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**The Surface Dynamics of the Northern Benguela Upwelling System
and its Relationship to Patterns of Clupeoid Production**

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DECLARATION

The analytical and written work contained herein is the sole and original work of the candidate unless acknowledged otherwise.

The research is based upon historical data that was not collected by the candidate. The various data sources can be divided into two categories: those collected and compiled locally, and those collected and/or compiled by overseas agencies. There have been no publications or theses focusing on the Northern Benguela Upwelling region which use the data collected and/or compiled by overseas agencies. The data that was collected and compiled locally formed part of ongoing research programmes in the region. Consequently this data has previously been used for a number of publications and theses. Nevertheless, the way the data has been handled and the emphasis of the analyses in this research are different to earlier studies. The maps of egg and larvae distribution in figures 5.3, 5.4 and 5.5 are the only products which are similar to earlier work. Nonetheless, even here there is an important distinction insofar as these maps were generated by computer interpolation routines rather than by hand.

Throughout this thesis, all the institutions and individuals who provided access to historical data have been fully acknowledged.

ABSTRACT

The environmental dynamics of the northern Benguela upwelling system was investigated primarily using a time series of mean, weekly satellite images of sea surface temperature (SST), and observed trends were related to patterns in the reproductive activity and recruitment success of the region's pilchard and anchovy stocks. Three main methods were used to look at environmental trends: overall and seasonal trends in the system's behaviour were derived from maps of mean SST and SST variability, charts of mean weekly SST per 0.5° latitude were constructed to show spatio-temporal variability in coastal upwelling activity, and standardised principal components analysis was employed to identify the major modes of spatial SST variability and to quantify the evolution of the system's spatial structure through time. Important new findings include the observation that interannual variability itself is largely due to interannual differences in conditions during February, March and April, and that longshore intrusions of warmer water from both ends of the system and onshore intrusions of oceanic water account for a large proportion of the system's temporal variability in spatial structure. Comparisons of clupeoid reproductive activity with environmental trends further confirms that spawning activity and anchovy larvae abundance tend to be greatest when upwelling activity is reduced and conditions are suitable for the retention of eggs and larvae. As regards recruitment variability, pilchard recruitment was found to have a generally positive relationship with SST conditions, whilst anchovy recruitment appeared to be favoured by cooler conditions than pilchard. Different 'domains' in the relationship between the system's spatial structure, as revealed by the principal components analysis, and inshore SSTs were found to correspond closely with differing levels of anchovy and pilchard recruitment between 1982 and 1987. Should these relationships hold when tested over more years, they might, in the future, provide a basis for predicting clupeoid recruitment success in the region.

"My young brother asked forgiveness of the birds: it seemed senseless, yet it is right, for all is like an ocean, all flows and connects; touch it in one place and it echoes at the other end of the world."

from Dostoevsky's 'The Brothers Karamazov'.

CHAPTER 1

Research Aims, Rationale and Global Background

1.1 OVERVIEW OF AIMS AND RATIONALE

The Benguela Current is one of the world's four major eastern boundary currents (Wooster & Reid 1963) and skirts northward along the coasts of western South Africa and Namibia (figures 1.1 & 1.2). The prevailing southerly and south westerly winds which drive the current, are responsible for frequent offshore Ekman transport and the upwelling of cool, nutrient rich water along the coastal edge of the continental shelf. This creates the necessary conditions for a highly productive food chain, which historically has maintained large commercial stocks of demersal and pelagic fish.

Effective management of the small, short-lived pelagic clupeoids, notably pilchard (*Sardinops sagax*) and anchovy (*Engraulis capensis*) has been especially difficult. The problem lies in their large population fluctuations, and the fact that density-independent factors may be equal to, or even more important than fishing pressure and density-dependent factors in driving the fluctuations. Consequently traditional fisheries management techniques based purely on density-dependent assumptions have proved inadequate for the management of these stocks.

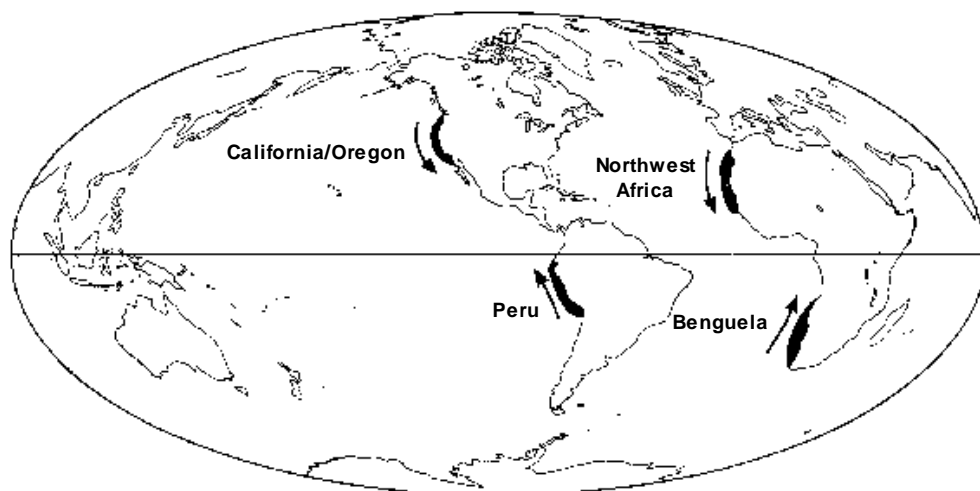


Figure 1.1. Eastern boundary coastal upwelling regions, adapted from Mann & Lazier (1991). Arrows indicate prevailing winds.

Despite conjecture as to the role of environmental variability in driving stock size fluctuations, since the beginning of this century, non-experimental investigations in the past have always been heavily constrained by poor data quality and limited quantity. However, two important developments in the last fifteen to twenty years have gone a long way to redressing the problems as regards environmental data; namely routine maritime remote sensing from satellites, and the compilation of global datasets on oceanic conditions from international shipping reports.

The purpose of this thesis is to investigate the oceanographic dynamics of the northern Benguela upwelling region, primarily using a time series of satellite images, and to relate observed environmental trends to existing information on the population dynamics and reproductive ecology of anchovy and pilchard stocks in the region. The ultimate goal being the identification of predictable environmental-fisheries interactions which in turn would enable the development of clupeoid management models for the region with environmental (i.e. density-independent) inputs.

The first two chapters will provide the background information relevant to the thrust of the research, and together act as an extended rationale and a summary of current knowledge. This chapter focuses on 'global' considerations whilst chapter 2 deals specifically with the northern Benguela region.

1.2 COASTAL UPWELLING: MECHANISM

Upwelling is said to occur whenever sub-surface water ascends to the surface. Biologically it is important because often it brings fresh supplies of nutrients into the sunlit surface layers, and so fuels the food chain by inducing high levels of phytoplankton production. The main areas of permanent upwelling include the equatorial Pacific, the Antarctic divergence zone at 70° S, and coastal regions along the eastern boundaries of the Atlantic and Pacific Oceans (figure 1.2). These areas are all characterised by high levels of biological productivity and can support large populations of fish, seabirds and marine mammals. (Mann & Lazier 1991; Lalli & Parsons 1993).

Coastal upwelling in eastern boundary regions is driven by the equatorward winds which prevail along their coasts (figure 1.2). The action of these winds on the sea surface is initially to induce along-shore surface flow. The Coriolis effect¹ then causes

¹ The Coriolis effect results from the Earth spinning on its axis, and accounts for why relative to the surface of the Earth a moving body of water swings to the right in the northern hemisphere and to the left in the southern hemisphere.

this flow to become progressively deflected offshore, and in order to replace the water which is being swept offshore, deeper water from over the continental shelf is brought to the surface along the coast. Typically this upwelled water comes from below the thermocline, and so on reaching the surface is very much colder and richer in nutrients than the surrounding surface oceanic water.

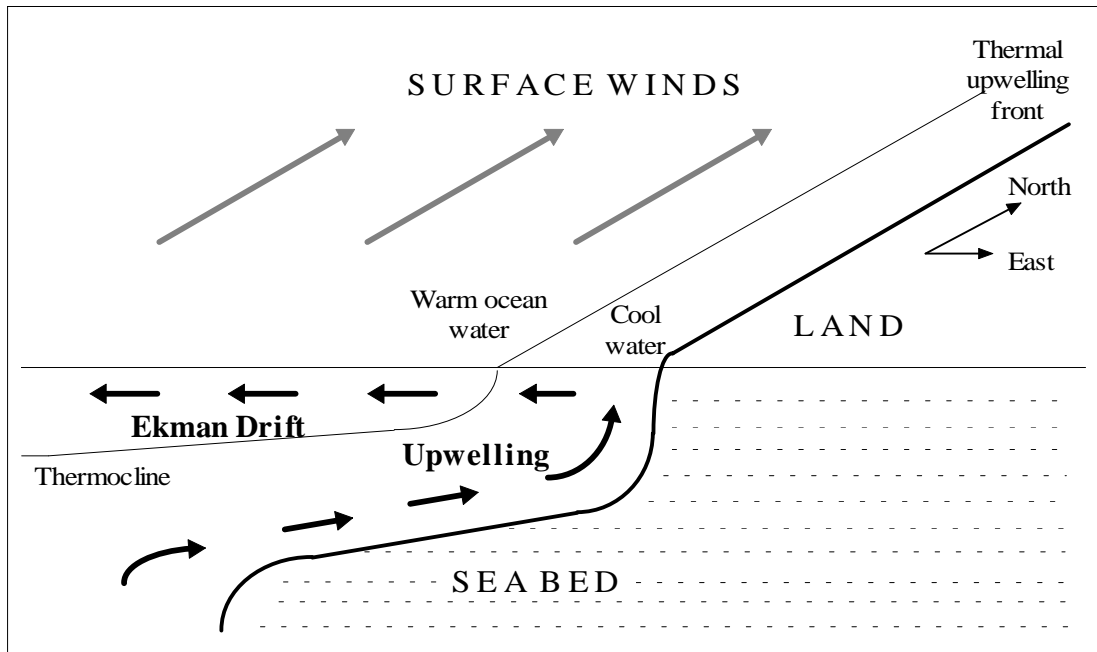


Figure 1.3. Schematic representation of eastern boundary coastal upwelling in the southern hemisphere, adapted from Mann & Lazier (1991).

Ekman theory addresses the balance of forces between wind drag, water movement and the Coriolis effect (see Mann & Lazier 1991 for a full discussion). The net flow of water within the layer affected by wind forcing, the Ekman layer, is at 90° to the direction of the wind; 90° to the right in the northern hemisphere, and 90° to the left in the southern hemisphere. The term given to this net flow is 'Ekman drift'. For the southern hemisphere figure 1.3 illustrates the general relationship between wind forcing, Ekman drift and coastal upwelling, including the presence of a thermal front between the cool upwelled water and the warmer surface oceanic water.

The mass (or volume) of water carried offshore per unit time and per unit length of coastline due to Ekman drift is termed Ekman transport, and can be estimated from the alongshore wind stress and a parameter for the Coriolis effect. Given that upwelling intensity will be proportional to the rate at which water is swept offshore, Ekman transport has often been used as an index of coastal upwelling activity (e.g. Bakun 1987).

In reality the behaviour of these coastal systems is a great deal more complex than indicated in figure 1.3. Fluctuations in the strength of upwelling favourable winds, changes in bathymetry along a coastline, dynamic instabilities in the flow of currents and remotely forced processes such as coastally trapped waves and warm water intrusions, can cause a high degree of spatial and temporal variability in upwelling activity. As a consequence the frontal region is almost never smooth, and is typically characterised by a complex pattern of eddies and filaments between the warm oceanic surface water and the cooler upwelled water as it is forced offshore.

Oscillations in the atmospheric pressure fields over the equatorial Pacific and Atlantic Oceans are important sources of interannual upwelling variability (Longhurst & Pauly 1987; Hisard 1986). During years in which these oscillations cause a weakening or reversal in the usual east to west flow of the equatorial trade winds these eastern boundary regions experience unusually warm conditions; known as el Niño's in the Pacific and Benguela Niño's in the Atlantic (Shannon *et al.* 1986). Typically they occur with periodicities of between 3 and 10 years and are characterised by intrusions of warmer water masses from the edges of the system, a deepening of the thermocline and subsequent reductions in the upwelling of cool nutrient rich water from below the thermocline. The biological impact of these events can be dramatic, and are associated with greatly reduced levels of productivity and the invasion of biota from neighbouring regions (Valdivia 1978; Boyd *et al.* 1985).

1.3 COASTAL UPWELLING: ECOSYSTEMS

Physical-biological interactions in the oceans and the scales at which they occur have in the last twenty years become an area of increasing theoretical and research interest. (Legendre & Demers 1984; Mann & Lazier 1991; Mann 1993). Marine ecosystems in general display tighter coupling between physical and biological processes than their terrestrial counterparts. Nowhere is this coupling more evident than in coastal upwelling systems, where the high levels of physical stress imposed by the degree and variability to which they are forced places important constraints on the types of marine life that they contain and the functioning of their ecosystems.

Upwelling ecosystems are all characterised by high biomasses, high productivities, low biodiversity, and a low number of trophic exchanges between primary production and fish production (Ryther 1969). The species composition and trophic organisation of one coastal upwelling region to another is very similar, and for the pelagic layer is generally much as illustrated in figure 1.4. The organisation of the mesopelagic and

demersal layers also tends to be very similar between systems, and in terms of commercially exploited fish they are often dominated by large populations of hake and horse mackerel (jack mackerel).

The high productivities and biomasses found throughout these ecosystems result from high levels of primary production, which in turn are a direct consequence of the injection of large supplies of nutrients into the sunlit surface layers during active upwelling. The number of trophic exchanges between primary production and fish production are low, in comparison to other marine systems, due to high nutrient concentrations and high levels of turbulence favouring phytoplankton which are large enough to be fed on directly by macrozooplankton and small fish.

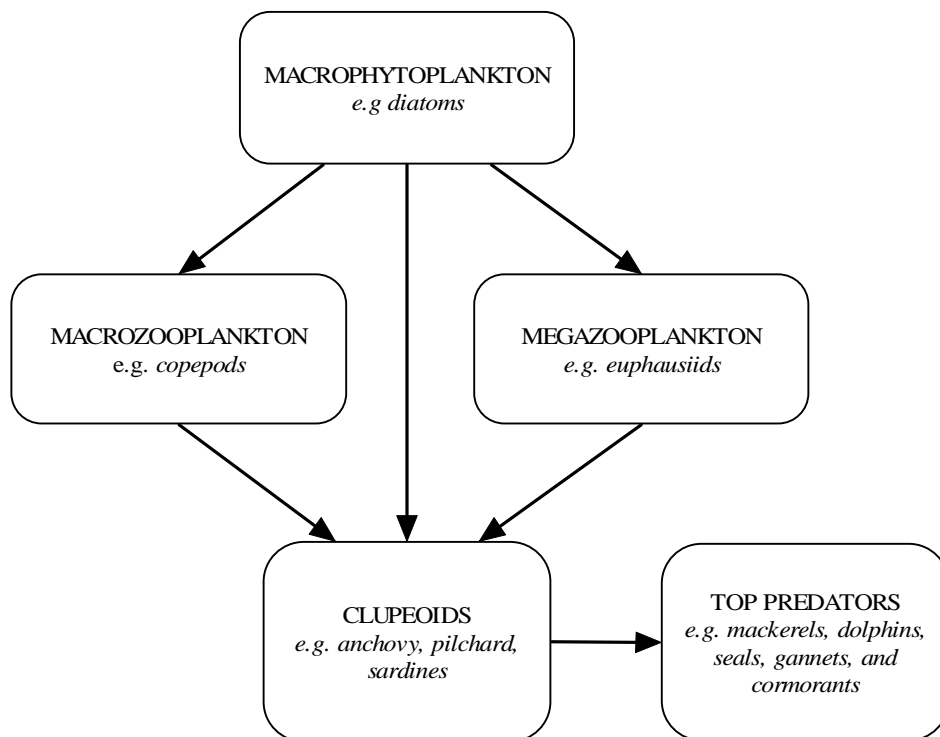


Figure 1.4. Major pelagic feeding relationships in an eastern boundary current upwelling system.

The low number of trophic exchanges between phytoplankton and fish have two consequences. Firstly, given the large losses associated with the transfer of energy between different trophic levels, a greater proportion of total primary production may become assimilated into fish biomass in upwelling regions than in other marine ecosystems. Secondly, they facilitate the propagation of environmental variability throughout the food web. High levels of spatial and temporal variability between upwelling activity, in which nutrients are injected into the photic zone, and calmer

conditions, as characterised by a stratified water column, are often reflected in equally variable patterns in primary production (e.g. Shannon & Pillar 1986). The small number of trophic exchanges will, to some degree, contribute to this variability in primary production having a relatively rapid knock-on effect throughout the food web (e.g. Branch *et al.* 1987). It is worth noting, however, that a more fundamental reason for this rapid propagation of variability results from upwelling ecosystems having very low levels of internal energy and material recycling, which in turn means they have little internal buffering against environmentally driven fluctuations in primary production (Baird *et al.* 1991).

The low biodiversity of these coastal upwelling systems may also be understood in terms their high levels of physical stress. In classical community ecology the magnitude, frequency and predictability of physical disturbances (i.e. physical stress) has long been considered important in influencing species richness (MacArthur 1975, Connell 1978). For instance, according to Connell's 'intermediate disturbance hypothesis' (Connell 1978) biodiversity will be maximised at intermediate levels of environmental disturbance, and minimised at both high and low levels of disturbance. The rationale being that systems with high levels of stress, such as coastal upwelling regions, only favour a few opportunistic species which can respond quickly after environmental setbacks, whilst systems with low levels of stress enable the development of climax communities in which competitive exclusion eventually limits species richness. (Systems with intermediate levels of disturbance thus favour biodiversity by allowing for the co-existence of both colonising and climax species, and by short-circuiting competitive exclusion).

1.4 CLUPEOIDS AND THE ENVIRONMENT

"...fish populations are neither self-determined, nor 'equilibrium seeking' entities, but rather that populations operate in response to short-term consequences of a cascading series of climate driven, oceanographic and ecological processes".
Sharp (1987)

Fish populations are regulated by a complex array of biotic and abiotic factors which operate across a wide spectrum of different scales, life history strategies and levels of causality. Increasingly, the view being held by fisheries experts is that variations in climatic forcing underpin natural² fluctuations in fish populations in terms of their

² i.e. not resulting from human activities.

biomass, recruitment³ success, and distribution (e.g. Crawford *et al.* 1991; Sharp 1987; Sharp 1995; Mann 1993; Bakun 1993). The establishment of the Large Marine Ecosystem (LME) concept (Sherman 1991) and global research programmes, such as the Climate and Eastern Ocean Systems (CEOS) project (Bakun *et al.* 1992), have now paved the way for current and future research into the behaviour of fish stocks to be conducted within their full physical, ecological and socio-economic contexts.

Clupeoid fishes are found in pelagic environments throughout the world's oceans. Species of sardine, pilchard, anchovy and herring form the largest stocks and are usually found in productive waters associated with upwelling areas, shallow continental shelves, and bays & estuaries. The relative ease with which they may be caught by purse seiners, due to their schooling behaviour, combined with the enormous biomasses reached by some populations has made them important economic resources. At the peak of the massive Peruvian anchoveta fishery in the early 1970's, clupeoids contributed roughly a third of total world annual catches, which at the time were in the region of 65 million tonnes. Except for the Atlantic herring, clupeoids tend to be short lived, rarely living beyond 5-10 years, and typically recruit to the adult stock between 1 and 3 years of age. (see Blaxter & Hunter 1982 for a thorough review of clupeoid biology and ecology).

Since the 1970s it has been recognised that density-independent environmental factors are more important in regulating clupeoid populations on a year to year basis than density-dependent factors (Cushing 1971, as cited by Blaxter & Hunter 1982). The main reason being that the small number of age classes allow environmentally driven fluctuations in recruitment success to translate rapidly into biomass fluctuations. Understanding the links between the environment and population dynamics of these species has become a research priority ever since the dramatic collapse of the Peruvian anchoveta fishery in the early 1970s due to a combination of over-fishing and adverse environmental conditions. The motivation is straightforward; namely the prevention of future collapses by the development of management techniques which take environmental conditions into consideration.

The rest of this section will take a broad look at the way in which the environment may influence clupeoid populations. The problems involved in managing these species, and the ways in which physical conditions determine reproductive success, according to the differential mortality of the planktonic early life-history stages, will be addressed in greater detail in the following two sections.

³ Throughout this thesis recruitment success is defined as the total number of new fish which become available to the fishing fleet each year.

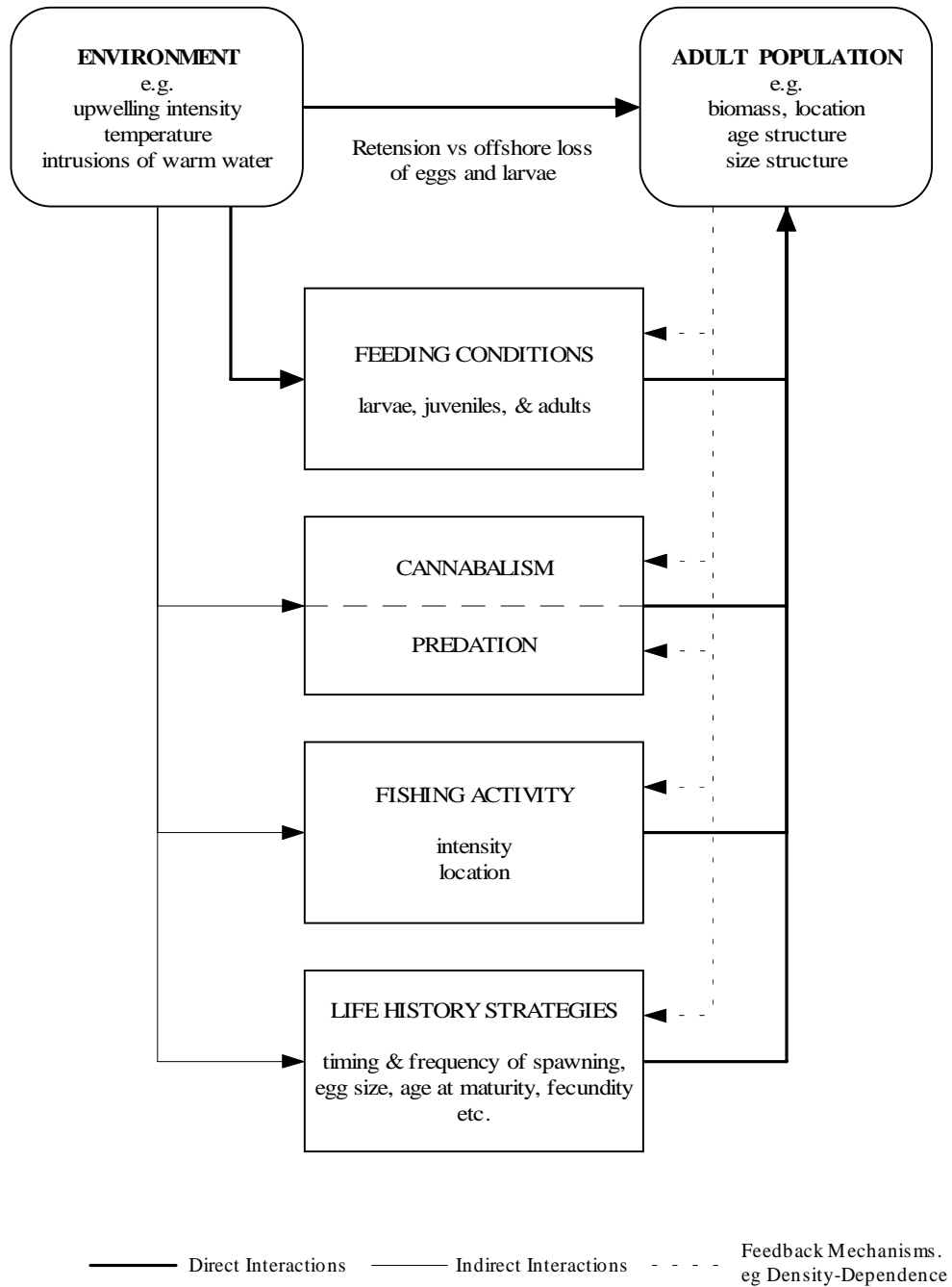


Figure 1.5. How environmental conditions can impact clupeoid populations in upwelling regions. See text for more details.

