveys indicate a significant but very small difference in densities (in two layers) between day and night (Figure 4.15). This means that diurnal vertical migration is not strong.

The multi-factorial analysis (an unbalanced ANOVA Type-III model) on acoustic densities was performed on the log-transformed data, testing differences in density averages between day and night vertical distributions as well as interaction between surveys and day / night. The ANOVA indicated that vertical layer had a low (<3% of the explained variance) influence, despite its high significance level ($P < 0.0001$). The effects of the day / night period was also significant ($P < 0.005$), although not important ($r^2 < 0.5\%$). The interaction between surveys and day / night was also significant ($P < 0.05$), although not important (<0.4%) (Table 4.11). In this model, the overall r^2 was very low ($r^2 = 5\%$), and is mainly caused by the survey and layer effects.

Table 4.11. Results of a multifactorial analysis done on variance of main effects plus 2 interaction on acoustic density. $r^2 = 0.046$

Source of Error	SS	df	MS	F-value	p-value
Model	32792677	9	3643630	7.36	<0.0001**
Error	674007077	1361	495229		
Corrected Total	706799755	1370			
Survey	6721946	1	6721946	13.57	<0.0002**
Day / Night	3530220	1	3530220	7.13	<0.0077*
Layer	18628329	3	6209443	12.54	<0.0001**
Day / night x Layer	815027	3	271675	0.55	0.6491 NS
Survey x day/night	2837161	1	2837161	5.73	<0.0168*

* = significant

** = highly significant

NS = not significant

4.4 DISCUSSION

The present analyses of the availability of both sardinella along the Angolan shelf using the survey data, indicate that the oscillations of the Benguela-Angola front system are partly responsible for the distribution of sardinellas. However, most sardinella occur well north of the front. In the past, several authors in the Congo-Angola region have done limited studies on the biology, distribution and evaluation of sardinella (e.g. Ghéno and Campos Rosado, 1972; Fontana and Pianet, 1973; Campos Rosado, 1974; Baptista, 1977; Boëly and Fréon, 1979; Troadec and Garcia, 1980; Thomas, 1984). They revealed that the movement of the sardinella stock is strongly influenced by the seasonal and the environmental conditions encountered in the area. Since 1985 to date, descriptions of the abundance and distribution of sardinella were based mainly on the acoustic density data recorded during the surveys by the R/V *Dr. Fridtjof Nansen*. However, an additional source of information on the mapped areas for the artisanal fishery is given by Lartigue and Kingombo (1996) (Figure 4.16). The artisanal fishery is becoming a major concern to the Angolan government, as the catch is used for food security by the coastal population. It is reported by Alberts (1990) that the artisanal fleet along the Angolan coast consists of approximately 3835 vessels.

The acoustic densities must be considered as relative indicators of sardinella abundance within the study area over a period of time. Absolute abundance estimates have not been attempted for two reasons: (1) horizontal avoidance of the boat almost certainly limits the encounter rate and (2) the difficulty of determining a correct average backscattering cross-section for the species (Rose and Leggett, 1988). Based on the size of the R/V *Dr. Fridtjof Nansen*, the inshore (<20m) and offshore (beyond 200 m) areas are not covered during the pelagic surveys.

This, in turn, means that a fraction biomass of this stock is not included in the overall biomass estimates (underestimation). As reported by Pereira (1991), in case of strong upwelling, schooling pelagic fish are usually forced to migrate further offshore, where they gather to feed on zoo- and phytoplankton. Similarly, Baptista (1977) pointed out

