

**CHARACTERIZING AND COMPARING THE
SPAWNING HABITATS OF SARDINE (*Sardinops
sagax*) AND ANCHOVY (*Engraulis encrasicolus*) IN THE
NORTHERN BENGUELA REGION**

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DECLARATION

I hereby declare that this dissertation is my own work. As a retrospective study, I obtained all the data from the Ministry of Fisheries and Marine Resource's institute: the National Marine Information and Research Centre (NatMIRC). The SWAPEL and Nansen surveys data were made available to me by Dr A. Kreiner, except for the SWAPEL environmental data which were provided by Mr D. Mouton, who was responsible for the environmental database (OCEANBASE). During my analysis, I was assisted by Mr L. Drapeau on development of a database and its usage, and the linkage of the SWAPEL survey's egg and environmental data, using the shortest distance, by exploring the spatial orientation of the data sets.

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SUMMARY

Spawning habitats of sardine and anchovy in eastern boundary systems are characterized in an attempt to understand the fluctuations observed in their abundance. These species have developed mechanisms that enable them to survive in these turbulent conditions. Spawning habitats were characterized by investigating the relationships between egg abundance and environmental data collected through two different survey programmes: SWAPEL surveys (1978 - 1985) and *Nansen* surveys (1999 - 2004). Single factor quotient techniques were used to define the selection of environmental conditions by these species for spawning. During the SWAPEL surveys, both species spawned over broad ranges of the variables (SST, salinity, dissolved oxygen and bottom depth) that were assessed. Anchovy was found to be less specific than sardine with respect to SST, salinity and oxygen, whereas sardine was less specific than anchovy with respect to bottom depth. During the *Nansen* surveys, sardine was found to be less specific with respect to the environmental variables than anchovy. Broad ranges of the environmental variables selected seem to be an effective mechanism to maximize survival of the early life stages in the varying environmental conditions that characterize eastern boundary regions. Both species have varied their preference seasonally relative to prevailing environmental conditions. These species also seems to have changed their preference with changes in their abundance on a longer period. Temperature-salinity diagrams were plotted to assess the distribution of the eggs in different water masses. These diagrams showed that

anchovy was distributed over a broader range of water masses than sardine during the SWAPEL surveys, whereas the reverse was found during the *Nansen* surveys. Sardine appears to adapt to environment conditions by varying its spawning habitats. Anchovy appears to maximize spawning success by timing its spawning activities to limit negative environmental effects on developmental stages. Spatial structure in egg distributions were assessed using experimental variograms. No coherent spatial structure in egg distributions was found for either of the two species during the SWAPEL surveys (1978 - 1985). This could be a result of the survey sampling strategies which resulted in high variability at short distances and low variability at long distances. Centers of spawning were identified for different periods for the two species by computing centroids from the egg distribution data. The spawning centers for both species occurred mainly in the area north of 22° S during both survey periods, which related to high concentrations of food found in this area. The current low biomass of anchovy and sardine requires adaptive management strategy that permits populations growth, in order to take advantage of vast volume of suitable spawning habitats and allow the quantification of spatial distribution.

Chapter 1. Spawning habitats of sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) in northern Benguela upwelling systems.

Abstract

Spawning habitats of sardine and anchovy in eastern boundary current systems are characterized in an attempt to understand the fluctuations observed in their abundance. The northern Benguela, as an eastern boundary current system, is characterized by turbulent conditions that seem to govern the variability observed in the abundance of these species. Sardine and anchovy have developed mechanisms that enable them to maximize productivity. In the northern Benguela, spawning intensity is historically known to be high in periods and vicinities where turbulence is reduced. However, it is believed that selection of conditions for spawning by these species may change with fluctuations in abundance of fish.

Introduction

The characterization of small pelagic species' spawning habitats was highlighted by the need to understand fluctuations in abundance of these species in the systems they inhabit (Lluch-Belda *et al.*, 1991a; van der Lingen *et al.*, 2001; Curtis 2004). Eastern boundary current ecosystems in which these species co-exist are defined by highly variable environmental conditions, which seem to govern the fluctuations observed in the abundance of these species (Shin *et al.*, 1998; Lluch-Belda *et al.*, 1989). In recent years several studies have focused on characterizing sardine and anchovy spawning habitats,

which, if spawning habitats impacts on population variability, is also essential for our understanding of population fluctuations of these species. In the southern Benguela, the spawning habitats of sardine and anchovy were found to be distinctively different in relation to environmental variables investigated, specifically salinity and SST. While anchovy was relatively specific in selection of environmental variables for spawning, sardine spawned over a broad range of environmental variables (van der Lingen *et al.*, 2001; Twatwa *et al.*, 2005). Similar results were also recorded for the California Current sardine and anchovy (Lluch-Belda *et al.*, 1991a). This indicates that sardine may be less affected than anchovy by changing climatic conditions, which could displace suitable spawning habitats (Twatwa *et al.*, 2005), because sardine can spawn in a greater variety of suitable habitats.

In the northern Benguela region, several studies have been done to define the spawning habitats of anchovy and sardine (O'Toole, 1977; Hewitson, 1987; le Clus, 1991). However, with the reduction in abundance of anchovy and sardine in the northern Benguela recorded over time, it is believed that the migration patterns may have changed (Crawford *et al.*, 1987; Boyer and Hampton 2001b). The purpose of this study is to compare the spawning habitats of sardine and anchovy in the northern Benguela region by characterizing their current spawning habitats, which may enable management to adapt strategies that permit population growth of these species by restricting anthropogenic impact to certain periods or areas.

The spawning habitats of sardine and anchovy are constrained by environmental conditions that characterize eastern boundary current systems. The northern Benguela system is described below with reference to conditions that are unique to eastern boundary regions. Variation in these conditions influences the fluctuations in abundance of sardine and anchovy (Shannon *et al.*, 1988), mainly due to recruitment failure that is related to environmental changes (Kawasaki 1983) and this maybe amplified by exploitation (Lluch-Belda *et al.*, 1989). Sardine and anchovy have adapted to these conditions by instituting several survival mechanisms (i.e. selecting their spawning habitats). Finally, the objective of the study is described with reference to specific questions about the spawning habitats.

Description of the northern Benguela region

The Benguela Current system, as an eastern boundary current system, is characterized by persistently strong equatorward winds that enhance unidirectional equatorward surface currents and offshore directed Ekman drift. The water moving offshore because of the coastal divergence is replaced by nutrient-rich, deep water during a process known as upwelling, which supports high rates of primary production (Shannon and Pillar, 1986; Bakun, 1996). The high primary productivity of these systems supports large commercial fisheries that contribute 17% of the total global fish catch (Carr and Broad, 2000). The major eastern boundary current systems are the Humboldt Current system off western South America, the California Current system off western North America, the Canary Current system off northwestern Africa and the Benguela Current system off southwestern Africa (Figure 1.1).

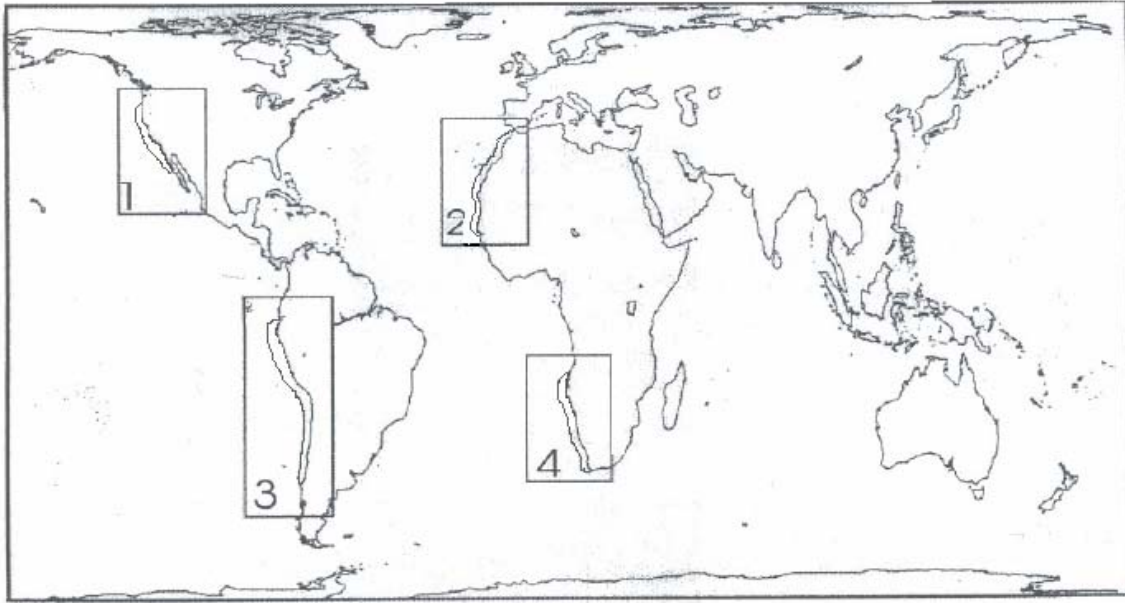


Figure 1.1: The major eastern boundary current systems of the world are indicated by the polygons in the boxes. 1) California Current system, 2) Canary Current system, 3) Humboldt Current system and 4) Benguela Current system (extracted from Jarre-Teichmann and Christensen, 1998).

The Benguela Current system is unique in the sense that it is bounded by warm-water currents on both equatorward (Angolan current) and poleward (Agulhas Current) sides (Shannon *et al.*, 1992). The Benguela system is split into northern and southern Benguela regions by the Lüderitz upwelling cell, with little vertical stratification, which acts as a semi-permanent barrier to longshore transport of pelagic eggs and larvae (Agenbag and Shannon, 1988).

The northern Benguela region (Figure 1.2) covers an area of about 150 000 km² along the western coast of southern Africa (Boyer and Bartholomae, 2000). The strong perennial upwelling cell off Lüderitz (27°-28°S) that separates it from the southern

Benguela region marks its southern boundary. The northern boundary is marked by the thermal front of warm Angolan water that varies in position between 14° to 17° S seasonally. The front is shifted further to the south during the first quarter of the year when southwesterly winds that drive surface water (upwelling) offshore are at minimum (Meeuwis and Lutjeharms, 1990). The coastal upwelling extends between 150 and 200 km offshore, with a further 600 km of filamentous mixing of upwelled water and oceanic water (Lutjeharms and Stockton, 1987).

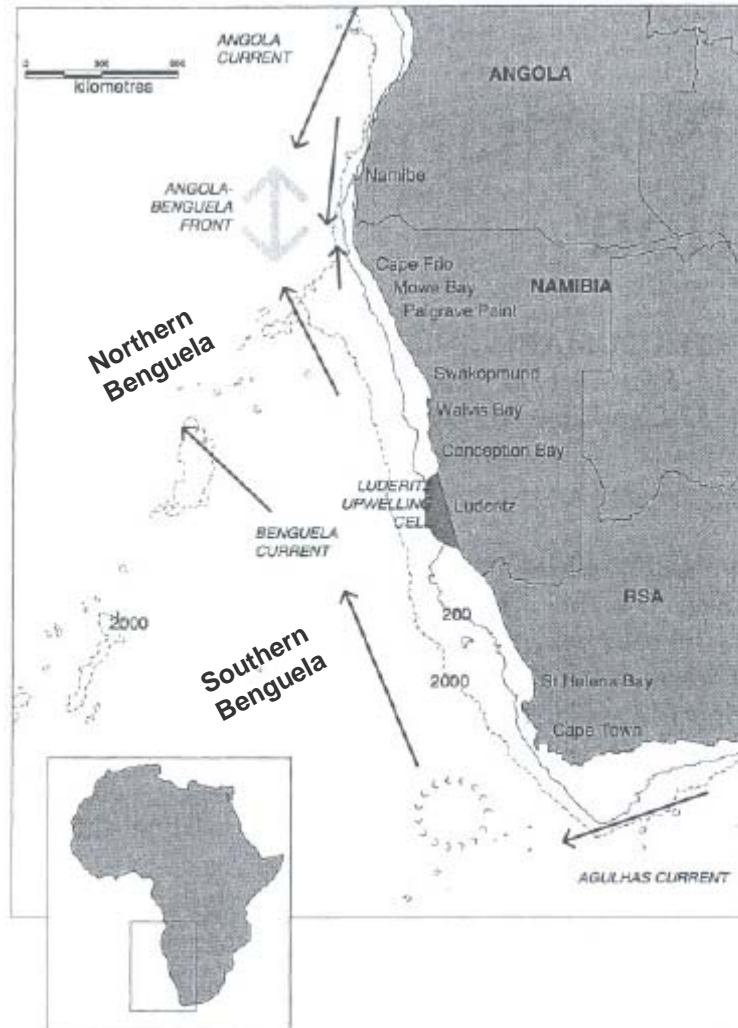


Figure 1.2: The Benguela Current system bounded by the warm currents; Angola Current (to the north) and Agulhas Current (to the south). The main surface circulations in the region are shown by the arrows. The Lüderitz upwelling region (shaded) separates the northern from the southern Benguela region, roughly along the broken line (extracted from Boyer *et al.*, 2000).

The continental shelf in the northern Benguela region is narrow between the northern boundary and Cape Frio ($18^{\circ} 30' S$) with a width of 20 – 30 nautical miles. The shelf widens (60 – 80 nm) southward to Walvis Bay ($23^{\circ} S$) (Boyd *et al.*, 1987) and narrows

again further south towards the Lüderitz region. The coastline tends to change orientation from broadly northwesterly to more northerly (Boyd *et al.*, 1987) where the continental shelf is narrower.

Circulation in the northern Benguela region is driven mainly by South Atlantic anticyclonic wind fields that primarily govern the prevailing southerly and southeasterly winds. The anticyclonic flow of air is entrained along the coast by the thermal barrier of hot air rising from the Namib Desert. The strength of the wind coupled with the width of the continental shelf determines the intensity of upwelling, with the strongest upwelling occurring where the shelf is narrow. The main upwelling cell is found off Lüderitz, with others off Cape Frio, Palgrave Point (20°30' S) and Conception Bay (24°00' S; Shannon, 1985). Upwelling activity in the south (south of 24° S) is reasonably consistent throughout the year but north of 24° S (north of Conception Bay) it is more pronounced in winter and spring.

The northerly flowing Benguela Current is the main geostrophic flow in the region. The current diverges to the northwest off Lüderitz and widens. Further north, the wind-driven upwelling currents are northwesterly flowing until deflected offshore at about 18° S, south of the frontal region between the cool upwelled water and the warm, saline, tropical Angola Current water (i.e. Angola/Benguela front). Occasionally, subsurface southerly-flowing saline Angolan water intrudes as far south as 23° 30'S (Boyd *et al.*, 1987) over the northern Benguela shelf (Figure 1.4). Remote forcing from the equatorial Atlantic has been implicated in the propagation of coastally trapped waves that are responsible for

strong poleward intrusion of Angolan water, suppressing upwelling of cool, deep, offshore water on to the coastal shelf (Shannon, 1985; Boyd *et al.*, 1987). Extreme cases of this intrusion result in low productivity due to deepening of the thermocline such that only the nutrient-impooverished layer is upwelled during upwelling. These extreme cases are referred to as Benguela *Niños* (Shannon *et al.*, 1986). Along the edge of the continental shelf, there is a poleward undercurrent flowing throughout the region (Nelson and Hutchings, 1983; Shannon, 1985).

Over the continental shelf, O'Toole (1980) studied the surface water distribution and identified three main water types. These are the low salinity Benguela Current Water (12 °C - 18 °C, 34.9 - 35.2‰) which is upwelled along the coast, moderate salinity oceanic and mixed water (16 °C - 20 °C, 35.2- 35.5‰) which moves onshore and offshore south of 19°S, and high salinity Angolan water (17 °C - 22 °C, 35.5 - 35.9‰) which intrudes southward along the shore. Boyd (1983) identified a fourth salinity water type (35.3 - 35.5‰) with a temperature lower than 15 °C which is upwelled off central Namibia in autumn, with origin from the north.

The seasonal variability of these water types have been described by several authors (O'Toole, 1980; Boyd, 1983; Shannon 1985) in terms of the distribution of temperature and salinity along the northern Benguela continental shelf. Boyd and Agenbag (1985) showed the occurrence of water cooler than 16°C along the entire coastline and extending up to 300 km offshore during winter to spring (Figure 1.3). During summer and autumn the area of cool water contracts meridionally and zonally, with the offshore temperature

gradient being stronger than the longshore gradient. The contraction of the cool water area reflects the intrusion of the warm, saline Angolan water onto the northern Benguela shelf further to the north, and the relaxation of the wind inducing upwelling to the south. The surface water is generally well mixed up to a depth of about 50 m during winter and spring but stratification is increased during summer and autumn due to insolation, advection and also relaxation of the wind (Shannon, 1985).

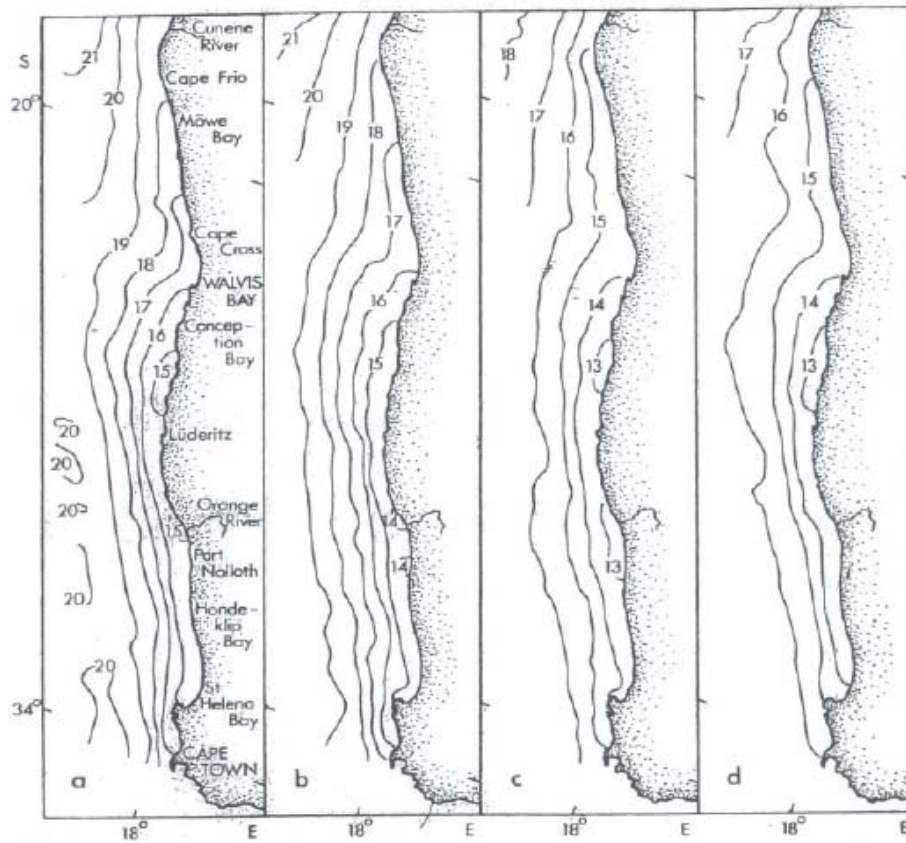


Figure 1.3: Mean seasonal sea surface temperature in (a) summer, (b) autumn, (c) winter and (d) spring. The warm water is displaced southwards in warmer periods as shown by the 16°C isotherm (extracted from Shannon, 1985).

The extent of the warm saline Angolan water intrusion has been studied to understand the interannual variability of water types along the northern Benguela shelf (Boyd *et al.*, 1987; Figure 1.4). The period of 1981 - 1983 and 1985 were associated with limited intrusion of Angolan water, which corresponded with a concomitant presence of cool temperatures. During the period of 1978 -1983, the autumn/winter of 1982 was found to be anomalously cooler, with associated low salinity water (Boyd and Agenbag, 1985). There was a transition from the upwelling winter of 1983 to massive intrusion of warm saline Angolan water in early 1984 (Boyd *et al.*, 1985). This extensive intrusion of the widely spread, warm, saline, relatively nutrient-poor, Angolan water observed during 1983/84 had a dramatic effect on the productivity of the region, and led to this period being termed a Benguela *Niño* season. The years of 1979, 1980 and 1984 had increased intrusion of warm saline Angolan water. Years of strong intrusion had maximum surface southerly penetration of warm saline Angolan water in March/April, whereas maximum penetration in years of limited intrusion occurred in February.

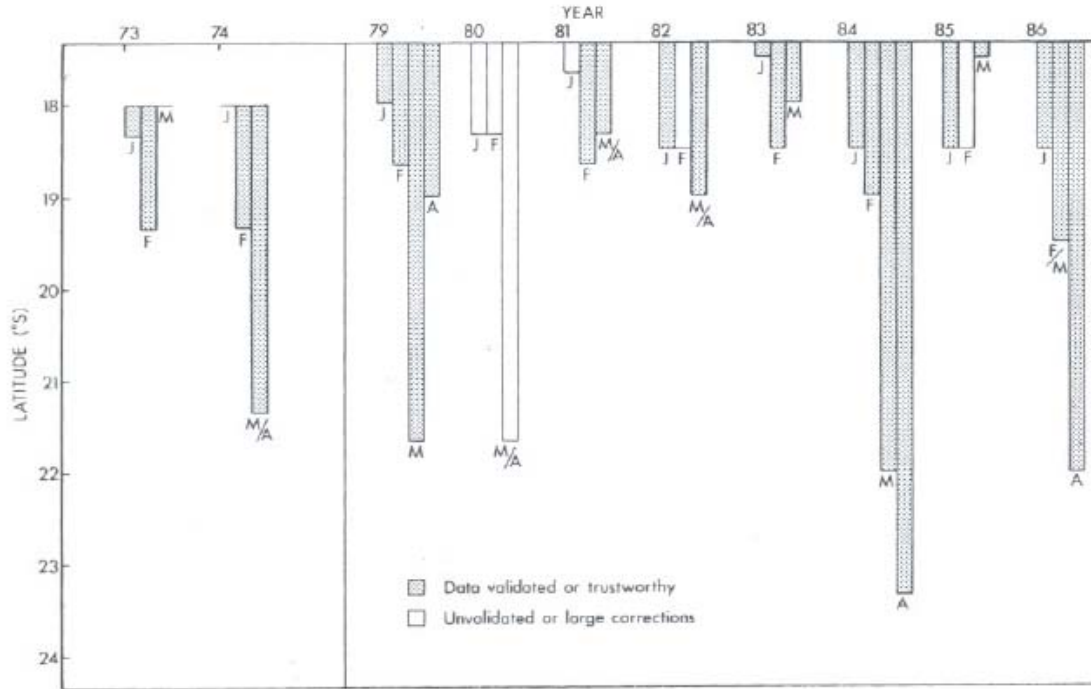


Figure 1.4: Interannual variation in the southward displacement of Angolan waters at the surface as indicated by the monthly latitudinal position of the 35.5 ppt surface isohaline at 35 n. miles offshore (from Boyd *et al.*, 1987).