Figure 1.5 illustrates the different ways in which environmental conditions may influence clupeoid populations in coastal upwelling regions. Offshore transport and levels of nutrient enrichment can directly affect recruitment success by influencing the survival and mortality of the vulnerable planktonic early life-history stages, (see figure 1.6). For instance offshore transport and surface currents control whether the eggs and

larvae are advected towards or away from suitable nursery areas (e.g. Parrish *et al.* 1983), whilst levels of nutrient enrichment and turbulent mixing in the water column determine the suitability of feeding conditions for the larvae (Rothschild *et al.* 1989).

The distribution of the adult population may also be directly influenced by the environment according to temperature preferences and feeding conditions. For example, during warm events anchovy and sardine stocks often contract to small areas adjacent to the coast where some localised upwelling is maintained (Longhurst & Pauly 1987; Thomas & Boyd 1985).

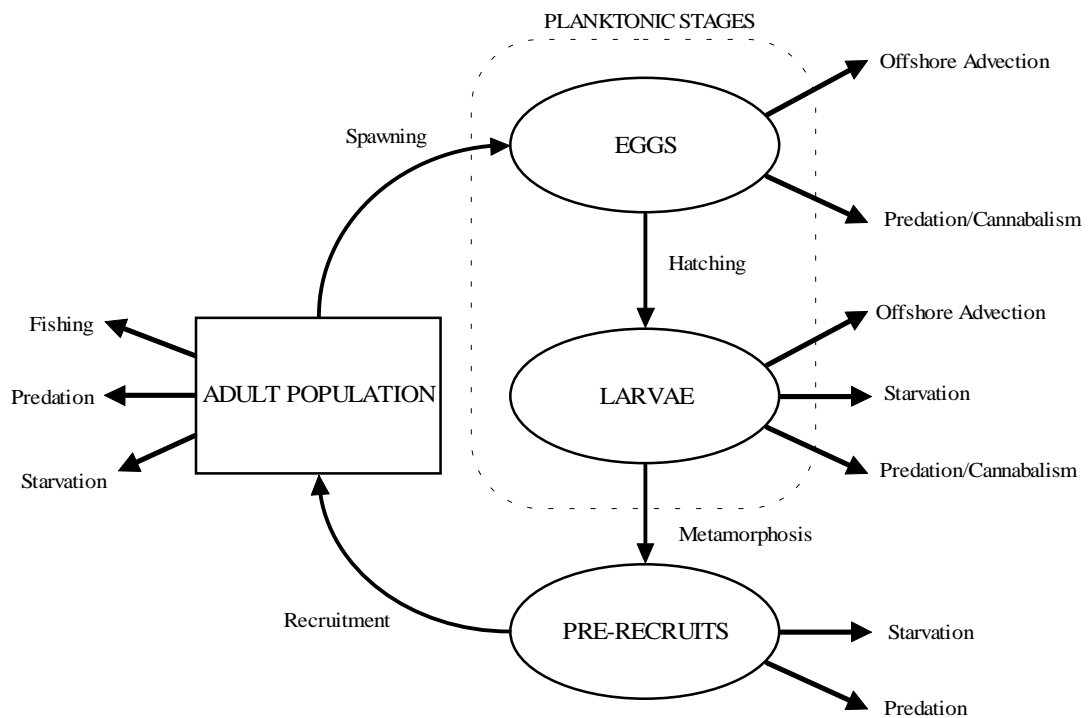


Figure 1.6. Generalised clupeoid life-cycle and major sources of mortality.

Insofar as environmental conditions can directly affect the distribution of adults and predators they can also indirectly influence juvenile and adult mortality via cannibalism, predation and fishing pressure. For example, the extent to which adult horse mackerel (*Trachurus murphyi*) feed on anchoveta in the Peruvian system is related to upwelling conditions and sea surface temperatures. Under normal upwelling conditions, the ranges of the two species do not overlap, but when there is warming, either in summer or due to an el Niño event, the horse mackerel move shoreward where they can feed on the anchoveta (Muck & Sanchez 1987; Muck 1989). Likewise contraction of clupeoid stocks into dense coastal concentrations during warm events not only makes them easier targets for fisherman, thus causing higher catches per unit effort (e.g. Thomas &

Boyd 1985), but may also result in increased competition for food and higher levels of cannibalism of eggs and larvae.

From an evolutionary perspective, the interaction between environmental conditions and reproductive success plays an important role in shaping the life-history strategies of these species. Pilchard, sardine and anchovy species in coastal upwelling regions all display similar life-history traits, such as serial spawning and early maturity, which allow 'bet-hedging' solutions (Stearns 1976) to the unpredictable survival of their early life-history stages. In other words, by maturing early and spreading their spawning activity over much of the year they greatly increase their chances of hitting a sequence of environmental events favourable to the survival and growth of the early life-history stages. Furthermore, evidence from simulation models have shown that herrings, sardines, and anchovies each have reproductive strategies which are best geared to breeding under differing temporal regimes of environmental variability (Armstrong & Shelton 1990), and that in reality we might expect to see a correspondence between the predominate spectra of environmental variability (i.e. weekly, seasonal, or interannual) in a particular region and the dominant clupeoid species .

The role that environmental variability is thought to play in driving fluctuations in clupeoid recruitment success and biomass is substantiated by the existence of good relationships between these fluctuations and various environmental indices, both at regional (e.g. Shannon *et al.* 1988; Cury & Roy 1989) and trans-oceanic scales (e.g. Kawasaki & Omori 1988; Lluch-Belda *et al.* 1989). Furthermore, long-term temperature records indicate that physical conditions may also play an important role in mediating the dominance of anchovy versus sardine/pilchard populations. For instance in the eastern Pacific, the relative dominance of anchovies versus sardines appears to be related to inter-decadal trends in temperature conditions (Sharp & McLain 1993); during warm periods with reduced upwelling, sardines tend to dominate, whereas during cool periods with enhanced upwelling anchovies dominate.

Since the end of the second world war fishing pressure has also had tremendous impact on the population dynamics of these species, and has often made it difficult for fisheries scientists to distinguish between the relative importance of fishing versus non-fishing related factors in driving population fluctuations. Nonetheless independent evidence for large natural variations in population size prior to the onset of industrialised fishing is provided by long-term records of guano harvests and by the relative abundance of clupeoid scales at different strata in coastal sediments (e.g. Souter & Isaacs 1974; DeVries & Percy 1982; Shackleton 1986; Crawford *et al.*

1987). The latter also confirms reversals in the relative dominance of anchovy and sardine/pilchard populations prior to the onset of heavy industrial fishing.

Whilst density-independent factors may be primarily responsible for driving the year to year population dynamics and distribution of clupeoids, density-dependent processes may also have some regulatory role, and are particularly likely to come into play after favourable environmental conditions have caused population booms. For instance, Kawasaki & Omori (1995) provide evidence for the far-eastern (i.e. Japanese) sardine population being regulated by both density-independent and density-dependent processes depending on what 'phase' the population was in. They argue that good environmental conditions may be what trigger population explosions when the population is small and located in coastal waters. Whereas, when the population is large and distributed in less productive oceanic waters, density-dependent competition for food between the adults leads to poor quality eggs which in turn leads to poor recruitment and population decline. In a similar fashion predation and cannibalism of eggs and larvae have been proposed as density-dependent mechanisms providing an upper limit to clupeoid population size off South Africa (Valdés *et al.* 1987).

1.5 THE MANAGEMENT PROBLEM

The history of the major clupeoid fisheries throughout the latter part of this century has been one of 'boom and bust' with sharp increases in catches often being followed by dramatic stock collapses. The collapse of the Californian sardine in the 1950s was the first to occur in a coastal upwelling system and was followed by the South African pilchard in the 1960s, the Namibian pilchard in the late 1960s and the Peruvian anchoveta in the early 1970s.

These trends are part of a wider decline in global fish stocks as a consequence over-fishing. Nearly all of the 200 fisheries monitored by the Food and Agriculture Organisation (FAO) are fully exploited and a third are either classified as 'depleted' or 'heavily over-exploited' (Anon 1994). Many separate factors are to blame, but essentially they fall into one of three categories; namely, the need to feed an ever increasing global population, technological advances in the ability to detect and catch fish, and the fact that unregulated fishing was the norm until the declaration of the first 200 nautical mile Exclusive Economic Zones (EEZs) in 1977.

Attempts have been made at managing fisheries since the first half of this century when it became apparent that the efficacy of industrialised fishing could lead to stock depletion (Cushing 1988). Despite some local successes, the current global situation

could, however, hardly be hailed as a triumph for management. Again there are many reasons, most of which boil down to a lack of political will, problems with the enforcement of fishery regulations, and in some instances scientific uncertainty as to the current status of fish stocks.

Political recognition of the need for management typically follows crises. Whilst this is by no means too late, it does mean that in order to implement the measures necessary for stocks to recover, even tougher political decisions need to be made than would have been the case had there been sufficient intervention at the first signs of over-fishing. All too often, however, the demands of management come second to other considerations; even after stocks have declined. An extreme example being the subsidies paid by European governments to their already over-expanded fishing fleets. Nonetheless there are also some good signs; notably with regards to individual states taking control of their own fish stocks via the establishment of 200 nm EEZs, the successful implementation of property-rights based fisheries management systems in countries like Iceland, New Zealand and Australia (Arnason 1993), and the increased, sometimes headline making, enforcement of fishing regulations.

Leaving the various human and political problems aside, the sustainable management of clupeoid stocks in upwelling regions poses a particular challenge to fisheries scientists. Large, natural population fluctuations, due to high levels of environmentally-driven recruitment success coupled with their short life spans, is a difficult backdrop against which to make management decisions. Most managers currently have no way of reliably predicting recruitment success, and what may be a conservative level of exploitation during years with good recruitment may prove disastrous in years with poor recruitment. The problem is exacerbated by over-fishing which via a reduction in the number of age classes in a population further increases its susceptibility to recruitment variability, and ultimately stock collapse if the number of age-classes becomes so reduced that the population is unable to bridge a string of years with poor recruitment success (e.g. Butterworth 1983).

Traditional fisheries management techniques for estimating sustainable yields and population size from catch statistics have proved to be of little worth. For instance the Schaefer surplus production model used in the Peruvian anchoveta fishery (Pitcher & Hart 1982) and the virtual population analysis (VPA) estimates of 'current biomass' used for the Namibian pilchard (Butterworth 1980) both failed to register substantial stock declines whilst the populations were in a state of collapse. These techniques were originally developed for long-lived ground fish with high levels of density-dependent population regulation, and as it turned out the assumptions from which they

worked proved inappropriate when applied to heavily exploited clupeoid populations. (See McGlade & Shepherd (1992) for a global overview of stock assessment methods and problems).

In the case of surplus production models the problems lies with their assumption of a 'steady-state' population primarily regulated by density-dependent interactions. Whereas for current biomass estimates from VPA the problems rests with the estimation of 'current year fishing mortality' using fishing effort as a scalar. Fishing mortality has typically been assumed to be linearly proportional to effort, which in turn assumes a homogenous distribution of fish and randomly directed fishing effort; assumptions which are a quite wrong for clupeoid fisheries. In reality the fact that clupeoids are tightly shoaling and that purse-seiners do not operate randomly leads to Palheimo-Dickie effects (Palheimo & Dickie 1964, as cited by Butterfield 1980), in which catch rates do not fall as quickly as stock size. Hence, during periods of stock decline, the use of fishing effort as a linear scalar can underestimate fishing mortality, and consequently overestimate stock size. Moreover, difficulties in quantifying these Palheimo-Dickie effects has precluded their incorporation into management models which utilise catch statistics.

There have been two responses to these problems with traditional techniques. The first is an increased reliance on direct surveys for estimates of current biomass prior to quota setting. Hydro-acoustic surveys are now the most widely used, although biomass estimates have also been derived from egg counts using to the egg-production method (e.g. Butterworth 1983; Hampton *et al.* 1990; Hampton 1992). The second, as touched on in the previous section, is an increase in the research effort directed at uncovering how environmental factors influence the population dynamics of these fish, particularly as regards driving recruitment variability.

Reliable forecasts of year class strength based on a clear understanding of the relationship between environmental conditions and recruitment success would be of great benefit in managing these volatile stocks. Not only would they improve the confidence with which fisheries managers could set quotas, but higher average catches resulting from the use of environmentally-sensitive management models also would benefit the fishing industry, (e.g. Cochrane & Starfield 1992). The next section will take a closer look at some of the mechanisms whereby environmental conditions may influence recruitment, and will discuss reasons why to date there has been a more or less universal failure in the actual prediction of recruitment success.

1.6 RECRUITMENT VARIABILITY

Recruitment variability is a characteristic feature of all marine organisms with planktonic life history stages. Marine ecologists started to be interested in recruitment during the late 1970s and early 1980s when it became apparent that many benthic and demersal communities were not the steady state equilibrium systems that had previously been assumed (Sale 1990), and that instead their organisation seemed to be largely determined by the recruitment variability of their constituent components (e.g. Roughgarden *et al.* 1984, Connell 1985, Caffrey 1985, Underwood & Fairweather 1989).

Fisheries biologists, however, have been aware of the potential importance of recruitment variability in influencing the population dynamics of fish stocks for much longer (e.g. Hjort 1914). Nonetheless fisheries management has until comparatively recently ignored this (e.g. see Allen & McGlade 1987), usually by assuming averaged relationships between stock size and recruitment. It is only in the last two decades that the issue of recruitment variability has come to be taken more seriously; largely as a consequence of the widespread increase in recruitment over fishing and incidences of stock collapse.

Recruitment success can be thought of as an integrated function of processes acting across a wide range of life-history stages, from the size and condition of the spawning population at one end to pre-recruit survival rates at the other. Although rudimentary stock-recruit relationships do exist for clupeoids (Lasker 1985), variable mortality of the vulnerable planktonic eggs and larvae is usually thought to be the main cause of year to year recruitment variability.

Theories of how recruitment success is influenced by the survival of these early life-history stages fall into two broad categories, as illustrated in figure 1.7: 'mechanistic theories' which deal with specific sources of egg and larval mortality, and 'synthesis theories' which attempt to unite the various mechanistic theories within a larger framework. Mechanistic theories can in turn be divided into three further categories: predation-cannibalism based, starvation based, and advection based (Hutchings 1992).

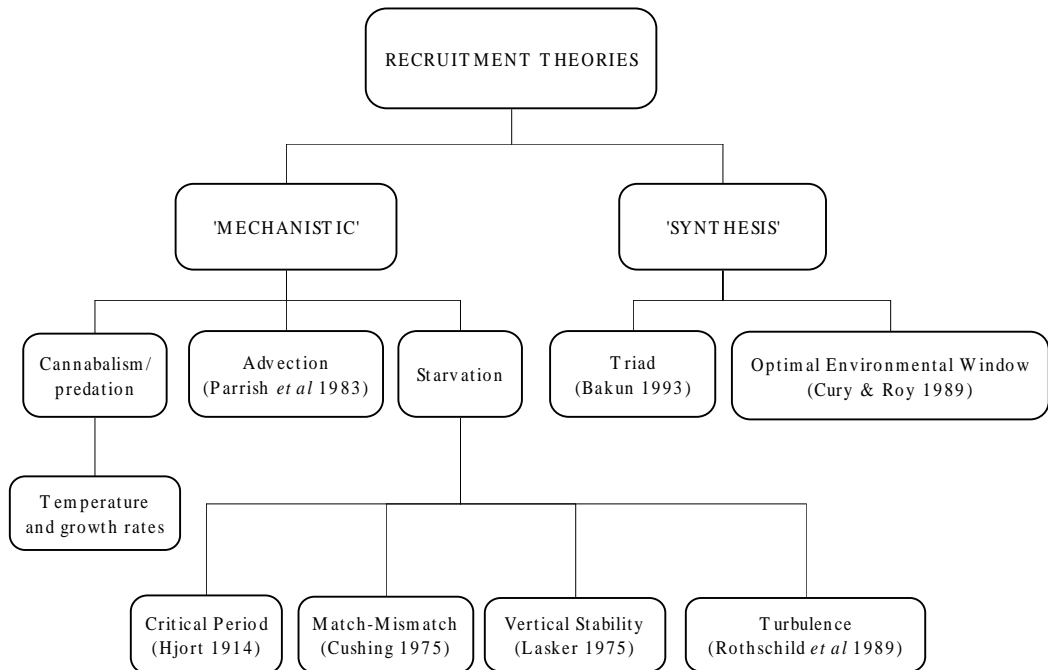


Figure 1.7. A classification of theories which address the causes of variable recruitment success in pelagic fish as a result of the differential mortality of the early life-history stages.

1.6.1 Mechanistic Theories

Starvation theories are based on the premise that if larvae do not encounter sufficient quantities of food after yolk-sac absorption they will die (Blaxter & Hunter 1982). Hjort's 'critical period' hypothesis was the first to work from this supposition, and prescribed the need for suitable food during the 'critical' transition between internal and external sources of energy, i.e. soon after yolk sac absorption, for successful recruitment (Hjort 1914, as cited by Pitcher & Hart 1982). Exactly what is the most 'critical' stage of larval development, in terms of final recruitment success, remains a matter of speculation, although for marine fisheries in general there is increasing evidence it is the later larval stages, and not the first-feeding stages, which are the most 'critical' (Cushing 1996). Nonetheless, the underlying premise of larval starvation has been expanded upon by a number of more modern theories.

Cushing's match-mismatch theory (Cushing 1975; Cushing 1996) developed from observations on fish stocks in the north-east Atlantic and North Sea, and concerns the timing of reproductive cycles with local productivity cycles, particularly with regards to larval development. The contention being that the greater the overlap between peak larval abundance and peak productivity the more larvae that will survive to

metamorphosis. Lasker's stability hypothesis was specifically tailored for pelagic fish in upwelling regions and prescribed the need for upwelling activity to be balanced by sufficiently calm conditions so that thermoclines and maximum chlorophyll layers (MCL) could form. The argument being that only in these MCLs would food concentrations, especially of dinoflagellates, be high enough to enable successful larval feeding (Lasker 1975, 1978). Finally, turbulence has also been hypothesised as mediating the feeding success of fish larvae according to its influence on encounter rates between larvae and food particles (Rothschild *et al.* 1989; Rothschild 1991).

'Advection' based theories concern themselves with the transport of eggs and larvae towards or away from suitable nursery areas (e.g. Iles & Sinclair 1982). They are of special concern in coastal upwelling regions due to the large offshore movement of water associated with Ekman drift. Comparative studies of these regions have shown that clupeoids tend to avoid spawning in areas and at times with strong upwelling when there would be a high risk of eggs and larvae being transported into unproductive oceanic waters (Parrish *et al.* 1983).

In practice, starvation and advection-based theories both prescribe similar environmental conditions for recruitment success in these regions; namely quiescent upwelling conditions to prevent the offshore loss of eggs and larvae, and to allow the development of chlorophyll maximum layers for successful larval feeding. Nonetheless it is important that calm periods are balanced with sufficient levels of upwelling. Poor recruitment has often occurred during warm events due to impoverished feeding conditions resulting from the suppressed upwelling of nutrient-rich water (e.g. Valdivia 1978; Boyd *et al.* 1985; Le Clus 1985).

Predation and cannibalism are also important sources of egg and larval mortality, and have received some attention as density-dependent mechanisms for maintaining the dominance of one clupeoid species over another and in placing upper limits on population size (e.g. Valdés *et al.* 1987; Valdés Szeinfeld & Cochrane 1992). As regards year to year recruitment variability, however, problems in quantifying their impact makes it difficult to assess whether these processes do in fact differ enough between years to explain this variability. Furthermore, even these 'density-dependent' sources of mortality are far from independent of environmental factors. Temperature is likely to be of particular importance insofar as it affects egg hatching and larval development rates. For instance, given that susceptibility to predation amongst marine organisms is largely size dependent, one would expect higher temperatures to promote the survival of early life history stages by inducing quick hatching and increasing the rate at which fish larvae can outgrow their predators (Laurence 1990).

1.6.2 Synthesis Theories

None of the mechanisms described above will be the sole process determining recruitment success in any particular system. For instance in an upwelling system, advective processes, vertical stability of the water column, temperature, food production and turbulence are all likely to some extent or another to be involved in influencing recruitment success according to the feeding, growth and retention of the early life-history stages. For this reason synthesis theories have been developed which attempt to bring the various mechanistic theories together within a single conceptual framework.

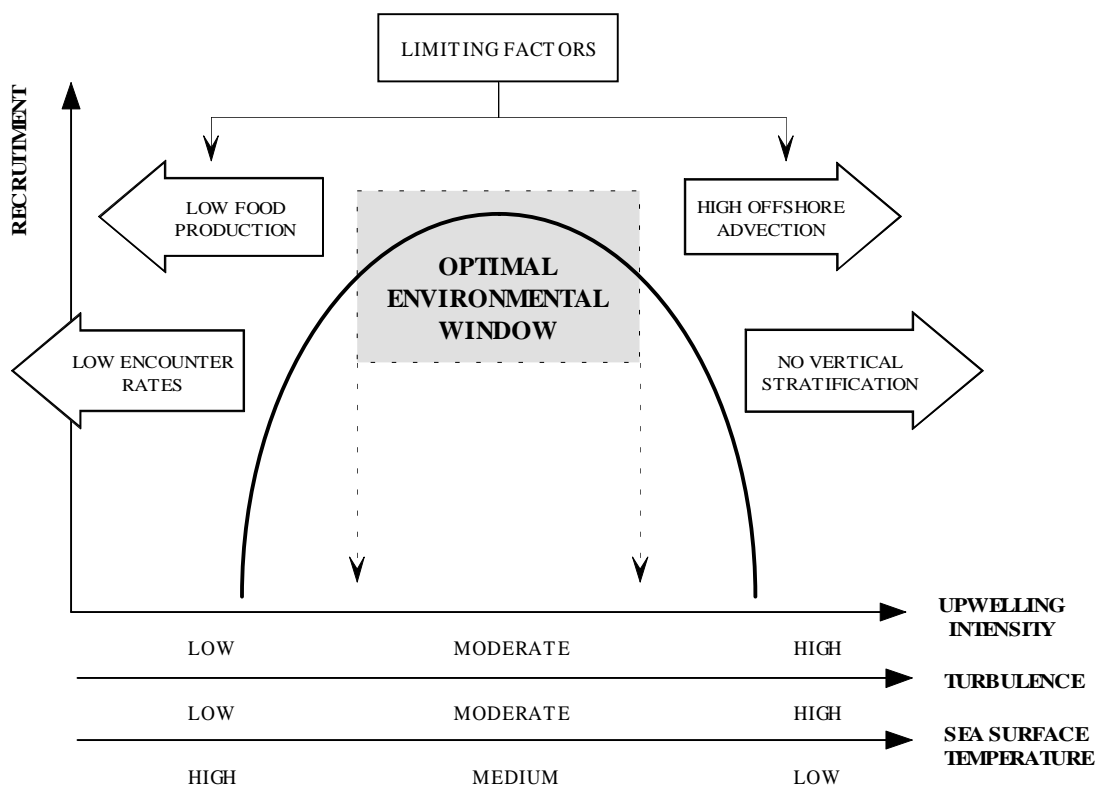


Figure 1.8. Schematic representation of the Optimal Environmental Window theory of clupeoid recruitment success in coastal upwelling regions. Adapted from Cury & Roy (1989).