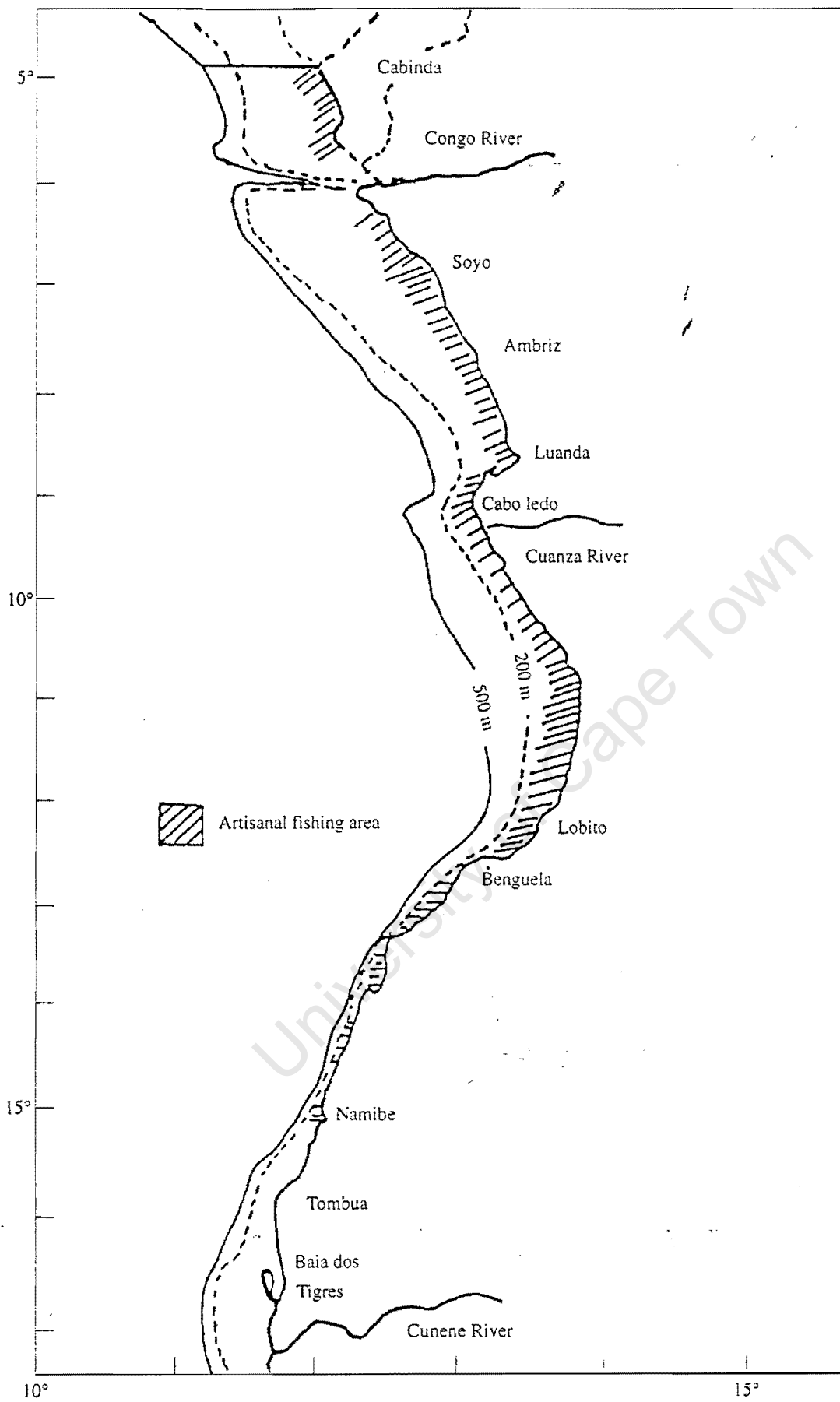


Figure 4.16 Artisanal fishing areas along the Angolan coast.
 [Source: IDPA-Luanda]

that an offshore movement of the species might cause the decreased availability of *S. aurita* during December and January, as they avoid lower temperatures during the cold season. Studies done in the mid 80s on pelagic resources, were also consulted (Thomas, 1984 and Wysonkinski, 1986) and compared with the findings of the R/V *Dr. "Fridtjof Nansen"*. There were similar findings on the biology and distribution of sardinella.

In recent years, a large difference in the distribution is clear between the two species, which can mainly be attributed to causes other than fishing. However, one can point out that coexisting species of pelagic fish that inhabit the same area of ocean can compete for food resources and space. Lasker and MacCall (1983) investigated this question indirectly by inferring the relative average sardine and anchovy stock sizes from the frequency distributions of sardine and anchovy scales found in anaerobic sediments. The average anchovy stock size during periods of high sardine abundance was found to be significantly smaller than in periods when sardine populations were low. The authors pointed out that this result is consistent with a competitive hypothesis, however there are other possible explanations, e.g. offshore distribution of small anchovies. An occasional response of an ecosystem when sardine abundance is low (e.g. off California) causes an increase in the population of anchovies, and alternatively, with ecosystems where anchovies were reduced (e.g. Peru-Chile), sardines in turn increased remarkably in number. Whether competition on a large geographic scale is the mechanism causing this has yet to be demonstrated.