These water types in the continental shelf region support small pelagic fish stocks that are well adapted to the variable conditions of the region, and have contributed to the economy of Namibia. The main small pelagic species being harvested here are anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*), as well as juvenile horse mackerel (*Trachurus trachurus capensis*).

Sardine and anchovy in eastern boundary current systems

All eastern boundary upwelling systems are inhabited by small pelagic fish species that are well adapted to the wind-induced variability in the environment. The species that have alternatively dominated the fisheries of these systems are sardine and anchovy (Schwartzlose *et al.*, 1999), as well as mackerel species (*Scomber* spp.) in some systems. The fluctuations of the pelagic species abundance have been termed “regime shifts” (Lluch-Cota *et al.*, 1997). The fluctuations of these species in some eastern boundary systems are in synchrony (Kawasaki, 1991). This was highlighted by empirical orthogonal function (EOF) analysis of sardine catches in the California, Benguela and Peru Current systems (Schwartzlose *et al.*, 1999). Crawford *et al.* (1991) also reported a positive correlation between the sardine catches in the California and Humboldt Current systems relative to ages at which sardine recruited to fisheries in the various systems.

The synchronous global fluctuations of sardine and anchovy catches in the major upwelling systems are influenced by global teleconnections (Kawasaki, 1991; Schwartzlose *et al.*, 1999). This was supported by the observation that oceanographic anomalies occurred at the same time in these systems (Crawford *et al.*, 1995). For

example, the correlation between catches of sardine in the Californian and Humboldt system in several years (1980, 1982, 1984 and 1985), suggest that the systems are being influenced by a climate operating at an oceanic scale. The mechanism that links climatic variability to sardine and anchovy catch fluctuations is not fully understood, although two categories of mechanisms have been proposed that may initiate or sustain fluctuations in pelagic catches. These are continuous modifications of habitat and episodic environmental events that trigger changes in the population and ecosystem (Schwartzlose *et al.*, 1999).

Modification of food availability and temperature have been reported to influence sardine and anchovy populations, because of increased spawning in periods of high food availability or favourable conditions (Schwartzlose *et al.*, 1999). Kawasaki and Omori (1998) suggested that variation in solar radiation leads to variation in primary production. An increase in primary production would benefit sardine than anchovy, as they are regarded as more of a phytoplankton feeder (i.e. feeding closer to the base of the food chain) than anchovy consuming more zooplankton. For example, in the Kuroshio system, on average, the fraction (0.65), by weight, of phytoplankton was greater in stomachs of sardine than of anchovy (0.39) (Li *et al.*, 1992). In the Peru and Benguela systems, although sardine do obtain their dietary input from small zooplankton by filter-feeding and particulate feeding (Konchina 1991; van der Lingen, 1994; 2002), they still utilize phytoplankton to a greater extent than anchovy. Thus, sardine (anchovy) increase in periods of phytoplankton (mesozooplankton) dominance (van der Lingen, 2002).

The distribution of sardine in eastern boundary systems has also been shown to change with temperature, expanding into cool regions during relatively warm periods and contracting into warm regions when it is cool. The Peruvian and Californian sardine expand polewards into cooler regions, whereas the Canary Current sardine expands northwards in warmer years. In the Benguela system, sardine move towards the cool upwelling cell in the centre (Lüderitz) in warmer years (Lluch-Belda *et al.*, 1989; 1991b).

Sardine and anchovy spawning habitats in eastern boundary current systems

The occupation of eastern boundary regions by anchovy and sardine comes at a cost. In order to survive in these regions, they have to adapt their survival strategy in a way that minimizes the detrimental effects on their survival of the turbulent conditions that characterize eastern boundary current regions. The Ekman drift advects eggs and larvae, along with surface water, offshore into unstratified and less nutritious area, where survival of the early life stages of these species is reduced. Thus, in eastern boundary current systems, the adults move away from the turbulent upwelling cell to find suitable spawning habitats (Laevastu, 1993). In the Iberian Peninsula (Spain), the spawning ground (Bay of Biscay) is located outside of the upwelling exposed region (Galician coast) to avoid the difficulties inherent in these regions (Shin *et al.*, 1998).

In mid latitude systems such as the Bay of Biscay (Spain) and the southern Benguela, this migratory adaptation has enabled small pelagic fish to take advantage of the coastal jet current that runs along the edge of the continental shelf towards the upwelling exposed region (Shin *et al.*, 1998). In the southern Benguela, once the eggs are spawned in the

spawning ground (Agulhas Bank), a shelf-edge jet current transports the eggs and larvae past the upwelling cell off the Cape Peninsula to the nursery ground along the west coast. Depending on the flow of the jet current, a substantial number of eggs and larvae are transported in the inner margin of the jet current where there is a high concentration of food particles as a result of the convergence of cold upwelled water with the warmer Agulhas water (Hutchings, 1992).

In selecting an area for spawning, many factors need to be considered, such as food and temperature, as well as the topography. Spawning of sardine and anchovy is known to correspond with areas of plankton concentration in eastern boundary current regions. A high concentration of plankton ensures a sufficient supply of energy to both spawners and early larval stages. Richardson *et al.* (1998) showed that anchovy spawning success is positively correlated with copepod concentration. Sardine have also been showed to time its spawning to period when copepod spawning is at maximum; providing eggs and nauplii that are ingested by sardine larval, and this coincide with high *chl a* concentrations providing food for spawning sardine adults (Richardson *et al.*, 2003). The length of the period of food availability is also important as it determines the length of the spawning season and growth of larvae (Laevastu, 1993; Twatwa, 2002).

Together with food, temperature is also an important factor affecting spawning success of small pelagic fish and the development of early life stages. Sardine, off California, have been reported to spawn over a wider range of temperature (13° - 25°C) than anchovy (11.5° - 16.5°C; Schwartzlose *et al.*, 1999). Lluch-Belda *et al.* (1992) concluded that

sardine off California tend to expand their spawning ground in warm periods. Warm periods may favor anchovy' abundance and expand its spawning range in the southern Benguela (van der Lingen *et al.*, 2001), which may explain the different in phase between regime shift in the southeastern Atlantic and other regions. Temperature ranges associated with abundance tends to coincide with high abundance of food, such as large copepods dominate in the temperature range of 16° -19°C, which are an important component of the anchovy diet (Richardson *et al.*, 1998).

Stratification and thermal constancy, which reduce the likelihood of abnormalities in egg development (which can occur in <14° C water for anchovy in southern Benguela; King *et al.*, 1978) and benefit larval growth, are found in areas where the continental shelf is wide or in coastal indentations such as bays downstream of intense upwelling centres. In such areas, coastal upwelling is minimized and circulation ensures retention of particles (larvae and plankton) and warming (Roy *et al.*, 1992; Shin *et al.*, 1998).

Spawning habitats of sardine and anchovy in the northern Benguela region

Sardine and anchovy in the northern Benguela region were known to spawn throughout the region, during the earlier years (1972 - 1985) from 22° S northwards (le Clus, 1991). There are two grounds where spawning intensity of sardine and anchovy was relatively high, one in the vicinity of Walvis Bay and the other further north between Palgrave Point (18° 30' S) and Cape Frio (20° 30' S, Figure 1.5). The southern ground, which was known to be the main spawning ground historically has diminished and declined considerably. Spawning in the northern ground tends to be relatively offshore of the

upwelling cell south of Cape Frio. This location is thought to be favourable due to the concentration of particles (i.e. enrichment and retention) by the Benguela/Angolan front. Spawning in this area peaks during January/ February when the upwelling wind stress is at a minimum. Also, onshore and poleward flow within the upper 50m is more pronounced during the first quarter of the year, facilitating retention (le Clus, 1991).

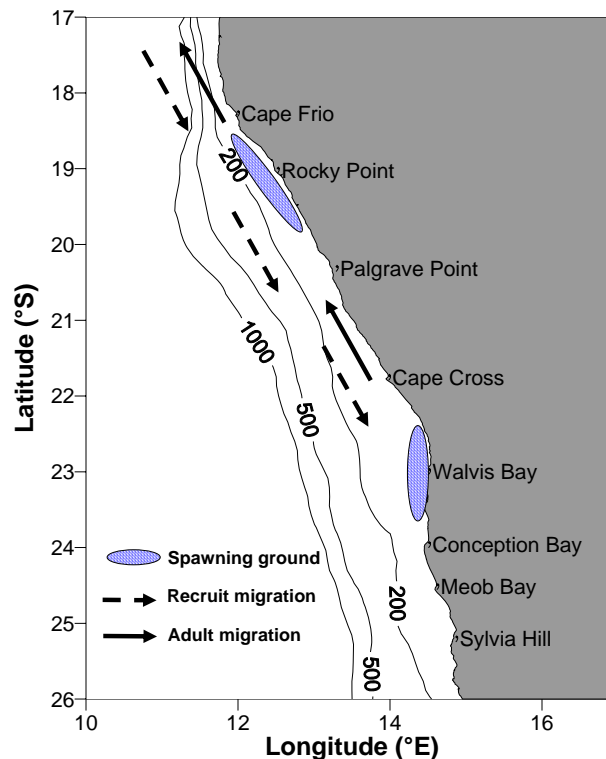


Figure 1.5: Historical spawning grounds and migration routes of sardine (diagram after drawing from Crawford et al, 1987).

The spawning ground in the vicinity of Walvis Bay is considered to be suitable because of the wide shallow shelf as well as the topography of the bay, which minimizes turbulence resulting from southeasterly winds that govern processes in this region. The upwelled water, carried by the main current from the Lüderitz upwelling centre, diffuses

in the bay and causes the formation of convection cells, reducing larval offshore advection as well as supplying the spawners and larvae with nutrients (le Clus, 1991; Shin *et al.*, 1998).

Sardine in the northern Benguela region spawn throughout the year with peaks in winter/spring (September - October) and in summer/autumn (February - March), whereas anchovy spawning is confined to summer/autumn (le Clus, 1991). Eggs of both species occur in water with a temperature range of 13° - 19°C and occur further south into cooler areas in warmer years (le Clus, 1991; Schwartzlose *et al.*, 1999).

Since the collapse of the sardine and anchovy stocks in the 1970s, spawning patterns are believed to have changed (Boyer and Hampton, 2001b). Crawford (1981) suggested that older fish would tend to spawn closer to the upwelling centre than younger ones. Thus, spawning around Walvis Bay could have declined after the collapse of the stocks, resulting in a reduced number of age classes. This is also supported by recent ichthyoplankton surveys (2000 - 2003), which indicate that the concentrations of eggs and larvae in the vicinity of Walvis Bay is very reduced and much less than in the area further north around Palgrave Point (van der Lingen *et al.*, 2006).

The change in abundance of sardine and anchovy in the northern Benguela have been associated with environmental changes (O'Toole and Shannon 1997; Boyer *et al.* 2001a; Boyer and Hampton 2001b). Daskalov *et al.* (2003) found a shift in the relationship between sardine recruitment and SST from positive over the period 1961 - 1983 to

negative from 1991 - 1999, when the biomass was significantly less than the former period. In addition, the relationship between sardine recruitment and wind speed switched from negative in the period 1961 - 1983 to positive in the period of 1991 - 1999 (Daskalov *et al.*, 2003).

The objective of the dissertation

The objective of this dissertation is to characterize the spawning habitats of sardine and anchovy populations in the northern Benguela in terms of space, time and the physical attributes of the waters in which the eggs of these fish were collected. Three key questions will be examined through a retrospective analysis of egg abundance and distribution data collected during research surveys made off Namibia over different periods: during the late 1970s and early 1980s (SWAPEL surveys) when sardine and anchovy species were relatively abundant in the northern Benguela system, and during the late 1990s and early 2000s when sardine and anchovy species were low compared to historical levels. The three key questions are:

1. Can sardine and anchovy spawning habitats in the northern Benguela be characterized in terms of physical parameters, and if so, are their characteristics different?

Sardine and anchovy are some of the few species that have adapted well to turbulent conditions that characterize eastern boundary systems. Therefore, in the northern Benguela system, as reported in other eastern boundary systems (Schwartzlose *et al.*, 1999; Lluch-Belda *et al.*, 1991a; Twatwa, 2002), these

species should have adapted their survival strategy in order to minimize the detrimental effect of these turbulent conditions. The occupation of similar niches by sardine and anchovy also means there should be a strategy that minimizes competition.

2. Do (did) sardine and anchovy in the northern Benguela show a temporal separation in the time of peak spawning?

Earlier studies (Mathews, 1964; le Clus, 1987) have shown that sardine in the northern Benguela region spawned throughout the year with peaks in winter/spring (July-October) and in summer/autumn (November – April), while anchovy spawning was reported to be mainly during the summer/autumn period (le Clus, 1985). The separation in spawning peaks could be explained by the difference in conditions preferred for spawning with certain period of the year being associated with specific environmental conditions, such as upwelling or stratification.

3. Do (did) sardine and anchovy in the northern Benguela show a spatial separation in the area in which peak spawning occurred?

Hydrographic features have been related to egg distributions of the two species (le Clus, 1991) than anchovy eggs. The location of the two species' spawning grounds overlap within the nearshore domain, but sardine eggs were found further offshore (extending to about 120 km). The northern and the offshore extent of the two species may be defined by the advection that occurs to the north and offshore

with wind stress. The extension of sardine further offshore than anchovy could be explained by the size and resilience of sardine to hydrographic conditions that characterize this region. It is hypothesized that differences in spawning habitats might minimize negative interaction between the two species (competition and predation), enabling the two species to occupy the same broad area.

The scope of the dissertation

The data used to characterize spawning habitats of sardine and anchovy are described in Chapter 2. Key question number one is addressed in Chapter 3, where the spawning habitats of the species are characterized in terms of physical variables. The single parameter quotient analysis was used to characterize the preferred ranges of variables in spawning habitats of sardine and anchovy, and temperature-salinity distribution plots were mapped to explore the spawning distribution of sardine and anchovy in water of different hydrological properties. Key question number two is also addressed in chapter 3 by examining the temporal variability of the preferred environmental conditions for spawning. The temporal analysis uses the SWAPELS data, which were of a better temporal scale than the *Nansen* data. The preferred spawning habitats are discussed with emphasis on differences in the selection by the two species, and their spawning habitats are compared to spawning habitats of sardine and anchovy in other eastern boundary regions.

Key question three is addressed in chapter 4, where the spatial and structural patterns of sardine and anchovy spawning distributions are examined. The spatial distribution of the spawning habitats is examined by computing centroids (centers of gravity), and the

structural patterns were examined by plotting experimental variograms. These outcomes are discussed with reference to the differences between the two species and are compared with results from other systems.

The final chapter (Chapter 5) synthesizes the results and defines the spawning habitats of sardine and anchovy in the northern Benguela. It emphasizes the implications of this study for improving our understanding of the spawning behaviour and the management of these species, and are compared with results from other eastern boundary systems.

Chapter 2. Data collection and processing

Abstract

Spawning habitats of sardine and anchovy were characterized by investigating the relation between egg abundance and environmental data collected through two different survey programmes (SWAPEL and *Nansen* surveys). The SWAPELS were conducted from 1978 to 1985 during the main spawning period (August to April) of sardine and anchovy covering the whole Namibian coastline. The *Nansen* surveys were conducted during 1999 to 2004 with spatial coverage over the central and northern region of Namibia. Comparably, more eggs were recorded during the SWAPEL than during the *Nansen* surveys. The data sets were cleaned and processed before being used for analysis in this study. The two periods' data sets have previously been used in other studies.

Introduction

Egg abundance and environmental data were collected through two independent survey programs; the SWAPEL and *Nansen* surveys. These two programs were different in terms of the period when they were conducted and their spatial coverage. The South West African Pelagic Egg and Larvae (SWAPEL) surveys were conducted monthly during the main spawning period (August to April) of sardine and anchovy from 1978 to 1985, with the sampling stations extending over the whole Namibian coastline. The *Nansen* surveys were conducted annually from 1999 to 2004 during the late summer (January – April) period, with sampling stations extending over the central and northern regions of

Namibia. The data used were made available by the Ministry of Fisheries and Marine Resources' research center (known as NatMIRC).

SWAPEL surveys

The (SWAPEL) surveys were part of the Cape Cross Programme, which was initiated in 1972 to investigate the state of the sardine fishery after the sudden decrease of sardine catches following the highest catches recorded in 1968 (O' Toole 1977). The primary objective of the SWAPELS was to investigate the abundance of commercially exploited pelagic stocks (mainly sardine and anchovy) from their spawning production (O' Toole 1977; le Clus 1985; Hewitson 1987).

Initially (1978 – 1980), the SWAPEL surveys were scheduled to cover the main spawning season (January and February) of anchovy but later the focus was shifted to sardine. Le Clus (1985) described how the larval distributions of both species given by O'Toole (1977) and anchovy average gonad mass per month for the period of 1970 - 1977 (Le Clus 1979) were used to guide the timing/planning of the surveys. Also, the survey were not regularly spaced throughout the spawning season because only one vessel was suitable and a refit has to be scheduled during the spawning season and the later summer period was considered more important for spawning (le Clus 1979).

The SWAPEL surveys covered the area from the Kunene River in the north to Lüderitz in the south, and up to 65 n. miles offshore (Figure 2.1). During the first two spawning seasons (1979/80 and 1980/81), a survey grid with an interval of 20 n. miles between

transects was followed, but in subsequent surveys the spacing between transects was increased to 30 n. miles for logistical reasons. The surveys commenced in the north at 17°20' S (south of Kunene River) for the first two seasons and at 17°30' S for the remaining seasons. The southern extent of the coverage varied with each survey because of time limitations, and the furthest extent was at 27°00' S (south of Lüderitz). The areas covered by the surveys are described in detail by Le Clus (1985) and Hewitson (1987).

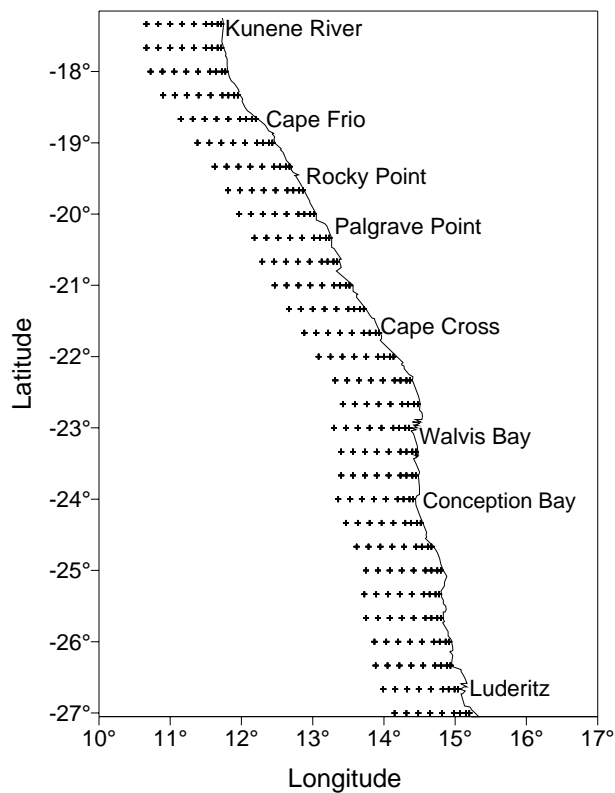


Figure 2.1: The spatial coverage of the SWAPEL surveys along the Namibian coastline.

The latitudinal interval between transects was 20 n. miles during the 1979 surveys.

Along each transect, 14 stations were located with a spacing of 5 n. miles. The stations were numbered from the coastline and the first station was 2 n. miles from the coast. The first four stations of 5 n. miles spacing, thereafter of 10 n. miles apart were sampled.

Ichthyoplankton were sampled with paired Bongo nets as described by Le Clus (1985). The Bongo net consisted of a 57 cm diameter fiberglass tube, a stainless steel band, a stainless steel neck, a net, a monofilament Becosyn gauze and a digital flowmeter. The net consisted of cylindrical and conical sections, which increased the surface area and also reduced clogging of the net by phytoplankton, which was common in the more productive areas along the Namibian coast.

Each net was fitted with a nylon monofilament Becosyn gauze, one net having a gauze with 0.3 mm mesh size, while the other net had a 0.5 mm mesh size. A digital flowmeter was suspended by means of a stainless steel rod at the center of the opening of each mouth tube to measure the rate of flow of water through the net. The number of revolutions recorded was used to calculate the volume of the water filtered through the net per tow. A digital electronic Bongo monitor clamped into a collar, which joined the paired Bongo nets, was used to measure the temperature and the water pressure (i.e. depth), and the monitor was also connected to the flowmeters. All information recorded by the monitor was transmitted through the towing cable to the deck unit on the ship and printed out on hard copy. The flow rate and the depth readout were used to regulate the depth and the speed of the nets through the water during deployment. In addition, measurement of temperature, salinity and oxygen were made at each station during the surveys (Kruger and Boyd 1984).

Ichthyoplankton were sampled by means of a double oblique haul. The net unit was lowered into the water by means of a cable while steaming at a speed of two knots until a depth of 50 m or 5 m from the bottom was reached. The net unit was allowed to stabilize for 30 seconds before being hauled to the surface. The unit was hauled up at a speed of 0.3 m while steaming at 2 knots. Prior to the use of the Bongo monitor, the depth of the net was regulated by reading off the slide of the bathythermograph, which was lowered with the nets.

On board, plankton were carefully flushed to the codend of the net and the samples were then emptied into a bucket. Large plankters (e.g. jellyfish) were discarded after their number and size had been recorded. The contents of the bucket were then filtered through a 0.30 mm sieve and the sample was then transferred into a 1 L plastic bottle and preserved using a 5% formalin solution.

Nansen surveys

The *Nansen* data were collected during surveys which were conducted during 1999 to 2004 as part of the Benguela Fisheries Interaction and Training (BENEFIT) project on horse mackerel recruitment. The objective of the project was to improve understanding of the environmental preferences and linkages between environmental processes and growth, distribution and abundance of the horse mackerel stocks. Initially the focus was to improve understanding of the reproductive biology and early life stages and to explain the spawning and recruitment dynamics of the two horse mackerel species (*Trachurus*

trachurus capensis and *Trachurus trachurus trecae*) in the region. The focus was expanded to include anchovy and sardine after the horse mackerel recruitment survey in 2001, when relatively high concentrations of anchovy larvae were observed.