The Optimal Environmental Window (OEW) theory stresses the importance of attaining a sufficient balance between the upwelling of nutrient rich water and calm conditions for encouraging successful clupeoid recruitment (Cury & Roy 1989; Roy *et al.* 1995), as illustrated by figure 1.8. It has been successfully tested on clupeoid populations off California, Peru and north-west Africa where it was found that recruitment success was maximised at intermediate levels of Ekman transport and

turbulence. The argument being that at low levels of upwelling and turbulence there is neither sufficient primary productivity nor high enough encounter rates between larvae and prey to enable successful larval feeding, whilst at high levels eggs and larvae are swept offshore, and the lack of any vertical stratification prevents the formation of maximum chlorophyll layers.

Bakun's Triad Hypothesis (Bakun 1993) generalises three broad categories of oceanographic process thought to be important in influencing recruitment success; namely *enrichment* of the food chain, *retention* of the eggs and larvae within suitable nursery areas, and *concentration* of food particles for the first-feeding larvae and subsequent developmental stages. Within a coastal upwelling system enrichment will result from the upwelling of nutrient-rich water from below the pycnocline; retention from a reduction in offshore transport and the advection of other water masses into the system; and concentration according to the formation of thermoclines and presence of fronts where food particles can be concentrated. Given that the physical conditions leading to enrichment versus retention and concentration are often mutually exclusive, it is recognised that the spatio-temporal variability in the physics of these systems will be important in determining whether there is a sufficient balance between these processes for recruitment success or not.

1.6.3 Towards the Prediction of Recruitment Success

To date there has been a more or less universal failure in the reliable year to year prediction of recruitment success, in spite of the successful testing of some of the theories described above and the existence of long-term relationships between environmental indices and recruitment. 'The complexity of marine of ecosystems' and an 'insufficient consideration of scale' are both reasons which have been put forward to account for this (Taggart & Frank 1990).

The wide number of different factors which can potentially determine recruitment success and the complexity of their interactions may simply preclude the effective prediction of recruitment from single environmental indices. This may explain why good correlations between environmental indices and recruitment sometime break down (e.g. see Shannon *et al.* 1988); as might occur, for instance, if a factor which is not reflected by the environmental index being used, suddenly assumes a more dominant role in determining final year class strength. Dealing with this problem requires a good understanding of the conditions under which different factors can influence recruitment, and a suitable multi-parameter model (e.g. Cochrane & Hutchings 1995). Neural networks may in the future prove to be particularly useful in

this regard, given their ability to 'learn' what the deterministic relationships are between multi-parameter inputs and single outputs (Jarre-Teichmann *et al.* 1995).

With regards to the problem of scale, fisheries and environmental parameters have often been measured and compared to each other at different, or inappropriate, spatial and temporal scales (Taggart & Frank 1990). For instance, in studies which have found good long-term relationships between single environmental parameters and recruitment, the environmental parameter has often been averaged over relatively long time intervals and measured from areas which are different in size or location from the distribution of the population under consideration (e.g. Cury & Roy 1989, Lluch-Belda *et al.* 1989, Shannon *et al.* 1988). Whilst this may reveal general relationships and give insight into the impact of remote forcing on fish populations, it will also mask variations in local environmental conditions and consequently is unlikely to provide a robust basis for recruitment prediction. For ultimately it is local conditions, irrespective of how they relate to wider processes, which determine spawning activity and the survival of the early life-history stages.

It should be remembered, nevertheless, that historically there have been enormous constraints on where, when and at what resolution environmental and biological data could be collected. Prior to the initiation of routine maritime remote sensing in 1978 (Sherman 1985) biologists and oceanographers were in the main limited to voluntary ships observations, coastal observations, weather reports, and the frequency with which research ships could be deployed. This has been a particular handicap in coastal upwelling systems where high resolution environmental monitoring is required in order to adequately capture their physical and biological variability.

Current developments in the field of maritime remote sensing, however, look like providing a solution to the problem of scale. In particular, the compilation of time series of sea surface temperature (SST) and ocean colour images by organisations such as NASA, NOAA (National Oceanographic and Atmospheric Administration of the United States) and the JRC (European Commission Joint Research Centre) represents an important step in our ability to resolve environmentally important patterns and events within an ecosystem. The main advantages of these datasets for examining environmental-biological interaction being as follows: firstly they allow the construction of environmental indices across a wide range of temporal and spatial scales, and secondly they open up the possibility of quantifying the behaviour of marine systems according to the evolution of their spatial structure through time.

If there is anywhere where recruitment success could be predicted from environmental conditions it should be in coastal upwelling systems with their high and

variable levels of physical forcing and tight environmental-ecological coupling. Given that many of the environmental features thought to influence recruitment, such as offshore transport, vertical stability of the water column, temperature, food production, turbulence, and warm water intrusions, co-vary with each other, there is good reason to believe that there may be some emergent environmental feature of these systems which would allow reasonable predictions of recruitment to be made. The compilation of oceanographic time-series of satellite images has now made further exploration of this possibility feasible.

1.7 THESIS STRUCTURE

The remainder of the thesis falls into three parts; namely background information about the northern Benguela and its fisheries, an evaluation of the environmental dynamics of the region, and investigations into possible relationships between the environment and the clupeoid fisheries.

Chapter 2 will act both as a summary of the current state of knowledge of the physics and pelagic fisheries of the northern Benguela, as well as covering the development of the industrial fisheries, fisheries management and events which have shaped marine research in the region. In chapters 3 and 4 the physical dynamics of the northern Benguela will be investigated, primarily via the analysis of a time series of sea surface temperature satellite images. In chapter 5 various aspects of the reproductive ecology of anchovy and pilchard, include spawning, larval survival and recruitment success will be examined to see whether they are in any way related to the environmental dynamics of the system, as revealed by the previous two chapters. A final chapter, chapter 6, will summarise the major findings of chapters 3, 4 and 5, and make recommendations for future research.

CHAPTER 2

The Northern Benguela

2.1 HISTORY OF MARINE RESEARCH

Marine research in the northern Benguela region has had a patchy history over the course of this century and has been subject to a shifting mosaic of political, economic and scientific developments. In his thesis, Alan Boyd (1987) gives a detailed description of the main developments prior to 1987 and has provided much of the material for this section. No attempt is made at matching his thoroughness, however, and unless indicated otherwise the reader may assume that much of the information and perspective on events prior to 1987 presented herein is from this source.

There have been various identifiable research periods each with different biases in the type of research carried out, as will be outlined in some detail below. In general there has been a progression, albeit a fuzzy one, from descriptive investigations into the meteorology, oceanography and species composition of the region, to more detailed evaluations of the system's physical and biological characteristics, and finally to high-tech acoustic stock assessment techniques and investigations into the functional relationships between various biotic and abiotic components of the ecosystem.

Aside from local monitoring conducted by the early German settlers after the turn of the century, and some larger scale hydrographic work conducted by British and German cruises between the two world wars, there was little marine research in the region until the after the second world war. It was only following the start of the industrial fishery from Walvis Bay in 1948, when South West Africa (as Namibia was then known) was under South African jurisdiction, that regular intensive research and monitoring began. It is this period from 1950 up to the present day to which greater attention is paid below.

Since the 1950s research by local¹ scientists has been primarily driven, and justified, by the need to understand the behaviour of the commercial fish stocks in order to enable effective management. Consequently research effort has been largely directed towards stock assessment, and on monitoring the biotic and abiotic environment so as

¹ Namibian, South West African, and South African

to better understand how the population dynamics of the fisheries, especially the clupeoid stocks, are influenced by factors other than fishing activity. The impetus behind this research received a boost following the disastrous collapse of the massive pilchard fishery during the late 1960s and 1970s, due to a combination of over-fishing and adverse environmental conditions (e.g. Butterworth 1983).

A fairly substantial body of research has also been conducted by foreign scientists; primarily on Spanish and Soviet research cruises since the 1960s, but also on German, American and British cruises. Whilst the initial motivation for these expeditions was likely to have been more in the "spirit of scientific enquiry" (Boyd 1987) than for local research, it would also be naive to suppose that during the 1960s and after there was no political and economic interest in the region's abundant fisheries, given that many stocks in the northern hemisphere had begun to seriously dwindle due to over fishing (e.g. Cushing 1988).

2.1.1 1950 - 1970

Major developments during this period include the building of a marine laboratory in Walvis Bay in the early 1950s, two oceanography cruises in 1950 by the *RRS William Scoresby*, and nine oceanographic cruises by the South African division of sea fisheries' research vessels, *Africana II* and *Sardinops*, between 1959 and 1961. In addition, important work into the physical and chemical oceanography of the region was conducted by Soviet and American cruises in the region during the 1960s.

Local research from the mid 1950s was geared towards regular coastal environmental and biological monitoring, and the sampling of fish stocks from catches landed in Walvis Bay. The environmental monitoring petered out in 1967 due to staffing problems, and what Alan Boyd also suspects to have been low morale following the introduction of factory ships in the region despite scientific warnings as to the danger of stock collapses.

In spite of these problems the research undertaken during this period led to an increased understanding of the region's physical and chemical oceanography (e.g. Hart & Currie 1960; Stander 1964; Stander & De Decker 1969; Moroshkin *et al.* 1970; Calvert & Price 1971), the distribution and abundance of its plankton (e.g. Kollmer 1963; Unterüberbacher 1964), and various aspects of the pilchard stock including its size, distribution, and reproductive biology (e.g. Matthews 1959; Matthews 1964; Newman 1970). In addition tagging studies confirmed that the South African and Namibian pilchard essentially form separate stocks (Newman 1970).

2.1.2 1970 - 1980

The main local research initiative during this decade was the Cape Cross Programme, which was designed to "research the pilchard fishery back to life" (Boyd 1987) following its collapse at the end of the 1960s. Its central tenant was the need for an improved understanding of the pilchard's population dynamics, in order to provide a more robust scientific base from which to champion the need for conservative levels of exploitation against the economic arguments of the fishing industry.

The programme essentially ran from 1970 to 1974, with particular emphasis placed on the following: investigating the spawning and larvae of pelagic fish with respect to environmental conditions, using combined aerial and acoustic surveys for deriving biomass estimates, and improving the biological monitoring of catches. The programme was of some immediate benefit in helping to limit catches, but staffing problems (Boyd 1987) combined with the apparent recovery of the stock (Cram 1981) resulted in the discontinuation of cruises and aerial surveys into 1975 and 1976. The lack of any scientific evidence as to stock size during these two years combined with "unchastened optimism" from the fishing industry resulted in increased quotas which ultimately contributed to a second stock collapse at the end of the 1970s.

Despite these management failings, the data collected by the programme led to the first insights into interactions between the environment and the reproductive ecology of pilchard and anchovy in the region (e.g. O'Toole 1977; King 1977), and further extended the understanding of the region's oceanography (e.g. O'Toole 1980; Shannon *et al.* 1987). In addition, the regular annual sampling of the age composition of pelagic stocks initiated by the programme continues up to the present day (e.g. Thomas 1985; Boyer *et al.* 1995), and the acoustics experience gained was valuable when acoustic biomass surveys were resumed in the late 1980s (e.g. Boyd *et al.* 1989). Moreover, the latter end of the decade saw a revival in basic research and environmental monitoring off Namibia, and in October 1978 environmental monitoring cruises and egg/larval surveys were once again resumed off Namibia.

International research activity during this period became centred around the International Commission for the South East Atlantic Fisheries (ICSEAF) in Madrid, founded in 1969. Although a number of research cruises were undertaken by foreign countries during this period it was not really until the 1980s that publications emerged; many of which can be found in the Collection of Scientific Papers of the International Commission for South East Atlantic Fisheries.

2.1.3 1980 - 1989

Local marine research during the 1980s in some ways picked up on where the Cape Cross Programme had left off, primarily with regard to a continued interest in environmental-fishery interactions using the data collected from regular environmental monitoring and egg/larval surveys, and a resumption of acoustic biomass surveys towards the end of the decade. Nevertheless, there were also important new developments during this decade; notably the launching of the Benguela Ecology Programme in 1982, and the opening up of new research opportunities due to the arrival of satellite remote sensing and the increasing availability of computers and computer databases for scientific research.

The increased availability of computers for research purposes from the late 1970s onwards resulted in two important developments. The estimation of stock size from catch statistics using virtual population analysis (VPA) was the first, and was used from 1980 onwards for estimating pilchard and anchovy biomass in the region (e.g. Butterworth 1980). The ability to process large quantities of environmental data from a wide variety of different sources was the second, and resulted in large scale investigations into the physical behaviour of the Benguela region using previously unused data sources, such as weather and sea surface data collected from commercial shipping (e.g. Parrish *et al.* 1983; McLain *et al.* 1985; Taunton-Clark and Shannon 1988).

The availability of remotely sensed sea surface temperature and ocean colour satellite data since 1978 (Sherman 1985) stimulated increased local interest in characterising and tracking the behaviour of mesoscale oceanographic features. Although the southern Benguela received greater attention than the north (e.g. Shannon 1985b), some important work was done in the north especially with regard to upwelling activity and behaviour of the offshore and longshore upwelling fronts (e.g. Lutjeharms & Meeuwis 1987; Lutjeharms & Stockton 1987; Meeuwis & Lutjeharms 1990; Kazmin *et al.* 1990; Lutjeharms *et al.* 1991).

Understanding of the relationship between environmental conditions and the reproductive success of pilchard and anchovy continued to increase over the course of the decade. The regular egg/larval surveys and environmental monitoring combined with the new-found capability to estimate recruitment from VPA were crucial to this. In addition the dramatic effects that the 1984 Benguela Niño event had on spawning activity, larval survival and ultimately recruitment success in these two stocks (Le Clus

1986; Le Clus *et al.* 1987) acted as an additional research stimulus. Sadly the regularity with which egg and larval surveys were conducted declined after the 1984/1985 spawning season from 4 to 5 per year to only 2 per year, and nothing appears to have been published from any survey data collected after March 1985.

The Benguela Ecology Programme played an important role in steering and co-ordinating research during the 1980s, and can take much of the credit for the decade's achievements (Rothschild & Wooster 1992). Overall the fusion between the introduction of new research tools, what had already been learnt of the system from the previous three decades worth of research, and the continued Cape Cross style sampling programmes resulted in important advances in understanding of the physical and biological behaviour of the northern Benguela.

No attempt will be made to summarise these advances here, given that what was learnt during this decade in many ways represents the current state of knowledge, and will be comprehensively covered in the rest of this chapter. Nonetheless the dramatic expansion in research activity and enthusiasm can be gauged by the sharp increase in the output of publications during this decade and the early 1990s (e.g. see Payne *et al.* 1987, 1992). In addition important syntheses of current knowledge about different aspects of the ecosystem appeared in the form of various substantial review articles (Nelson & Hutchings 1983; Shannon 1985a; Chapman & Shannon 1985; Shannon & Pillar 1986; and Crawford *et al.* 1987).

International research interest in the region continued throughout the decade. Of particular note were two joint Spanish/South African cruises during 1985 and 1986 to investigate physical-biological coupling in the region (e.g. Barange *et al.* 1991; Barange 1990; Olivar & Barange 1990), and a number of surveys of the demersal and mesopelagic fisheries by Spanish and Soviet scientists (e.g. Macpherson & Roel 1987; Mas-Riera *et al.* 1990; and Sedletskaya 1988).

With the end of the decade came tremendous political changes which were to have a profound effect on marine research in the region. The long war of independence which had plagued Namibia since the late 1960s finally came to an end in April 1989 when the United Nations moved in. From May of that year the independence process began in earnest, and with it came the dismantling of the old South African regime (the South West African administration). South Africa ceased to be responsible for marine research and fisheries management in the region, and most of the marine scientists who had been working in Namibia moved to Cape Town. With them went the accumulated experience of 40 years research and many of the research and monitoring programmes which had been built up over the previous 20 years.

2.1.4 1990 - 1996

Namibia formally declared independence on the 21st March 1990, and in 1991 the newly created Ministry of Fisheries and Marine Resources took over responsibility for fisheries research and management. Research was initially a problem, given that most of the experienced marine scientists in the region had returned to South Africa during the independence process. Namibian scientists, many of whom had no previous marine experience, were recruited as research staff to the ministry. Money, however, was not a problem. Towards the end of 1992 a new research centre, which had largely been built and equipped with international aid money, was completed in Swakopmund (The National Marine Information and Research Centre), and in 1994 the Namibians took delivery of a new research vessel, the *RV Welwitchia*, which had been donated by the Japanese government. Prior to its delivery shipboard research and data collection had been conducted from the rapidly ageing *RV Benguela*.

Beyond the provision of hardware, overseas agencies have and continue to be heavily involved with helping to launch research programmes, particularly as regards stock assessment, and with the training of Namibian scientists and research personnel. Foremost amongst them is the NORAD (Norwegian Agency for Development and Co-operation) sponsored Nansen programme, which via complementing the stock assessment cruises carried out by the *RV Benguela* and *RV Welwitchia* from the *RV Dr Fridtjof Nansen* has also provided valuable training in acoustic and 'swept-area' surveying methodologies (Boyer² pers. comm.).

The Food and Agriculture Organisation of the United Nations (FAO) and the Danish International Development Agency (DANIDA) have also provided valuable training in a number of fields, especially stock assessment. Other contributors include ICEIDA, the Icelandic overseas development agency, who continue to provide training and support for the manning of research vessels, and the British Overseas Development Agency (ODA) who donated and supervised the installation of satellite receiving equipment in Swakopmund in 1994 (Boyer pers. comm.).

There has understandably been a certain amount of disorientation amongst the Namibian scientific staff, largely due to their initial lack of expertise, the huge social and political upheavals that accompanied independence and the involvement of a bewildering array of overseas agencies. This is reflected by the fact that no new

² David Boyer, National Marine Information and Research Centre, PO Box 912, Swakopmund, Republic of Namibia

publications, other than internal research reports, have emerged from within the country during the 1990s.

Nonetheless there are good signs. With help from the various overseas agencies involved in the region, Namibian scientists have rapidly gained expertise over the past six years and are increasingly taking full control of their research activities. In addition new collaborative links have been established with South African and Angolan scientists. Of particular importance is the Benguela Fisheries Interactions and Training (BENEFIT) programme, which will act as a regional forum for co-ordinated and co-operative research between the three countries bordering the Benguela system. For Namibia the renewed links with South Africa should prove especially fruitful given that many South African marine scientists have a great deal of experience of the northern Benguela from the years prior to independence.

2.2 PHYSICS AND PLANKTON PRODUCTION

"...nearly all of the physical, chemical and biological properties of the current exhibit discontinuity or irregularity both in time and space. The Benguela Current consists of a series of anticyclonic eddies of interlocking tongues of cool and warmer water which are in a constant state of change or flux. This quality of irregularity is in fact one of the features which emphasise the discrete character of this upwelling region."

(Hart & Currie 1960)

The Benguela Current forms the eastern limb of the South Atlantic subtropical gyre (Stramma & Peterson 1991). From the Cape of Good Hope it skirts equatorward along the coast of South Africa and Namibia until offshore of Lüderitz where it deflects to a more north-westerly direction, as illustrated by figure 2.1. The prevailing southerly and south westerly winds which drive the current are responsible for frequent Ekman transport and the upwelling of cool nutrient rich water along the coastal edge of the continental shelf.

Coastal upwelling commonly occurs between Cape Agulhas in the south to southern Angola in the north (Shannon 1985a). The intensity of this upwelling is far from uniform with tremendous spatio-temporal variability according to local bathymetry, fluctuations in the wind fields, coastally trapped waves, and periodic intrusions of tropical water from both the northern and southern ends of the system (Boyd 1987). Strong perennial upwelling off Lüderitz (27° - 28° S) effectively splits the system into

northern and southern regimes, and acts as a semi-permanent environmental barrier to the longshore transport of pelagic fish eggs and larvae (Boyd & Cruickshank 1983; Agenbag & Shannon 1988). Areas of strong upwelling activity are generally associated with headlands, where alongshore windstress is locally intensified, and narrow continental shelves, where cool deep water lies close to the coast. Conversely upwelling activity tends to be sluggish in bays and where the continental shelf is wide (see figure 2.1).

The Benguela is unlike other eastern boundary current upwelling regions in that it is bounded at both its equatorward and polarward ends by warm water currents. To the north are the tropical waters associated with the Angola basin and the southerly flowing coastal Angola current. Whereas to the south is the Agulhas current which flows round the southern tip of Africa from the tropical Indian Ocean. Both boundaries are characterised by strong thermal fronts, whose exact location depends on the dynamic balance between upwelling activity and the flow of these tropical waters. During the austral summer the northern boundary contracts to around 18° S, whilst in the south it expands as far as Cape Agulhas (35° S 20° E). During winter the situation reverses; in the north upwelling expands as far as 15° S, whilst in the south it contracts to around 31° S. (Shannon 1985a, Lutjeharms & Meeuwis 1987).

Research into the physics of the northern Benguela has been based on coastal monitoring stations, surveys, drogue tracking, merchant shipping data, and some use of remote sensing. In general, there is a good understanding of the oceanography of the region in terms of the relationship between local and remote forcing on upwelling activity, vertical stratification and major current flows. Mesoscale processes and features, however, are less well understood. The main reason has been due to the lack of direct current measurements in the region. Aside from a few drogue studies, most of the inferences on mesoscale currents have been made on the basis of salinity distributions, sea surface temperatures and dynamic topography maps (see Boyd 1987, Boyd *et al.* 1987, Shannon 1985a). None of which are wholly satisfactory for resolving wind driven surface flows, due to the fact that wind driven flows are rapidly attenuating phenomena which can occur over short length scales, whereas salinity distributions, sea surface temperatures and dynamic topographies all tend to persist over longer time and length scales .

High resolution sea surface temperature data from satellite imagery, however, has enabled some insight into the spatial dynamics of the offshore upwelling front, as regards the formation of eddies and filaments, and also into the dynamics of the Angola-Benguela frontal region (e.g. Lutjeharms & Stockton 1987, Meeuwis &

Lutjeharms 1990, Kazmin *et al.* 1990). Nonetheless relatively little is known about a possible cyclonic gyre lying off the continental shelf between 18° S and 25° S (Nelson & Hutchings 1983), and the dynamics of the coastal 'convergence zone' between 22° S and 23° S where water from the vigorous upwelling off Lüderitz meets the comparatively sluggish water over the wide Swakop shelf.

The purpose of this section is to describe the main oceanographic features and behaviour of the northern Benguela, and the climatic and hydrodynamic forces which drive them. For more detail the reader is referred to Alan Boyd's thesis (Boyd 1987) and the following review articles: Nelson & Hutchings (1983), Shannon (1985a) and Chapman & Shannon (1985).

2.2.1 Meteorology & Surface Winds

Coastal winds in the Benguela are governed by three main weather systems and their interaction with local topography; namely the south Atlantic anticyclone, the African subcontinent pressure field, and eastward moving low pressure cells along the Southern Ocean westerly wind belt to the south of the African continent (Shannon 1985a).