Survey results indicate that there were seasonal changes in the distribution of sardinella species along the coast of Angola (Luyeye and Misund, 1998, Figs. 4.5-4.7), probably due to the seasonal variability of the hydrographic regime, as well as the distribution of phyto- and zooplankton. It should be noted that although the marked seasonal changes only affect the upper 100m or so of the water column, high productivity is available here over wide depth ranges.

Due to higher temperatures in 1995 (Benguela-El niño), sardinellas were redistributed in the northern region over depths more than 700 meters (Anon, 1995). As already pointed out by Dias (1983), greater activity of the Angolan current may cause seasonal (March-May) movement of single schools as observed in 1983, as far as

waters off northern Namibia, (Thomas, 1984). The increase and decrease in biomass estimates observed during 1985 to 1996 indicated a possibility of north-south movements that are connected to upwelling and the Angolan current.

At the end of May the changes of season start with a reduction in the surface temperature (22°C) apparently starting in the north. This may be the start of the upwelling which reaches its maximum in August-September and probably ceases towards the end of the year. This may affect the distribution of the plankton feeding fish (e.g. sardinellas). In the warm season (February), the warm water of the Angolan current moves towards the southern area in the open water some 20 nm outside the shelf edge. These variations result in a displacement in a north-south direction of the frontal zone between the water masses of the Angola and Benguela currents. This regime influences the seasonal and inter-annual variations in the position of the frontal area and then is likely to result in changes in the distribution of the pelagic fish.

The upwelling causes intensified primary production which affects fish production and their distribution. Baptista (1977) showed that movement of the sardinella stock results in seasonal fishing in certain areas along the Angolan coast (Appendix IV). As may be seen from this table, similar patterns were observed during the time series of estimates done on the R/V "*Dr. Fridtjof Nansen*". It is common knowledge that, especially in the sardinella species, their behaviour is strongly influenced by the seasonal and environmental conditions encountered in the area (Anon, 1991). Acoustic sampling has the advantage of covering fish resources in a relative short time, i.e. giving a snapshot of the abundance of pelagic species.

This method however suffers from a series of biases and sources of variance that are difficult to evaluate and reduce (MacLennan & Simmonds, 1992). Some of the problems are related to the behaviour of fish, due to the day-night variations in fish distribution and density, near surface distribution as well as vessel avoidance. These factors may influence the acoustic biomass estimates significantly. However, comparisons of acoustic recordings and distribution areas for different seasons are probably marginally affected.

The relationship was roughly linear between school areas and biomass as established by sonar measurements as well as echo integration of selected schools (Figure 4.8). The relationship does not have predictive capacity due to a wide variance. This suggests that the areas of entire schools, as recorded by sonar, cannot be accurately converted to fish density. During the survey, measurements were conducted in three different areas with a large number of schools that were encountered close to the surface. The relationship is therefore based on a selection of representative schools close to the surface off Angola, and cannot therefore be used to convert the daytime sonar recordings of school areas to biomass in later abundance estimations. Sardinellas seem to maintain rather dense shoals at night, however should a different relationship exist between the area and biomass of the night- and daytime shoals, it is not known as yet. The school measurements revealed an average packing density of more or less 3 fish m^{-3} in sardinella schools which is comparable to herring schools of similar length (Misund and Floen, 1993).

During the cruise a large number of surface schools were sighted. These surface schools seem most active during early morning and in the afternoon, with a minimum of surface activity during mid-day. The numbers of surface schools seem inversely related to the level of solar radiation (Misund *et al.*, 1998).

To produce comparable biomass estimates for the pelagic fish resources of Angola, a single target strength (TS) was used. Although this target strength to size relationship has been used for a number of fish species (horse mackerel, pilchard, anchovy and sardinella), it is probably not ideal for some of the species encountered during these surveys such as some of the socially aggregated sardinella. In addition to possible problems associated with shadowing in dense schools especially when using the EK400 echo integrator, the question arises whether the average target strength (TS) of fish remains constant when fish change their depth and tilt angle during diel vertical movements, a behaviour commonly associated with changes in aggregation (Woodhead, 1966; Dembiski, 1971; Blaxter, 1975). Accurate hydro-acoustic assessments of biomass of a particular species have been limited by the difficulty of objectively differentiating among taxonomic groups of sound scatterers.