The *Nansen* surveys covered the area from Tombua (15°30' S) in southern Angola to Sandwich Harbour (23°30' S) in central Namibia (Figure 2.2). For most of the surveys transects started on a line at 23° 30' S and progressed northwards with lines spaced at 40 - 50 n. mile intervals. Sampling was also done along the diagonal lines (northeast-southwest) that joined the parallel (east-west) transects. Stations were located every 20 n. miles in the offshore region and every 15 n. miles in the near shore region.

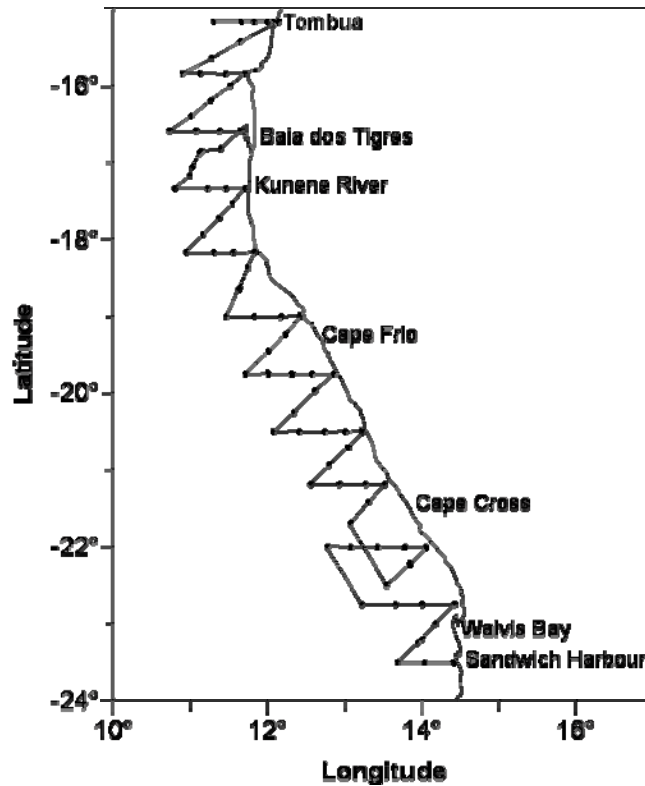


Figure 2.2. The spatial coverage of the April 2002 *Nansen* survey along the Namibian coastline (Stenevik *et al.*, 2002).

Ichthyoplankton were sampled with a hydrobios multinet plankton sampler having 5 nets with a mesh size of 405 μ m and a mouth opening of 0.5 x 0.5 m sampled at depth intervals of 0 - 10 m, 10 - 20 m, 20 - 40 m, 40 - 60 m and 60 - 100 m. When bottom depth was less than 100 m, the deepest net was sampled from 10 m above the bottom to the nearest depth interval upper limit. A flow meter was mounted in the mouth of the multinet, and a Scanmar depth recorder with acoustic transmission to the vessel was mounted on top of the multinet. The multinet was lowered to depth and retrieved at a speed of 0.5 - 1.0 ms^{-1} while the vessels maintained a speed of about 2 - 2.5 knots. In addition to ichthyoplankton sampling a Seabird 911 CTD was deployed to collect data on

temperature, salinity and oxygen concentration between the surface and 10 m off the bottom at every station (Stenevik *et al.*, 2002).

On board, the codends were removed from the multinet and the samples were poured into measuring cylinders to determine the volume of the sample by displacement. The samples were then transferred into petri dishes and examined on-board with a stereomicroscope. Fish eggs were identified, counted, staged and their diameter measured.

Data processing

Data obtained from SWAPEL surveys were stored electronically in ichthyoplankton and an environmental datasets. The ichthyoplankton dataset, which was made available for use by Dr Anja Kreiner (NatMIRC), was stored in a Microsoft Excel format while the environmental dataset was stored in ASCII format and was obtained from the NatMIRC ocean database (OCEANBASE). The SWAPEL surveys egg data were reported as numbers of eggs in a matrix format of lines (transects) and stations. I transformed these data into a column format presenting the number label of transect, the number label of the station along each transect and the number of anchovy and sardine eggs per station, using the Pivot table tool in Microsoft Excel (Microsoft ® Office Excel 2003). The lines were labeled in numerical sequence from the northern point of the region, and the stations along each line from inshore to offshore. I converted the labels into geographical coordinates based on the spacing intervals between lines and the distance of the stations from the coastline.

SWAPEL surveys environmental data were stored as depth profiles and I exported the files to Microsoft Access and summarized the data based on the number of times a station was sampled. As a result, three separate files were created; a file containing the observations at each station as a depth profile, a file depicting the month and year (surveys) a station was sampled, and a file showing the geographical coordinates of each station. I linked the station file to the surveys (or month and year) file using the coordinates of each station. Subsequently, the observations recorded as depth profiles were linked to the stations using the survey file.

Environmental data were not collected every survey, and in order to link environmental observations to the egg observations I used a least distance likelihood, based on the geographical coordinates and date of the survey conducted to estimate the environmental conditions when these were not measured. I obtained the likelihood distance by spatial exploration of the two data sets in Arcview software with the assistance of L. Drapeau (IRD). The environmental depth profiles were averaged for the top 50 m of the water column, and I considered this value to be the representative for that specific station. The reason for averaging the environmental data was because eggs were only sampled using an oblique haul and not over a discrete depth (as was the case during the *Nansen* surveys) and it was assumed that the eggs only occurred within surface waters, based on O'Toole's (1977) work which showed that most anchovy and sardine eggs were concentrated above the thermocline in the top 20 m.

I linked the two data sets in Microsoft Access using positions and dates of the stations. Once the files were linked, 150 of the total cases were deleted, due to incomplete data and only a place holder of -9999 was recorded. A total of 12 321 cases remained for all the SWAPEL surveys. The total number of eggs recorded is shown in Table 1.

Data obtained from the *Nansen* programme were stored in a Microsoft Excel format and were also made available by Dr Anja Kreiner (NatMIRC). The data consisted of three files, the eggs, stations and environmental data sets, which I transferred to Microsoft Access. An average for each environmental variable per sampled depth range was calculated and station numbers were used to link environmental data to ichthyoplankton data. A total of 1991 cases were recorded during these surveys. The total number of eggs recorded is shown in Table 2.1.

Table 2.1: The total number of sardine and anchovy eggs collected during the SWAPEL and *Nansen* surveys and the stations where eggs were recorded.

SWAPEL surveys					
EGGS (Bongo net)	Sardine		Anchovy		Environmental Data (CTD)
	Number	(+) stations	Number	(+) stations	
	300247	228	1412298	451	Temperature Salinity Oxygen Sounding
Nansen surveys					
EGGS (Multinet)	Sardine		Anchovy		Environmental Data (CTD)
	Number	(+) stations	Number	(+) stations	
	1518	49	936	31	Temperature Salinity Oxygen Sounding

Earlier studies where these data were used.

Several authors have previously used the data from the SWAPEL surveys to investigate the spatial, temporal and hydrographic variability of egg and larvae of pelagic species during their spawning seasons. O'Toole (1977) investigated the seasonal distribution and abundance of larval stages of some species (sardine, anchovy, horse mackerel (*T. trachurus capensis*), hake (*Merluccius capensis*), west coast sole (*Austroglossus microlepis*) and bearded goby (*Sufflogobius bibarbatus*)) in relation to hydrographical conditions. Le Clus (1985) and Hewitson (1987) studied the seasonal, geographical and hydrographical trends, and spatial and temporal distribution patterns of anchovy in the northern Benguela region, respectively.

The Nansen survey data are summarized in corresponding survey reports. Stenevik and Kreiner 2004 studied the spawning habitat of northern Benguela sardine and anchovy for the period of 2003 and 2004 using Nansen surveys data.

Chapter 3. Characterizing and comparison of sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) spawning habitats using single parameter quotient analysis and T-S diagrams

Abstract

Spawning habitats of sardine and anchovy were characterized using single factor quotient analysis and temperature-salinity (T-S) plots. During the *SWAPEL* surveys, both species spawned over broad ranges of the variables (SST, salinity, dissolved oxygen and bottom depth) that were assessed. Anchovy was found to be less specific than sardine with respect to SST, salinity and oxygen, whereas sardine was less specific than anchovy with respect to bottom depth. During the *Nansen* surveys, sardine was found to be less specific than anchovy with respect to all the environmental variables. The selection of broad ranges of these variables has enabled these species to vary their preference seasonally relative to the prevailing environmental conditions. Over a longer period, fluctuations in abundance of these species may have a noticeable impact on the selection of environmental variables for spawning by both species. Temperature-salinity diagrams showed that anchovy was distributed over a broader range of water masses than sardine during the *SWAPEL* surveys, whereas the reverse was found during the *Nansen* surveys. Sardine appears to be better adapted than anchovy because it is better able to vary its spawning habitats. Anchovy might maximize spawning success by timing spawning activities to limit detrimental environmental effects on developmental stages.

Introduction

The occupation of eastern boundary regions by anchovy and sardine comes at a cost. In order to survive in these regions, they have to adapt their life history strategy in a way that minimizes the detrimental effects of the turbulent conditions that characterize eastern boundary current regions. The Ekman drift advects eggs and larvae, along with surface water, offshore into unsuitable areas for survival of the early stages of these species. Thus, in eastern boundary current systems, adult fish generally move away from the turbulent upwelling cells to find suitable spawning habitats (Laevastu 1993).

In selecting an area for spawning, other factors also need to be considered, such as food and temperature, as well as the topography. Spawning of sardine and anchovy is known to correspond with areas of plankton concentration in eastern boundary current regions. A high concentration of plankton ensures a sufficient supply of energy to both spawners and early larval stages. Together with food, temperature is also an important factor in determining spawning success of small pelagic fish and the development of early life stages. Sardine, off California, have been reported to spawn over a wider range of temperature (13° - 25°C) than anchovy (16° - 19°C), (Schwartzlose *et al.*, 1999). Lluch-Belda *et al.* (1992) concluded that sardine off California tend to expand their spawning ground in warm periods, whereas van der Lingen *et al.* (2001) suggested that the opposite might be the case in the southern Benguela region. In the northern Benguela region, warm periods are associated with strong southward displacement of warm, saline Angolan water, often associated with low oxygen concentrations, on to the Namibian continental shelf (Boyd *et al.*, 1987). These infrequent intrusions are referred to as

Benguela Niños, and example of such a warm event occurred during the 1984/1985 spawning season and reduced the productivity of the region (Shannon 1985). Stratification and thermal constancy, which reduce the likelihood of abnormalities in egg development (which can occur in $<14^{\circ}$ C water for anchovy in southern Benguela; King *et al.*, 1978) and benefit larval growth, are found in areas where the continental shelf is wide or in coastal indentations such as bays downstream of intense upwelling centres. In such areas, coastal upwelling is minimized and circulation ensures retention of particles (larvae and plankton) and warming (Roy *et al.*, 1992; Shin *et al.*, 1998).

Spawning habitats of anchovy and sardine are characterized in this chapter by examining the selection of environmental variables by these species, as determined by the ranges of environmental variables in which their eggs were observed. The preferred environmental conditions were derived from data collected during the SWAPEL and *Nansen* surveys. Two techniques were used to define the selection of environmental variables by sardine and anchovy spawners and the distribution of eggs in different water masses; namely SPQ and TS. These are described below.

Analysis techniques

Single parameter quotient analysis

Single factor quotient analysis was used to determine habitat selectivity by each species for different environmental variables. Single factor quotient analysis is a relatively simple technique that is considered to be an exploratory data analysis tool which describes the relationship between egg abundance and environmental variables (Drapeau 2004).

First, for each environmental variable range of observed values was divided into 30 equally sized classes to ensure that maximum frequency of occurrence per class did not exceed 20% of all measurements. Percentage frequency of occurrence ($\% p_c$) of each class (c) was determined as follows:

$$\% p_c = \frac{p_c}{\sum_{c=1}^{30} p_c} * 100 \quad (2.1)$$

The same procedure was applied to egg abundance data, with the number of eggs (egg abundance) associated with each environmental class (e_c) expressed as a percentage of the total number of eggs of that species collected during each survey:

$$\% e_c = \frac{e_c}{\sum_{c=1}^{30} e_c} * 100 \quad (2.2)$$

The percentage of total eggs in each environmental range was then divided by the percentage frequency of occurrence of that particular environmental class.

$$Q_c = \frac{\% e_c}{\% p_c} \quad (2.3)$$

This resultant quotient value (Q_c) is used to assess the selection by fish for spawning over a particular range of that environmental variable. If the quotient value is greater than one, fish are assumed to select that variable range for spawning, but if it is less than one the variable range was assumed to be avoided (van der Lingen 2001; Twatwa 2002), and the quotient was plotted over the environmental range observed. The resultant quotient curves describe the relationship between egg abundance and the environmental variables and the quotient curves were smoothed using a 3 point running mean because of the high interpoint variability in the data.

Single parameter quotient techniques have been used to characterize spawning habitats of pelagic fish species in different eastern boundary systems (Luch-Belda *et al.*, 1991a; van der Lingen *et al.*, 2001; Twatwa 2002; Twatwa *et al.*, 2005; Claramunt and Serra 2004; Bernal *et al.*, 2004; Angélico 2004). It is however important to emphasise that this technique does not serve as a substitute for any of the statistical techniques used to investigate complex correlations, such as GLM or GAM models.

Temperature-salinity diagrams

Temperature-salinity diagrams are used to characterize water masses in the ocean (Sverdrup *et al.*, 1942), ideally isolated from external influences such as heat exchange, precipitation and runoff. T-S diagrams can also be used to characterize preferred water masses for spawning by pelagic fish (Checkley 2004a).

The SWAPEL surveys' data used were restricted to the period 1980 to 1985 for both species as no records of sardine eggs were obtained prior to the 1980 season. Temperature and salinity are plotted on a diagram and egg abundance is overlaid, as a third dimension parameter, to indicate the preferred combination of temperature and salinity. This preference was enhanced by applying a threshold of $>0.1\%$ (total egg abundance) on egg abundance to ensure that only stations with higher numbers of eggs were presented.

It is again important to emphasise that T-S diagrams, as exploratory techniques, must be interpreted with caution, especially for pelagic fish stocks that spawn close to the surface of the water column, where external sources may have an influence on the properties of the water masses, particularly temperature.

Results

Spawning habitats selected during SWAPEL surveys (1978 - 1985)

The aggregated data for over the SWAPEL surveys indicate that both species selected a wide range of SST ($> 14\text{ }^{\circ}\text{C}$) for spawning (Figure 3.1 a), with anchovy preferring slightly cooler waters than sardine and sardine showing high selection for warmer ($> 19.5\text{ }^{\circ}\text{C}$) waters. The warmest temperatures selected by both species were not defined as the selected range may have extended beyond the SST class range observed here. Anchovy (sardine) eggs occurred in waters of temperature $> 11.25\text{ }^{\circ}\text{C}$ ($>11.5\text{ }^{\circ}\text{C}$). Of the ranges selected, most spawning occurred in the range between $16\text{ }^{\circ}\text{C}$ and $19\text{ }^{\circ}\text{C}$, which contained more than 40% (60%) of the eggs for anchovy (sardine). This range overlaps

with the mean SST (14 – 18 °C) range reported by Parrish *et al.* (1983) on spawning grounds in four eastern boundary current systems. Inter-annually, no particular trend could be deduced from selections by both species for spawning (Figure 3.2 a and 3.3 a). However, there appears to be a shift from cool to warm SST ranges in preference by both species during some of the spawning seasons, especially for sardine (Figure 3.2 b and 3.3 b).

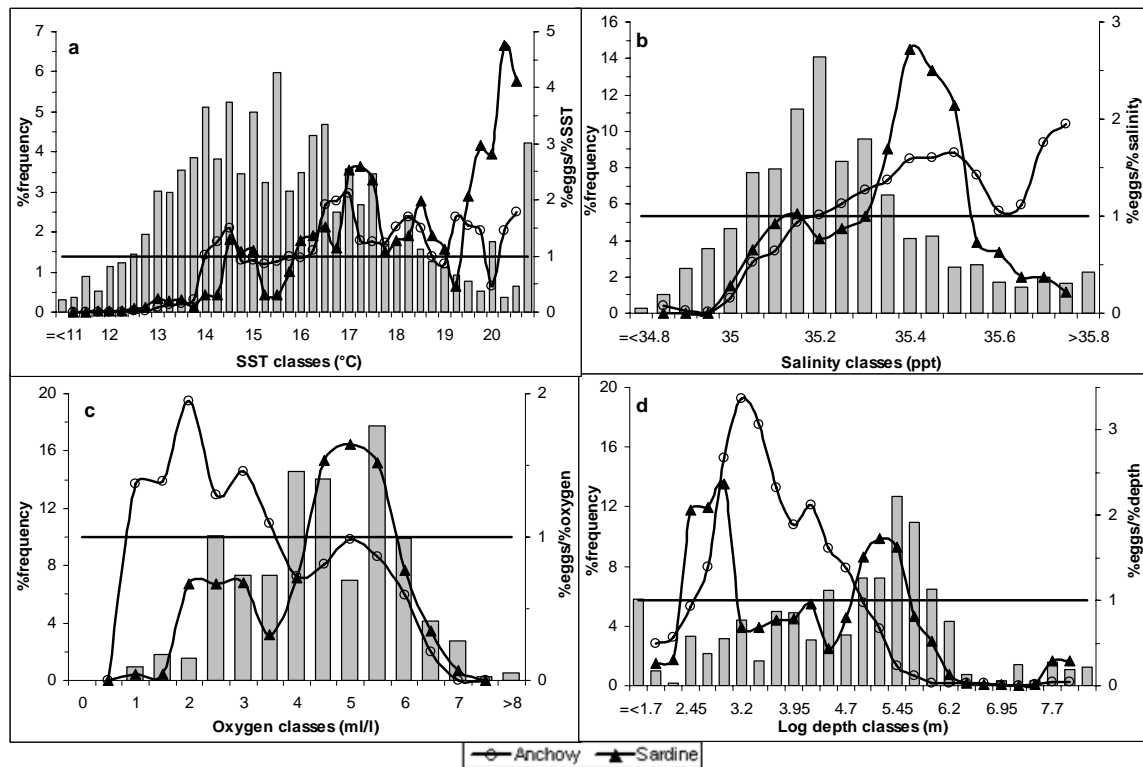


Figure 3.1: Percentage frequency distribution (histograms) environmental variables for all SWAPEL surveys combined (a) SST, (b) salinity (c) dissolved oxygen and (d) log-transformed depth. Quotient curves (3-point running mean) are shown for sardine (triangle) and anchovy (open circle) eggs. A quotient value of 1 is plotted as the selection threshold.

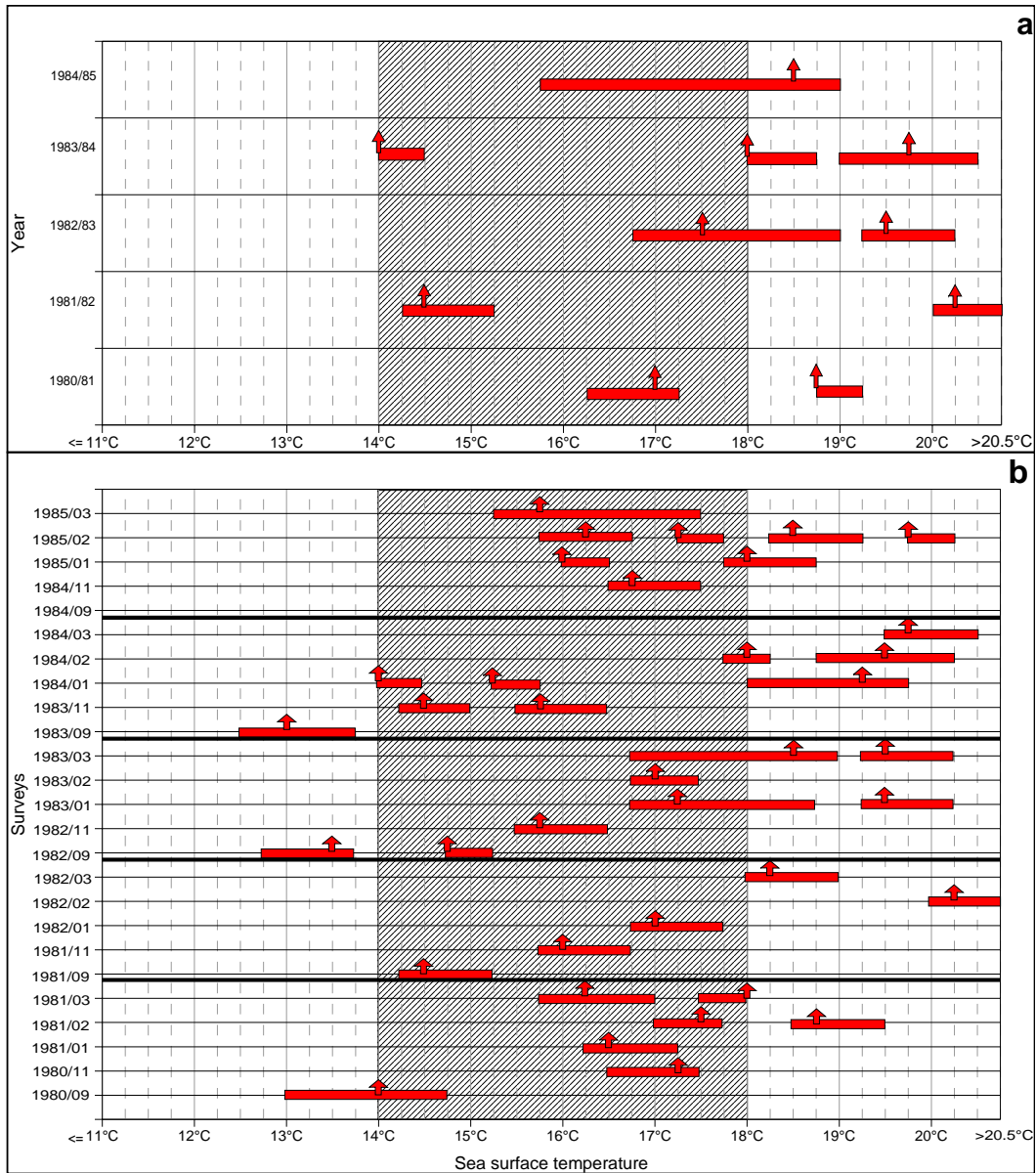


Figure 3.2: Sardine selection of SST for spawning during the SWAPEL surveys, showing (a) different years (aggregated monthly data) and (b) individual surveys. The (red) bars indicate the SST ranges selected ($Q > 1$), with arrows showing the peaks of the selected range. The thick horizontal solid line separates the different seasons. The shaded area represents the SST range reported in sardine and anchovy spawning grounds in four eastern boundary regions (Parrish *et al.*, 1983).