The south Atlantic anticyclone causes the prevailing southerly and south-easterly winds responsible for Ekman drift and upwelling throughout the system. The anticyclonic flow of wind is entrained northwards along the coast by a thermal barrier of hot air rising off the coastal plain. This thermal barrier is particularly strong north of 31° S where the Namib desert runs along the coast. Seasonally the anticyclone migrates about 800 km and moves in tune with the Inter Tropical Convergence Zone (ITCZ). In winter it is centred around 27°S 10°W and in summer around 32°S 5°W (Peterson & Stramma 1991). These movements directly influence the seasonality, in both incidence and magnitude, of upwelling favourable winds. In general the maximum pressure gradient along the coast occurs in spring, although towards the northern end of the Benguela this tends to be earlier in the year due to a time lag as the anticyclone moves south.

The African subcontinent pressure field changes from being a low pressure system during the summer to a weak high pressure system during the winter, concomitant with the seasonal movement of the ITCZ. In the southern Benguela these summer lows contribute to upwelling favourable winds by intensifying the pressure difference between the south Atlantic anticyclone and the coast. During autumn and spring large high pressure systems occasionally develop over the southern part of the continent, and can cause strong easterly winds off south western Africa, known as Berg winds. These

Berg winds 'escape' the central continental plateau and blow out to sea along much of the Benguela coastline, often bringing dust storms with them. Typically they last about four days and may suppress macroscale upwelling, whilst at the same time intensifying local upwelling in water less than 10 km offshore.

Eastward moving low pressure cells along the Southern Ocean westerly wind belt are important in influencing the pulsing of upwelling events in the southern Benguela according to their interaction with wind fields from the south Atlantic anticyclone, but have little impact on events in the northern Benguela.

The main seasonal and latitudinal trends in upwelling favourable winds (i.e. alongshore winds) are illustrated in figure 2.2. In the northern Benguela the strongest upwelling favourable winds are found off Lüderitz (25° S - 27° S) and in the vicinity of Cape Frio. Conversely the lowest alongshore winds are found between 19° and 23° S, where the coastline is generally concave.

Seasonality, with respect to both variance in wind direction and strength of upwelling favourable components (i.e. southerly components), is much greater to the south of Lüderitz than to the north. South of 31° S the most favourable winds for upwelling occur during the austral summer and spring. During winter there is a much higher frequency of winds with westerly components and in general upwelling is suppressed. Between 24° and 31° S the southerly winds are greatest from the late winter through to summer (August to February) and least during autumn and early winter. North of 25° S they are greatest during late winter/spring (August to November) and least during summer (November to February). In addition, north of 18° S there are also peaks in upwelling favourable winds during autumn (March-April).

A great deal of shorter term diurnal and 'event' scale variability is superimposed over these general seasonal trends. Diurnal variability is primarily due to the development of sea breezes. These result from the differential heating of the land and coastal waters, and typically cause a strengthening of the southerly wind component throughout the day until the mid afternoon. 'Event' scale variability manifests itself as 5-12 day cycles in the strength of these southerly components, as deduced by the spectral analysis of wind data from Pelican Point (Boyd 1987).

2.2.2 Macroscale Currents

The main macroscale features of surface circulation are presented in figure 2.1. The Benguela Current originates as northward flow near the Cape of Good Hope. At about 30° S it starts to head north-west and in doing so separates from the coast and begins

widening rapidly. The current is topographically steered in that it accelerates over areas with steep bathymetry and meanders over bathymetric plains (Shannon 1985a). The current is primarily fed by water from the south Atlantic Current, which in effect is the southern limb of the south Atlantic subtropical gyre. Nonetheless it also receives some input from the Agulhas Current and from sub-Antarctic surface water (e.g. see Shannon *et al.* 1989).

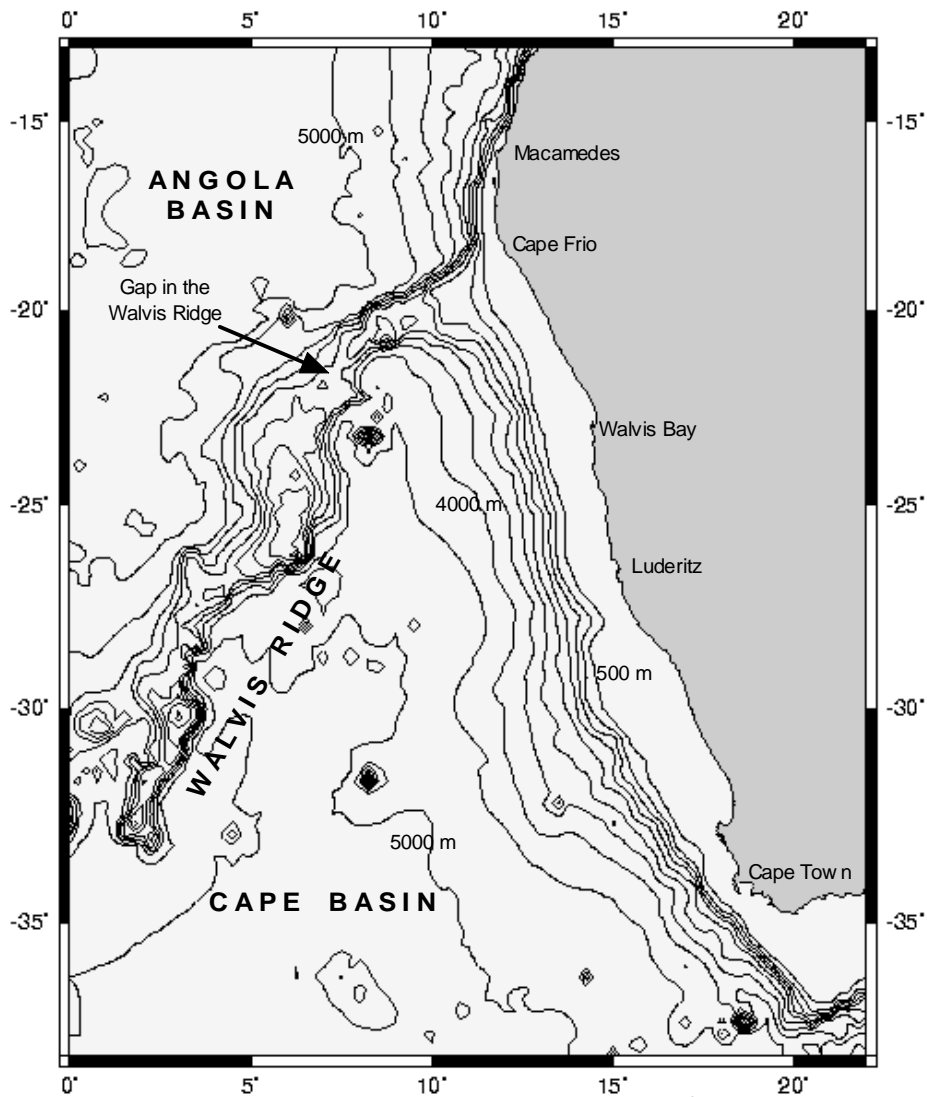


Figure 2.3. Bathymetry of the south east Atlantic. The depth contours are at 500m intervals.

South of 23° S the predominant offshore currents coincide with the anticyclonic wind fields. Between 30°-35° S there is convergence between equatorward and westerly flow. Off Lüderitz the main geostrophic flow of water turns west, with the likelihood of a surface stream flowing towards the gap in the Walvis Ridge at 22° S 7°30' W (Nelson & Hutchings 1983) shown in figure 2.3. The cyclonic gyre proposed

by Nelson & Hutchings (1983) occurs to the east of this stream with the Walvis Ridge acting as the northern boundary.

North of 23° S surface currents are more complicated. Moroshkin *et al.* (1970) conclude that a divergence zone exists offshore of 20° S, where the main north-westerly Benguelan flow splits into east and west branches, possibly due to the action of a cyclonic gyre present in the Angolan Basin. The western branch heads west and the eastern branch heads northwards as a semi-permanent flow between 100 and 200 nm offshore.

Further inshore the wind driven upwelling currents are north-westerly flowing until about 18° S, near the Angola-Benguela frontal region, where they start to be deflected offshore (see Boyd & Agenbag 1985). Close inshore and to the north of the front there is a pronounced southerly counter current flow of warm saline Angolan water (the Angolan Current). The latitudinal extent of this flow and the position of the Angola-Benguela front are, however, subject to strong seasonal and inter-annual variability as will be described in greater detail below.

As regards sub-surface currents, the existence of a polarward undercurrent flowing along the edge of the continental shelf as far as the Cape of Good Hope has been well established and is often characterised by low oxygen concentrations (Nelson & Hutchings 1983; Shannon 1985a). Further inshore, subsurface intrusions of saline Angolan water often make their way south over the central Namibian shelf during summer/autumn, and may do so concurrently, or independently from surface intrusions (Boyd *et al.* 1987). Consequently, when there is upwelling off central Namibia at this time of the year it may be water of Angolan origin which often is brought to the surface.

2.2.3 Upwelling Activity and Mesoscale Features North of 28° S

North of 28° S, upwelling activity is closely linked to the magnitude of the southerly wind fields and local bathymetry. Diurnal and 'event' scale pulsing in the strength of coastal winds drive high levels of short term variability in upwelling activity which in turn are superimposed over more general seasonal and interannual trends. The main upwelling cells are found in association with headlands and/or narrow steep continental shelves; notably off Lüderitz, but also Cape Frio (18°-19° S), Palgrave Point (20°-21° S) and Conception Bay (24° S). Response times between increases in alongshore windstress and enhanced upwelling activity are short, and for the main upwelling cells

may be measured on the scale of hours rather than days (e.g. Kazmin *et al.* 1990, and Walter 1937 as cited by Shannon 1985a).

Wind and bathymetry are, however, not the only factors influencing upwelling activity. Remote forcing from the equatorial Atlantic has been implicated in the propagation of coastal trapped waves along the coast of southern Africa, and during Benguela Niño years is responsible for strong polarward intrusions of Angolan water into the northern Benguela. The effect of the latter being to suppress the upwelling of cool nutrient rich water during summer and early autumn (as described more fully in section 2.2.4), whilst that of the former possibly being to 'prime' upwelling (Boyd & Agenbag 1985; Shannon 1985a; Boyd 1987). Indeed off Walvis Bay, Boyd (1987) noted a seasonal intrusion of cold water ($<12^{\circ}$ C) over the shelf between July and October, which he attributed to coastally trapped waves given that the intrusions were more regular than the corresponding fluctuations in mean monthly equatorward wind speeds.

Seasonal variation in upwelling activity is greater off northern and central Namibia than off southern Namibia, due to latitudinal differences in the forcing of the system. Upwelling is reasonably consistent throughout the year between 24° and 28° S, whereas north of 24° S there is a marked contrast between the vigorous upwelling activity during winter and spring and the more sluggish conditions during summer and autumn. In general, the state of the upwelling system between 15° and 24° S is reflected by the presence or otherwise of four different surface water types (O'Toole 1980), namely: cool upwelled water of south Atlantic central water origin (12° - 18° C, salinity: 34.9-35.2 ‰); warmer saline upwelled water probably of Angolan origin (15° C, salinity: 35.3 ‰); warm saline Angolan surface water (17° - 22° C, salinity: 35.5-35.9‰); and oceanic water of mixed origin (16° - 20° C, salinity: 35.2-35.5‰).

The width of the coastal upwelling regime is on average between 150 and 200 km, and is separated from the surface south Atlantic waters by a highly convoluted thermal front characterised by eddies and long upwelling filaments (Hart & Currie 1960, as cited by Shannon 1985a; Lutjeharms & Stockton 1987; Kazmin *et al.* 1990). These upwelling filaments penetrate far out into the south Atlantic into a 'filamentous mixing area', which may extend a further 600 km or so offshore of the main upwelling front (Lutjeharms & Stockton 1987).

The vertical structure of the water column in the region is a function of wind induced turbulence, solar heating of the surface layers, and intrusions of warmer water masses. Consequently the frequency with which thermoclines are found throughout the region varies with area and season. Shallow thermoclines are most frequently found in

sheltered areas during summer, whereas deep thermoclines may occur in more exposed regions due to inward advection of warmer water masses. (e.g. see Du Pleiss 1967 and Boyd 1987).

The remainder of this section will take a more detailed look at upwelling activity, water flows and mesoscale features within three subdivisions of the northern Benguela upwelling system, namely: the northern Namibia region³ (15° - 19° S), the central Namibian region (19° - 24° S), and the Lüderitz region (24° - 28° S).

NORTHERN NAMIBIA REGION (15°-19°S)

The oceanography of this region is dominated by the meeting of upwelled and tropical surface waters at the Angola-Benguela front. Temperature gradients across the front are commonly as high as 4° C per 1° latitude. The position of the front varies, and depends on the dynamic balance between the southerly flowing Angola Current and the north-westerly flow of upwelled water (Meeuwis & Lutjeharms 1990).

The front is furthest north during winter, when coastal upwelling commonly occurs as far north as 15° S (Parrish *et al.* 1983, Lutjeharms & Meeuwis 1987, Lutjeharms & Stockton 1987). During summer and autumn (November to April) the northern boundary of cold water upwelling shifts to the south and so does the mean position of the front. Where the midpoint of the front meets the coast will usually be anywhere between 10° and 20° S, although on average it is found between 14° and 16° S with a 2°-3° shift in its average seasonal position (Meeuwis & Lutjeharms 1990).

Surface flow is complex in the region. Eddies result from the shear between the Angolan current and the upwelling currents as they turn offshore, and upwelling filaments often develop off Cape Frio and the Kunene estuary during in winter and spring (May to October) (Lutjeharms & Stockton 1987). During summer and early autumn (November to March) short-period pulsings in the position of the front are common, as are 'tongue-like' polarward intrusions of warm Angolan water along the coast, and high levels of vertical stratification (Meeuwis & Lutjeharms 1990). In addition dynamic topography maps indicate the possibility of some eastward flow in the region at this time of year (Shannon *et al.* 1987); perhaps in association with the presence of these frontal eddies (see also Boyd 1987).

³ It should be noted that this region also includes the waters off southern Angolan

CENTRAL NAMIBIA REGION (19°-24° S)

This region is characterised by moderate upwelling favourable winds, and the wide shallow Swakop shelf which prevents the upwelling of water from deeper than 150-200 m. Consequently it is an 'intermediate' area of low intensity upwelling in which the seasonal insolation cycle is more important than wind driven turbulence in determining vertical stratification (Boyd 1987), and shallow thermoclines are especially common in summer and early autumn (November to March) (Du Pleiss 1967; Boyd 1987). Exceptions to this regime occur at Palgrave Point and (20° 20'S) and Conception Bay (24° S) where the continental shelves are steeper and narrower (Shannon 1985a; Boyd 1987).

Onshore and alongshore flow of warmer waters into the region is commonest during summer and early autumn when upwelling activity reaches a seasonal low. From the north may come surface and sub-surface intrusions of tropical Angolan water (Boyd *et al.* 1987), whereas from the east and north-east there may be intrusions of oceanic water (O'Toole 1980). O'Toole (1980) also observed that when strong upwelling occurred simultaneously off Lüderitz and Cape Frio, oceanic water appeared to be drawn inshore into the central region between these two upwelling centres.

The area between 21° and 23° S is of particular interest as a 'semi-permanent convergence zone' between the Lüderitz and northern/central Namibian regimes (see Shannon 1985a). This is especially so during late summer and early autumn (January to March) when the longshore contrast between the perennial upwelling conditions of Lüderitz and the stable stratified conditions off central Namibia are at their greatest. In terms of water movement little is known about its dynamics, although there has been speculation as to the role of 'semi-enclosed circulation' in promoting the maintenance of large euphausiid populations (Barange & Boyd 1992). Moreover, the likelihood of some eastward flow is supported by the area's wind fields having a net onshore component (Boyd 1987), and by dynamic topography maps indicating the presence of eddies along the upwelling front between 19° and 20° S with associated onshore flow between 21° and 23° S (see Stander 1964 as cited by Shannon 1985a, and also Barange *et al.* 1992).

LÜDERITZ UPWELLING REGION (24°-28° S)

This region has the most intense and consistent upwelling activity in the whole Benguela system, by virtue of its strong southerly wind fields and narrow deep continental shelf. Shelf edge upwelling is common around 26° S, and upwelled water

typically rises to the surface from depths of 250-350 m. The 'semi-permanent' environmental barrier between the northern and southern Benguela is maintained to the north of Lüderitz by a north-westerly moving tongue of freshly upwelled water, with high levels of turbulence and low levels of vertical stratification (Boyd & Cruickshank 1983, Agenbag & Shannon 1988). Whilst to the south, between 27° and 28° S, onshore movement of oceanic water is common. Seasonal differences in upwelling intensity are relatively small. Nonetheless upwelling is usually strongest between August and October (late winter/spring), and weakest during autumn/early winter.

Eddies and filaments are common features of the upwelling front off Lüderitz. Occasionally 'superfilaments' are formed which can extend over 1000 km into the South Atlantic. These 'superfilaments' may result from a combination of intense upwelling and offshore 'entrainment' by warm water rings which have been advected north after 'budding' off from the Agulhas current (Lutjeharms *et al.* 1991). Tongues of warm water from the Agulhas current are also occasionally advected up the south-west African coast. Usually these intrusions have little effect on upwelling activity north of about 30° S, but an especially strong intrusion during the second half of 1986 resulted in the suppression of cold water upwelling in the region (Shannon & Agenbag 1987).

2.2.4 Interannual Variability

Upwelling activity and water flows in the northern Benguela are subject to high levels of inter-annual variability, in addition to the seasonal and shorter term trends described above. Analysis of long time series of SST measurements from shipping reports has revealed the existence of a weak 8-10 year cycle between alternating cool and warm periods (Taunton-Clark & Shannon 1988); cool periods being associated with the enhanced upwelling of cool water, and vice versa for warm periods.

BENGUELA NIÑOS

Anomalously warm years are known as Benguela Niño's due to their similarity, in terms of underlying physical mechanisms and biological consequences, to the el Niño events in the eastern Pacific (Shannon *et al.* 1986). They have occurred several times this century (Taunton-Clark & Shannon 1988), with especially strong events recorded in 1963 (Stander & De Decker 1969), 1984 (Boyd *et al.* 1985) and more recently in 1995 (O'Toole pers. comm.).

Benguela Niños usually last six months or more, beginning around January and February, and may be considered an extension of the seasonal summer warming in the

northern and central regions. In particular, the Angola-Benguela front is displaced much further south than usual, and warm saline surface water advects along the Namibian coastline, sometimes as far 25° S. These intrusions typically cause a deepening of the thermocline with the result that when upwelling does occur it will often be from the nutrient impoverished layers above the thermocline. During strong Niño events this nutrient impoverishment is particularly severe and is associated with marked declines in biological productivity (Boyd *et al.* 1985). Other local environmental features associated with these events have been documented in Shannon *et al.* (1986).

In a similar fashion to el Niños being driven by trans-Pacific 'anomalies' in atmospheric pressure gradients (Longhurst & Pauly 1987), Benguela Niños are thought to originate from 'anomalous' atmospheric conditions in the western tropical Atlantic (Hisard & Henin 1987; Hisard 1986). The proposed mechanism is as follows. A weakening or reversal of the easterly trade winds disrupts the usual east to west flow of surface water, and in doing so causes a relaxation in the usual east to west thermocline tilt⁴ which sets up eastward propagating Kelvin waves along the equator. When they hit the African coast these Kelvin waves are then refracted to the north and south. Off south-western Africa this leads to enhanced counter current flows (i.e. the Angolan current), higher sea levels (e.g. Brundrit *et al.* 1987) and warm water intrusions into the northern Benguela.

Although these warm water events are often referred to as 'anomalies', it should be remembered that in fact they merely represent the extreme boundaries of semi-cyclical interannual oscillations in the magnitude of regular trans-oceanic seasonal changes. What happens during a Niño year is no more than an exaggeration of what happens seasonally every year. Moreover, these particularly warm years seem always to be preceded by very cold years⁵ in which stronger than usual easterly trade winds ultimately lead to lower sea levels, shallower thermoclines, and enhanced cold water upwelling along the eastern boundaries of ocean basins (e.g. Hisard 1986, Sharp & McLain 1993).

LONGER TERM FLUCTUATIONS

Equatorward windstress in the Benguela appears on average to have increased over the course of this century (Taunton-Clark & Shannon 1988). Similar trends have also been found in other eastern boundary currents since 1950, which Bakun (1990)

⁴ Under usual conditions the thermocline is shallower in the eastern tropical Atlantic than in the west.

⁵ In the Pacific these very cold years are known as la Niñas (Sharp & McLain 1993)

discusses as being indirect evidence for global warming. He argues that the inhibition of night time cooling and the enhancement of daytime heating might cause a deepening of the continental low pressure systems adjacent to these upwelling systems. This in turn would lead to enhanced inshore-offshore atmospheric pressure gradients, greater alongshore wind speeds, and thus an overall trend towards increased upwelling activity. This interpretation has, however, been challenged by Mann (1993) on the basis that the average surface temperature of the earth actually fell between the 1940s and the 1970s.

2.2.5 Phytoplankton

The phytoplankton community can be split into two groups. Diatom communities dominate in recently upwelled water, and are responsible for the high and fluctuating primary productivity of the region. Microflagellate and dinoflagellate communities tend to dominate during warm stable conditions, and reach their highest concentrations shortly after the transition from cool upwelling to warmer and more stratified conditions (Pieterse & van der Post 1967 as cited by Shannon & Pillar 1986; Mitchell-Innes & Pitcher 1992). Red tides are common along the coast during these stable periods, and are caused by sharp increases in dinoflagellate numbers. Often they are associated with fish and shellfish mortality, and off Namibia are commonest during summer (Shannon & Pillar 1986).

The mesoscale dynamics of phytoplankton blooms and their trophic relationships are better understood for the southern Benguela, where they have been studied in greater detail than to the north. Nonetheless it is clear that the large scale distribution and abundance of phytoplankton in the northern Benguela is closely related to the hydrodynamics of the region.

During active upwelling conditions the offshore movement of surface water, and a one to three day time lag between the introduction of nutrients into the surface layers and the development of phytoplankton blooms generally results in the highest chlorophyll concentrations being found in bands offshore and parallel to the coast (Chapman & Shannon 1985 as cited by Shannon & Pillar 1986). During the quiescent upwelling conditions these bands are found closer inshore and further to the south (see Kruger & Boyd 1984; Shannon *et al.* 1984; Estrada & Marassé 1987). In line with this, the shift to quiescent upwelling conditions also appears to be accompanied by a shift from predominately inshore-offshore gradients in phytoplankton concentration to longshore gradients (e.g. see Barange *et al.* 1991).

From the literature it appears as if the highest phytoplankton concentrations are found during 'intermediate' levels of upwelling, when there are sufficient nutrient concentrations for the development of blooms and yet the mixed layer is still shallow enough for the phytoplankton cells to receive plenty of light (Shannon *et al.* 1984, and see also Kollmer 1962, Kruger & Boyd 1984). For instance, Kollmer (1962) found the highest phytoplankton concentrations off central Namibia during November and December, which are transitional months between the vigorous late winter/early spring upwelling season and the quiescent summer months. Moreover, the southward shift in chlorophyll maxima during 'quiescent periods' off central Namibia may be due to sufficient reductions in wind driven turbulence and offshore transport in the Lüderitz region for the development of inshore phytoplankton blooms (Shannon *et al.* 1984).