Identification methods most commonly used are based on trawl sampling in close proximity to the acoustic targets as well as on visual interpretation of echograms

based on previous knowledge of species shoaling patterns. In many cases, however, these techniques have not enabled objective discrimination between co-occurring fish species (Rose and Leggett 1988). Species mixing in aggregations may also lead to errors in the proportion of the measured acoustic energy allocated to a particular species. This method does not reveal knowledge of the fish size distribution within the schools (Robinson *et al.*, 2000).

The introduction of the EK500 in 1992 may to some extent have affected the comparability of the time series of stock estimates which the previous surveys provide. The possibility of underestimation by saturation in the previous system (EK400) existed especially where dense schools occurred close to the surface, which is a characteristic behaviour for sardinella. In that case high values would be suppressed. This type of bias would be greatly reduced by the wide dynamic range of the EK500 system.

A diurnal cycle in fish density was observed. Large variations also existed in the measurement of biomass between successive surveys, with densities on average being opposite lower at night than during the day. Fréon *et al.*, (1993) found that lower densities were recorded by day than by night through an analysis of acoustic data obtained from tropical locations covering 18 surveys. They concluded that lateral avoidance of the survey vessel by near surface shoals is the primary reason for underestimation by day. However preliminary findings by Roel and Armstrong (1991), suggest that sardine schools in South Africa show very little or no signs of avoidance reaction to the presence of a research vessel. Fréon *et al.*, (1993) also concluded that in their analysis of acoustic data, the bias due to fish being too close to the surface at night could account for only about 10 % of the day/night differences.

Fréon *et al.* (1993) also indicated some factors for the underestimation of fish during the night like a higher range of variables in tilt angles of the fish at night than during the day as well as the use of light on a vessel which produces a strong avoidance reaction, and in some cases changes the echo abundance below the vessel. During the acoustic surveys conducted in Angola, the effect of the light intensity on the research vessel was reduced during the night which in turn does not cause a strong reaction and allows the vessel to move close to the fish or pass over them. It is evident from this

study that differences in day and night densities are not important. It is therefore suspected that the day/night differences in abundance estimates may be caused by diurnal change in schooling behaviour with related vertical displacement of the fish and/or vessel avoidance. Further studies in the comparison of sonar and echo sounder estimates of fish biomass could assist in highlighting vertical migration biases as well as those caused by avoidance.

Since the advent of the echo sounder, it has become possible to determine the variations and extent of vertical migration of fish populations. Since pioneering work done by Runnstrøm during the early 1940's (Runnstrøm, 1941, cited in Blaxter and Holliday, 1963), numerous authors have reported on the phenomenon of vertical migration particularly by clupeids. General patterns of vertical migration seem to be an upward movement at night followed by a spreading out of the fish.

Several reasons have been suggested as to why fish migrate vertically. These include changes in vertical distribution in relation to changes in food availability, avoidance of predators, the following of a preferred light intensity as well as changes in the thermal and salinity structure of water columns (Blaxter and Hunter, 1982). It seems likely that control of vertical migration is extremely complex, depending on a number of external factors, the effect of which will be modified by internal factors such as the age and physiological state of the fish. In this study, it has been found that the range of vertical distribution of sardinella is large (80 m) but that diurnal vertical migrations are low and or exceptionally variable or underestimated by the surface dead-zone of the acoustic equipment.

In both of these surveys, a significant difference of day/night between the average densities was found in the shallow water, possibly indicating that fish were missed above the transducer. However, constraints due to the typical scale of one to five nautical miles imposed by the echo integrator, limited the extraction of further detailed information from the acoustic data or echo charts (Reid and Simmonds, 1993).

Using sonars to detect when fish are too close to the surface has increased in recent years (Gerlotto *et al.*, 1994; Soria *et al.*, 1996). As it would probably be inappropriate to survey sardinella only during the day due to time constraints, the use of sonar may be useful in alerting scientists during routine surveys as to the presence of surface shoals. In these instances surveys should be combined (echo sounder + sonar).

The distribution of sardinella is very dynamic, and these species are fast-swimming fish with significant changes in behaviour during the day (Figure 4.10). The most common feature for the sardinella in Angolan waters is the concentration in schools at daytime, often close to the surface (Figure 4.14). At night the schools tend to dissolve and the fish are spread in somewhat deeper layers, however, still in the upper part of the water masses.

In this work the methodological survey on pelagic schooling fish resources off Angola have confirmed earlier observations of some authors (e.g. Pitcher and Partridge, 1979; Fréon and Misund, 1999) that surface schooling of sardinella causes significant underestimation of fish abundance by conventional echo integration in the area.