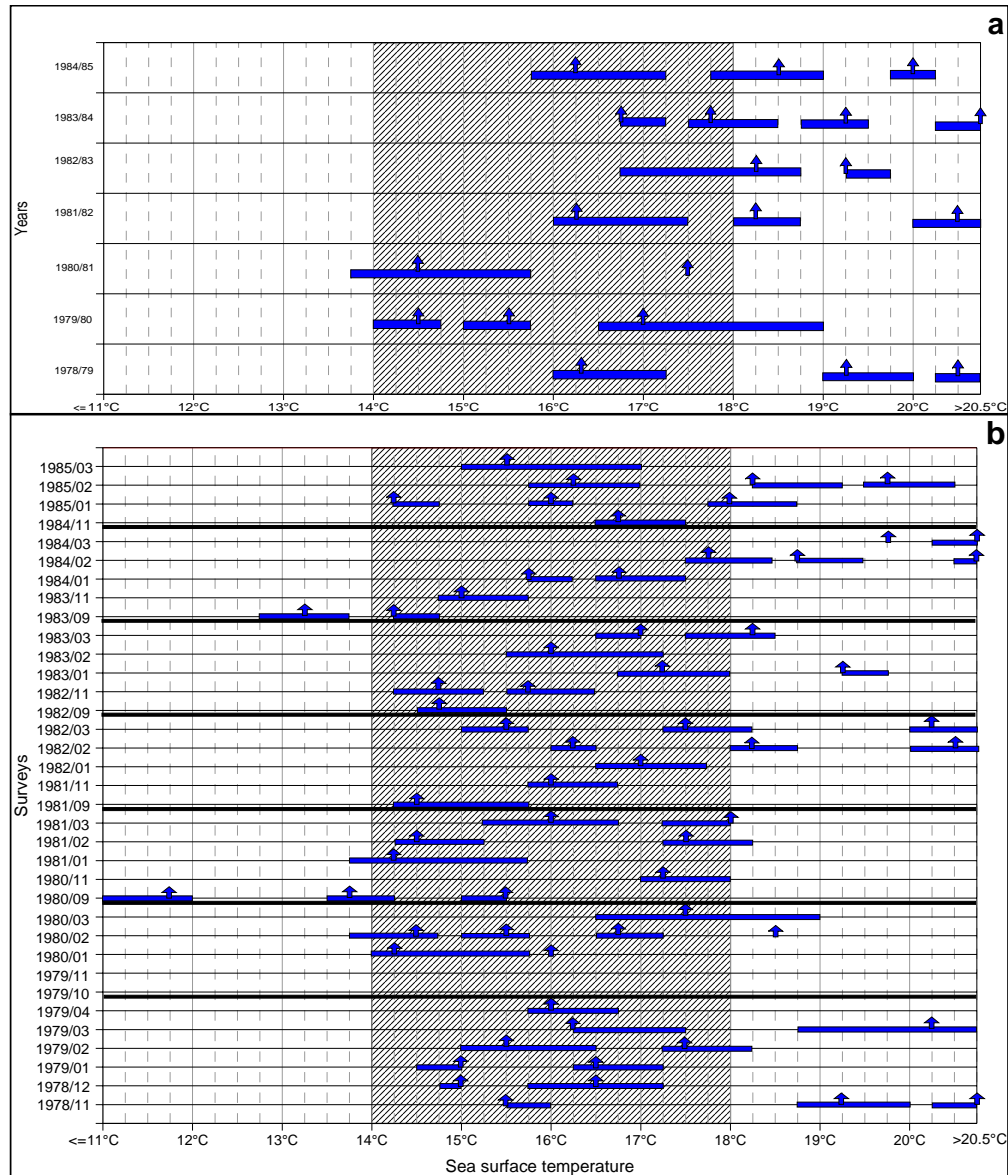


Figure 3.3: Anchovy selection of SST for spawning during the SWAPEL surveys, showing (a) different years (aggregated monthly data) and (b) individual surveys. The (blue) bars indicate the SST ranges selected ($Q > 1$), with arrows showing the peaks of the selected range. The thick horizontal solid line separates the different seasons. The shaded area represents the SST range reported in sardine and anchovy spawning grounds in four eastern boundary regions (Parrish *et al.*, 1983).

Similar to the selection of SST for spawning, the aggregation data showed that anchovy and sardine preferences for salinity during spawning were comparable (Figure 3.1 b). Both species eggs occurred from 34.85 ‰ to 35.75 ‰. Anchovy selected to spawn in water of salinity greater than 35.2 ‰ whereas sardine selected a narrow range of 35.3 - 35.55 ‰ (Figure 3.1 b). The upper end of the range selected by anchovy was not well defined, indicating that spawning could have occurred in more saline water than the range shown here. Of the range selected, spawning mainly occurred between 35.2 - 35.6 ‰, which contained more than 70% of the anchovy eggs. Water type of this salinity range was identified as the moderately saline oceanic and mixed water over the continental shelf of the northern Benguela region (O'Toole 1980). As was the case with SST, no particular trend could be deduced from the selected ranges for spawning by both species, annually (Figure 3.4 a and 3.5 a), although in 1983/1984 both species tended to choose high salinity water and low salinity water in 1984/1985. During some seasons trends of shifting preference towards more saline water could be deduced, which matched the shift to warmer SST (Figure 3.4 b and 3.5 b).

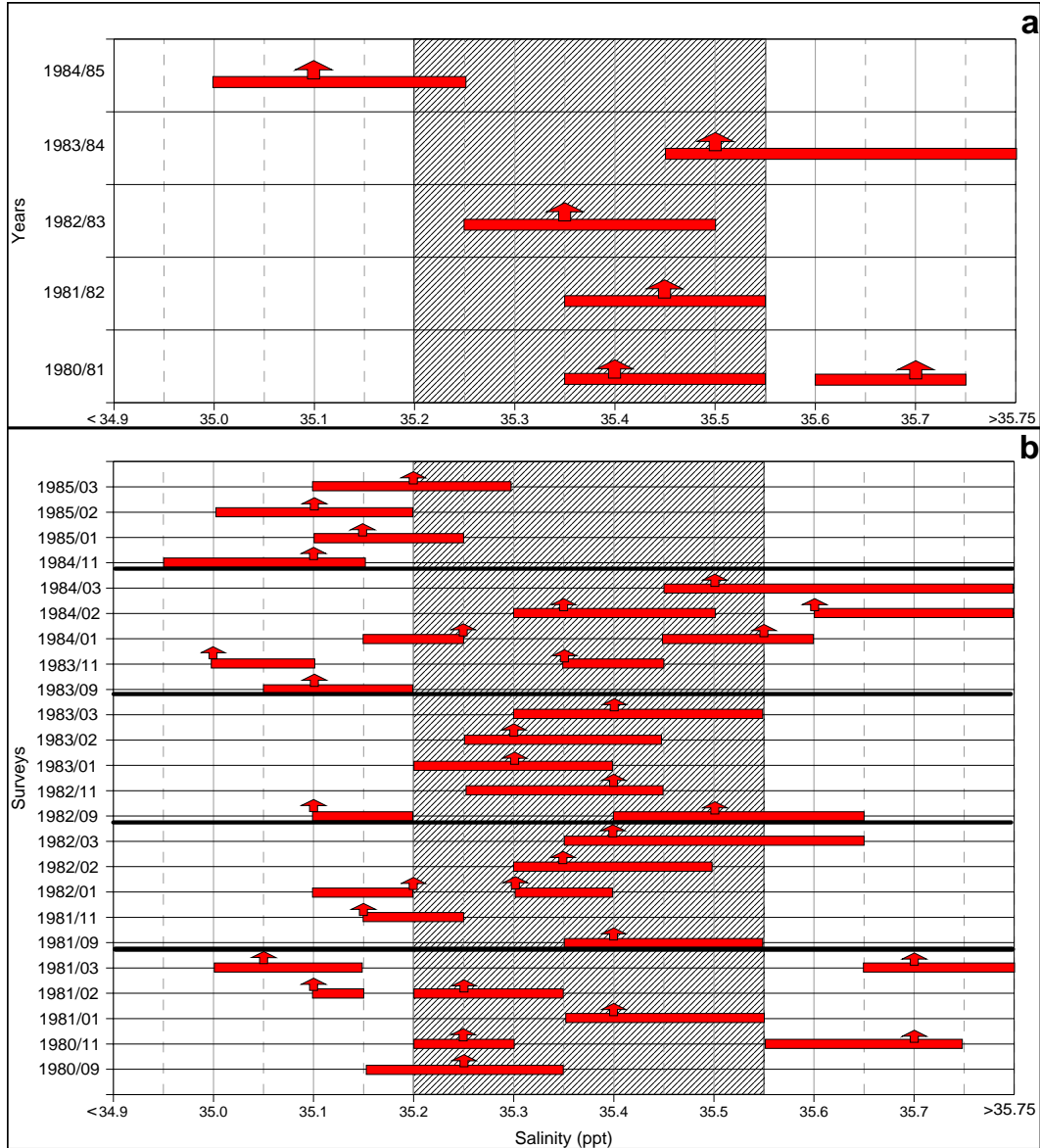


Figure 3.4: Sardine selection of salinity for spawning during the SWAPEL surveys, showing (a) different years (aggregated monthly data) and (b) individual surveys. The (red) bars indicate the salinity ranges selected ($Q > 1$), with arrows showing the peaks of the selected range. The thick horizontal solid line separates the different seasons. The shaded area represents the salinity range of oceanic and mixed waters found over most of the Namibian continental shelf area (O'Toole 1980).

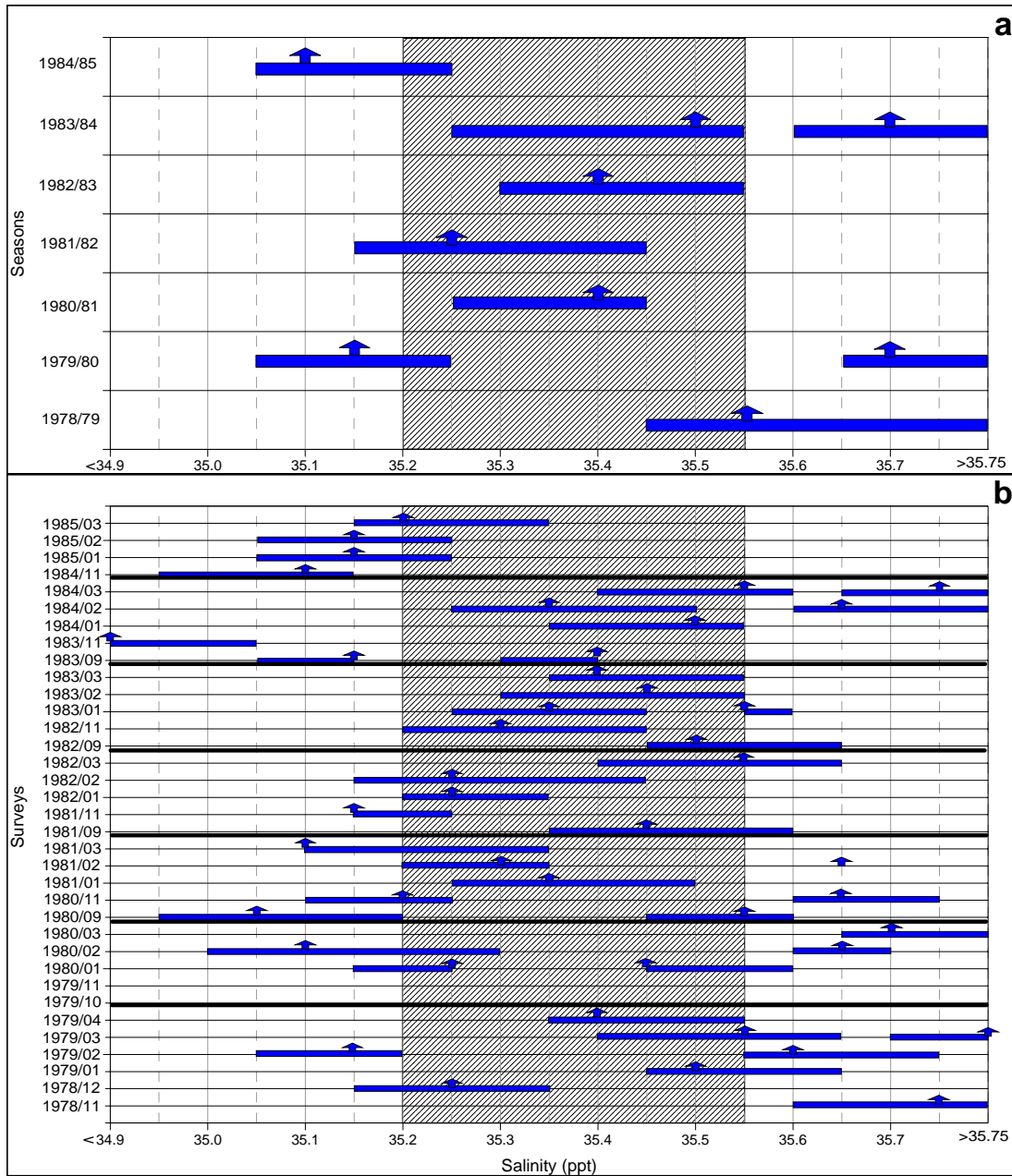


Figure 3.5: Anchovy selection of salinity for spawning during the SWAPEL surveys, showing (a) different years (aggregated monthly data) and (b) individual surveys. The (blue) bars indicate the salinity ranges selected ($Q > 1$), with arrows showing the peaks of the selected range. The thick horizontal solid line separates the different seasons. The shaded area represents the salinity range of oceanic and mixed waters found over most of the Namibian continental shelf area (O'Toole 1980).

The aggregated data showed no overlap in the selection of dissolved oxygen ranges for spawning (Figure 3.1 c). Anchovy eggs occurred from 1 ml l^{-1} to 7.5 ml l^{-1} , whereas sardine occurred from 1 ml l^{-1} to 7 ml l^{-1} of dissolved oxygen. Anchovy seems to have a higher tolerance for low oxygen conditions than sardine and appear to have selected to spawn in waters of 1 ml l^{-1} - 3.5 ml l^{-1} of dissolved oxygen, although this may be an artifact as there were few observations in the low dissolved oxygen waters. Sardine selected relatively a narrower range and higher oxygen concentration (4.5 ml l^{-1} - 5.5 ml l^{-1}) than anchovy. On an annual basis, both species seem to avoid hypoxic water except during 1980/1981, when eggs of both species occurred in hypoxic conditions (Figure 3.6 a and 3.7 a). This was also the only time that eggs were found in water of dissolved oxygen below the threshold (2.0 ml l^{-1}) at which organisms may require physiological adaptation to survive (Kreiner *et al.* submitted). During the 1980/1981 season, there seemed to be a shift from spawning in high to low oxygen water (Figure 3.6 b and 3.7 b).

There was relatively little overlap between the two species with respect to selection of bottom depth for spawning. Both species eggs were observed over broad bottom depth range of 7 m (log 1.95 m) to 2800 m (log 7.95 m). Anchovy selected, on aggregation, a bottom depth range with a peak around 25 m (log 3.2 m) for spawning whereas sardine selected a broader bottom depth range with two peaks; within shallow water (20 m; log 2.95 m) and offshore (200 m; log 5.2 m) (Figure 3.1 d). Both species' eggs occurred over the whole bottom depth range with most of the eggs counted being found in the range 9 – 299 m (12 – 141 m) bottom depth for sardine (anchovy). On an annual basis, Sardine spawning was variable with selected bottom depth extending beyond the continental shelf

in 3 years (Figure 3.8 a). Anchovy spawning was confined to the continental shelf (<200 m) for all the years (Figure 3.9 a). There was no particular pattern in the bottom depth range selected for spawning on a monthly basis (Figure 3.8 b and 3.9 b), although anchovy selected bottom depth ranges beyond 200 m during some months.

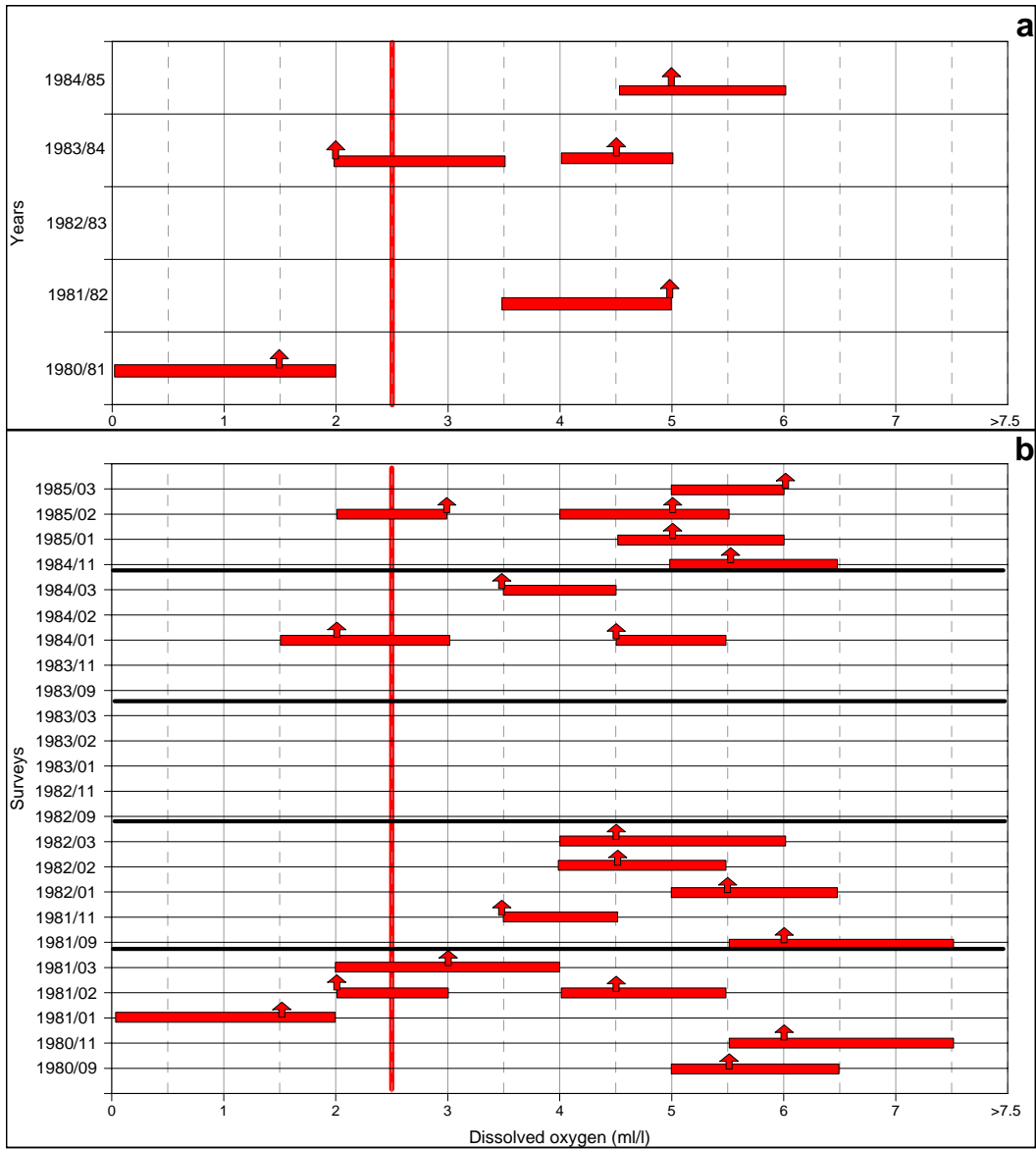


Figure 3.6: Sardine selection of dissolved oxygen for spawning during the SWAPEL period, showing (a) season and (b) individual surveys. The (red) bars indicate the dissolved oxygen ranges selected ($Q > 1$), with arrows showing the peaks of the selected range. The thick horizontal solid line (black) separates the different seasons. The vertical line (red) represents the dissolved oxygen concentration threshold below which physiological behaviour of the fish will be affected (Ekau and Verheye 2005).

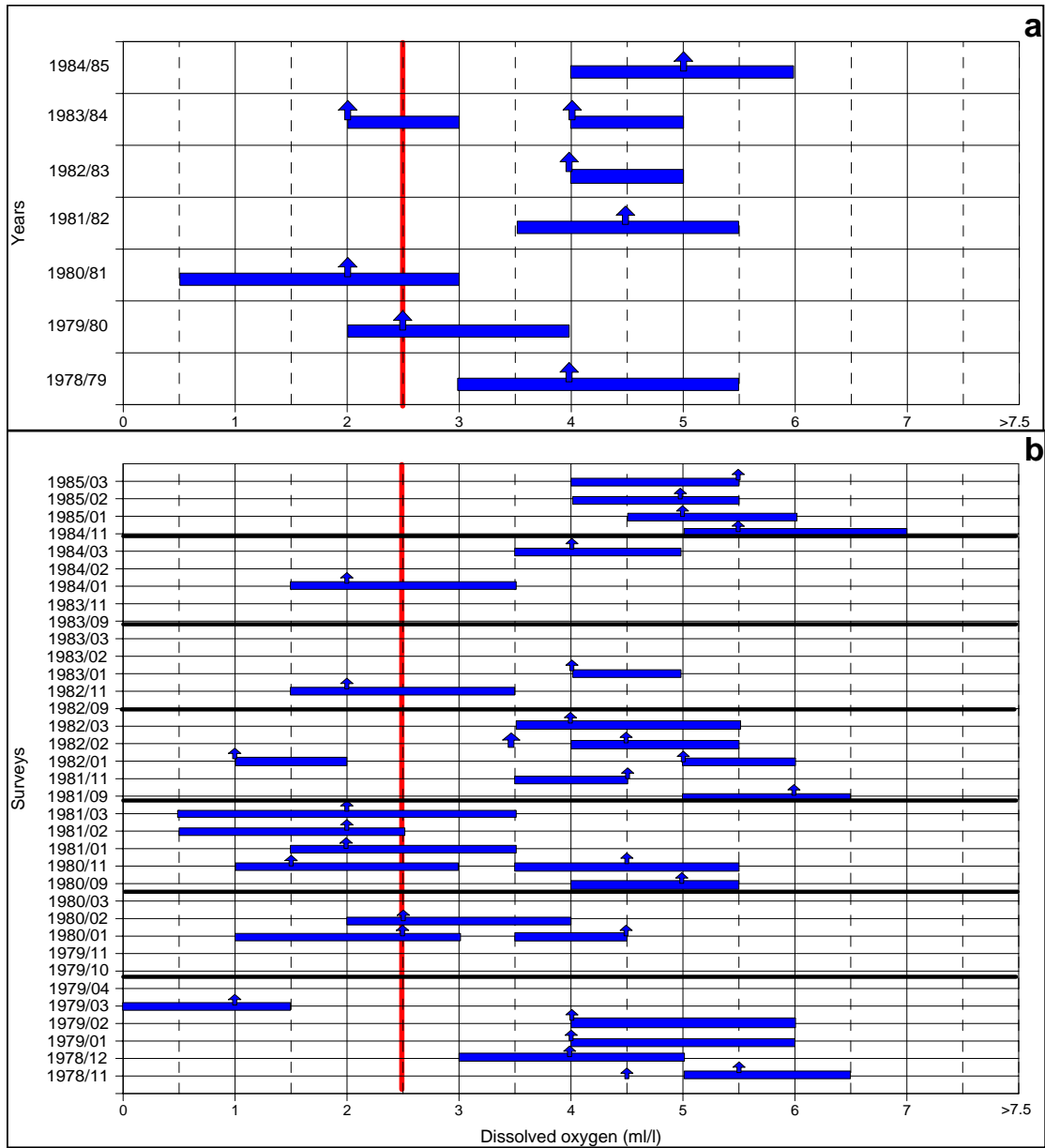


Figure 3.7: Anchovy selection of dissolved oxygen for spawning during the SWAPEL period, showing (a) season and (b) surveys. The bars (blue) indicate the dissolved oxygen ranges selected ($Q > 1$), with arrows showing the peaks of the selected range. The thick horizontal solid line (black) separate the different seasons. The vertical line (red) represents the dissolved oxygen concentration threshold below which physiological behaviour of the fish will be affected (Ekau and Verheye 2005).