Although little work has been done on the mesoscale dynamics of phytoplankton blooms and distribution in the northern Benguela, the maps of chlorophyll and phytoplankton distribution presented in the various publications cited above, clearly indicate high levels of mesoscale patchiness. Various interacting factors will be responsible for this; namely, horizontal turbulent diffusion, the growth of phytoplankton blooms due to nutrient enrichment, and mesoscale water movements (e.g. Legendre & Demers 1984). Grazing may also play an important role, as suggested by mesoscale overlapping of high zooplankton densities and reduced phytoplankton concentrations (Kruger 1983; Kruger & Boyd 1984; Barange & Boyd 1992).

2.2.6 Zooplankton

Copepods and euphausiids have been the most studied zooplankton in the northern Benguela, primarily due to their large population sizes and their importance as fish food. Indeed Armstrong *et al.* (1991) estimated that 90% of the diet of pelagic and mesopelagic fish in the northern Benguela is composed, in more or less equal proportions, of mesozooplankton (i.e. mainly copepods) and euphausiids. In general, however, like phytoplankton there is a greater understanding of zooplankton trophodynamics and the interaction between zooplankton populations and hydrological processes in the southern Benguela. Zooplankton were regularly monitored in the north during the SWAPELS cruises but unfortunately little has been published from the data collected (Shannon & Pillar 1986).

Nonetheless it is safe to assert that environmental conditions will have important effects on the region's zooplankton populations. In particular their distribution and

abundance will in the main be dependent on local currents and patterns of phytoplankton availability. Although it should also be remembered that physiological and behavioural adaptations will enable the zooplankton to 'dampen out' environmental variability to a greater extent than phytoplankton can (e.g. Caddy & Sharp 1988). For instance, their ability to store energy reserves allows them to 'ride out' lean periods when there is little food, and the harnessing of different currents via vertical migration provide them with a degree of active control over their distribution (e.g. Barange 1990; Barange *et al.* 1992; and Verheye *et al.* 1992).

The main trends to have been observed in the region may be summarised as follows. The highest zooplankton concentrations off northern and central Namibia are found in belts parallel to the coast which are located further offshore than the corresponding belts of maximum phytoplankton concentration (Kruger 1983; Shannon & Pillar 1986; Barange & Boyd 1992). Like phytoplankton the main gradients in zooplankton abundance appear to be inshore-offshore during active upwelling and north to south during quiescent periods (Olivar & Barange 1990; Barange *et al.* 1991). Abundance and cross shelf distribution is similarly linked to upwelling conditions, with the highest abundances being found during active upwelling (Timonin 1990). Seasonal peaks in abundance occur during late spring/early summer (November-December) and autumn (March-May) (Unterübacher 1964), and coincide with similar peaks in phytoplankton abundance (Kollmer 1963).

Again there has been little work at the mesoscale level in the northern Benguela, although Barange & Boyd (1992) do speculate on the likelihood of a 'semi-enclosed circulation system' in the central Namibia convergence zone promoting the maintenance of large euphausiid populations in the area. Furthermore, tight coupling between phytoplankton production and zooplankton production is indicated by the co-occurrence of seasonal trends in abundance, and is supported by studies in the southern Benguela which have found copepod fecundity to be directly related to phytoplankton abundance (Mitchell-Innes & Pitcher 1992).

Copepods and euphausiids are both omnivorous. Whilst their overall abundance is thought to be mainly regulated by phytoplankton availability, their impact on other zooplankton groups is completely unknown in the Benguela. Similarly little is known about the trophic impact of carnivorous zooplankton groups in the region such as ctenophora, siphonophora, jellyfish, chaetognatha, amphipods and crustacean larvae (Gibbons *et al.* 1992). However, given that jellyfish have been found to be significant grazers of zooplankton and ichthyoplankton in other part of the world (e.g. Purcell 1989; Cowan & Houde 1993), a dramatic increase in jellyfish abundance in the

northern Benguela during the 1970s resulted in some speculation as to their impact on ichthyoplankton in the region (Fearon *et al.* 1993).

2.3 ANCHOVY AND PILCHARD

2.3.1 Exploitation of the Fisheries: A Brief History

The Namibian purse seine fishery developed shortly after the end of World War II (Crawford *et al.* 1987). Adult pilchard (*Sardinops sagax*) have been the most heavily targeted pelagic fish due to their suitability for canning and human consumption, as well as their superabundance during the 1950s and 1960s (see figure 2.4a). Anchovy (*Engraulis capensis*), juvenile horse mackerel (*Trachurus capensis* & *T. trecae*), and juvenile pilchard have also been targeted, or caught as by-catch, primarily for processing into fish meal and oil. Walvis Bay has been the main port and processing centre. A southerly shift in fish distribution after the 1963 Benguela Niño also led to the establishment of processing and canning facilities in Lüderitz. By 1974, however, these facilities had been shut down due to the fish having moved back north. (See Crawford & Shannon 1988; Crawford *et al.* 1987).

The history of the pilchard fishery has been one of expansion and increasing catches until the late 1960s, followed by a series of stock collapses and a subsequent contraction in the size of the purse seine fleet (Crawford *et al.* 1987). The industrial effort directed on the pilchard peaked between 1966 and 1971 when in addition to the activities centred around Walvis Bay and Lüderitz South African factory ships were also operating in the region (Butterfield 1983).

Since the start of the industrial fishery there have been three stock collapses, as illustrated in figure 2.4a; namely from 1965 to 1970, 1975 to 1980, and 1992 to 1996. The first two collapses between them accounted for a drop in catches from 1.4 million tonnes in 1968 to 11,000 tonnes in 1980. Although superficially less dramatic, the most recent collapse is equally severe to the first two, as testified by the slide in landings from 115,000 tonnes in 1994 to an all time low of 2,000 tonnes in 1996 (Boyer pers. comm.).

Whilst no data exist for recruitment strength after 1987, in each case it appears that a string of years with poor recruitment (see figure 2.5) combined with the maintenance of large catches, as indicated by increasing catch:biomass ratios in figure 2.4c, are to blame for the collapses. The final death bell was sounded when catches fail to reach

annual quotas, as shown in figure 2.4b. Furthermore, the failure of the stocks to recover to their pre 1970s levels during periods of strong recruitment, such as from 1971-1973 and during the early and mid 1980s, has been due to increased landings; resulting in what Butterworth (1983) calls "the piggy back effect of a series of good year classes that could lead to significant stock recovery never being given the chance to develop".

The erosion of the population's age structure since the late sixties (figure 2.4d) is another consequence of widespread over fishing. As has already been mentioned in section 1.5, this has the effect of further reducing the population's natural stability by increasing the degree to which overall biomass is subject to recruitment variability, and consequently will have also contributed to the stock collapses by reducing the population's ability to bridge a string of years with poor recruitment success.

Between 1978 and 1983 anchovy replaced pilchard as the most heavily exploited clupeoid stock (see figure 2.7a). Since then fluctuations in anchovy catch and biomass have if anything been more variable than for pilchard. This, however, is unsurprising given that anchovy is shorter lived than pilchard, and so in terms of population size will be more susceptible to fluctuations in recruitment success than pilchard.

Full year by year reports on the status and behaviour of the anchovy, pilchard and horse mackerel stocks during the late 1970s and 1980s may be found in the Collection of Scientific Papers of the International Commission for South East Atlantic Fisheries.

2.3.2 Diet and Predators

Early studies off Namibia found pilchard and anchovy to have broadly similar feeding habits with juveniles primarily consuming zooplankton and adults primarily consuming phytoplankton (King & Macleod 1976). These findings have, however, been contradicted by more recent investigations off South Africa which indicate that the adults of both species are principally carnivorous (James 1987, James 1988). Even so, it remains likely that phytoplankton will be somewhat more important to clupeoid diets off Namibia than off South Africa given there is a higher abundance of chain forming diatoms in Namibian waters (Brown & Hutchings 1987 as cited by Hewitson & Cruickshank 1993). As regards larval diets, unfortunately there is no information for either anchovy or pilchard; not least because of the difficulty of catching samples with food in their digestive tracts (King & Macleod 1976, van der Lingen⁶ pers. comm.).

⁶ Carl van der Lingen, Sea Fisheries Research Institute, Roggebaai 8012, Cape Town, Republic of South Africa.

In spite of the similarities between pilchard and anchovy diets, experimental studies on food particle clearance rates indicate some degree of resource partitioning between the two species. South African pilchard have been found to be more efficient at feeding on particles with diameters smaller than 580 μm whereas anchovy are more efficient at clearing particles with larger diameters (Anon 1993).

Both species are important prey to a number of different predators including gannets, cormorants, seals, odontocete cetaceans, and predatory fish (especially chub mackerel, snoek and ground fish). There are few quantitative estimates of predation rates in the northern Benguela. Nevertheless they are likely to be broadly similar to the southern Benguela, where in the early 1980s, for instance, predation was thought to account for 73% of all mortality in the anchovy population (Bergh *et al.* 1985 as cited by Crawford *et al.* 1987; see also Baird *et al.* 1991 for a complete trophic energy flow network for the southern Benguela).

2.3.3 Reproductive Ecology, Distribution and Migration

Anchovy and pilchard are both serial spawners and generally spawn within the upper 50 m (Olivar 1990) in the area of minimum alongshore windstress between 18° S and 25° S (Boyd 1987, Le Clus 1990, Parrish *et al.* 1983). On average, anchovy tend to spawn closer inshore than pilchard (Cruickshank 1983); with pilchard eggs commonly being found within 120 km of the coast, and anchovy eggs within 60 km (Le Clus 1991). Pilchard maintain a background level of spawning activity throughout the year, whereas anchovy spawning is mainly confined to summer and autumn. Figure 2.10 gives a highly schematised representation of the major spawning grounds and migrations undertaken by both stocks.

Pilchard have two main spawning grounds; one centred over the 200m isobath between 19° S and 21° S where spawning peaks in late summer/autumn during stratified conditions when temperatures are between 16° and 22° C, and the other off Walvis Bay where spawning peaks during mid spring/early summer in water between 12° C and 16.5° C (Crawford *et al.* 1987). It is thought that the latter spawning ground was mainly used by older fish, and since the first stock collapse in the early 1970s it has diminished in importance. Le Clus (1992) found that the mid spring/early summer spawners produced larger eggs, which she discusses as being an adaptation for promoting larval survival during cooler conditions.

Anchovy spawning is mainly concentrated inside the 200m isobath between the mouth of the Kunene river and 22° S, although there is also some spawning to the

south of Walvis Bay (Le Clus 1991). For both species most spawning occurs when sea surface temperatures are anywhere between 15° and 22° C, and increased spawning activity is observed during periods of reduced upwelling and increased vertical stratification (O'Toole 1977; Le Clus 1991).

In general little is known about the distribution and retention of clupeoid larvae within the system. O'Toole (1977) reported that during summer and autumn, the highest concentrations of pilchard larvae were generally found between Möwe Bay and Cape Cross, whilst Hewitson (1987) noted that the highest concentrations of anchovy larvae tend to be found in offshore bands anywhere between the Kunene River and Walvis Bay. For both species the horizontal distribution of larvae at any particular moment is likely to reflect the balance between the offshore movement of upwelled water, onshore movements of oceanic water, and southerly intrusions of Angolan water, as well as any 'local' currents associated with mesoscale features in the region (Olivar 1990).

Southward moving 6-10 month old pilchard recruit to the fishery off Walvis Bay between March and August. The newly recruited juveniles then migrate northwards along the coast as far as southern Angola. Adults are thought to move south again for spawning (see Crawford *et al.* 1987), although there is some evidence for the maintenance of a sexually active adult population in Angolan waters around Baie dos Tigres (16°30' to 17° S) (Boyer pers comm.). Anchovy show broadly similar trends, with southward moving juveniles recruiting to the fishery off Walvis Bay from May onwards and then migrating back to the waters north of Cape Cross (Schülein 1986, Le Clus *et al.* 1988).

Both species recruit to fishery at standard lengths (L_C) of about 8 cm onwards. Anchovy start to spawn when they reach 9-10 cm even before they are one year old, whereas pilchard tend to become sexually mature at about 18 cm when they are a year and a half old (Le Clus 1979, Le Clus pers. comm.). Nonetheless the size and age at which both species become sexually mature varies according to the condition of the fish, growth rates and the size of the stock. Some density dependence is indicated given that during the first two pilchard stock collapse there were corresponding increases in growth rate (Butterworth 1983), increases in mean gonad mass (Thomas 1986), and decreases in the age and length at maturity (Butterworth 1983).

The stock-recruitment plots for pilchard and anchovy (figures 2.6 & 2.9) also indicate some degree of density-dependent recruitment regulation; with recruitment tending to be proportionally smaller with respect to parent stock when the stock is large, and vice versa. For pilchard this is also illustrated by figure 2.5b, in which the

general trend has been for relative recruitment success (i.e. relative to the adult stock) to increase as the stock decreases (figure 2.4a). Nonetheless, although density dependence can account for much of the long term variation in recruitment success, it tells us very little about year to year differences. For instance, figure 2.6 illustrates that within the two periods 1970 to 1977, and 1978 to 1987 the variation in pilchard recruitment was far greater than the corresponding variation in stock size, with figure 2.9 showing the same for anchovy between 1981 and 1987.

In order to explain these strong density-independent recruitment fluctuations, local and overseas scientists from the late 1970s onwards became increasingly interested in looking for environmental features and trends that might influence the reproductive ecology and recruitment success of these two stocks.

2.3.4 The Effects of Environmental Variability

Evidence for the environmental control of clupeoid recruitment in the northern Benguela is provided by Shannon *et al.* (1988), insofar as they found significant positive correlations between large scale sea surface temperature anomalies and the year class strengths of pilchard and anchovy for selected. Otherwise there have been relatively few direct 'environmental investigations' into recruitment variability. Nonetheless the effects of the unusual conditions during the 1984 Benguela Niño and during the winter of 1986, when the Lüderitz upwelling cell broke down, both received fairly substantial coverage.

During the 1983/1984 spawning season the maximum production of pilchard and anchovy eggs, respectively, was a quarter and twentieth of the previous annual maximum production means (Le Clus 1986). This resulted from poor adult feeding conditions due to the dramatic reductions in primary and secondary production during this period (Boyd *et al.* 1985). Anchovy recruitment consequently turned out to be disastrous (figure 2.8). To the surprise of some, however, pilchard recruitment relative to its stock size was better than average (see figure 2.5b). In retrospect it was concluded that enhanced larval survival due to the stratified conditions and reduced levels of offshore transport, associated with the influx of Angolan water, more than compensated for the poor pilchard spawning (Boyd *et al.* 1985).

1987 was an excellent year for anchovy recruitment and a good year for pilchard too (see figures 2.5 and 2.8). This, however, may have had little to do with events in the northern and central Namibian upwelling regimes, and more to do with the northerly advection of larvae which had been hatched in the southern Benguela. The theory

being that the suppression of the Lüderitz upwelling cell during the winter of 1986, which normally acts a barrier to the longshore transport of clupeoid larvae, was during this time unable to prevent their passage into the northern Benguela (Shannon & Agenbag 1987). Nevertheless a lack of relevant egg & larval survey data has prevented this theory from being adequately tested (Le Clus *et al.* 1988), as will be discussed in greater detail in section 5.4.3.

Other studies in the region, although not drawing direct correlations with year class strength, also indicate important interactions between the environment and the distribution and behaviour of these two stocks. For instance, Crawford & Shannon (1988) found latitudinal shifts in pelagic catches to be related to interannual differences in average SSTs; Parrish *et al.* (1983) noted that in general spawning was most intense in areas of increased vertical stratification and reduced offshore transport; Le Clus (1990, 1991) demonstrated a positive relationship between trends in the timing and distribution of spawning activity with average monthly SST anomalies and levels of vertical stratification; and various authors have found patterns in the distribution and abundance of pelagic ichthyoplankton (including horse mackerel) to be associated with calm stratified conditions, especially with regard to the Angola-Benguela frontal region and the seasonal southerly intrusions of warm saline water (O'Toole 1977; Badenhorst & Boyd 1980; Shannon & Pillar 1986; Hewitson 1987; Olivar 1990).

2.4 MANAGEMENT OF PILCHARD AND ANCHOVY STOCKS

Throughout the Namibian fishery's history various methods have been used to manage the anchovy and pilchard stocks; including the use of fishing seasons, closed areas, minimum mesh sizes, restrictions on the types of vessels operated, and the setting of annual catch quotas (Butterworth 1983; Boyer pers. comm.). As is often the case with short lived species, there has been a reliance on short term management policies with the initial fishing season, closed areas, and quotas often being modified according to catch trends as the season progresses.

2.4.1 Political and Economic Factors

Prior to independence most of the fishing activity off Namibia was conducted by South African and other foreign owned fleets. Consequently, Namibia itself derived very little benefit from these fishing activities as most of the profits were siphoned off overseas. Furthermore, despite earnest attempts by Namibian and South African scientists to maintain conservative levels of exploitation, scientific evidence as to the

status of the stocks during the 1960s and 1970s tended to be patchy and their quota recommendations were often steam-rolled by the economic concerns of the fishing industry. Indeed, each of the pilchard stock collapses, including the most recent, can be attributed to the maintenance of high or increasing quotas in spite of poor recruitment and declining populations, as was outlined in section 2.3.1. Circumstances surrounding the most recent collapse, however, do differ somewhat the others in that this time there was clear evidence from acoustic surveys that the stock was in a state of decline, as illustrated by figure 2.4a.

After independence the Namibian government committed itself to taking control of the region's marine resources, so that the profits from the fishing industry remained within the country instead of 'disappearing' overseas, and to ensuring a policy of 'sustainable management'. Indeed Helmut Angula, the then Fisheries Minister, went as far as saying, "we believe that a responsibly managed fisheries sector has the potential of becoming the engine of growth for the Namibian economy".

The economic forecasts were certainly rosy. It was estimated that after a full recovery of the demersal and clupeoid stocks, both of which had been depleted prior to independence, 1.3-1.5 million tons of fish could be harvested per annum (Van Den Bussche 1992). Depending on domestic processing capacity, this would represent foreign export earnings of between US \$225 million and US \$450 million; equivalent to 41-82% of total foreign export earnings in 1990. Although in retrospect these forecasts were overly optimistic, given the recent collapse in the pilchard stock and evidence for decline in the hake fishery (Boyer pers. comm.), they do indicate the degree to which the fishing industry could potentially benefit the country's economy.

Soon after independence Namibia declared a 200 nm EEZ and subsequently banned all vessels not licensed in Namibia from operating within the region. Poaching, especially by Spanish fishermen, was initially a problem but a policy of strict enforcement, via the use of helicopter surveillance, fast patrol vessels and strict sentencing for those caught, resulted in the numbers of illegally operating fishing vessels thought to be operating at any one time in Namibian waters dropping from 30-35 to between three and five from 1990 and 1991 (Van Den Bussche 1992).

Other important developments soon after independence included the provision of a legal framework for the fishing industry (Sea Fisheries Act 1992), the development of a new quota system in which fishing concerns were allocated a certain proportion of the global quota for a particular stock, and granting of fishing licenses to a limited number of vessels. In addition, Namibian involvement in the industry was encouraged via a number of policies; notably the granting of preferential quotas, licenses and catch levies

to Namibian fishing concerns, and to joint ventures between Namibian and overseas companies (Boyer pers. comm.).

2.4.2 Fishing Seasons and Closed Areas

Since 1951 closed seasons have been set for the purse seine fleet in order to avoid seasonal spawning and low oil yields, as well as to curtail fishing effort (Butterworth 1983). Since 1971 purse seining has in general been permitted from February/March to August/September.

After 1982 the season was split according to mesh size and vessel type. Prior to May/June purse seining has been limited to Refrigerated Seawater (RSW) vessels with 28 mm nets. Only after have unrefrigerated vessels and 11 mm nets been permitted (Thomas 1983; Thomas & Boyd 1985). This measure was taken in an attempt to reduce the by-catch of pilchard recruits, and to ensure that the adult pilchard landed were in good condition. The reasoning being that by limiting directed fishing on anchovy until after May/June the pilchard recruits would have been given enough time to outgrow the anchovy recruits, after which they would cease to school with the anchovy, and so would be less susceptible to by-catch (Butterworth 1983). This strategy has been subject to periodic season closures if too many pilchard recruits are considered to have been caught (Thomas & Boyd 1985).

Closed areas have been used from time to time since 1971, especially in the north from where catches often returned in poor condition prior to the widespread introduction of RSW vessels (Crawford *et al.* 1987). Also after 1978, when anchovy catches overtook pilchard, they have been used on an *ad hoc* basis to reduce the by-catch of juvenile pilchard with anchovy (e.g. Anon 1985).

2.4.3 Quotas and Stock Assessment

Global quotas for all pelagics were introduced in 1954, although they were not set according to any scientific assessment of stock size until the inception of the Cape Cross programme in 1971. Ironically their introduction was considered important in guarding against a Californian style pilchard collapse.

In spite of warnings on over-exploitation from the director of the Sea Fisheries Research Institute in Cape Town and the South West African Marine Research Laboratory (Boyd 1987), there was a steady increase in quotas between 1959 and 1968. This was in part due to apparent increases in pilchard abundance, but more

importantly from 1966 was in response to pressure from the local fishing industry following the deployment of South African factory ships in waters outside the 12 nm coastal region (which the South West African administration had no control over).

In 1969, quotas were not filled which led to requests for the removal of the factory ships, and by the end of the first pilchard stock collapse in 1971 quotas had been reduced and the last of the two factory ships had left Namibian waters. In 1972 the global quota was split between pilchard and other species, and in 1978 separate quotas for anchovy were introduced. Also in 1978, separate pilchard canning quotas were introduced in an attempt to reduce the dumping of fish unsuitable for canning. (Butterworth 1983)

With the start of the Cape Cross programme in 1971, pilchard quotas began to be set on a scientific basis according to relative biomass estimates from combined aerial and acoustic surveys. Surveys were undertaken during 1971-1974 and 1977, but were suspended in 1975 and 1976 as discussed in section 2.1.2. When in 1978 anchovy replaced pilchard as the most caught species, these surveys were finally stopped because anchovy schooling behaviour was less consistent than pilchard, thus making it harder to estimate their biomass from aerial shoal counting techniques.

1978 also saw a revision of quota setting policy due to the second collapse of pilchard, and anchovy having become the most important stock in terms of landings. Anchovy were first caught in the mid 1960s when 11 mm meshed nets were introduced, but it was not until the 1970s when catches started to approach those of pilchard (see figure 2.7a). Prior to 1978 management policy had been to encourage as much fishing on anchovy as possible in an attempt to boost the recovery of pilchard by minimising the potential for competitive interactions with anchovy (Crawford *et al.* 1987).

Anchovy quotas between 1978 and 1985 were set according to average catches during the 1970s (Butterworth 1983), estimates of maximum sustainable yield (MSY) from dynamic Schaefer production models, and projected biomass estimates for the forthcoming fishing season from virtual population analyses (VPA) (Le Clus & Melo 1981, 1982, 1983; Le Clus 1984, 1985). These quotas were then subject to modification during the fishing season depending upon how good recruitment appeared to be from the catch statistics. Nonetheless catches fell drastically short of quotas in 1982 and 1984, and it became apparent that quota setting according to these models was not feasible in view of the combined effects of high recruitment variability (figure 2.8), poor stock-recruitment relationships (figure 2.9), and the fact the anchovy fishery is mainly dependent on recruits. From 1985 onwards, no anchovy quotas appear to

have been set, and by 1987 recommendations for closed seasons were the main basis for management (Le Clus *et al.* 1987). Since 1990 management has purely been on the basis of effort limitation through the use of vessel licenses and closed seasons (Boyer pers. comm.)