CHAPTER 5.

DISCUSSION AND CONCLUSIONS

This thesis has covered many aspects, such as distribution, migrations, diet and schooling behaviour. The two species are congeneric and largely sympatric species with a very similar geographical distribution that includes the continental shelf along the eastern Atlantic. They have common characteristics that differentiate them from other genera of Clupeidae. Flat sardinella is identified as a species of limited migration and no cases of wide scale migrations are known. However, the migratory cycle of adults of round sardinella is known along the Eastern Central Atlantic. The two species of sardinellas are zoo- and phytoplankton filter feeders of which the main diet is zooplankton. The spawning activity for the two species occurs over protracted periods throughout the year with several minor and one major peak (Roy *et al.*, 1992)

Results on the biology (e.g. mean fish lengths) indicate that both sardinella species, along the Angolan coast, are influenced mostly by seasonal variations (Figures 3.5 and 3.10). During the warm season, which is characterized by more stratified water masses and higher temperatures, more than 50% of sardinella species biomass is found in the region Benguela-Luanda. In contrast, during the cold season which is characterized by upwelling and colder surface waters, more than 50% of the sardinella are found in the northern region from Luanda-Cabinda (Figure 4.4). Based on the above results, it is clear that the distribution pattern of sardinella appears to be different in the two seasons. The sizes of fish available are also dependent on season, larger specimens being present in the cold season as compared to the warm season. It was found that the period with intensive fishing (1985-1991) led to a decrease in mean fish lengths (Figs. 3.9 and 3.14). This finding supports the idea that the stock was negatively affected by the intensive fishing by Soviet fleets.

Round sardinella showed here adequate results indicating that both males and females reach 50% maturity at sizes 23 and 24 cm total length, respectively (Figure 3.4).

The sex ratios for round sardinella in both seasons and among the three zones was statistically different from unity. Only a few ratios slightly favoured males, whereas females were frequently dominant (Table 3.2). In contrast, for flat sardinella the sex ratios favoured few females, whereas males were dominant (Table 3.3). This study has shown for the first time in Angolan waters the relative importance of season, geographic zone, and inshore-offshore distribution of sardinellas.

The GLM without interactions for the two species revealed that season as an independent variable had little contribution to the total variance in the GLM (<4% for round sardinella, while flat sardinella is <5%), despite its highly significant *P*-value (Figs 3.5 and 3.10). Highly significant *P*-values and a low r^2 may occur when there are many degrees of freedom (df) in the model. In contrast, in the GLM of flat sardinella without interactions, the depth and zone had little contribution to the total variance in the GLM (<7% for zone, while the depth is <10%), despite their highly significant *P*-values (Table 3.8). The highly significant value for the depth as an independent variable may indicate that the juveniles of flat sardinella occur inshore of adults (Anon, 1994). The significant interaction between season and zone in the GLM of flat sardinella indicates that flat sardinella vary differently in size at different season and zone (Table 3.9).

The use of acoustic data has enabled a “snapshot” of the spatial dynamics of sardinella populations. Although there are many factors known to cause a change in catch composition for *S. aurita* (7% for the 1998 and 1% for the 1999), this change may be attributed to the “niche competition theory” between both species or the reduction of the migration patterns of the round sardinella. The reduction of migration patterns of the round sardinella may occur due to the fishing pressure based on the distance between spawning and the feeding areas.

There appeared to be some change with time in the mean biomass estimates of sardinella along the Angolan coast. Within the main regions of distribution of sardinella, (i.e. from Benguela to Cabinda), there was a decline in mean tonnage from 310 000 tonnes (4 surveys, 1985) to 255 000 tonnes for two surveys in 1986 and down to 195 000 tonnes for the three 1989 surveys. However, the estimates increased to 260 000 tonnes in 1991 and 280 000 tonnes in 1992 (Figure 1.3, see Appendix II).

The same trend of increase in the average biomass was observed from 1994 to 2000. From 1985 to 1989, a decline in the average biomass may be attributed to the intensive fishing by the Soviet fleets. Furthermore, the information used in this study collected by the R/V "Dr. Fridtjof Nansen" is concentrated on specific areas, targeting particularly the pre-adult pelagic fishes and, therefore, does not provide a or representative sample of pelagic fishes in the whole region.