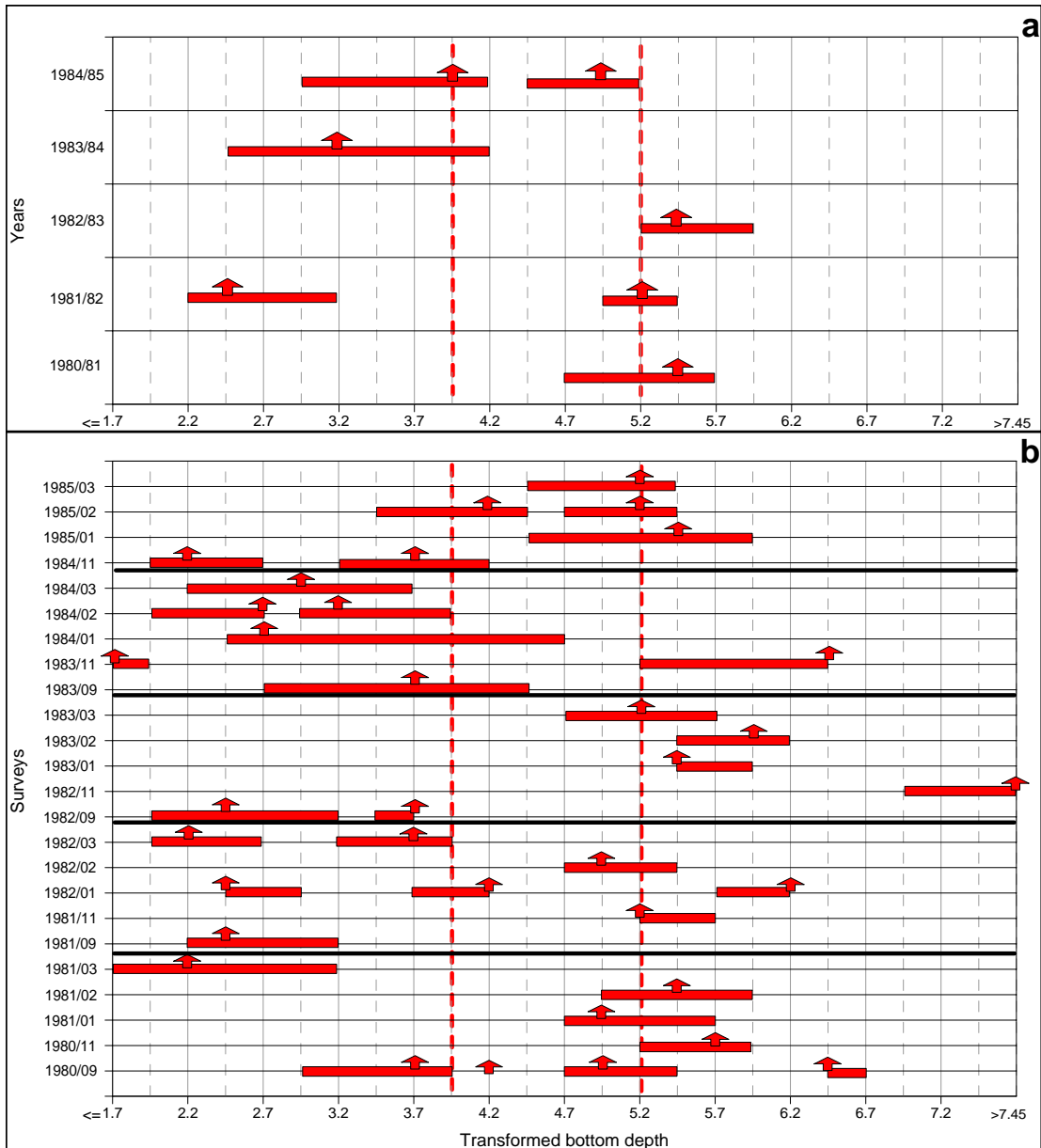


Figure 3.8: Sardine selection of (log-transformed) bottom depth for spawning during the SWAPEL period, showing (a) different years and (b) individual surveys. The (red) bars indicate the bottom depth ranges selected ($Q > 1$), with the arrows showing the peaks of the selected range. The thick horizontal solid line (black) separate the different seasons. The bottom depths of 50 and 200 m are depicted by the vertical dotted lines (red).

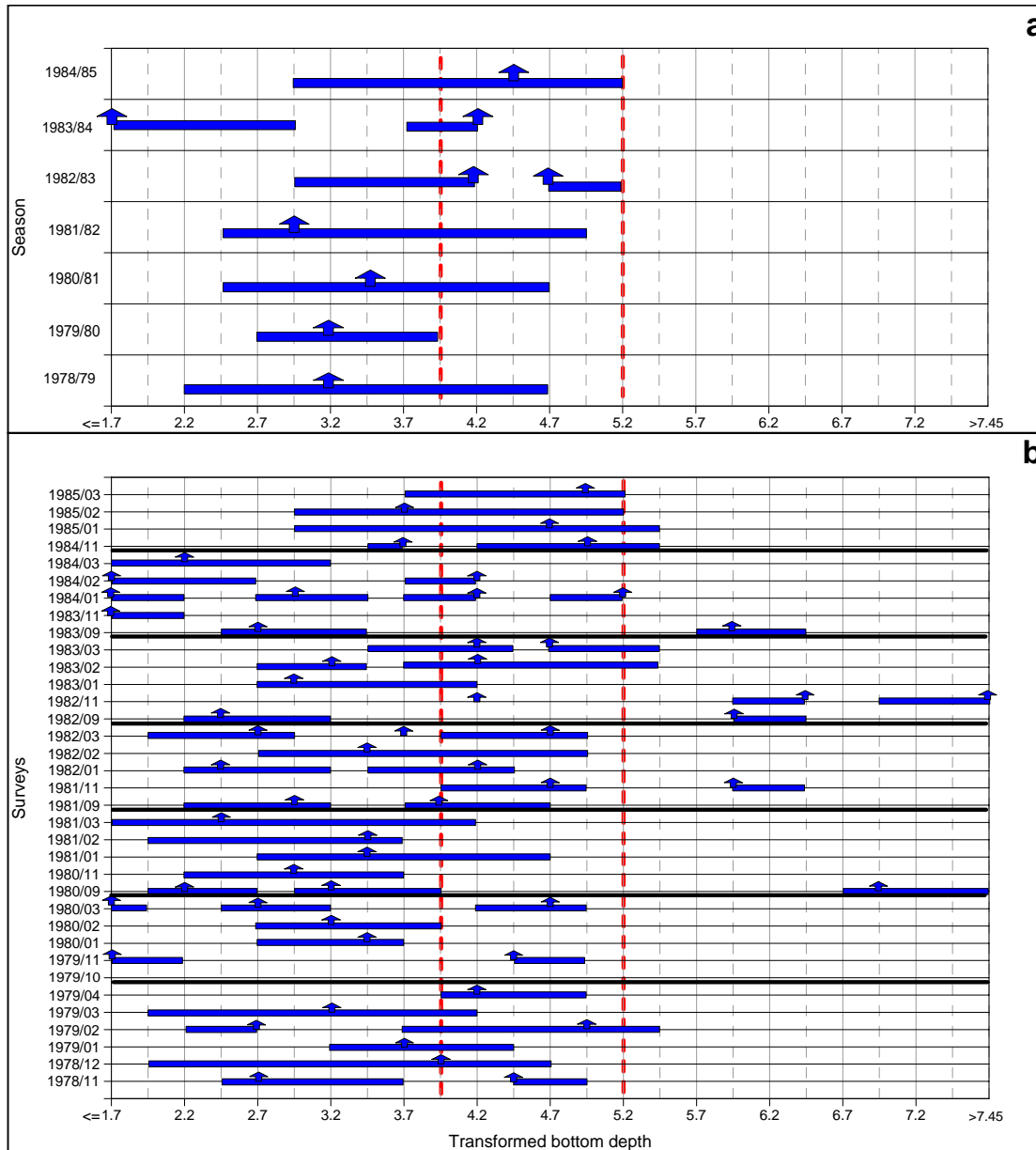


Figure 3.9: Anchovy selection of (log-transformed) bottom depth for spawning during the SWAPEL period, showing (a) different seasons and (b) surveys. The (blue) bars indicate the bottom depth ranges selected ($Q > 1$), with the arrows showing the peaks of the selected range. The thick horizontal solid line (black) separate the different seasons. The bottom depths of 50 and 200 m are depicted by the vertical dotted lines (red).

Spawning habitats selected during Nansen surveys (1999 - 2004)

The SST range selected by the two species for spawning over the *Nansen* survey period overlapped (Figure 3.10 a). Anchovy eggs were found from 14 °C to 19.75 °C and sardine eggs were found from 12.5 °C to 19.75 °C. Anchovy spawned within a very narrow range with two peaks, whereas sardine spawned over a broad range with three peaks within the range of 14.8 °C - 19.8°C, with the main peaks for both species overlapping. The only time that the three ranges preferred by sardine observed in the aggregated dataset were selected for spawning was during the January 2004 survey (Figure 3.11 a). In the other years sardine showed as single quotient peak lying roughly within the range (14 - 18 °C) defined for anchovy and sardine in eastern boundary regions (Parrish *et al.*, 1983). In years when anchovy eggs were recorded there was a preference for a range between 16 -19 °C for spawning (Figure 3.11 b).

From aggregated data, anchovy eggs were found over salinity range of 35.1 ‰ - 35.8 ‰ and sardine eggs were found over a range of 35.3 ‰ - 35.8 ‰. Anchovy selected one salinity range for spawning, whereas sardine selected two ranges (Figure 3.10 b) on aggregation. The less saline range selected for spawning by sardine overlapped with the range preferred by anchovy. The higher salinity range for sardine was not defined, which may indicate that spawning may have extended beyond the range shown here. Again this maybe an artefact of low percentage frequency observed at those levels. It seems as if both species shifted their preference from high to low salinity water over time (Figure 3.12), except during the 1999 survey when sardine preferred the lowest salinity range of all the ranges selected for spawning.

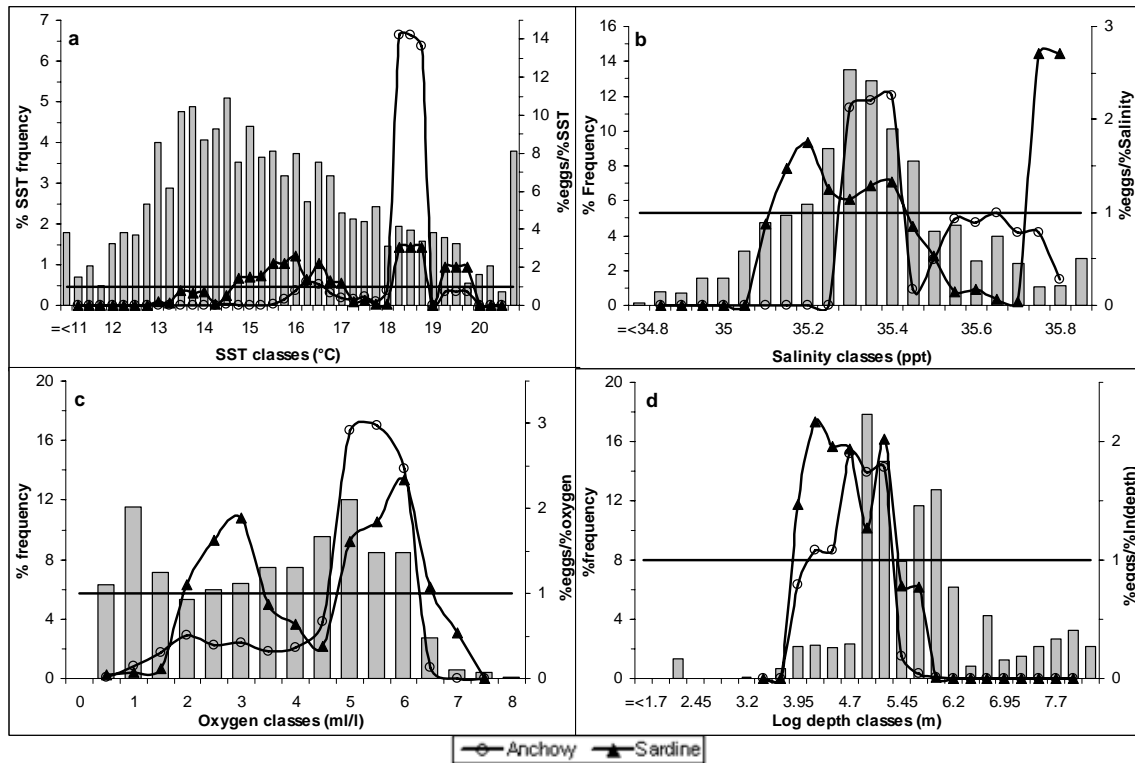


Figure 3.10: Percentage frequency distribution (histogram) of environmental variables for all *Nansen* surveys combined (a) SST, (b) salinity (c) dissolved oxygen and (d) log-transformed depth. Quotient curves (3-point running mean) are shown for sardine (triangle) and anchovy (open circle) eggs. A quotient value of 1 is plotted as the selection threshold.

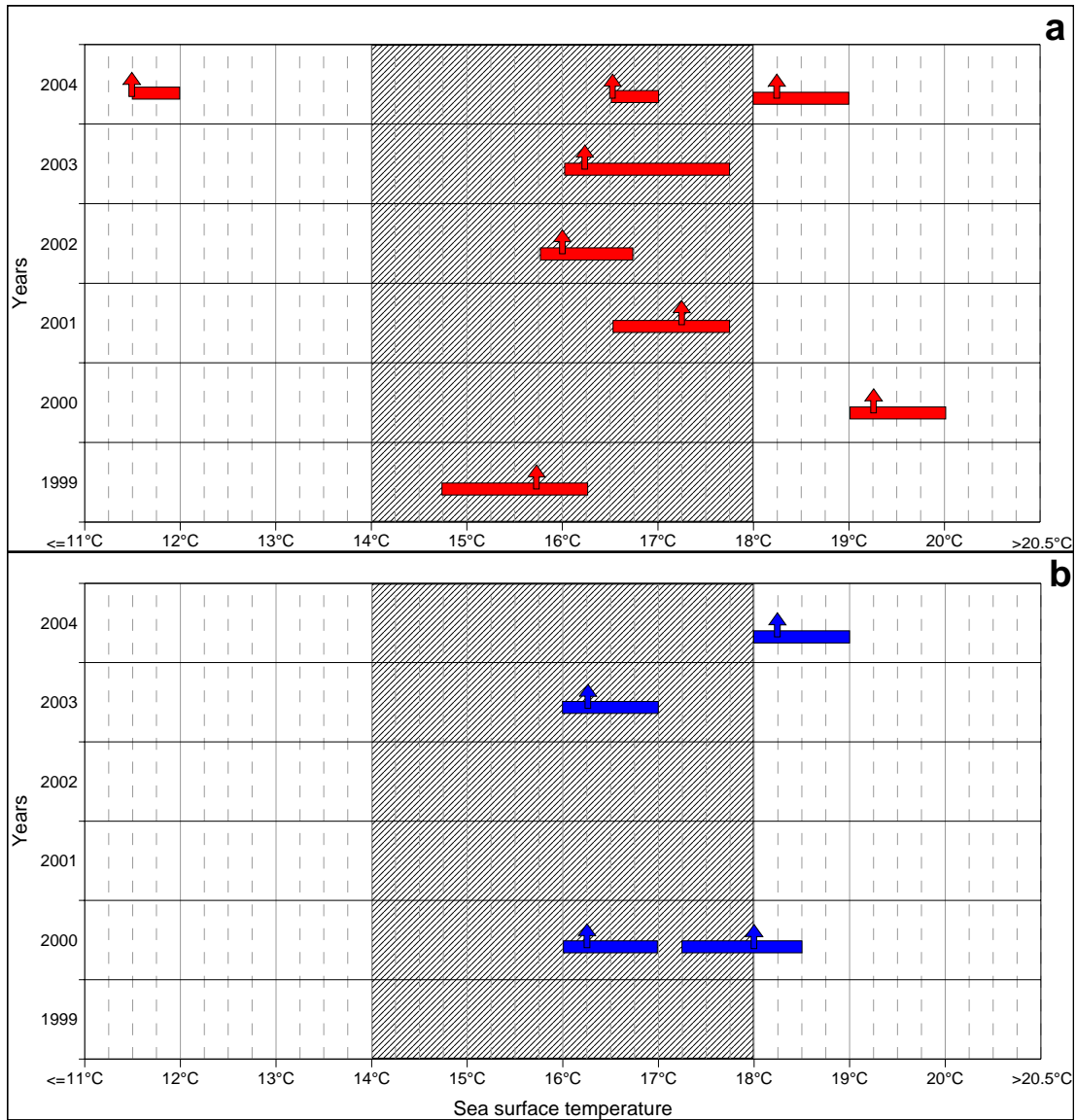


Figure 3.11: Sardine (a) and Anchovy (b) Selection of SST for spawning during the *Nansen* surveys. The bars indicate the SST ranges selected, with arrows showing the peaks of the selected range. The shaded area represents the SST range reported in sardine and anchovy spawning grounds in four eastern boundary regions (Parrish *et al.*, 1983).

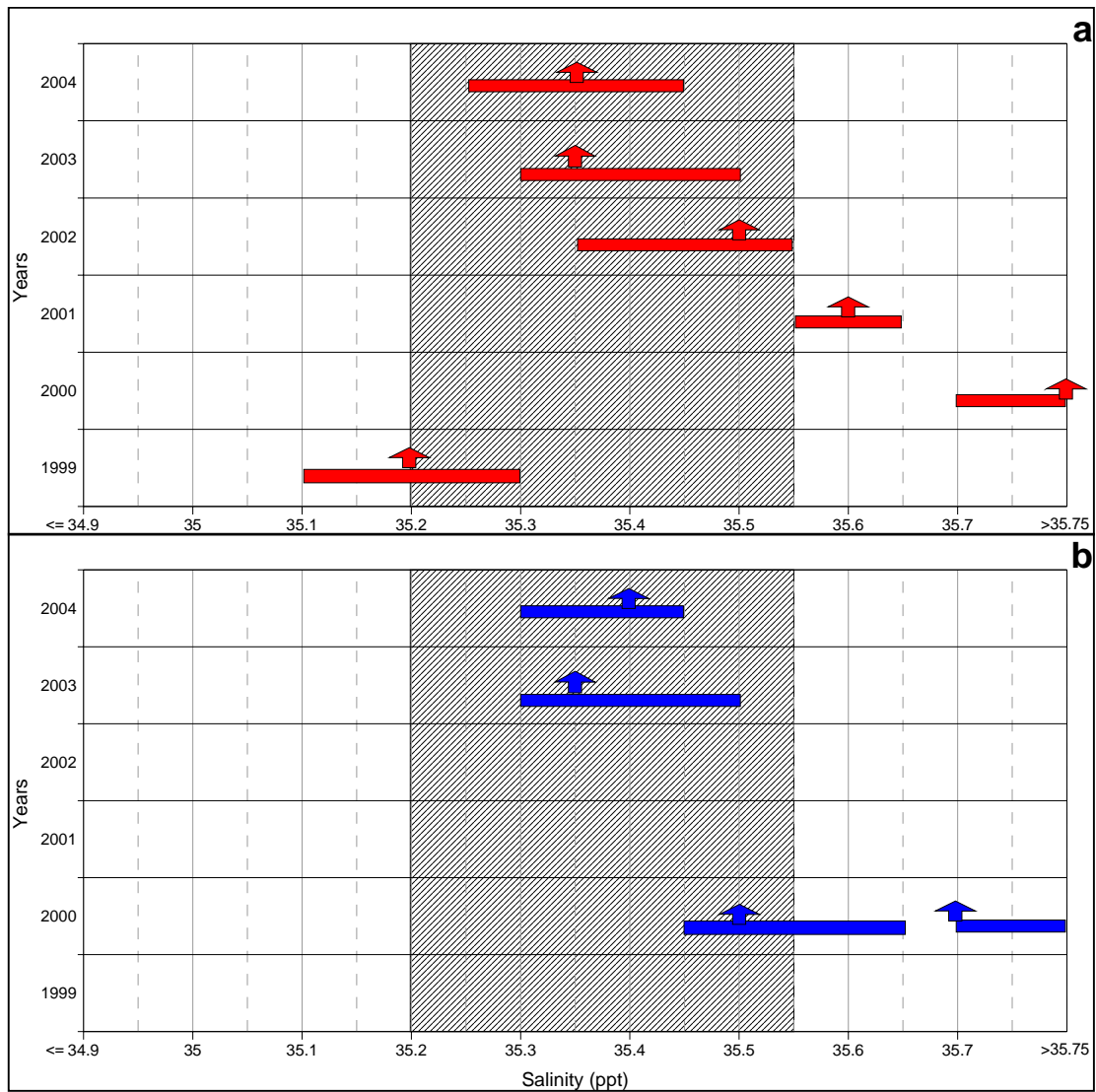


Figure 3.12: Sardine (a) and Anchovy (b) Selection of salinity for spawning during the *Nansen* surveys. The bars indicate the SST ranges selected, with arrows showing the peaks of the selected range. The shaded area represents the salinity range of oceanic and mixed waters found over most of the Namibian continental shelf area (O'Toole 1980).