Pilchard quotas between 1978 and 1987 were based on acceptable fishing mortalities from VPA biomass projections for the forthcoming fishing season, with 'projected' recruitment strength commonly being estimated according to averaged stock:recruitment relationships (Butterworth 1980; Le Clus & Thomas 1981, 1982; Thomas 1983; Thomas & Boyd 1985; Thomas 1986; Le Clus *et al.* 1987).

Whilst VPA is considered to provide reasonably accurate biomass estimates for previous years, estimates of current year biomass are subject to error (see section 1.5). For the Namibian anchovy and pilchard these errors appear to have fairly consistently led to an over-estimation of the current year biomass, as illustrated in figure 2.11. These biases will have to some degree facilitated over-fishing via the setting of inappropriately high quotas, and in the case of pilchard will have played a part in preventing a full stock recovery during the early 1980s despite strong recruitment in 1980, 1981 and 1984. Moreover, the use of average stock-recruitment relationships for making biomass projections, prior to quota setting, may have further exacerbated the problem due to there being a high level of density-independent driven variability about an average stock-recruitment relationship, as illustrated by figure 2.6.

From 1988 onwards, quotas and other management recommendations for pilchard and anchovy have been based on hydro-acoustic surveys (Boyd *et al.* 1989; Hewitson *et al.* 1989; Boyer *et al.* 1995). The general scientific policy both before and after Namibian independence has been to make quota recommendations based on 20 % of the most recent biomass estimates (Boyd *et al.* 1989; Boyer *et al.* 1995).

Biomass estimates from acoustic surveys undertaken since Namibian independence are considered to have been good indicators of the general state of Namibian pilchard stock. Nevertheless the precision of individual survey estimates is thought to be poor largely due to variable errors associated with changes in the distribution and behaviour of the fish (Boyer *et al.* 1995). Particular examples include ship avoidance behaviour (e.g. see Misund 1993), and when fish are concentrated close inshore or near the surface where they are beyond the reach of research ships and their acoustic equipment (e.g. see Le Clus *et al.* 1987).

In addition there has been criticism of the Namibian acoustic surveys due to the lack of a methodological survey design (Hampton⁷ pers. comm.; Barange⁸ pers. comm.). Surveys have not been conducted to pre-set random sampling criteria (e.g. Jolly & Hampton 1990), but have proceeded on a look and see basis according to where fish have been found. The criticism being that this non-random sampling introduces appreciable biases into the biomass estimates.

Nevertheless, given that these surveys have been primarily aimed at assessing pilchard abundance they have been defended on the basis of pilchard shoaling ecology (the criticism came from scientists who were primarily involved with South African anchovy surveys). It is argued that because pilchard have a tendency to shoal very much more tightly than anchovy, there would be the danger with randomly selected transects of missing too many shoals from which to make reasonable biomass estimates (Boyer pers comm.; Ona⁹ pers. comm.). Another reason for using an adaptive survey strategy was that the distribution of pilchard is often almost totally unknown prior to the start of the survey. This problem has become worse throughout this decade as the population has decreased and its range has contracted (Boyer pers. comm.).

2.4.4 Illegal Practices

In theory the Namibian fishing industry should be relatively easy to monitor given that most of the fishing and all of the processing activity is centred around one port only. Nevertheless illegal practices will have caused some inaccuracy in the catch statistics. Cram (1981) details three main types: namely under-recording of catches, species mis-identification after the introduction of split quotas in 1971, and dumping, especially of pilchard in poor condition or too small for canning.

These illegal practices are thought to be of minor importance these days, although there are currently two practices which are likely to cause some inaccuracy in the statistics (Boyer pers comm.). The first is the cutting loose of nets when the wrong size or species of fish are caught. Although perfectly legal, few of the fish 'cut loose' probably survive. The second is uncontrolled fishing in Angola, which is thought to have been a particular problem during 1995 and 1996. This second practice is particular concern given that in the past Angolan waters may have been an important refuge from heavy fishing off Namibia.

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⁸ Manuel Barange, Sea Fisheries Research Institute, Private Bag X 2, Rogge Bay 8012, CApe Town, Republic of South Africa.

⁹ Egil Ona, Institute of Marine Research, P/B 1870, Bergen 5024, Norway.

2.5 SUMMARY OF THE MAIN POINTS

1. Since the end of World War II marine research in the northern Benguela has been subject to a wide variety of technological, scientific, economic and political factors. Namibian independence in 1990 disrupted the relatively smooth flow of research conducted since the 1950s by South African and South West African scientists. Nevertheless with help from various overseas agencies Namibian scientists have rapidly gained experience and expertise. The recently launched Benguela Fisheries Interactions and Training Programme (BENEFIT) will have a significant impact on research programmes in the region, and represents the start of a new era in scientific collaboration between Angola, Namibia and South Africa.
2. The oceanography of the northern Benguela is well understood in terms of the effects of local and remote forcing on upwelling activity, vertical stratification and major current flows. The dynamics of mesoscale features have, in contrast, received less attention. Although there have been a number of studies which use remotely sensed data, the relative lack of direct current measurements has been a major obstacle to resolving the patterns of water flow associated with mesoscale features.

In a similar fashion the general relationship between the physical environment and the population dynamics and species composition of phytoplankton and zooplankton communities have been fairly well documented, especially as regards the effect of different levels of upwelling activity and vertical stratification. The mesoscale dynamics of plankton populations and their relationship to environmental conditions have, however, received comparatively little attention.

3. The general ecology of pilchard and anchovy in the region has been well described in terms of migrations, reproductive activity, and major predators. The state of the environment is thought to play a major role in influencing these stocks insofar as differing environmental conditions have been found to correspond with trends in the distribution of adults, spawning activity, larvae abundance and distribution, and, to a limited degree, recruitment success. Diet is an area in which there still remain some important unanswered questions particularly with regard to the relative importance of phytoplankton vs. zooplankton, and larval feeding habits. Shoaling behaviour and ecology is another area about which relatively little is known, but which is beginning to receive greater attention given its impact on acoustic survey strategies and biomass estimates.

4. Since the onset of industrial fishing in the 1950s the pilchard fishery, in particular, has been subject to heavy over-exploitation. Pilchard catches have fallen from a peak of 1.4 million tonnes in 1968 to an all time low of 2,000 tonnes in 1996. Three separate collapses in the stock can be identified: 1965 to 1970, 1975 to 1980, and 1992 to 1996. In each case the trends are the same; namely a string of years with poor recruitment, the maintenance of large or increasing catches, and finally catches not reaching the set quotas.

Various methods have been used to manage the stocks including the use of fishing seasons, closed areas, minimum mesh sizes, restrictions on vessel type, and the setting of annual quotas. Stock assessment has been conducted using a variety of different techniques, including aerial surveys, egg surveys, and the application of Virtual Population Analysis and Schaefer Production models to catch and effort statistics. Since Namibian independence, and for some of the years before, acoustic surveys have been the preferred method of assessment. Their main advantage being that they give a fairly good idea of current biomass prior to the setting of quotas.

CHAPTER 3

Data Evaluation and General Environmental Trends in the Northern Benguela from 1981 to 1990.

3.1 INTRODUCTION

The advent of remote sensing marked a new era in the observation and monitoring of the marine environment. The first remote observations of the ocean surface from space were from the TIROS-2 satellite during the early 1960's, and in 1978 the first sensors specifically designed for marine research were deployed with the launching of the Seasat, TIROS-N, and Nimbus satellites (Sherman 1985). Since then, many more sensors with marine observation capabilities have been placed in orbit, and remotely sensed information is now used for a wide variety of purposes including shipping, fishing operations, scientific research, coastal zone management, pollution control, and living resources management.

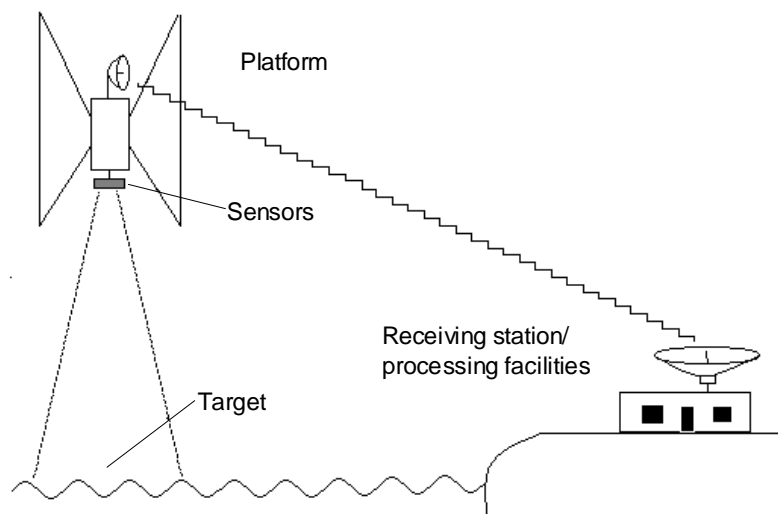


Figure 3.1. The main components of a remote sensing system

Remote sensing systems have four main components as illustrated in figure 3.1; namely, a target feature or property which requires monitoring, sensors for measuring levels of electromagnetic radiation, a platform for mounting the sensors on, and

facilities for receiving and processing the raw data. Three different types of sensor are commonly used for oceanographic purposes; those which measure reflected radiation, emitted radiation and back scattered radiation, as illustrated in figure 3.2. Sensors which fall into the first two categories are known as passive sensors, whereas those that fall into the latter are known as active sensors.

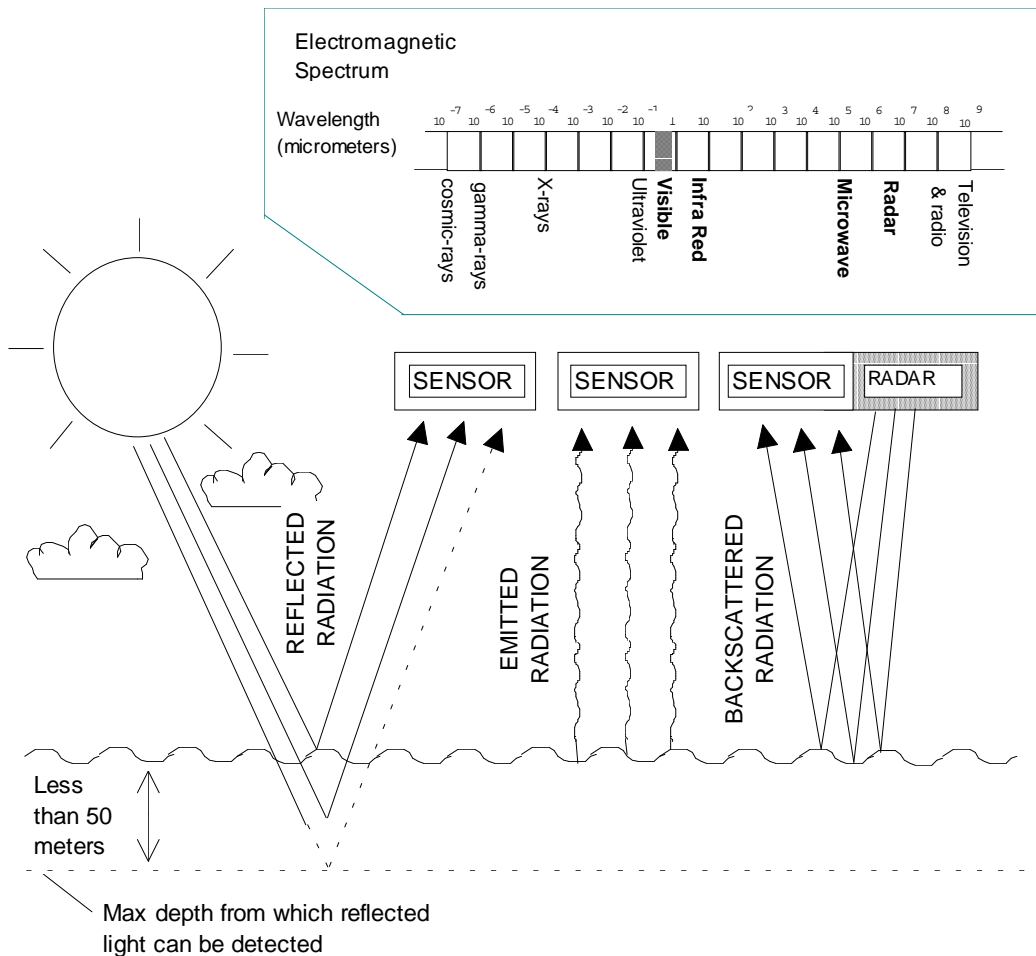


Figure 3.2. Schematic representation of the three classes of sensor most commonly used for marine remote sensing. The electromagnetic spectrum included in the inset is modified from Lillesand & Kiefer (1987).

Sensors which measure reflected radiation operate in the visible portion of the electromagnetic spectrum (EMS) and are used for monitoring chlorophyll concentrations and other factors which affect 'ocean colour', such as coastal sediments and pollutants. Sensors which measure emitted radiation operate in the infra red and microwave portions of the EMS and are typically used for deriving sea surface temperatures estimates. Active sensors which measure back scattered radiation operate in the radar section of the EMS. They are used for directly measuring sea level, wave

height and surface roughness, and as such may be used for indirectly estimating other environmental parameters such as surface wind stress and wind driven surface flow (e.g. Brucks *et al.* 1984; Carter 1993). A summary of the sensors used for marine monitoring and their various applications is provided in table 3.1. For a more complete description the reader is referred to the following publications: Robinson (1985), Salzman (1985), Victorov (1996), Robinson & Guymer (1996).

The main advantage of using satellites for marine research is their ability to sample large areas of ocean on a considerably more frequent basis, and with better spatial coverage than shipboard oceanographic surveys. For this reason remote sensing has caught the imagination of fisheries scientists as a tool for investigating links between the environment and the behaviour of commercial fish stocks.

'Ocean colour' images of chlorophyll concentration, and sea surface temperature (SST) images from infra red radiometry have been the most commonly used 'satellite products' for fisheries research. From these images it is possible to identify particular features known to influence the distribution and abundance of fish stocks, such as upwelling activity, frontal systems, and patterns of food abundance. To date, though, it is the distribution of fish populations, not their fluctuations in abundance, which have received the most attention.

For example satellite images have been used to investigate anchovy spawning off southern California in relation to upwelling activity and phytoplankton concentration (Lasker *et al.* 1981; Fielder 1983¹), the distribution of temperature fronts and albacore tuna in the California Current system (Laurs *et al.* 1984¹), the relationship between seasonal warming and the distribution of bluefin tuna in the Atlantic (Roffer *et al.* 1982¹), and for forecasting the distribution of commercial fisheries in the Arabian Sea off north-west India with respect to thermal variability (Kumari *et al.* 1994). Nonetheless their potential for investigating environmental effects on fish stock population dynamics is illustrated by studies such as that by McGlade (1987), in which remotely sensed SST data was used to assess the influence of Gulf Stream gyre activity on pollock recruitment off Nova Scotia.

Poor resolution environmental data collected, or averaged, over inappropriate spatio-temporal scales was one of the reasons discussed in chapter 1 (section 1.6.3) for the widespread failure to predict recruitment success in clupeoids on a year to year basis. Remote sensing offers a powerful solution to this problem, especially the compilation of SST and ocean colour satellite image time series. These time series have

¹ As cited in Laurs & Brucks (1985)

begun to be used for investigating physical variability and changes in chlorophyll concentration (e.g. Nykjaer & Van Camp 1994; Weeks & Shillington 1994), but their use for investigating environmental effects on fish recruitment remains fresh territory and presents exciting research opportunities.

Despite the benefits of visible and infra red remote sensing to fisheries research, there are, however a number of limitations which need to be taken into account. The most serious relate to cloud cover and limitations on the depth from which the sensors receive radiation. Visible light is typically only reflected from the upper few meters of the water column, whereas infra red radiation is emitted solely from a thin layer of water at the surface, known as the 'surface skin'.

Cloud cover can seriously limit the spatial coverage of satellite images, whilst 'depth limitation' can lead to biases in the representation of phytoplankton concentrations and sea surface temperature. For instance, if large concentrations of phytoplankton are found below the upper few meters, as may happen when a maximum chlorophyll layer (MCL) forms in association with a moderately deep thermocline, these will be missed by ocean colour measurements. Similarly, biases may creep into SST measurements due to disparities between the temperature of the 'surface skin' and the 'bulk temperature' of the mixed layer immediately below. For instance, negative disparities may result from evaporation across the air-sea interface during surface heating, whereas positive disparities may occur during periods of warm calm weather due to strong solar heating and the formation of a very shallow diurnal thermocline. The latter phenomena, when present, will be strongest during the early to mid afternoon, and the temperature fluctuations involved may be large enough to mask underlying oceanographic features (e.g. Flament *et al.* 1994).

Remotely sensed data has been used on a number of previous occasions in the northern Benguela for observing oceanographic processes, and to a lesser degree for investigating chlorophyll distribution and concentrations. Particular features and processes which have received attention include the following: upwelling dynamics (Lutjeharms & Meeuwis 1987; Kazmin *et al.* 1990), behaviour of the Angola-Benguela front (Shannon *et al.* 1987; Meeuwis & Lutjeharms 1990), characteristics of the upwelling front (Lutjeharms & Stockton 1987), upwelling filaments (Lutjeharms *et al.* 1991; Shillington *et al.* 1992), and the large scale dynamics of chlorophyll concentrations in the region within the context of the Southeast Atlantic and Indian Oceans (Weeks & Shillington 1994).

This chapter will introduce a time series of weekly and monthly SST composites for the northern Benguela between 1981 and 1990. It has three main aims: firstly, to

evaluate the quality of the data; secondly, to describe the environmental dynamics of the region during the 1980s, in terms of its major spatio-temporal trends in SST; and finally, to assess the extent to which SST trends reflect changes in wind forcing and vertical stratification. The structure of the chapter reflects these aims, with a section devoted to each one of them followed by a final discussion section.

3.2 DATA SOURCES

CORSA SEA SURFACE TEMPERATURE IMAGES

Weekly and monthly sea surface temperature (SST) images of the northern Benguela were extracted from the Cloud and Ocean Remote Sensing around Africa (CORSA) data set held at the European Joint Research Centre (JRC) at Ispra in northern Italy. The data set consists of weekly, monthly and annual 'level 3' SST composites for the area from 45° S to 45° N and 30° W to 51° E from July 1981 to December 1990. It was processed in the Marine Environment Unit at the JRC from level 1 Global Area Coverage (GAC) Advanced Very High Resolution Radiometer (AVHRR) data, under a data sharing agreement with NASA.

The daily polar-orbiting satellite passes from which the AVHRR GAC data were derived fell between 11:30 GMT for the Indian Ocean waters off eastern Africa and 16:00 GMT for the Atlantic waters off western Africa. Level 2 processing for SST and cloud masks was performed using standard techniques according to 'thresholds' and conditional relationships between the 'brightness temperature' values of channels 2, 4, and 5. The output SST values for each pixel were then subjected to feasibility tests according to the SSTs of the surrounding pixels. Pixels which failed the test were included in the cloud mask. (Villacastin² pers. comm.).

Level 3 processing involved averaging the daily level 2 SST images into weekly, monthly and annual composites. Four weekly composites were produced per month; with the first three composites being seven day averages and the final composite being an average of all the remaining days in the month. Equatorial regions aside, the level 3 composites were then successfully validated with SST data from the COADS (see below), NASA MCSST, and GOSTA (Global Ocean Surface Temperature Atlas) data sets. The composites have a resolution of 4 km at the equator, and have been

² Carlos Villacastin, Institute for Remote Sensing Applications, European Commission Joint Research Centre, 1-21020 Ispra (Va) Italy.

georeferenced according to the Mercator projection. The mean monthly composites from July 1981 to December 1990 are presented in appendix I.

COMPREHENSIVE OCEAN-ATMOSPHERE DATA SET (COADS)

The COADS data set is the result of a co-operative project to collect global marine weather and sea surface temperature observations from merchant ships since 1854 into a compact and easily used data set. It allows for the extraction of mean monthly environmental parameters for user-defined areas at resolutions down to 0.5° latitude X 0.5° longitude. In this study the data set was used for the extraction of SST values, and northerly and easterly wind pseudo-stress vectors. For the purposes of quality control, SST observations which exceeded 2.8 standard deviations about the mean were excluded from the calculation of monthly means.

Organisations involved in the compilation and distribution of this dataset include: The National Oceanic and Atmospheric Administration (NOAA), L'Institut Français de Recherche Scientifique pour le Développement en Coopération (ORSTOM), the National Climate Data Centre (NCDC), the Cooperative Institute for Research in Environmental Sciences (CIRES), and the National Centre for Atmospheric Research (NCAR). For a full description of the data set please refer to Woodruff *et al.* (1987) and Roy & Mendelsohn (1997), and for data extraction details to Mendelsohn & Roy (1996).

WIND READINGS FROM COASTAL WEATHER STATIONS

Thrice daily wind measurements from the Pelican Point and Möwe Bay coastal weather stations from 1978 to 1986 were kindly made available by Chris Bartholomea of the Namibian National Marine Research and Information Centre. The dataset was originally compiled at the Namibian National Weather Bureau in Windhoek. Wind speed and direction were estimated using pressure plate anemometers (du Pisani Pers. comm.). The data for Pelican Point is complete, whereas missing measurements are common for the Möwe Bay dataset, especially after 1984.

CTD MEASUREMENTS FROM SHIP SURVEYS

Environmental data from various research surveys along the Namibian coast between 1981 and 1985 were made available by Alan Boyd from the Sea Fisheries Research Institute in Cape Town. CTD measurements from twenty-one surveys were used in this study and were derived from routine environmental surveys and the South West African Pelagic Egg and Larval Surveys (SWAPELS). Details of the dates and latitudinal extent of each survey may be found in appendix II.

3.3 QUALITY OF THE CORSA DATASET

The purpose of this section is to evaluate the quality of the CORSA data by assessing the problem of 'cloud contamination', validating the SST values, and by placing the dataset within the context of longer term SST trends in the region. The term 'cloud contamination' is used to describe the presence of zero pixel values in the weekly SST composites due to the presence of cloud cover at a particular site throughout the entire week represented by the composite. Examples of cloud contamination can be found in in figures 3.3b & c.

Long-term sea surface temperature trends in the northern Benguela have already been investigated by several authors including Mclain *et al.* (1985), Walker (1987), Taunton-Clark & Shannon (1988) and Shannon & Taunton-Clark (1989). Nevertheless amongst these publications the most recent year for which SST trends were included was 1986. In order to fully place CORSA data within the context of any longer term environmental fluctuations it was considered important that this study should examine trends up until 1990.

3.3.1 Method

Cloud contamination in the northern Benguela was estimated both through time, for the whole time series of weekly SST composites, and across space, for each separate composite. Maps of percentage cloud contamination through time were generated from the CORSA dataset by applying a reclassification routine followed by a simple algorithm for calculating the percentages. The reclassification converted the original weekly composites into Boolean images, in which non-cloud contaminated pixels were given a value of 1 and cloud contaminated pixels remained at 0. These Boolean images could then be summed and the percentage cloud contamination values at different sites calculated. Conversely, levels of spatial cloud contamination for the whole area and each of the four sub-areas, illustrated in figure 3.4, were estimated by simply counting the number of zero value pixels within each area per composite.

Validation of the CORSA dataset was performed by comparing mean SSTs from the monthly composites with mean monthly SSTs from the COADS dataset. Two areas with relatively high numbers of merchant shipping observations were chosen: an inshore area corresponding to the main fishing grounds, and an offshore area corresponding to the main Atlantic shipping lanes to and from South Africa, as illustrated in figure 3.3a. The inshore and offshore areas were validated at different

spatial resolutions, $0.5^\circ \times 0.5^\circ$ and $1^\circ \times 1^\circ$ respectively. It was not possible to use $0.5^\circ \times 0.5^\circ$ boxes for the offshore area due to insufficient coverage from merchant ships.