Acoustic density values (S_A -values) describe the diurnal behaviour of sardinellas in this work. A weak diurnal variation in sardinella densities per layer was noted with sardinella densities being lower at night than during the day (layer 0-20 m, mean day = 4.09 g. m^{-2} , SD = 2.17 and mean night = 3.40 g. m^{-2} , SD = 1.90); layer 40-60 m, mean day = 1.41 g. m^{-2} , SD = 2.00 and mean night = 1.05 g. m^{-2} , SD = 1.35) (Tables 4.6 and 4.7). The diurnal cycle in density measured during acoustic surveys is difficult to investigate quantitatively from the data set of two surveys (1994, 1997) because the signal depends mainly on the spatial variability and/or horizontal fish migrations. However, the situation is usually as follows in many tropical areas: A diurnal cycle is observed with the highest density values during the night and the lowest during the day. This is due to a number of biases : overestimation at night and under estimation during the day. Nonetheless, opposite biases exist but are out weighed by the previous one (see Table 1, 222 p in Fréon *et al.*, 1993).

The spatial structure of schools is therefore important information for understanding the biology of the fish and for the survey design. It was clear from this study that sardinella are mostly dispersed at night, although limited shoaling still persists during the night as observed in other areas (Fréon *et al.* 1996). This was evidenced in the difference of both the day and night densities. The distribution of sardinella species is very dynamic, and these species are fast swimming fish with significant changes in behaviour during the day.

From the ANOVA model, the survey effect has a small contribution to the total variance in the ANOVA (<0.9%, Table 4.10), despite its highly significant P -value. This finding could theoretically be explained by the irregular survey track in all surveys. The survey track should more regular and kept consistent in all surveys. The resolution of the sampling unit used in all surveys is probably not adequate to

understand the finer structure of the distribution. Thus, increasing the sampling units by higher resolution (1nm instead of 5 nm) would both provide more information on the distribution structure of the stock. These findings indicate that sardinella undergo diel vertical migrations and may not always be available to acoustic sampling at night. It is recommended that future surveys incorporate the use of the new methodologies (e.g. sampling methodology for imaging schools with multibeam sonar (e.g. Soria *et al.*, 1996), looking - forward sonar and sightings surveys, in addition to sonar techniques, amenable for sardinella in Angolan waters) suggested during the BENEFIT Distance- Sampling Workshop at Marine and Coastal Management (M&CM, Dec. 1999) in Cape Town.

During this workshop it was concluded that in the short to medium term, sonar estimates of absolute abundance in the region (Angola, Namibia and South Africa) will tend to be very imprecise, and should be used more as indices of abundance (e.g. as relative estimates) to detect trends and support other data than as absolute estimates. The only way to overcome these limitations of the vertical acoustic methodology and the use of a sonar is in a complementary way with the vertical echo sounder, as developed by Misund and Aglen (1992) in sampling methodology for imaging schools in 3- dimensions (e.g. multibeam or omnidirectional sonars with very narrow individual beams). The method developed by Misund and Aglen (1992) has limitations in relating the horizontal observation to the vertical data (Misund, 1997).

The distribution of migration direction of the tracked schools (Figure 4.15) showed that eastwards and westwards movements dominated. It was however found that tracking of school movements, using sonar, suggested that horizontal shoal movements might have a diurnal pattern, being shorewards at night, but it has also become evident that such studies must be linked to more detailed studies (e.g. migratory behaviour). This migration behaviour could possibly be linked to large internal waves on the continental shelf off Angola. The internal waves mix plankton in the water column, and near the coast the fronts of breaking internal waves are visible as bright stripes at the surface parallel to the coast.

For commercial fishing by purse seining, the surface appearance of the sardinella schools eases detection of the schools and fishing is possible without sophisticated

equipment. For conventional acoustic surveys by echo integration through a hull-mounted transducer, the surface distribution may lead to substantial under-estimation of biomass. This study is a good indication of the amount of variation that can occur due to changes in spatial distribution of fish populations in both the horizontal and in vertical layers, as well as in behaviour of fish populations in relation to time and the environment. These changes might be understood throughout the linked research studies between resources and environmental conditions, planned in part of the BENEFIT Research Programme.

Due to many difficulties encountered in data collection, the data series analyzed are only from surveys carried out in Angolan waters. The survey data of the Congo region should be included in this study due to the issue of transboundary migrations of sardinella. These data used are not weighted in any way, but were meant to give a general first overview of the population.