The selection for spawning with respect to dissolved oxygen was also similar for the two species, with sardine spawning in a broader range than anchovy (Figure 3.10 c) anchovy eggs occurred in dissolved oxygen of 0.5 ml l^{-1} to 6.5 ml l^{-1} and sardine eggs from 0.5 ml l^{-1} to 7 ml l^{-1} . Sardine and anchovy selected high dissolved oxygen waters (5 ml l^{-1} - 6.5 ml l^{-1}) but sardine also selected a second range (2 ml l^{-1} - 3 ml l^{-1}) in the low dissolved oxygen range. Both species spawned mostly in water with dissolved oxygen above critical hypoxic conditions. However, of the three surveys when anchovy eggs were recorded, anchovy eggs were disproportionately high in low oxygen waters in 2000 (Figure 3.13 b).

Both species' eggs occurrences range from about 50 m (log 3.95 m) to as deep as 500 m (log 6.2 m) bottom depth. In broad terms, both species selected a bottom depth range from 50 m (3.7) to just about 200 m (5.45). Sardine spawn over a slightly broader range than anchovy extending into shallower waters (Figure 3.10 d). During individual surveys (Figure 3.14), there was no noticeable variation in the bottom depth range preferred for spawning.

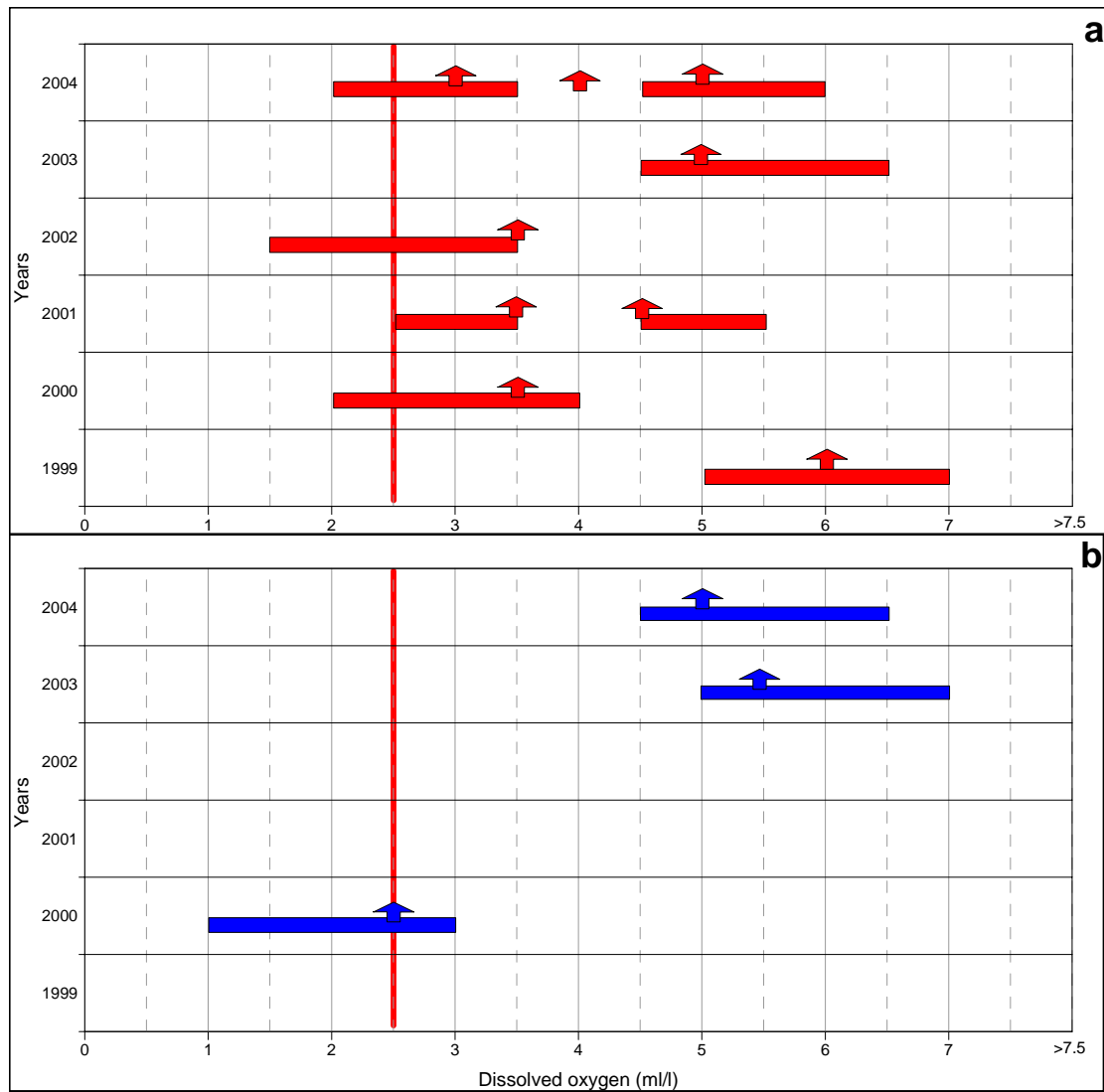


Figure 3.13: Sardine (a) and Anchovy (b) Selection of dissolved oxygen for spawning during the *Nansen* surveys. The bars indicate the dissolved oxygen ranges selected. The vertical line (red) represents the dissolved oxygen concentration threshold below which physiological behaviour of the fish will be affected (Ekau and Verheye 2005).

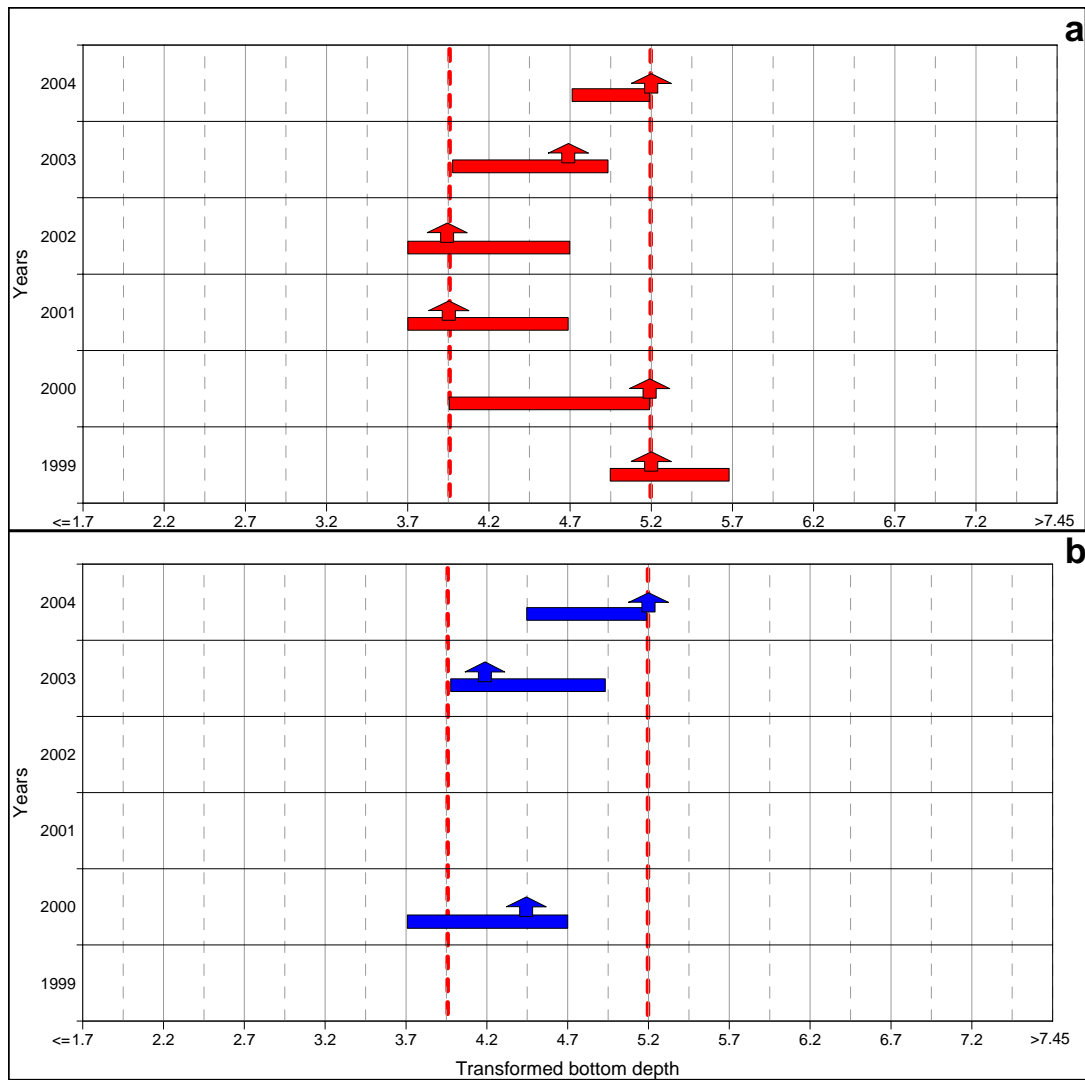


Figure 3.14: Sardine (a) and Anchovy (b) Selection of bottom depth (log-transformed bottom depth) for spawning during the *Nansen* surveys. The bars indicate the bottom depth ranges selected. The bottom depth of 50 and 200 m are depicted by the vertical dotted lines (red).

Temperature-salinity diagrams

This section describes the distribution of sardine and anchovy eggs in relation to the water mass in which the eggs were observed.

SWAPEL surveys (1980 - 1985)

The aggregated temperature-salinity plot indicates that anchovy eggs were found in all three of the water types reported for this region (O'Toole 1980), whereas sardine was restricted to oceanic and mixed water and Benguela Current water only (Figure 3.15). Both species eggs mostly occurred in oceanic mixed water during the period 1980 - 1983 (Figure 3.16) and shifted to Benguela Current water during the 1984/1985 season.

Nansen surveys (1999 - 2004)

The aggregated temperature-salinity plot shows that sardine eggs were found over a broader T-S range than anchovy eggs (Figure 3.17). Anchovy spawning was mostly confined to oceanic mixed water during all the surveys when the eggs were recorded (Figure 3.18). The only times that sardine did not spawn in oceanic mixed water were during the first two years (Figure 3.18); in 1999 sardine spawned in Benguela Current water and in 2000 spawned in Angola Current water.

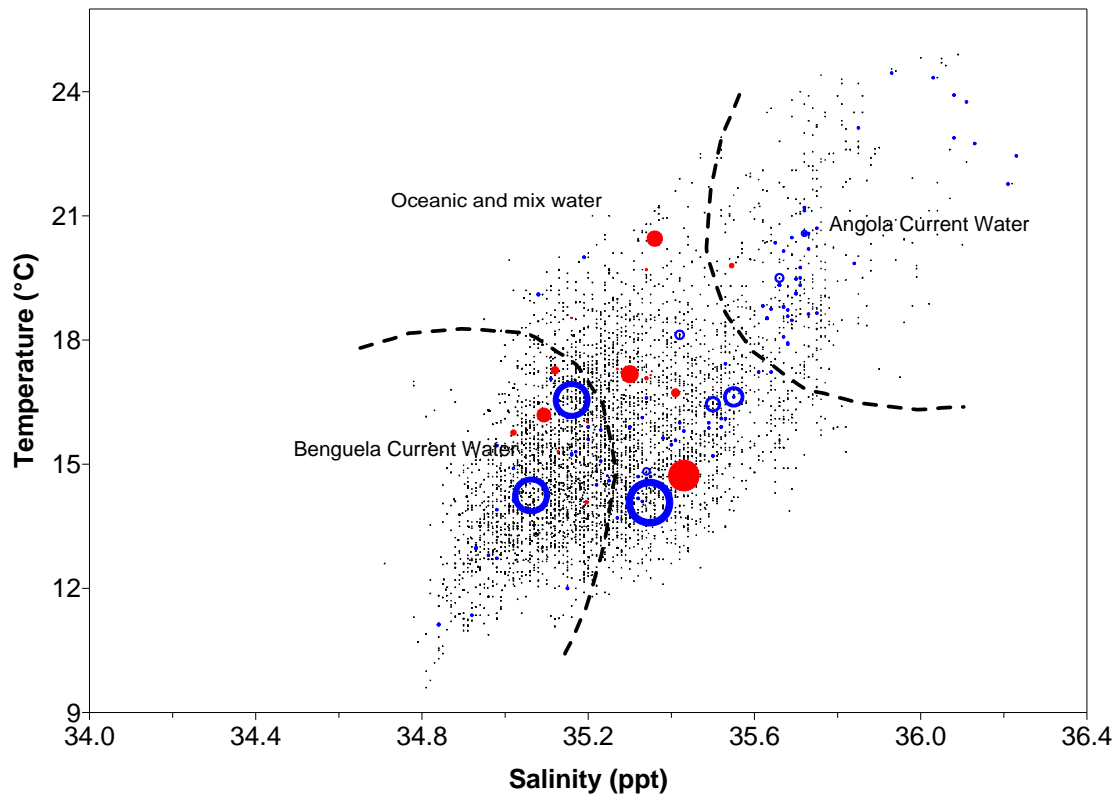


Figure 3.15: Temperature-salinity plot showing eggs of sardine (red) and anchovy (blue) during the spawning seasons from 1980 - 1985 from SWAPEL surveys. The percentage of the eggs is shown by the solid circles (sardine) and open circles (anchovy), with circles being proportional to eggs abundance. The black crosses represent the stations sampled. The different water types are separated by the dotted arcs.

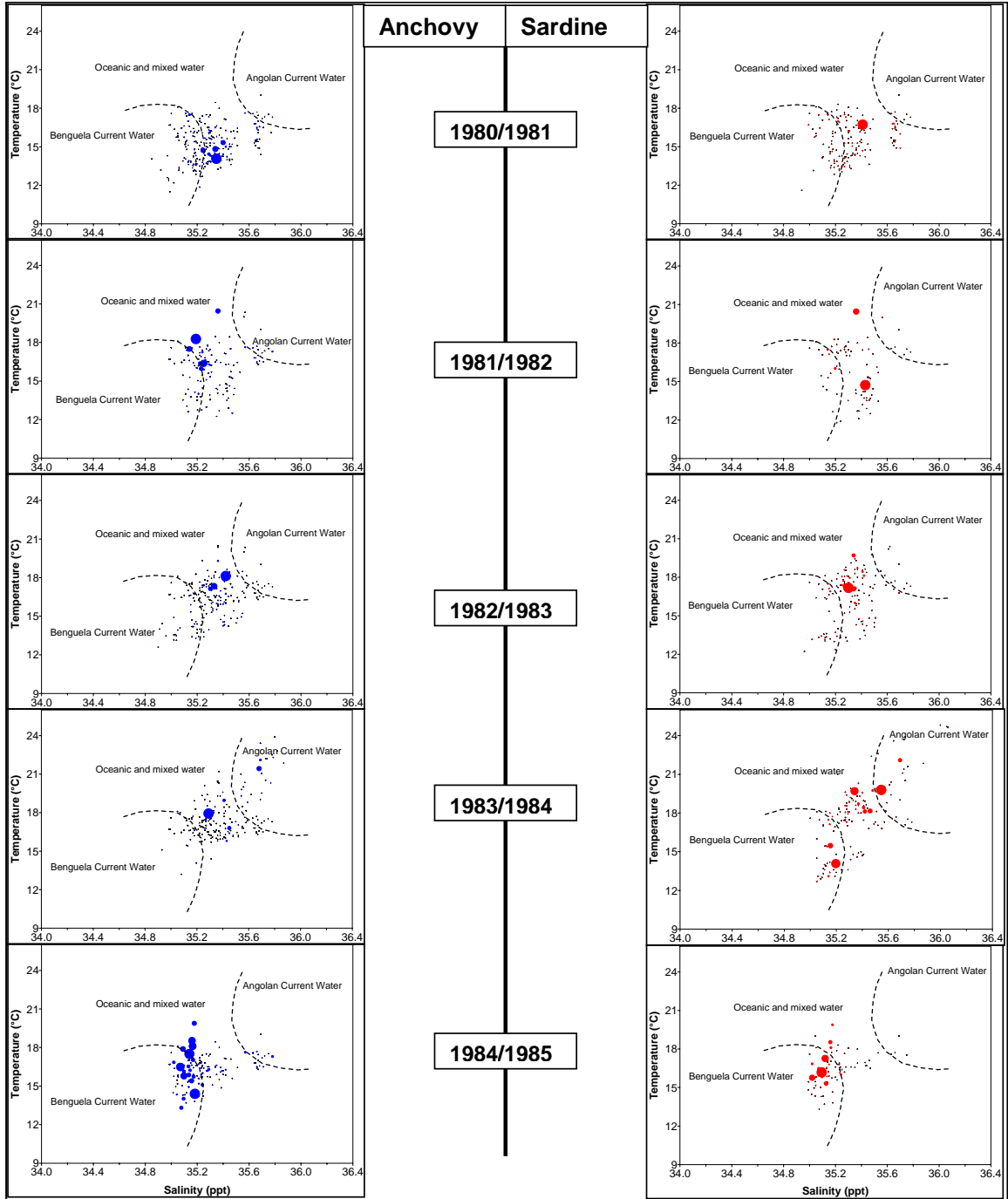


Figure 3.16: Temperature-salinity plots showing anchovy eggs (left) and sardine eggs (right) during the spawning seasons from 1980 - 1985 from the SWAPEL surveys. The black crosses represent the stations sampled and the solid circles represent the percentage of positive stations, with circles being proportional to eggs abundance. The different water types are separated by the dotted arcs.

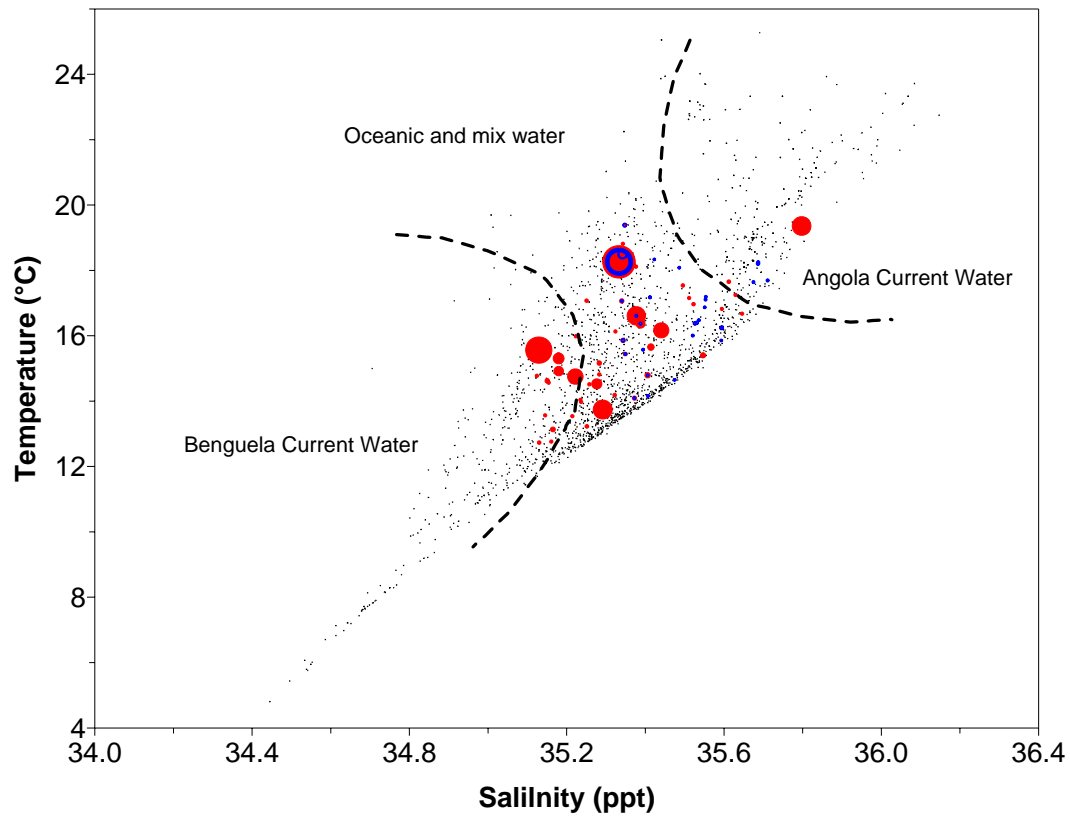


Figure 3.17: Temperature-salinity plot showing sardine eggs (red) and anchovy eggs (blue) during the *Nansen* surveys. The percentage of the eggs is shown by the solid circles (sardine eggs) and open circles (anchovy eggs), with circles being proportional to eggs abundance. The black crosses represent the stations sampled. The different water types are separated by the dotted arcs.