Mean SST values per box from the two datasets were only matched with each other if the following criteria were met. Firstly, that the mean monthly SST value from COADS was calculated from more than 20 samples; and secondly, that there was less than 50% cloud contamination per box in all four of the weekly SST composites corresponding to the monthly SST composite in question. For both areas the CORSA and COADS SST values were then plotted against each other. A linear regression curve was fitted to assess the strength of association between the SSTs from the two datasets, with COADS SST acting as the dependent variable.

Long term SST trends in the region were examined also using the COADS dataset. Mean monthly SST values from 1960 to 1990 were extracted for each of the 1° latitude \times 1° longitude boxes illustrated in figure 3.3b. A mean SST for each month for the whole area was then derived by averaging the monthly SSTs from all the $1^\circ \times 1^\circ$ boxes. (An alternative approach would have been to extract the mean monthly SST for the whole region as a single block. This, however would not have allowed any control over possible shifts in the sampling distribution within the area). In order to resolve interannual trends a 13-point smoothing routine (Chatfield 1996) was applied to the monthly 'whole area' means, which were then presented as 'smoothed monthly SST anomalies' after removal of the 30 year mean SST. Decadal trends were also resolved by plotting the overall mean SST anomaly for each decade.

Spectral analysis was performed on the smoothed monthly anomalies in order to resolve the dominant periods associated with interannual fluctuations in temperature conditions. The analysis was performed using Santis (version 1.1) with a Hanning lag window (see Chatfield 1996). (Various lag windows were experimented with. The Hanning window was found to give the smoothest output power spectrum).

3.3.2 Results

CLOUD CONTAMINATION

The overall distribution of cloud contamination is shown in figure 3.4. There are two clear trends; firstly, that the highest levels of cloud contamination are found in the north-west off southern Angola and the lowest are in the south-east off southern Namibia, and secondly, that between 18° S and 23° S there is more contamination adjacent to the coast than further offshore. This last trend ties in with fog being

common feature of the central Namibian coastline (Shannon 1985a). Throughout the entire coastal region levels of cloud contamination are generally less than 25 %.

With regards to levels of spatial cloud contamination, figure 3.5 shows that for the main coastal area in figure 3.4 over 80 % of the composites images in the time series have less than 25% cloud contamination. Table 3.2 gives the frequency distribution of different levels of spatial cloud contamination within each of the sub-areas in figure 3.4, and as such mirrors the results in figure 3.4 in that the highest levels of contamination are found in the north.

Seasonal trends in cloud contamination are illustrated by the monthly maps in figure 3.6. The greatest seasonal variation is found in the north and north-west where levels of contamination are highest ($> 70\%$) during late winter (August and September) and lowest (0-10 %) during late autumn (April and May). In the south there is very much less seasonal variation and levels of contamination are generally below 30% throughout the year.

Because cloud contamination reflects the continual presence of cloud cover throughout an entire week, daily levels of cloud cover in the region are higher than the levels of cloud contamination found in this analysis. For example, Parrish *et al.* (1983) found daily cloud cover along the coast to be between 40 and 70%. One problem which has not been possible to address is the quantification of partial cloud contamination due to areas being under cloud for part of the week. This problem will be greatest when there are only one or two cloud free days per week for a particular area. This is illustrated in figure 3.3b where south of 23° S jagged discontinuities between areas with different SSTs shows how partial cloud contamination can mask the mesoscale thermal structure of the system.

Straight line boundaries between areas with different sea surface temperatures are also found in some weekly composites (e.g. see later in figures 5.6m and 5.6r). These boundaries have nothing to do with cloud cover, but instead result from areas falling outside the scanning range of the sensors (the swath width) for one or more of the satellite passes during a particular week.

VALIDATION

The regression fits in figure 3.7 clearly indicate that in general the CORSA dataset provides an accurate representation of SST values in the northern Benguela. The slope and intercept values of the regression curves do however indicate small negative biases in the CORSA SST values. For both the inshore and offshore areas the CORSA values

are typically 0.5° - 1° C lower than the COADS values. Given the region's proximity to the equator it is quite likely that these negative biases are due to evaporation across the air-sea interface as a consequence of intense solar heating. Nonetheless these biases are very small in comparison to the large SST fluctuations in the region and do not pose a problem for data quality.

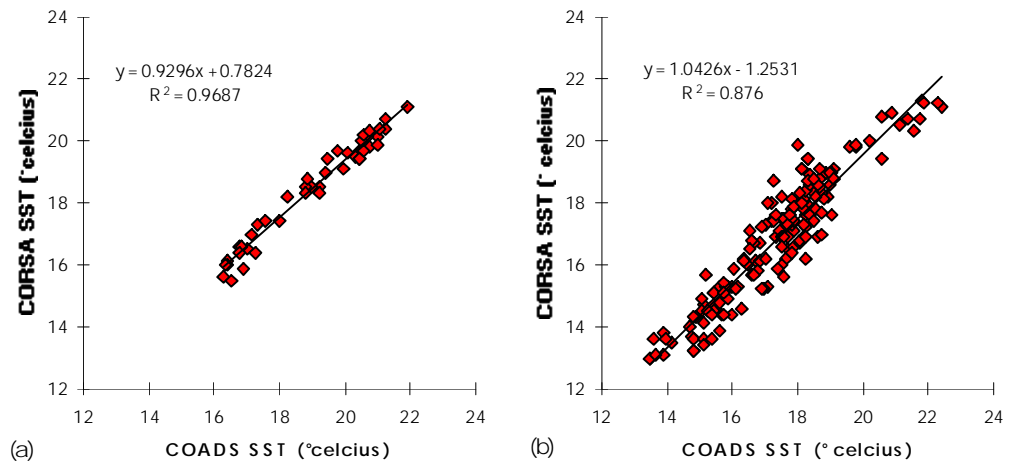


Figure 3.7. Validation of (a) offshore and (b) inshore mean monthly SSTs from the CORSA dataset with the equivalent mean monthly SSTs from ships of opportunity measurements in the COADS dataset.

In the introduction to this chapter diurnal surface warming was also discussed as being a potential source of bias in remotely sensed SST measurements. However, even if diurnal warming was a common problem in the northern Benguela it would not be detected by this validation technique for two main reasons. Firstly, given that the phenomena is likely to occur over short time scales (hours to days) it is unlikely to be resolved from mean monthly SST values. This is exacerbated by the fact that the COADS database does not allow for the separate extraction of day time and night time SSTs. Secondly, it is questionable whether it would be detected from ships of opportunity observations at all, especially from bucket measurements³, given that these surface measurements are likely to be taken from above, or close to a shallow diurnal thermocline, should one exist (Flament 1994). Nonetheless, given the generally high levels of wind driven turbulence in the northern Benguela, it is safe to assume that any biases due to diurnal surface warming will be fairly minimal.

³ As opposed to temperature readings from the sea water intake for engine cooling.

A final look at the scatter and R^2 values in figures 3.7a & 3.7b shows that the regression for the inshore area is less significant than for the offshore area. It is likely, however, that the reason for this lies mostly with inaccuracies in the COADS data rather than with the CORSA data. The COADS dataset provides no information on the spatial distribution of the SST samples within each box, nor on how the samples are temporally distributed within each month. Hence, given the higher levels of spatial and temporal SST variability associated with coastal upwelling in the inshore region, appreciable biases in the mean monthly COADS SST values will almost certainly result from the individual SST measurements not being uniformly distributed in space and time.

DECADAL TRENDS IN SEA SURFACE TEMPERATURE

The 30 year time series of smoothed monthly SST anomalies, and mean decadal anomalies are presented in figure 3.8a. The temporal sampling coverage in the COADS dataset from which these anomalies were calculated, in terms of the total number of individual SST measurements per month within the boxes in fig 3.3b, is shown in figure 3.8b. Predominately warm periods occurred during 1963, 1972-1974, 1980-1981, and 1984-1990, whereas cool periods occurred during 1964-1971, 1976-1980, and 1982-1983. The strong 'Benguela Niño' warm events in 1963 and 1984 stand out particularly clearly. The presence of dominant interannual cycles of around eleven and six years is indicated by the power spectrum peaks in figure 3.8c.

Despite the general trends being the same, there are some minor disagreements with the results in Taunton-Clark & Shannon (1988) for the Namibian coastal region. They found the periods from 1964-1971 and 1975-1978 to be warmer than figure 3.8a suggests. Aside from errors due to low sampling intensities, and taking into consideration the fact that their SST anomalies were calculated from a longer term average, an explanation may lie with the fact that they did not appear to control for possible shifts in the spatial distribution of samples within the region.

Finally, figure 3.8a shows that the years covered by the CORSA dataset (1981-1990) are on balance approximately 0.3°C warmer than the previous twenty years, with 1982 and 1983 being the only years with strong negative SST anomalies. It is tempting to speculate that global warming may be behind the trend towards increasing SSTs over this thirty year period. Nevertheless, it is not possible to draw any firm conclusions for three reasons. Firstly, given the inherent variability of upwelling systems, it is unlikely that thirty years is a long enough time span in which to observe the effects of global changes; secondly, the low number of temperature readings during

the early 1960s and early 1970s, as illustrated in figure 3.8b, casts some doubt as to the accuracy of the mean monthly SST values during these periods; and lastly, contrary to the trends in figure 3.8a, one might expect global warming to cause enhanced equatorward windstress, greater upwelling activity and hence long term decreases in mean SST (Bakun 1990) (see section 2.2.4 for a full explanation).

3.4 SST TRENDS IN THE NORTHERN BENGUELA DURING THE 1980s

The main features of the northern Benguela's oceanography have already been reviewed in some detail in chapter 2. This section seeks to describe the major spatial and temporal environmental features of the system using SSTs from the CORSA dataset, and to derive an upwelling index for the region which is relatively unbiased by seasonal trends in surface heating.

3.4.1 Method

DESCRIPTIVE STATISTICS

Descriptive statistics of SST conditions in the region were generated from across the entire CORSA time series and presented as colour maps using ERDAS Imagine's™ Model Maker and Map Composer. Maps of mean SST, standard deviation, and coefficient of variation were produced for the entire period as well as for each month of the year. Missing data points due to cloud contamination were omitted from the calculations.

LATITUDE-SPECIFIC WEEKLY SEA SURFACE TEMPERATURE AND UPWELLING INDICES

Mean weekly SSTs between 20 km and 50 km offshore, per 0.5° latitude were extracted from the CORSA dataset and the results presented as colour charts. The areas from which the mean SSTs were taken are shown in figure 3.3c. Missing SST values due to total cloud contamination within the 0.5° latitudinal areas accounted for less than 5% of all the values extracted, and were interpolated according to the average SST of the surrounding eight cells in the colour charts.

Two attempts were made to derive upwelling indices from these latitude-specific mean weekly SSTs. The first technique was broadly similar to that used by Nykjaer & Van Camp (1994) according to the difference in SST between water close to the coast and water further offshore. In this case, however, it proved to be unsuccessful, as the

offshore temperature conditions were not sufficiently independent of inshore conditions. The offshore SSTs were extracted from the COADS dataset for areas which were on average 800 km offshore. As it turned out this was not far enough to escape the cooling effects of intense inshore upwelling activity. Insufficient coverage by ships of opportunity prevented the extraction of SSTs from even further offshore

The second method was devised in response to these problems. It involved removing the regular seasonal fluctuations from the SST colour charts using a Fourier analysis technique. The rationale being that sea surface temperature on its own would provide an adequate scalar of the upwelling of cool nutrient rich water if it were not for seasonal changes in the intensity with which the surface layers are warmed by solar heating.

The main difficulty involved separating out seasonal SST fluctuations due to changes in solar heating from seasonal SST fluctuations due to other effects, such as changes in upwelling intensity due to seasonal shifts in the position of weather systems. In this case it was assumed that seasonal fluctuations in solar heating are much more regular, as regards both timing and amplitude, than seasonal changes in other factors which influence SST, and hence will always correspond to exactly one cycle per year (as opposed to somewhat longer and shorter period cycles).

A Fast Fourier Transform was used to convert the whole nine year colour chart of latitude and time-specific SSTs into a corresponding Fourier magnitude spectrum. High amplitude seasonal frequencies (1 cycle per year) were clearly identifiable and were masked out using a rectangular Gaussian mask with lower and upper boundaries of 0.84 and 1.125 cycles per year respectively. The deseasonalised SSTs were then derived by applying an Inverse Fast Fourier Transform to the 'masked' magnitude spectrum. The success of the technique was evaluated by comparing the deseasonalised SSTs with the original SST values across the entire time series. For a full description of Fourier analysis techniques for image processing the reader may wish to refer to Lillesand & Keifer (1987) and ERDAS (1995).

3.4.2 Results

GENERAL FEATURES OF THE UPWELLING SYSTEM

Perennial coastal upwelling polarward of 17° S is confirmed by the predominately inshore-offshore mean SST gradients south of this latitude in figures 3.9a and 3.10. These figures also confirm that the highest levels of cold water upwelling are found in

the Lüderitz region, between 24° and 28° S, and that upwelling activity within the entire region is seasonally at its greatest between June and November and at its least between December and May.

The standard deviation values in figure 3.9b act as an absolute index of the variability of temperature conditions throughout the region. As such, they highlight the contrast between the consistently high levels of coastal upwelling activity in the Lüderitz region versus the more variable conditions further north along the coast from 23° S to the Angola-Benguela frontal region. These trends are mirrored, albeit to a lesser degree, in figure 3.10 where to the north of 23° S average seasonal SSTs over the shelf can be seen to vary by as much as 6° C over the course of a year, whereas to the south they rarely vary by more than 3-4° C.

A relative index of temperature variability throughout the region is provided by the coefficient of variation values in figure 3.9c. In contrast to the standard deviation map, figure 3.9c draws attention to the high levels of environmental variability associated with coastal upwelling, and provides further support that 17° S is the northernmost point at which upwelling activity can be expected to occur throughout the year.

ANGOLA-BENGUELA FRONTAL REGION

The Angola-Benguela frontal region is characterised by high levels of SST variability due to the dynamic flux between cool and warm water masses in the vicinity of the front (e.g. Shannon 1985a; Shannon *et al.* 1987; Meeuwis & Lutjeharms 1990). As such, the general location of the front anywhere between 14° S and 18° S is indicated by the elevated standard deviation values in figure 3.9b.

Seasonal shifts in its position can be seen in figure 3.11. On average it is at southernmost point during March/April, where the zone of elevated standard deviation values is centred over 17°30' S, and at its northernmost point in July, where there is a faint band of elevated standard deviation values between 14°30' S and 15° S. These seasonal shifts can also be seen from the seasonal coefficient of variation maps in figure 3.12, albeit to a lesser degree.

THE CENTRAL NAMIBIAN CONVERGENCE ZONE (21° - 23° S)

The area over the wide Swakop shelf between 21° S and 23° S has generated interest as a transitional zone separating the consistent Lüderitz regime from the more seasonal upwelling regimes further north (Shannon 1985a; Boyd & Agenbag 1985; Barange & Boyd 1992). Figure 3.9a indicates that the region is characterised by

relatively strong longshore gradients in mean SST, and by inshore SSTs generally being higher than both to the north and to the south. These longshore gradients are at their strongest during summer and early autumn, as illustrated by figure 3.10, when there is often extensive seasonal warming in the central Namibian region.

Semi-enclosed circulation has been hypothesised as a possible mechanism promoting the retention of plankton in the region (Barange & Boyd 1992). Although these results reveal little about circulation patterns, substantial mesoscale activity between waters with different SSTs is suggested by the elevated levels of coastal SST variability within the convergence zone as illustrated in figures 3.9b & c.

INTERANNUAL TRENDS

Before commenting on differences between the individual years an important observation is that the presence of large inter-annual differences in coastal temperature conditions is largely a function of what happens during the months of February, March and April (i.e. late summer/early autumn). SSTs during the other months are very similar from year to year, and so have relatively little impact in determining interannual trends. Support for this observation comes from the much higher levels of inshore SST variability in figures 3.11 and 3.12 for these three months. Moreover a quick inspection of figure 3.13 confirms that these elevated levels of variability are principally due to high levels of SST variability between years rather than within the months themselves.

By extending the observation window to cover the months from January to May the inshore SSTs in figure 3.13 mark out 1984, 1988, 1989 and 1990 as the warmest years; 1982, 1983 and 1987 as the coolest years; and 1985 and 1986 as years with intermediate temperatures. The existence of two different types of summer/autumn warming patterns along the inner Namibian shelf between 17° and 24° is an additional feature of the system's behaviour drawn attention to by figure 3.13; namely warming due to surface intrusions of warm Angolan water along the coast, and warming in the absence of these intrusions.

Surface warming due to southwards intrusions of warm water from Angola during 1984, 1986 and 1988 is indicated by the extensive presence of SSTs greater than 25° C south of 14° S, and by the time dependent latitudinal staggering of elevated SSTs as the warmer water is advected southwards along the coast. The prolonged presence of high SSTs over the shelf between February and April during 1984 was a feature of the Benguela Niño that occurred in that year (see chapter 2). The 1986 and 1988

intrusions might also qualify as belonging to Benguela Niño events, albeit less intense ones, depending upon what the conditions in the equatorial Atlantic were at the time.

In contrast, southerly intrusions do not appear to account for the more modest summer and autumn warming trends during the other years in the time series. Seasonal warming during these years will be solely due to some combination of reduced upwelling, increased solar heating, and coastal intrusions of oceanic surface water. Sub-surface intrusions of Angolan water along the shelf during these months may also play a part, given that if upwelling does occur during these sub-surface intrusions it will be water that is warmer than the usual South Atlantic central water (Shannon 1985a) that comes to the surface (Boyd & Agenbag 1985, Boyd *et al.* 1987).

The contrast between coastal warming due to southerly intrusions of Angolan water versus coastal intrusions of oceanic water is illustrated by the weekly composites in figures 3.3b & c. The distinction between these two short-term warming trends is unlikely to be always this clear cut, however. For instance when there is reduced upwelling activity in the northern Namibian region (i.e. off Cape Frio) intrusions of warmer water may occur from both the north and the west.

UPWELLING INDICES

The time series of deseasonalised SSTs is presented in figure 3.14d. A comparison with figure 3.14a shows that the Fourier technique effectively removed a large component of the seasonal signal, and that much of the seasonality that remains is due to the superimposition of interannual trends onto the normal seasonal cycle. Furthermore, confirmation that the technique is sensitive to latitudinal differences in the seasonality of the system is illustrated during the second half of 1986 in figures 3.15b-d; where in the northern part of the system (figure 3.15b) the trend was towards increasing deseasonalised SSTs whilst in the south the trend was towards decreasing deseasonalised SSTs (figure 3.15d).

Nevertheless, the plots in figure 3.15 also indicate that deseasonalisation of the original time series was not sufficiently uniform between years for the deseasonalised SSTs in figure 3.14d to be used as upwelling indices. All four plots in figure 3.15 reveal the same problem, namely that those years in the middle of the series were deseasonalised to a greater extent than those at either end.

The results from this study are encouraging nonetheless, and the use of Fourier techniques for deriving upwelling indices is considered worthy of further investigation. For instance, the disparities in the extent of deseasonalisation between different parts of

the time series may be due to end effects, which are a common problem with Fourier analysis. Potential solutions for which include buffering the end of the time series with zeros, or linking several copies of the time series end to end prior to performing the analysis.

Finally, by pure serendipity figure 3.14c draws attention to a previously uncommented on feature of the system's behaviour. Namely the existence of a weak biannual cycle in SST variability. Inspection of figure 3.13 indicates that this may be partially due to the presence of secondary warming trends in autumn/early winter. For instance during 1984, 1985, 1988 and 1989 it can be seen that after the main period of warming, during summer/early autumn, there is some cooling which is shortly followed by a second period of warming.

3.5 WIND FORCING, SST AND VERTICAL STRATIFICATION

Wind-forcing is the main factor driving offshore transport and coastal upwelling in eastern boundary regions. Nevertheless, the use of Ekman transport as an index of offshore transport and upwelling activity is limited by the assumption that surface flow is determined solely by the action of wind drag on the ocean surface combined with the Coriolis effect, and that within a biological context there is a consistent relationship between offshore transport and the upwelling of cool nutrient rich water from below the pycnocline.

In reality, upwelling activity and surface circulation in these regions are also subject to a number of other local and remote factors; examples of which include bathymetry, coastally trapped waves, and inertial forces such as the remotely forced intrusion of warmer water masses. These factors not only disrupt the relationship between wind-forcing and upwelling activity by introducing time lags and non-linearities, but in extreme cases, for instance during Pacific and Atlantic Ocean warm events, they may completely block the upwelling of cool nutrient rich water altogether. Offshore transport and upwelling activity can therefore only be partially represented by wind based indices.

In contrast to wind indices, sea surface temperature is an emergent property of a system's oceanography, and as such reflects the dynamic balance between a wide spectrum of different forcing factors. In eastern boundary systems SSTs will be largely determined by the 'play' between the upwelling of cold water, solar warming of the surface layers, and the advection of warmer water masses from the edges of the system. As such they should provide a better representation of the physical state of an upwelling system than wind-based indices, and consequently are likely to be more useful for studies of environmental-fisheries interactions.

One problem with SSTs, however, is that they cannot directly reflect the presence or otherwise of sub-surface features such as thermoclines. Nonetheless given that the formation of thermoclines in the northern Benguela is also largely a function of solar heating, upwelling activity and intrusions of warmer water masses (Boyd 1987), there is likely to be some kind of relationship between surface temperatures and levels of vertical stratification.

The purpose of this section is, firstly, to examine the relationship between Ekman transport and sea surface temperatures in the region at two different spatio-temporal scales, and secondly to evaluate the extent to which coastal sea surface temperatures reflect levels of vertical stratification in the water column.

3.5.1 Method

LOCAL SHORT-TERM WIND FORCING AND SST TRENDS

Thrice daily Ekman transport indices were constructed for Möwe Bay and Pelican Point between July 1981 and January 1986. Alongshore wind stress was calculated using the bulk aerodynamic formula and modifying the results according to the coriolis parameter, as outlined in Peixoto & Oort (1992). The drag coefficient and air density values used for calculating wind stress were 0.0013 and 1.22 kg/m³ respectively (Bakun 1987; Roy⁴ pers. comm.). The thrice daily values were then averaged in such a way so as to give four mean weekly Ekman Transport values per month which fully coincided with the mean weekly SST values from the weekly CORSA composites.

Mean weekly inshore SSTs were extracted from the colour charts in figure 3.13 for the areas from 19° to 20° S and from 22°30' S to 23°30' S, for Möwe Bay and Pelican Point respectively. The relationship between changes in wind forcing and SST for the two areas was evaluated according to the difference in Ekman Transport, and SST between successive weeks. The strength of any relationship between the two variables was assessed using standard linear regression, with Ekman Transport acting as the independent variable.

LARGE SCALE SEASONAL WIND FORCING AND SST TRENDS

Mean monthly sea surface temperature, northerly wind pseudostress, and easterly wind pseudostress were extracted from the COADS dataset for each of the areas between 16° S and 22° S illustrated in figure 3.18e between 1965 and 1990. Alongshore pseudostress was derived from the northerly and easterly pseudostress vectors. Ekman transport was then calculated by modifying alongshore pseudostress by the Coriolis parameter, and the same drag coefficient and air density values used above with the coastal wind data. Spreadsheets with the COADS extraction and Ekman Transport calculations were kindly provided by Philippe Cury and Claude Roy.