Recommendations for research

Ideally, there should be synchronization between Congolese and Angolan surveys to address the issue of transboundary migrations. It is important to cover the entire population of sardinella during the surveys, not only the pre-adults and adult fish, for better understanding of the spatial and temporal distribution. This means a small boat should be adequate to cover the shallow water (<20m). The survey data are not sufficient for giving all the information needed in the population analysis.

It is therefore important to implement a national sampling programme on landings for all components of the fishery each year including both catch and effort data, and equally reliable information should be collected on the spatial and temporal distribution of this effort i.e. the areas in which fishing is taking place, and when it is taking place. This will allow determination of whether changes in CPUE are due primarily to changes in abundance of the stocks, or whether they are due to changes in catchability or in the area or time of fishing.

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APPENDIX I

SUMMARY OF THE AVAILABLE SURVEY DATA

Survey (period)	Sounder	Sonar	Area
Nansen 1985	*Echograms, SA-Values	**	Cunene-River - Cabinda
Nansen 1986	*Echograms, SA-Values	**	Cunene-River - Cabinda
Nansen 1989	*Echograms, SA-Values	**	Cunene-River - Cabinda
Nansen 1991	*Echograms, SA-Values	**	Cunene-River - Cabinda
Nansen 1992	*Echograms, SA-Values	**	Cunene-River - Cabinda
Nansen 1994	***Echograms, SA-Values	**	Cunene-River - Congo-River
Nansen 1995	***Echograms, SA-Values	**	Cunene-River - Congo-River
Nansen 1996	***Echograms, SA-Values	Echograms	Cunene-River - Congo-River
Nansen 1997	***Echograms, SA-Values	Echograms	Cunene-River - Congo-River
Nansen 1998	***Echograms, SA-Values	Echograms	Cunene-River - Congo-River
Nansen 1999	***Echograms, SA-Values	**	Cunene-River - Congo-River
Nansen 2000	***Echograms, SA-Values	**	Cunene-River - Congo-River

Source: Nansis-database, IMR-Bergen

* = SA-values not available in the Bergen Echo Integrator

** = School volume data not available in the Bergen Echo Integrator

*** = SA-values available in the Bergen Echo Integrator

APPENDIX II

ESTIMATES OF BIOMASS OF SARDINELLAS BY REGIONS AND SURVEYS (* 000 TONNES)

Survey	Cunene-Benguela	Benguela-Luanda	Luanda-Cabinda	TOTAL
1/85	25	220	80	325
2/85	110	190	180	480
3/85	0	70	190	260
4/85	0	200	110	310
1/86	10	140	110	260
2/86	10	130	130	270
1/89	40	200	60	300
2/89	20	40	130	190
3/89	40	100	60	200
1/91	*	180	120	300
2/91	*	68	154	222
1/92	*	119	161	280
1/94	*	410	100	510
2/94	*	245	290	535
1/95	*	140	24	164
2/95	*	277	297	574
1/96	49	175	70	294
2/96	*	130	233	363
1/97	*	195	300	495
1/98	75	389	79	543
2/98	*	233	159	392
2/99	0	228	135	363
2/2000	0	179	174	353

* = not estimated

[Source: Nansis-database, IIP-Angola and IMR-Bergen]

Appendix III

Catch composition of the two species during cold and warm seasons.

Cold season			
		<i>S.aurita</i>	<i>S.maderensis</i>
Year	%	%	%
1991(2)	25		75
1992(2)	9		91
1994(2)	17		83
1994(2)	5		95
1995(2)	30		70
1996(2)	36		64
1998(2)	7		93
1999(2)	1		99
2000(2)	30		70
Warm season			
		<i>S.aurita</i>	<i>S.maderensis</i>
Year	%	%	%
1994(1)	17		83
1995(1)	12		88
1996(1)	21		79
1997(1)	33		67
1998(1)	25		74

APPENDIX IV

Seasonality of sardinella fishing on individual sectors of the Angolan Coast (Baptista, 1977) and seasonal variation of survey biomass estimates.

		Season						
		Feb	March- April	May-June	July- Aug	Sept-Oct	Nov	Dec- Jan
Zone								
Northern	Fishery	good	highest	good	weak	increasing	good	weak
	Biomass	+			++			
Central	Fishery	highest	good	decreasing	weak	increasing	good	weak
	Biomass	++			+			
Southern	Fishery	average	average	weak	weak	increasing	aver.	weak
	Biomass	--			--			

+ good, ++ higher, -- weak