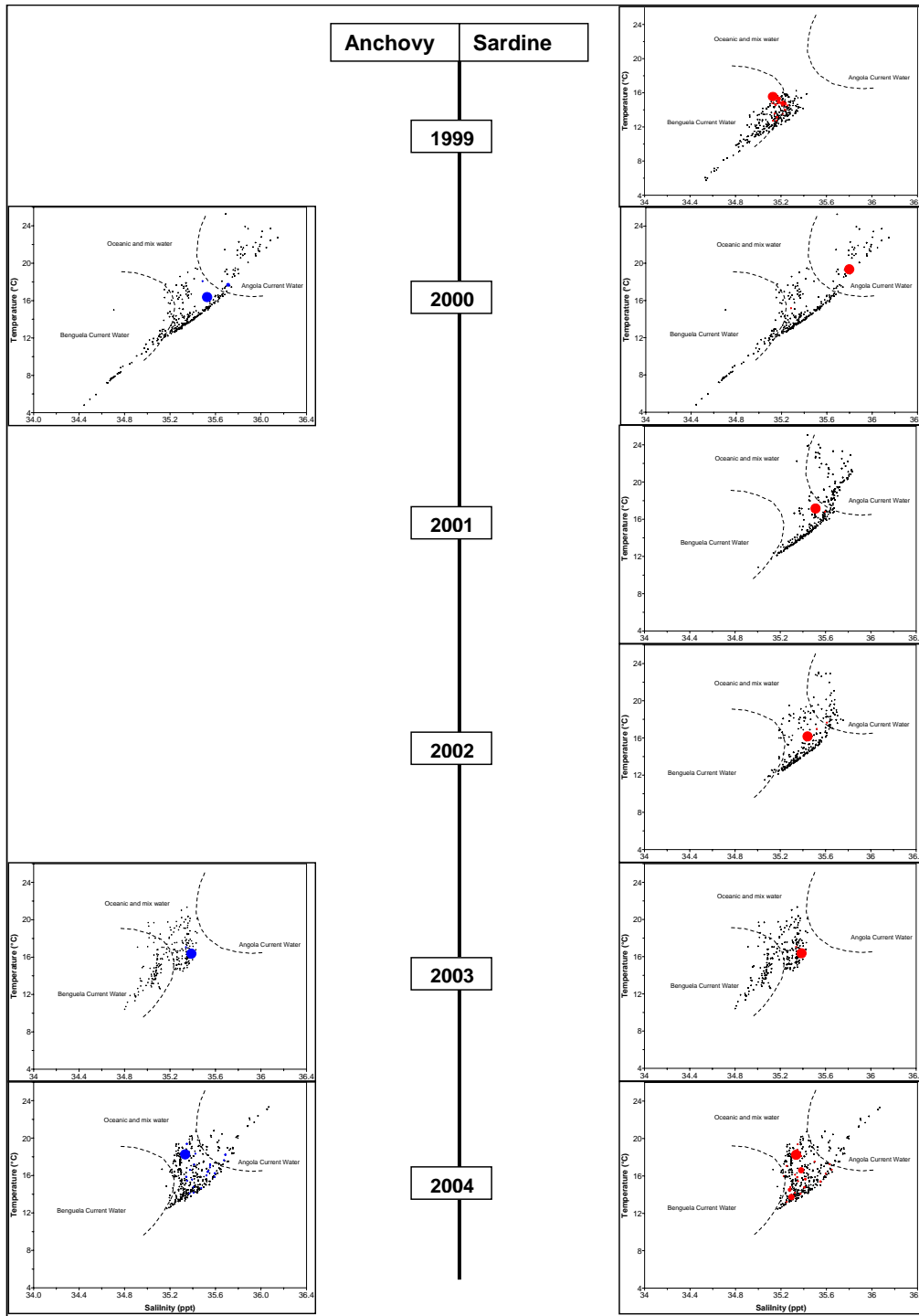


Figure 3.18: Temperature-salinity plot showing anchovy eggs (right) and sardine eggs (left) during the *Nansen* surveys (1999 - 2004). The black crosses represent the stations sampled and the solid circles represent the percentage of positive stations, with circles being proportional to eggs abundance. The different water types are separated by the dotted arcs.

Discussion

Spawning habitat of sardine

During the SWAPEL surveys, sardine eggs were selected ranges in waters of a broad SST ranges (>14.5 °C), a narrow range of salinity (35.3 ‰ - 35.55 ‰), high dissolved oxygen (4 – 6.5 ml/l), and broad bottom depth ranges (9 m - 25 m and 110 m - 300 m). In contrast, during the *Nansen* surveys, sardine spawning selection was over a broad range of SSTs (14.8 °C - 17 °C and 18 °C - 19.8 °C) and salinity ranges (35.1 ‰ - 35.45 ‰ and >35.8 ‰), in low (2 ml/l - 3.5 ml/l) and high (4.5 ml/l - 6.5 ml/l) dissolved oxygen waters, and within a relatively narrow bottom depth range (40 m - 230 m). Le Clus (1991), who studied the impact of large environmental features of spawning distributions of northern Benguela sardine and anchovy from 1972 - 1985, reported that sardine spawned in the temperature range from 15 °C - 19 °C. Similar temperature ranges were also reported for other eastern boundary regions; a range of 13 °C - 25 °C was reported for Californian sardine (Lluch-Belda *et al.* 1991a) and one of the ranges (15.2 °C - 18.2 °C and 17.4 °C - 21.1 °C) reported for southern Benguela sardine (van der Lingen *et al.*, 2001, Twatwa *et al.*, 2005). Off Morocco, sardine have been shown to spawn over wide range of SST with multiple peaks ranging from 15.5 °C to 22 °C (Ettahiri and Berraho 2004). The spawning of sardine over broad ranges of SST has been linked to its patchy spawning behaviour. In the southern Benguela region, Fowler (1998) reported that sardine occupied broad areas for spawning, with no particular spatial dominance in order to take advantage of the variable conditions that characterize eastern boundary regions in which sardine occur.

The results presented here indicate that sardine in the northern Benguela selected multiple ranges of temperature for spawning. These multiple ranges appear separated in time and space, with spawning within the cool water (13 °C – 16.5 °C) occurring mainly during November and December in the Walvis Bay area and spawning in warm water (16.5 °C – 22 °C) occurring during February and March in the area north of Palgrave Point (King 1997b). The selection of multiple temperature ranges for spawning by sardine had also been observed in other eastern boundary regions. In the southern Benguela, Twatwa (2005) also used quotient curve analysis to characterize spawning habitats of sardine, and she reported bimodal distributions peaks (15.5 °C - 17.5 °C and 21 °C - 22°C) with respect to SST. Similar selection of SST for spawning was also reported for Californian sardine (Lluch-Belda *et al.*, 1991a), which showed two peaks over a wide temperature range. The selection of two temperature ranges by sardine seems to be an effective mechanism for withstanding the variable conditions that characterize eastern boundary regions, so that the second peak can become the major peak when conditions are unfavourable (Alheit 1989).

The seasonal variation in selection of temperature and salinity by sardine coincides with the displacement of the Benguela/Angola front. Sardine spawn in cool water at the beginning of the season and shift towards warm water towards the end of the season in summer. King (1977a) indicated that sardine spawned in cool water during November and December and in warm water during February and March. During summer there is a southward shift in the location of the Angola/Benguela front, leading to intrusion of the warm, high salinity tropical Angolan water (Boyd *et al.* 1987, Shannon 1985). The

strongest intrusion was experienced during the 1983/1984 season, during the 1984 Benguela *Niño*. This is also the season that sardine showed the largest increase in selected SST, from 12.5 °C to 20.5 °C. The period of 1981 – 1983 was classified as cool (le Clus 1990), with minimal intrusion of the warm Angolan water (Boyd *et al.*, 1987). Boyd *et al.* (1987) also stated that the same period tended to have the most southerly extent of warm water in February, whereas periods of strong intrusion had maximum surface intrusion in March/April. Although the intrusion in 1982 was limited, the maximum intrusion was in March/April and not in February. The correspondence of sardine spawning selection with displacement of warm, saline Angolan water southwards indicates sardine tolerance for varying environmental conditions.

The selection of temperature for spawning can also be explained in terms of locality. Le Clus' (1990) work demonstrates that sardine extends its spawning ground southwards to the Lüderitz upwelling cell in the northern Benguela when it is anomalously warm. This finding is supported by this study, because sardine tended to adjust its area of spawning with the expansion of warm water southwards (see Chapter 4). The same pattern of expanding spawning grounds with respect to temperature was also reported for other eastern boundary systems (Humboldt and California, Lluch-Belda *et al.*, 1992). Twatwa's (2002) and Twatwa *et al.* 2005 findings also indicate that sardine shifts its spawning distribution into cool water (or inshore) when the wind driven upwelling is at its minimum and vice versa. Studies on Japanese sardine indicate that sardine migrates according to environmental conditions, which exhibit seasonal and annual fluctuations (Kondô 1988).

Sardine showed an affinity for moderately saline oceanic and mixed waters as defined by O'Toole (1980). This water mass generally occupies most of the continental shelf, depending on the hydrographic processes (i.e. upwelling/intrusion) impacting on the shelf at a given time. The preference of sardine for this water can be explained by the overlap of sardine selected spawning temperature range and this water temperature (16 °C - 20 °C) range. The low salinity Benguela Current water could be too cold for sardine egg survival and successful development (King 1997a), and the high salinity Angola Current water is poor in productivity (Mitchell-Innes *et al.*, 2001) and may not be nutritious for sardine adults and larval development.

Spawning habitat of anchovy

Anchovy spawning selection was within a broad SST range (> 14 °C), broad salinity range (> 35.2 ‰), low dissolved oxygen (1 ml l⁻¹ - 3.5 ml l⁻¹) and relatively shallow (12 m - 141 m) bottom depth during the SWAPEL surveys. During the *Nansen* surveys, anchovy eggs were found in water with a SST range of 16 °C - 19 °C, a narrow salinity range (35.3 - 35.4 ‰), high dissolved oxygen (4.5 ml l⁻¹ - 6 ml l⁻¹) and relatively shallow bottom depths (67 m - 181 m). Wide temperature ranges for spawning were reported for both anchovy and sardine by le Clus (1991). The selection of this wide temperature range was considered significant by Motos *et al.* (1996), who studied the spatio-temporal pattern of anchovy spawning in the Bay of Biscay. Once sea surface temperature rises above 14 °C, anchovy eggs are found, and spawning activities increased with increasing surface temperature (Motos *et al.* 1996), reaching a peak during the transition from

winter to summer when the temperature is at its warmest. This adaptive behavior allows anchovy to search for time-space environmental windows that have favorable conditions for egg and larval survival (Cury and Roy 1989).

The results indicate that anchovy preferred cooler water than sardine during the SWAPEL surveys. This finding is supported by le Clus' (1991) work relating hydrographic features with anchovy and sardine spawning. Le Clus (1991) concluded that while sardine spawn early in the season when upwelling is strong, anchovy spawn more frequently in cool waters inshore than do sardine. Anchovy preference for cool upwelled waters is not well understood, but in California anchovy was also found to spawn in these waters (Lluch-Belda *et al.*, 1991a). It was suggested that anchovy spawning is related to intense upwelling, which results in cold temperatures. In contrast, southern Benguela anchovy seem to be better adapted to warm waters and their spawning activity is poorly related to upwelling intensity (van der Lingen *et al.*, 2001; Twatwa 2002) as anchovy spawn exclusively on the Agulhas bank. This finding was supported by anchovy feeding conditions that were associated with warm temperatures (Richardson *et al.*, 1998).

The feeding ground of anchovy in the northern Benguela was within a distance of about 15 km - 20 km from shore (Le Clus 1991), where the concentration of phytoplankton in the northern Benguela reaches a maximum during the spawning season (Kruger 1983, Shannon and Pillar 1986, Mitchell-Innes *et al.*, 2001), with zooplankton abundance extending even further offshore (Verheye *et al.*, 2001). This distance coincides with the bottom depth range selected for spawning by anchovy, indicating that this depth range

may coincide with that needed for energetic reasons. Le Clus (1991) also concluded that anchovy spawn inshore but extend offshore in some seasons (warm periods). This depth range is known to be within the frontal zone of the cold upwelled water and warm oceanic water, which is closely related to the shelf break (Stenevik and Kreiner 2004). In the Bay of Biscay, anchovy have also been shown to spawn within frontal regions where hydrographic features enhance particle retention and stratification (Motos *et al.*, 1996; Bakun 1996).

The occurrence of anchovy eggs within shallow water coincided with the low oxygen waters that are common on the shelf (Chapman and Shannon 1985). The results indicate that anchovy have a high tolerance for oxygen deficient conditions, spawning well below the oxygen depletion threshold, as defined by Monteiro *et al.* (2006). The tolerance for low oxygen conditions by anchovy may be associated with its small size and inferior swimming abilities compared with sardine, which confines anchovy to nearshore areas (Dotson and Griffith 1996) where low oxygen water is a permanent feature from the poleward flowing sub-surface current (Monteiro *et al.*, 2006).

Comparison of sardine and anchovy spawning habitats

The selection of environmental variables by sardine and anchovy for spawning indicates that their preferred spawning habitats were generally similar. Sardine selection of a broad bottom depth seems to be associated with a narrow salinity range. Anchovy selection of a narrow bottom depth range for spawning is associated with a broad salinity range. The broad salinity range selected shows that anchovy spawned in different water masses that

were introduced on to the shelf during upwelling or the intrusion of warm high saline Angolan water. In contrast, sardine appear to prefer spawning in oceanic water that occupies most of the shelf, avoiding cool less saline upwelling water and the warm saline Angolan water associated with low oxygen. The variability in sardine geographic habitat is reported to be the result of its superior swimming when compared with anchovy (Dotson and Griffith 1996). Sardine are larger and longer-lived than anchovy, and are more able to cope with large scale hydrographic variability (Curtis 2004).

The similarity of sardine and anchovy spawning habitats in the northern Benguela contrasts with the spawning habitats of these species in other systems. Although the California sardine and anchovy temperature preferences were characterized to be similar, sardine spawned over a wider temperature range and was better adapted than anchovy to spawn in warm water (Lluch-Belda *et al.*, 1991a). Sardine in the southern Benguela were also characterized to be different from anchovy (Twatwa *et al.*, 2005), with sardine spawning over a wider temperature range than anchovy. However, anchovy was better adapted to spawn in warm water than sardine (van der Lingen *et al.*, 2001). The lack of a difference in spawning habitat may challenge the hypothesis of regime shifts in the northern Benguela, although environmental conditions and fishing pressure have been postulated to preclude steady growth of the sardine population in the northern Benguela (Schwartzlose *et al.*, 1999).

Comparing the two surveys

Although the comparison of the two surveys is limited by the difference in survey intensity and spatial coverage, some differences were noticeable. SWAPEL surveys have a better spatial coverage and extended over the whole spawning period. *Nansen* annual surveys were limited to the central and northern regions of the northern Benguela.

Anchovy spawning habitat selection was broad during the SWAPEL surveys, whereas it was much narrower during the *Nansen* period. The shift in range selection may be explained by the density dependence of anchovy spawning. Although evidence of density-dependence is scarce (Blaxter and Hunter 1982), clupeoid populations have been shown to reduce their preference range with a decrease in abundance (Bakun 1996; Schwartzlose *et al.*, 1999). Anchovy populations in the northern Benguela have decreased drastically between the two survey periods. Catches averaged around 200 000 tonnes per annum during the SWAPEL surveys, but have reduced to virtually zero during the *Nansen* surveys (Boyer and Hampton 2001b). In the Bay of Biscay, Motos *et al.* (1996) reported that anchovy concentrate their spawning activity in sites which maintain minimal sustaining conditions for anchovy populations. These authors showed that anchovy selected specifically waters with low salinity even in isolated sites further offshore. It was also shown in the southern Benguela that anchovy will first choose an optimal temperature (16 – 18°C) range then expand its range with an increase in population size (Twatwa 2002).

Sardine displayed single peaks with respect to salinity and oxygen during the SWAPEL surveys, but bimodal peaks during the *Nansen* surveys. The change in selectivity indicates that sardine changed their spawning habitat with time. As there has not been a significant drop in sardine abundance in comparison to the early 1980s (Boyer and Hampton 2001b), the change in spawning habitat may be attributed to environmental conditions. In recent years a high frequency of warm events was reported (Bartholomae and van der Plas 2007), which have been shown to affect sardine distribution (Crawford *et al.*, 1987). In other systems, sardine also were reported to broaden their selectivity range as a strategy to adapt to turbulent conditions (Alheit 1989; Lluch-Belda *et al.*, 1991a; van der Lingen *et al.*, 2001).

Conclusions

The spawning habitat of sardine and anchovy was characterized by assessing the value of environmental variables in waters in which eggs were observed, using single factor quotient analysis. The results indicated that the two species selected generally similar conditions for spawning, with some important differences. Sardine spawning habitats were characterized by a broad range of temperature and bottom depth, well oxygenated waters and a narrow range of salinity during the SWAPEL surveys. During the *Nansen* period, sardine spawning was broad with respect to salinity and oxygen (i.e spawning in different water masses and in low oxygen waters). Anchovy spawning habitat was characterized by broad temperature and salinity ranges, and was confined to low oxygen waters within the shallow areas during the SWAPEL surveys. During the *Nansen* surveys, anchovy spawning habitat was characterized by specific ranges with respect to

all the variables assessed. The selection of broad ranges of the environmental variables seems to be an effective mechanism to maximize survival of the early life stages in these varying environmental conditions that characterize eastern boundary regions. Both species have varied their preference seasonally relative to prevailing environmental conditions. These species also seem to have changed their preference with changes in their abundance over a longer period. Sardine seems to be better adapted to varying conditions by changing its spawning habitat in order to avoid conditions that may not be beneficial to successful development of the early stages. On the other hand, anchovy has adapted to varying conditions by tolerating a wide range of different conditions, and timing its spawning such that the effect on the development of early stages is minimal.

Thus anchovy are more specific than are sardine, as shown in other systems (Checkley 2004b, Twatwa *et al.*, 2005), when selecting habitat for spawning, and this implies that anchovy could be more vulnerable to variability in environmental conditions than sardine.

The current low biomass of anchovy and sardine requires careful management to allow populations to increase, in order to improve the chances of successful spawning and development. The increase in anchovy populations could allow anchovy to expand their niche and take advantage of the favourable conditions further offshore.

Chapter 4. Spatial structure in egg distributions of sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) and location of spawning centers.

Abstract

The spatial structure in egg distributions of sardine and anchovy, and variability in the location of spawning centers (center of gravity) were explored to assess spawning behaviour within the spawning habitats of the two species. Experimental variograms were computed to assess the spatial patterns, and centroids (center of gravity) were computed to analyze changes in location of the spawning centers. No coherent spatial structure in egg distributions was found for either of the two species during the SWAPEL surveys (1978 - 1985). This could be a result of the survey sampling strategies, which resulted in increased variability at short distance and reduced variability over long distances. The spawning centers for both species occurred in the area north of 22° S during both SWAPEL and *Nansen* surveys. Spawning activity in this area is related to high concentrations of food, which are important for early life stage development.

Introduction

Most knowledge of spawning behaviour in clupeoids, such as determination of peak spawning periods and associated environmental conditions, comes from studies on their egg distributions. Several studies have been directed towards quantifying the spatial distribution of eggs of small pelagic fish, with variograms being used frequently as the analyzing technique (Curtis 2004). In the southern Benguela, Barange and Hampton (1997) compared the spatial structure of adults and eggs of anchovy and sardine

and concluded that anchovy exhibited greater structure than sardine at the sampling scale of 9 km. Their findings were complemented by those of van der Lingen *et al.* (1998), who indicated that patchiness in sardine egg distributions can be resolved partially by increasing sampling effort. A similar study by Curtis (2004) in the southern California Bight showed that sardine was spatially more structured than anchovy at a smaller sampling scale than the scale reported by Barange and Hampton (1997). Curtis (2004) attributed the spatial structure of eggs to species, population size and age structure, spawning intensity and characteristic physical scale of the spawning habitat. Sardine have better superior swimming ability than anchovy, and this allows organization at a larger scale and with greater movement during spawning, which results in a more structured spatial distribution. The greater mobility of adult sardine also results in spatio-temporal variability of their spawning proximity in relation to the spawning area of anchovy. Also, the patchiness in sardine school distributions increases the pattern in spatial structure of eggs at small scales/ short range (~ 1 n. mile).

Studying the spatial distribution of sardine and anchovy eggs is central to understanding the spawning behaviour of these species, this behaviour is also central to better understanding and characterizing their spawning habitats. This chapter aims to investigate the spatial structure of sardine and anchovy adults during spawning in the northern Benguela by analyzing the spatial distribution of their eggs, and the variability in these distributions among years.

Methods

Egg data collected during the SWAPEL surveys (1978 - 1985) were used for assessing spatial structure of both species. Nansen surveys (1999 - 2004) were not used for spatial structural studies because of the paucity of data. However, data from both surveys were used to assess the spatial variability (movement) of spawning activity by computing centers of spawning activity (centroids). During the SWAPEL surveys, eggs were sampled at a scale of 5 n. miles between stations along transects, and at an interval of 20 n. miles between transects in the early years, then 30 n. miles in later years (see Chapter 2; Figure 2.1).

Analysis techniques

This section presents the experimental variograms and gravity center of activity techniques used to assess the spatial structure and calculate the variability of centroids for sardine and anchovy adults during spawning.

Experimental Variogram

The computation of experimental variograms is described in detail in Burrough and McDonnell (1998) and is summarized below. Generally, spatial techniques acknowledge that the spatial variability of any continuous variable is often too irregular to be modeled by a simple, smooth mathematical function. The experimental variogram method, as a spatial technique, calculates a localized average, and also the size, orientation and shape of the neighbourhood from which the data points were sampled, with the uncertainties associated with the interpolated value. It also ensures that the predictions of the attribute

values at unvisited points are optimal in terms of the assumptions made. The technique assumes that the spatial variation of any variable can be expressed as the sum of three major components: (i) a structural component ($m(x)$) of the variable Z at x (location), having a constant mean or trend; (ii) a stochastic locally varying but spatially dependent residual ($\varepsilon'(x)$) from the structural component, known as the variation of the localized variable; and (iii) a spatially independent (uncorrelated) Gaussian noise or residual error term (ε'') having zero mean and variance. This can be expressed mathematically as follows:

$$Z(x) = m(x) + \varepsilon'(x) + \varepsilon'' \quad 4.1$$

If it is assumed that the structural component is equal to the mean value of the data points, and the average or expected differences between any two points separated by a distance h is zero, and the variance of the differences depends only on the distance between the points, then this equation can be rewritten as:

$$\gamma(h) = \frac{1}{2n} \sum_{i=1}^n \{z(x_i) - z(x_i + h)\}^2 \quad 4.2$$

The semivariance $\gamma(h)$ is derived from the number (n) of pairs of data points sampled of variable (z) separated by a distance (h). A plot of the semivariance against distance is known as the experimental variogram (Figure 4.1). The experimental variogram provides information for interpolation and determining the spatial pattern. The plot displays three important features for interpolation purposes. (i) The distance (h) at which the

semivariance levels off implies that there is no spatial dependence between points separated beyond this **range**. (ii) The curve rises from a low value of semi-variance to a point where the semi-variance of the differences does change with the sample separation distance. This horizontal part is called the **sill**. (iii) The third feature is the intercept of the curve, which does not pass through the origin. This represents the variance or residual (spatially uncorrelated) noise of measurement error combined with that from spatial variation at distances much shorter than the sample spacing, and is known as the **nugget**.

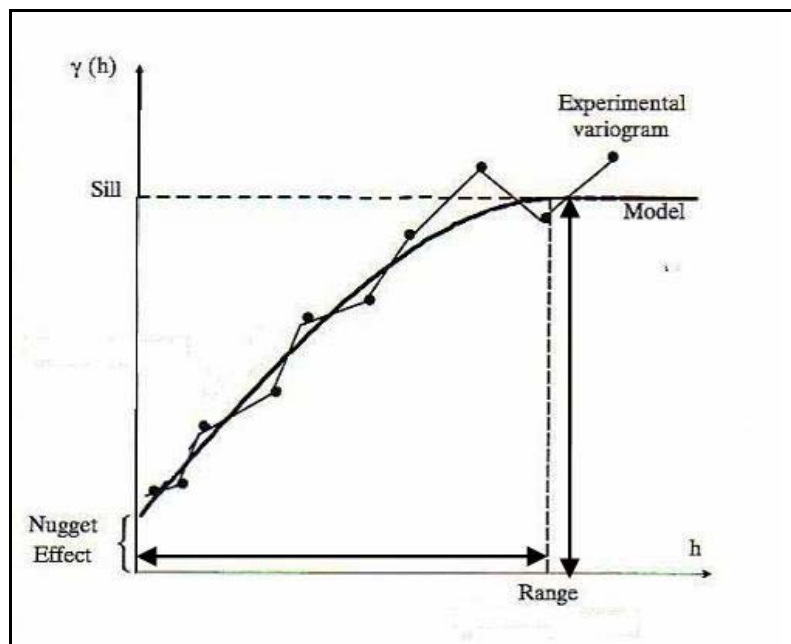


Figure 4.1: An illustrative variogram model depicting the experimental variogram. The three features (range, sill and nugget) depicting the general pattern of a model are also shown (derived from Geostatistics 1997).

The inputs into the computations of experimental variograms were the geographical information (latitude and longitude) of each station and the log-transformed number of eggs recorded at each station during the SWAPEL surveys. The latitude positions were converted to distance from the 200 m isobath to investigate if there were any structural patterns related to hydrographic features. The experimental variograms were only computed for some of the surveys, selected on the basis of a comparable period between the two species and a high number of eggs to investigate the structural trend in spawning behaviour. The variograms were analyzed using Surfer, version 8.0 (2002).

Centroids

The spatial changes (movement) of spawning location between surveys were determined using a synthetic measure known as the centroid (also known as the center of gravity or center of activity, Hayne 1949), which is defined as the geographical mean of the egg distributions. It is determined by weighting (W) the geographical coordinates for each station (i) by the ratio of the number of eggs (z) per station and the total number of eggs over all stations per survey.

$$W_i = \frac{z_i}{\sum_{i=1}^n z_i} \quad 4.3$$

The sum of the weighted coordinates for longitude (X_w) and latitude (Y_w) determines the geographical position of a centroid:

$$X_w = \sum_{i=1}^n X_i * W_i \quad ; \quad Y_w = \sum_{i=1}^n Y_i * W_i \quad 4.4$$

The variability around the centroid is determined by computing the variance (σ^2) along the geographical dimensions for all the stations of a survey. The dimension with the greater variance (magnitude) is referred to as the major axis (α), whereas the other dimension's variance is referred to as the minor axis (β), with a constant factor ($\varepsilon = 5.9915$, Jenrich and Turner ellipse; Jenrich and Turner 1969). The deviation of the major axis from the main dimension is also determined and is referred to as the axis angle (θ).

$$\sigma_x^2 = \frac{\sum_{i=1}^n (X_i - X_w)^2}{n-1} \quad ; \quad \sigma_y^2 = \frac{\sum_{i=1}^n (Y_i - Y_w)^2}{n-1} \quad 4.5$$

$$S_{XY} = \frac{\sum_{i=1}^n [(X_i - X_w) * (Y_i - Y_w)]}{n-1} \quad ; \quad 4.6$$

$$\lambda = \left[(\sigma_x^2 - \sigma_y^2)^2 + 4(S_{XY})^2 \right]^{\frac{1}{2}} \quad 4.7$$

$$\alpha = \left[\left((\sigma_x^2 + \sigma_y^2)^2 + \lambda \right) \frac{\varepsilon}{2} \right]^{\frac{1}{2}} \quad 4.8$$

$$\beta = \left[\left((\sigma_x^2 + \sigma_y^2)^2 - \lambda \right) \frac{\varepsilon}{2} \right]^{\frac{1}{2}} \quad 4.9$$

$$\theta = \frac{-2S_{XY}}{\text{Arc tan} \left((\sigma_x^2 + \sigma_y^2) - \lambda \right)} \quad 4.10$$

Results

Spatial pattern

The egg distributions of sardine and anchovy did not show obvious structural patterns when all the data from the SWAPEL surveys were analyzed together (Figure 4.2). The variograms for each species indicated that there was a high nugget effect, thus structural variability could not be explained using the available sampling range. When individual survey years were analyzed, anchovy showed some structural pattern, with a relatively small nugget effect, whereas sardine did not (Figure 4.3). The plots shown in Figure 4.3 are only for February 1985, as there were few differences in the observed patterns in comparison to the other surveys and the number of eggs observed relative significant. The increase in variance with distance to about 15 n. miles followed by a decrease is mainly a consequence of the sampling pattern. The number of stations that can be paired decreased with distance along transects, so most of the pairs occurred within short distances. At distances greater than 15 n. miles the variance decreased because there were relatively more data points that could be paired between transects. At ranges above 50 n. miles, the variance increased as the pairs were from data points inside and outside egg patches.

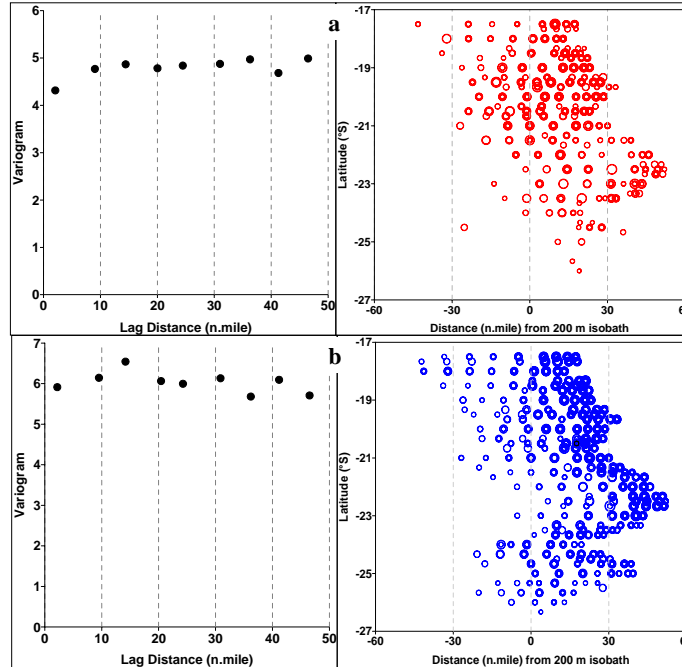


Figure 4.2: Experimental variograms for sardine (a) and anchovy (b) eggs and distributions for all SWAPEL surveys (1978-1985). The size of the circle symbol in the distribution map indicates the log-transformed number of eggs per station.

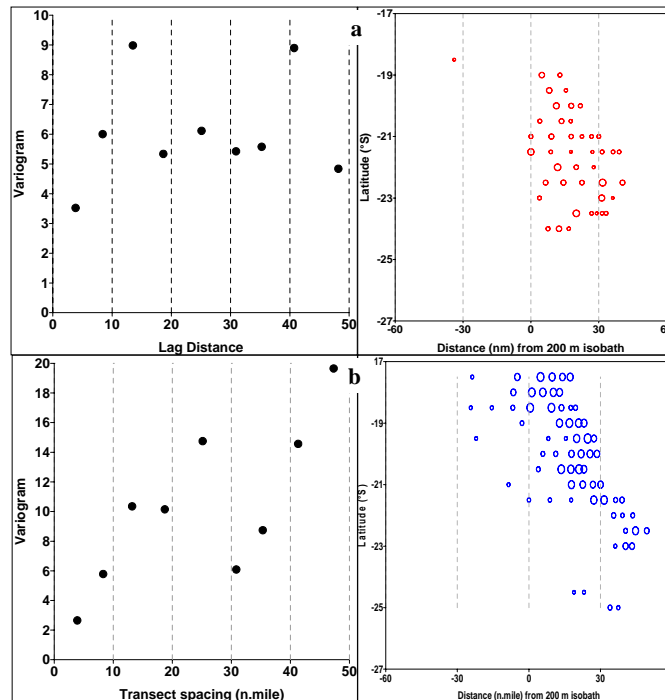


Figure 4.3: Experimental variograms for sardine (a) and anchovy (b) eggs and distributions during February 1985. The size of the circle symbol in the distribution map indicates the log-transformed number of eggs per station.

Movement of centroids

The center of spawning activity of sardine and anchovy was variable along the coast but most of the activity was confined to the area north of 22° 00' S (Figure 4.4 and 4.5). There were some periods when the center of spawning was shifted to south of 22° 00' S. Sardine seemed to shift its spawning center to the south mainly towards the end of a season. Anchovy mostly maintained its spawning center in the area north of 22° 00' S. In more recent years, both species mainly maintained their spawning centers within the area north of 22° 00' S (Figure 4.6), and in 2000 spawning also occurred in the far north, off southern Angola.

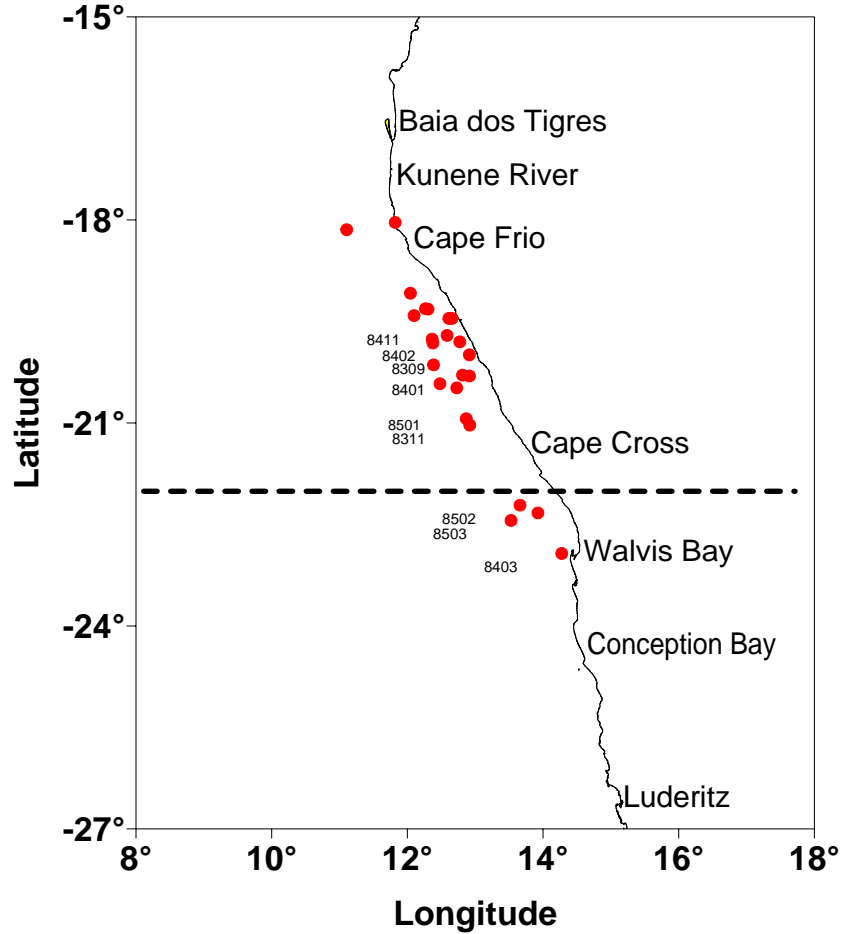


Figure 4.4: Sardine centroids for all the surveys during the SWAPEL surveys. A selected number of surveys are labelled (the first two digits of the number indicate the year and the last two indicate the month) to demonstrate the shift in centroids during the spawning season from 1983 to 1985. The two spawning grounds defined by le Clus (1990) for sardine and anchovy were separated along the 22° 00' S latitude.

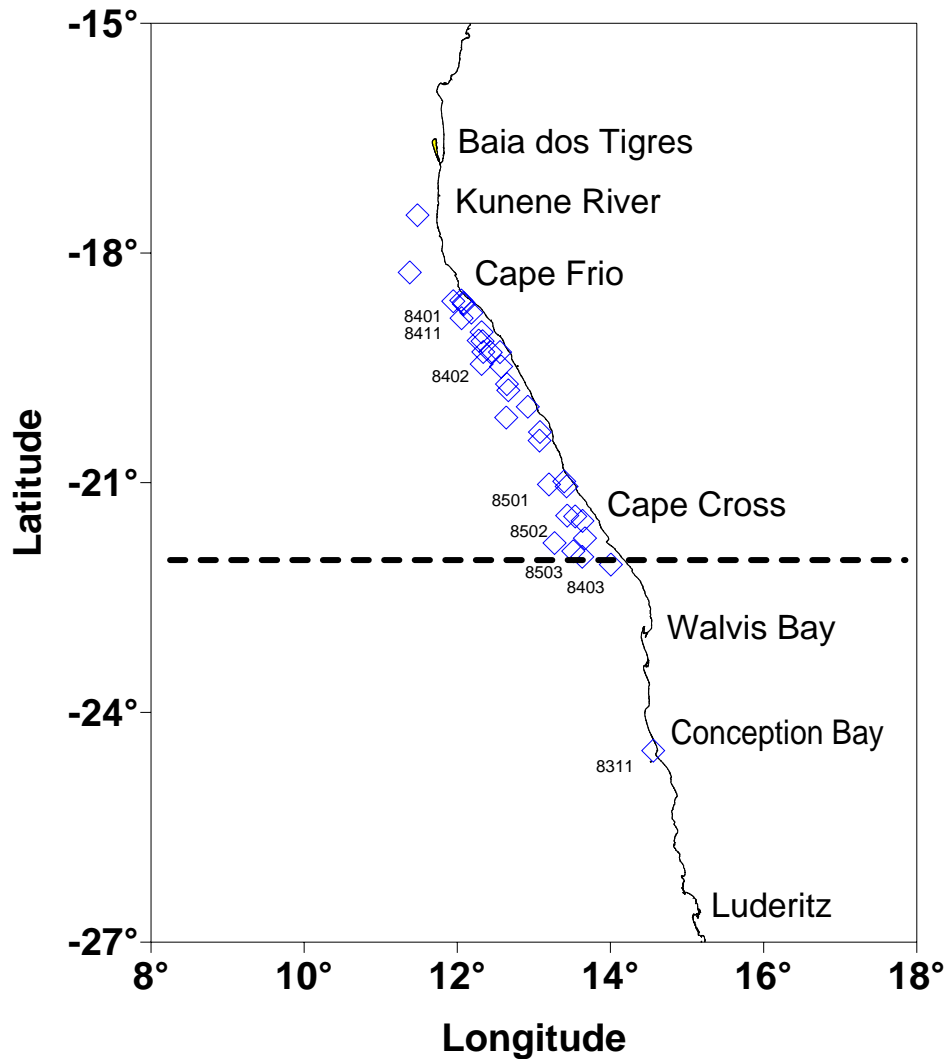


Figure 4.5: Anchovy centroids for all the surveys during the SWAPEL surveys. A selected number of surveys are labelled (the first two digits of the number indicate the year and the last two indicate the month) to demonstrate the shift in centroids during the spawning season from 1983 to 1985. The two spawning grounds defined by le Clus (1990) for sardine and anchovy were separated along the 22° 00' S latitude.

Discussion

The results showed little spatial structure in the distribution of sardine and anchovy eggs. This lack of spatial structure can be attributed to several factors, including the low abundance of eggs observed, the large distances between stations, spawning behaviour of these species, physical processes or combinations of these factors (Curtis 2004). In the context of the northern Benguela region, it seems that the distance between sampling stations was the most significant factor to which the none coherent spatial distribution was attributed to. With wide sampling intervals of about 10 n. miles, many of the egg patches were probably not detected. In order to detect a patch of eggs, the sampling interval should be less than the diameter of the patch to ensure that it is detected at least once (Fletcher and Summer 1999). Barange and Hampton (1997) studied the spatial structure of sardine and anchovy eggs in the southern Benguela using data from acoustic surveys integrated over an interval of 1 n.mile and 5 or 10 n.miles for net hauling. They concluded that anchovy eggs showed greater spatial coherence than did sardine at this sampling scale and argued that the sampling interval was more appropriate for anchovy, which is more structured at a population level, than for sardine. Van der Lingen *et al.* (1998) studied the spatial distribution pattern of sardine eggs at a fine sampling scale of 1.4 n. miles and showed that sardine showed greater spatial structure as distance between samples decreased. Similar findings were also reported in other areas such as off California, where sardine egg distributions showed a smaller nugget effect than anchovy eggs at a fine scale (Curtis 2004).

Sampling at wide ranges gives rise to high variability. The variance increases at sampling ranges that paired the positive egg stations with the negative egg stations outside the egg patches. Alternatively, sampling at wide ranges reduces the variance when negative egg stations are being paired missing the small egg patches (Fletcher and Summer 1999).

Work that has been done on spatial structure of sardine and anchovy in other regions attributed the structured spawning distribution observed to spawning behaviour of these species. No spawning structural patterns were observed in the northern Benguela, where the coarse sampling scale may have influenced the results. However, the distribution of the adults of the two species could influence the distribution of eggs. Sardine, which are known to be larger than anchovy and faster swimmers, show structural patterns at a finer scale than anchovy. The difference is attributed to feeding ecology of these species, with anchovy mainly feeding on large zooplankton by particle-feeding and sardine mainly feeding on small zooplankton and phytoplankton by filter-feeding (van der Lingen 1994). Thus, sardine have to maintain a minimum distance between individuals for feeding, whereas anchovy do not benefit energetically from maintaining a constant school density (Barange *et al.*, 2005).

Historically, two spawning grounds for sardine and anchovy were defined in the northern Benguela to the north and south of 22° 00' S (le Clus 1990). However, both species appear to spawn in the same vicinity, mainly in the northern spawning area. This area could be favoured because elevated plankton concentrations result from the blocking effect on the Benguela of the southward intrusion of Angola Current waters (le Clus

1991). Plankton food is important for early life stage development. The difference in feeding behaviour, which reduces competition between these species, might also enable them to occupy the same area (Barange *et al.*, 2005).

Understanding of spawning behaviour in relation to spawning habitats is important for identifying environmental conditions that influence the variability observed in abundance of these species, for improving management of these resources and for understanding ecosystem health. It is therefore important that further studies be conducted on egg and spawner distributions, using a finer sampling resolution than used in existing data sets, so that the distribution scales of these species can be captured adequately.

Chapter 5. Conclusion

Spawning habitats of sardine and anchovy in other eastern boundary current systems were characterized (Twatwa 2002, Lluch-Belda *et al.*, 1991a) in attempts to understand the fluctuations observed in their abundance. In an attempt to understand the variability in abundance of sardine and anchovy in the northern Benguela, this dissertation characterized the spawning habitats in these species. Historically, the spawning activities of these species were known to be high in periods and vicinities where turbulence is reduced. However, with low abundance of both species observed in recent years it is believed that selection of conditions for spawning may have changed.

This dissertation is formulated to characterize the spawning habitats of sardine and anchovy populations in the northern Benguela in terms of space, time, and the physical and biological attributes of the waters in which the eggs of these fish are collected. The spawning habitats were characterized through a retrospective analysis of egg abundance and distribution data collected during research surveys made off Namibia. The surveys were the South West African pelagic egg and larvae surveys (SWAPELS) and more recent ichthyoplankton surveys conducted by the Dr. Fridtjof Nansen.

The spawning habitats of sardine and anchovy were characterized and compared by using single factor quotient analysis to define the preferred ranges of environmental variables in spawning habitats. Temperature-salinity distribution plots were mapped to explore the spawning distribution of sardine and anchovy in water of different properties. The spatial

and structural patterns of sardine and anchovy spawning distributions were examined by computing centroids (centers of gravity) and plotting experimental variograms.

The focus of this chapter is to synthesize the results of the dissertation and define the spawning habitats of sardine and anchovy in the northern Benguela. It also emphasizes the implication of this study for improving our understanding of the spawning behaviour and the management of these species.

The spawning habitat of sardine and anchovy was characterized with the two species selecting similar conditions. However, some differences were evident in their environmental variable preference. Both species' spawning habitats were characterized by a broad range of temperature, with sardine spawning habitat being also characterized by a broad range of bottom depth, well oxygenated waters and a narrow range of salinity, whereas anchovy spawning habitat was characterized by broad salinity ranges and was confined to low oxygen waters within the shallow areas during the SWAPEL surveys. While anchovy spawning habitat was characterized by specific ranges with respect to all the variables assessed, sardine spawning habitat was characterized by broad range with respect to salinity and oxygen (i.e spawning in different water masses and in low oxygen waters) during the *Nansen* period. Broad ranges of the environmental variables selected seem to be an effective mechanism to maximize survival of the early life stages in these varying environmental conditions that characterize eastern boundary regions. Both species have varied their reference seasonally relative to prevailing environmental

conditions. These species also seems to have changed their preference with changes in their abundance over a longer period.

No coherent spatial structure in egg distributions was found for either of the two species during the SWAPEL surveys. This could mainly be as a result of the survey sampling strategies, which resulted in increased variability at short distance and reduced variability over long distances. The spawning activities of both species was concentrated in the area north of 22° S during both SWAPEL and *Nansen* surveys. Spawning activity in this area is related to high concentrations of food, which is important for early life stage development.

Sardine seems to be better adapted to varying conditions by changing its spawning habitat in order to avoid conditions that may not be beneficial to successful development of the early stages. On the other hand, anchovy has adapted to varying conditions by tolerating a wide range of different conditions, and timing its spawning such that the effect on the development of early stages is minimal. Thus anchovy are more specific than sardine when selecting habitat for spawning, and this implies that anchovy could be more vulnerable to variability in environmental conditions than sardine.

The current low biomass of anchovy and sardine requires careful management to allow populations to increase, in order to improve the chances of successful spawning and development. An increase in anchovy populations could allow anchovy to expand their niche and take advantage of favourable conditions further offshore.

Understanding of spawning behaviour in relation to spawning habitats is important for identifying environmental conditions that influence the variability observed in abundance of these species, for improving management of these resources and for understanding ecosystem health. It is therefore important that further studies be conducted on egg and spawner distributions, using a finer sampling resolution than used in existing data sets, so that the distribution scales of these species can be captured adequately.

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