The relationship between Ekman Transport and sea surface temperature was examined across the whole area (16°-22° S) for four seasonal intervals; namely January to March, April to May, June to September, and October to December. Plots were made of mean Ekman Transport versus mean SST over the whole area for each season,

⁴ Claude Roy, Océanographe, UR 15 - Département TOA, Centre ORSTOM de Brest - BP 70 - 29280, Plouzané, France.

and standard linear regression was used to assess the strength of any relationship between the two variables (again with Ekman Transport as the independent variable).

VERTICAL STRATIFICATION AND SST

Raster maps representing levels of vertical stratification were constructed from 21 ship surveys between August 1981 and March 1985. The dates and latitudinal extent of the surveys are presented in appendix II. At each CTD sampling station an index of vertical stratification was calculated according to the difference in temperature between 30 metres and the surface (0.01m). A distance-weight interpolation procedure was then applied to the stratification per station values to create the raster maps. The interpolation was performed using the *interpol* module in IDRISI™, according to a six-station search radius and a distance-weight exponent⁵ of 2.

Temperature difference between 0-30 m will in general be a good indicator of vertical stratification over the shelf, given that thermoclines if they occur tend to be found at depths shallower than 25m. The only major exceptions to this will be at the edges of the upwelling region where thermoclines may form at depths greater than 30 m due to the inshore or southward advection of warmer surface water masses (see Boyd 1987 for a full discussion).

Levels of stratification were compared with SSTs on a survey by survey basis for the three areas illustrated in figure 3.19. Within each of these areas the mean 'vertical stratification' was plotted against the mean SST from the weekly SST composite which overlapped with the dates when the temperature measurements were taken (see appendix II). Linear regression curves were fitted in order to evaluate the strength of any relationship between them, with SST acting as the dependent variable.

3.5.2 Results

LOCAL SHORT TERM WIND FORCING AND ITS RELATIONSHIP WITH SST

The Ekman transport and SST time series for both Möwe Bay and Pelican Point are presented in figure 3.16. From figure 3.17 it is clear that the expected relationship between changes in the two variables, i.e. that increases in Ekman Transport are matched by decreases in SST and vice versa, holds true at a statistically significant level ($P < 0.001$) for Möwe Bay only. Nonetheless even this is not a clean relationship as

⁵ 2 was the default exponent value used by *interpol*. For a smoother result one would need a lower exponent value, conversely for a coarser result one would use a higher exponent value.

witnessed by the low R^2 value, and the fact that decreases in Ekman Transport often coincide with decreases in SST and vice versa.

For both sites it can be concluded that there is nothing like a consistent relationship between fluctuations in Ekman transport and the upwelling of cooler water. Although these results do highlight the constraints of using Ekman Transport as an upwelling index at these spatial and temporal scales, they are subject to two limitations. The first is that neither Pelican Point nor Möwe Bay are noted for their high levels of upwelling activity, which limits the extent to which these findings can be generalised along the entire coastline. The second is that time lags between changes in Ekman Transport and changes in SST have not been taken into account, although it should be added that this is unlikely to be large problem given that previous investigations have found response times between changes in wind stress and surface temperature to be considerably less than a week (Walter 1937 as cited by Shannon 1985a, Kazmin *et al.* 1990).

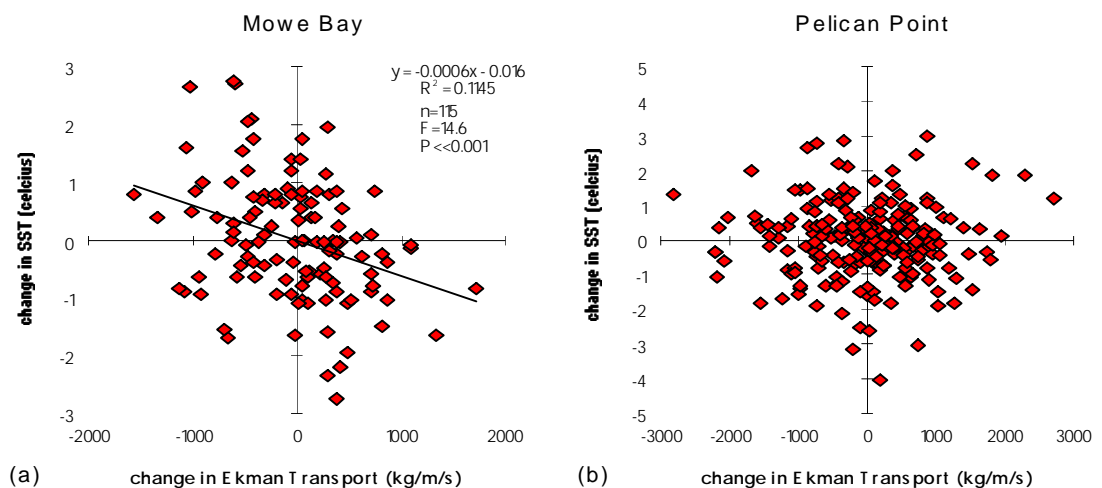


Figure 3.17. Relationship between fluctuations in Ekman Transport and SSTs off (a) Möwe Bay and (b) Pelican Point, according to the difference in mean Ekman Transport and SST values between successive weeks. Regression statistics are included for the Möwe Bay plot. For Pelican Point the relationship between the two variables was found to be insignificant.

Nonetheless, the fact that for Möwe Bay there is a significant relationship between the two variables, whereas for Pelican Point there is not, can be accounted for by differences in their bathymetry and oceanography. Any theoretical relationship between Ekman Transport and changes in SST off Pelican Point is likely to be scrambled by factors associated with its position in the central Namibian 'convergence zone'; namely its wide continental shelf and its proximity to the Lüderitz upwelling region. Indeed previous authors have concluded that interference from cold water upwelling off Lüderitz and solar warming over the shelf are more important in determining the

oceanographic dynamics of the region than upwelling favourable wind stress (Boyd & Agenbag 1985, Boyd 1987). In contrast, the narrower continental shelf off Möwe Bay, and its being beyond the reach off the Lüderitz upwelling cell, explains why it has a more consistent relationship between changes in Ekman transport and changes in the upwelling of cool water.

LARGE SCALE SEASONAL WIND FORCING AND ITS RELATIONSHIP WITH SST.

Plots of mean seasonal Ekman Transport versus seasonal SST are shown in figure 3.18. In none of the four seasons was there a significant relationship between the two variables. This is surprising given that higher mean levels of Ekman transport might be expected to cause greater upwelling activity and thus result in lower mean sea surface temperatures, and vice versa. Moreover, at this scale time lags and local conditions cannot be cited as reasons for the absence of a relationship between the variables.

Assuming that sea surface temperatures do provide a more integrated and realistic representation of the system's environmental dynamics than Ekman Transport, these results suggest that even when averaged over large space and time scales Ekman Transport does not adequately capture any of the main environmental trends between 16° and 22° S in the northern Benguela.

VERTICAL STRATIFICATION AND SST

Maps showing levels of stratification for the selected cruises are presented in figure 3.19. As was found in other studies (e.g. Shannon 1985a, Boyd 1987, and Le Clus 1991), the highest levels of vertical stratification occur in the central Namibian region over the broad Swakop shelf between 21° and 23° S. With regards to interannual trends, levels of stratification during the cool summers of 1981/82 and 1982/83 were much less than during the warmer summers of 1983/84 and 1984/85.

Plots of SST versus vertical stratification for each of the three areas in figure 3.19 are displayed in figure 3.20 with their regression statistics. The general trend for all the areas is the same, namely that higher SSTs are associated with higher levels of vertical stratification. There are, however, some differences between each area. General levels of stratification are greater in the south than the north (note that the y-axis scales are different for figures 3.20a, b & c), and both the R^2 and F values show that the relationship between SST and vertical stratification becomes tighter and more significant as one moves south.

In spite of the likelihood of there being some non-linearity in the relationship between the two variables, these plots do indicate that increases in SSTs will on average be associated with increased vertical stratification. Moreover, these relationships are likely to hold true over a wide range of conditions, given that upwelling and mixing in the surface layers will disrupt the presence of thermoclines, and that calm conditions, insolation and advection of warmer water masses from the system's edges will induce their formation (Shannon 1985a; Boyd 1987). An exception, however, may occur during unusually strong intrusions of tropical Angolan water, when warm water moves south over the entire depth range of the continental shelf. This phenomena was reported during the 1984 Benguela Niño (Boyd *et al.* 1987), and is evident between 21° and 22° S as an area with low stratification during March 1984 (see figure 3.19p).

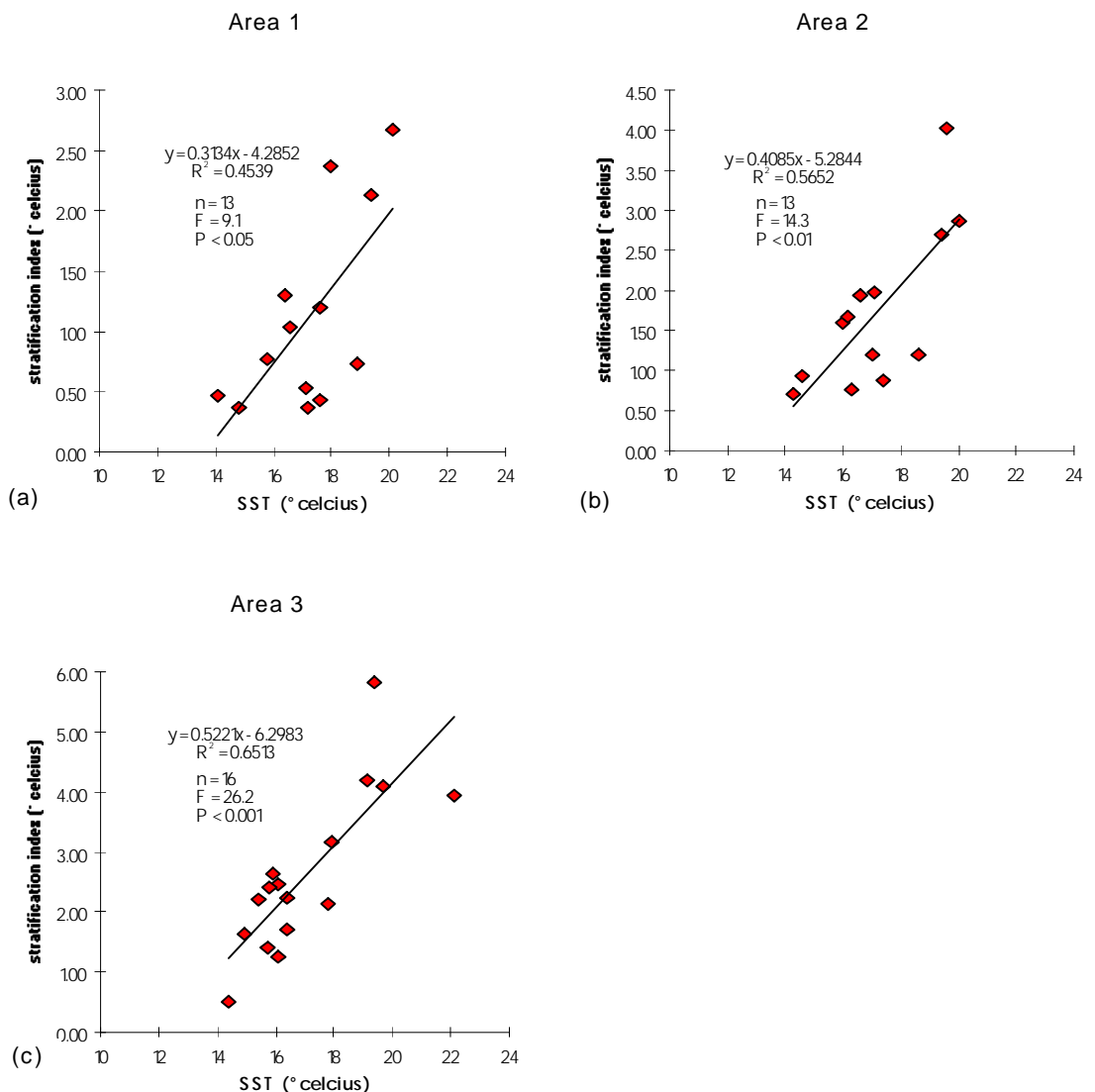


Figure 3.20. Mean SST versus vertical stratification for the three areas shown in fig 3.19a. Vertical stratification is approximated as the difference between SST and temperature at 30m.

3.6 DISCUSSION

3.6.1 Quality of the CORSA Data

The validation exercise confirms that the CORSA dataset provides an accurate representation of mean weekly sea surface temperatures in the northern Benguela. Cloud cover is more of a problem. Nevertheless figures 3.2 and 3.5 show that on the whole levels of cloud contamination through time are less than 30 % within the region, and figure 3.6 shows that within the coastal region nearly 90 % of the individual weekly composites have less than 30 % cloud contamination. The main problems are in the north especially during late winter/spring (July to October), where contamination values in excess of 30 % might, for instance, seriously hamper investigations into the mesoscale dynamics of the Angola-Benguela frontal region.

Nonetheless, the generally moderate levels of cloud contamination are unlikely to compromise the identification of large scale advective processes. Moreover, the upwelling filament between 25° and 27° S in figure 3.3a shows that when there is no cloud contamination, the temporal resolution of dataset is more than sufficient for the identification of reasonably permanent mesoscale features. It should be noted, however, that the dominant 3-10 day period in the event scale pulsing of upwelling activity (Boyd 1987) will inevitably mean that some of the event scale variability and mesoscale structure will have been smoothed out during the construction of the mean weekly composites.

3.6.2 Environmental Indices and Fisheries Studies

In choosing environmental indices for fisheries research there are four considerations: what are the environmental processes and features that are related to the question being asked; what in theory is the best way to measure them; how easily and cheaply can they be measured in practice; and finally, what indices have been collected in the past. Because non-experimental fisheries research is by its nature retrospective and often needs long time-series, this final 'consideration' also acts an important restraint. Moreover, it helps explain why it is only comparatively recently that time-series of satellite data have been processed for the purposes of fisheries research; despite the existence of routine oceanographic remote sensing since 1978.

The environmental features that we want to measure are likely to fall into the three broad categories of oceanographic process generalised by the Triad hypothesis (Bakun 1993) as described in chapter 1; namely *enrichment* of the food chain, *retention* of the early life history stages, and *concentration* of food particles for the first-feeding larvae. The ideal indices for monitoring each of these processes might be as follows: nitrate, phosphate and chlorophyll concentrations for measuring enrichment; current readings for measuring offshore transport; sea surface temperature readings for locating the presence of fronts and intrusions of warmer water; temperature based indices of vertical stratification for recording the presence or otherwise of thermoclines; and wind speed cubed for measuring turbulence in the water column.

Nonetheless of these seven indices, nitrate and phosphate concentrations, surface currents, and vertical temperature profiles cannot currently be directly sampled at sufficient spatial and temporal scales to be of much empirical value. This is due to their reliance on oceanographic surveys, and hence the frequency with which research ships can be deployed. (The placement of moored buoys with oceanographic monitoring capabilities may, however, provide a means whereby these parameters could be sampled frequently enough for fisheries applications in the future).

In practice sea surface temperature and various wind indices have been the most commonly used physical indices for looking at relationships between the environment and the behaviour of fish populations, in terms of their recruitment success, distribution and spawning activity. There are a three main reasons for this. Firstly, they are cheaply and regularly collected, both at sea by ships of opportunity and along the coast by research institutes. Secondly, records of these environmental parameters are typically very long and may stretch back as far as the last century. Thirdly, they often directly or indirectly represent environmental processes thought to influence the dynamics and distribution of fish populations.

Nonetheless with respect to this last reason the results presented in figures 3.17 and 3.18 show that sea surface temperatures and Ekman Transport either appear to be unrelated to one another, or do not covary as strongly as might be expected given the theoretical relationship between equatorward wind stress and upwelling intensity. Given that SST is an emergent property of a wide range of forcing factors, of which surface wind stress is only one, this suggests that SSTs provide a more realistic representation of the northern Benguela's behaviour than Ekman Transport. The implication for fisheries studies in the region being that SST is likely to be a more useful environmental index.

Remote sensing has clearly been an important development insofar as it has vastly increased the spatial and temporal resolution at which environmental data can be collected. Indeed, one need look no further than figure 3.13 to appreciate the value of time series of satellite images, in terms of allowing us to extract high resolution summaries of a system's dynamics. Furthermore, by adding chlorophyll concentration to the list of environmental indices that can be cheaply and intensively collected remote sensing has also provided a means of directly measuring levels of *enrichment*.

Nonetheless, the greatest value of satellite image time-series may lie in their ability to provide detailed spatial representations of the physical state of marine systems through time, rather than just acting as high resolution databases for environmental parameters. This is clearly illustrated in figures 3a-c where patterns in the gradient structure of the images allow us to visually identify particular features and processes associated with *enrichment*, *retention*, and *concentration*, such as upwelling activity, upwelling filaments and intrusions of warmer water masses.

The application of pattern analysis and recognition techniques to time series of satellite images might enable the behaviour of marine systems to be successfully quantified in terms of their spatial structure, and thus provide meta-level indices of physical behaviour for use in fisheries and ecological research. The difference from more traditional approaches being that a system's behaviour would be classified according to its entire spatial structure, rather than according to the absolute value of indices extracted from specific areas within the images (e.g. as in figure 3.13). This topic of pattern analysis will be returned to in the next chapter, where the region's spatio-temporal dynamics will be investigated by applying principal components analysis to the time series of weekly CORSA images.

3.6.3 Environmental Dynamics of the Northern Benguela

The surface oceanographic features of the northern Benguela are primarily a consequence of the dynamic balance between physical conditions which promote upwelling activity versus those which suppress it. Given that upwelling causes surface cooling and that its suppression results in warming, many of these features can be identified and their temporal characteristics evaluated according to patterns and gradients in the distribution of sea surface temperatures. The results presented in this chapter are the most complete and detailed representation of the surface behaviour and variability of the northern Benguela during the 1980s. As such they lend support to previously described features and trends, whilst also providing some new insights;

principally with regards to the post 1986 behaviour of the system, and to the nature of interannual variability itself. These results have already largely been placed in the context of previous investigation in section 3.4.2, and the remainder of this section is intended will act mainly as a summary.

General features of the northern Benguela upwelling system highlighted by these results include the following: 17° S being approximately the northernmost latitude at which cold water upwelling occurs throughout the year; the consistently high levels of upwelling activity off Lüderitz in contrast to the weaker, more variable upwelling off northern and central Namibia; and seasonal trends in cold water upwelling, with the highest levels generally occurring during late winter/spring (July to October) and the lowest during late summer/autumn (January to April).

Although direct observation of mesoscale phenomena is not possible from figures 3.9 to 3.12, these maps do highlight the high levels of SST variability associated with the Angola-Benguela front, seasonal shifts in the position of the front, and the presence of elevated levels of mesoscale activity in the central Namibian convergence zone (21° to 23° S). Any semi-enclosed circulation which may occur off central Namibia, as a result of this mesoscale activity, is likely to be most pronounced during late summer/early autumn (January to March), when the convergence between southerly flow over the northern & central Namibian shelf and northerly moving water from the Lüderitz upwelling region is at its greatest (Boyd & Agenbag 1985, Boyd *et al.* 1987).

Except for 1982, 1983, and 1987, the 1980s were generally warmer than the previous twenty years, with particularly warm conditions during the summers of 1984, 1988, 1989 and 1990. The interannual differences themselves were largely a consequence of the extent to which seasonal warming occurred during the months of February, March, and April. Two different types of warm water intrusions were associated with warming during these summer and autumn months; namely, southerly intrusions of tropical surface water from Angola (as occurred during 1984, 1986, and 1988), and shoreward intrusions of oceanic water.

The observation that inter-annual variability is largely due to conditions during late summer/early autumn is of consequence because it is often just before and during this time of the year that peak spawning occurs in the region's pilchard and anchovy stocks. Given that the physical behaviour of the northern Benguela during these months is likely to be important in determining the survival, or otherwise, of the early life-history stages, the implication is that year to year differences in physical conditions during late summer/early autumn are likely to play an important role in influencing year to year fluctuations in recruitment success.

3.7 SUMMARY AND CONCLUSIONS

1. The CORSA dataset provides a good representation of macroscale surface thermal features in the northern Benguela. Relatively long-lasting mesoscale features may also be identified if levels of cloud contamination are low. Small negative biases (0.5° - 1.0° C) in the recorded SSTs are likely to be due to evaporation across the air-sea interface. General levels of cloud contamination are reasonably low. For example, 90% of the composites in the time series had less than 30 % spatial cloud contamination within 200 km of the coast. High levels of cloud contamination (greater than 30 %) are a problem only in the northern part of system (equatorward of 19° S) between the months of July and October.
2. In comparison to the 1960s and 1970s, the 1980s were on balance a warm decade. 1963, 1972-1974, 1980-1981, and 1984-1990 were predominately warm periods, whilst 1964-1971, 1976-1980, and 1982-1983 were predominately cool. Dominant five and eleven year cycles in interannual SST fluctuations were found during these years.
3. The derivation of mean SSTs and indices of SST variation through time from the CORSA images confirm previously documented features of the northern Benguela, particularly as regards the following: the northern limit of upwelling activity, differences in levels of upwelling activity along the coast, seasonal trends in upwelling activity, seasonal trends in the position of the Angola-Benguela front, and elevated levels of mesoscale activity in the central Namibian convergence zone.
4. Derivation of a reliable upwelling index based on SST values proved difficult. Nonetheless, initial attempts at using inverse fourier transforms for removing the seasonal component in SST fluctuations, due to regular seasonal trends in solar insolation, were promising and are worthy of further investigation. An upwelling index based on SSTs would be preferable to wind based indices, given that SST is an emergent property of the system's behaviour and that either no or poor relationships between Ekman Transport and SST were found to the north of 23° S.
5. Interannual variability in inshore SST conditions is primarily a consequence of year to year differences in the extent to which warming occurs during late summer/autumn (February to April). This seasonal warming is due to combination of reduced upwelling activity, solar heating, longshore intrusions of warm water from the north and/or inshore intrusions of oceanic water. The extent and nature of

this warming may have an important impact on the reproductive success of the pilchard and anchovy stocks, given that peak levels of spawning activity are often found just before and during this time of the year.

CHAPTER 4

An Analysis of the Spatial and Temporal Patterning of Sea Surface Temperatures in the Northern Benguela

4.1 INTRODUCTION

The notion of quantifying the behaviour of marine systems according to their spatial structure was introduced towards the end of the previous chapter (section 3.6.2). The purpose of this chapter is to evaluate the use of principal components analysis (PCA) on the CORSA time series for the northern Benguela. The broad justification being that patterns in the thermal gradient structure of the CORSA images may tell us more about the oceanographic behaviour of the coastal region than area-averaged mean SSTs (e.g. figure 3.13) on their own.

PCA aims to reduce large multidimensional datasets to a smaller number of uncorrelated principal components (e.g. Chatfield & Collins 1980). It has been most commonly applied to remotely sensed data as a method of data compression in multi-channel sets of satellite images. Often there are high levels of redundancy in the information carried by different channels which PCA can remove by extracting fewer than n principal components from an n -channel dataset, thus allowing the original dataset to be replaced by the components (Lillesand & Kiefer 1987). Increasingly, however, it is also finding use as a method of investigating patterns of spatio-temporal change in time series of satellite images. Examples include the evaluation of changes in vegetation across Africa (Eastman & Fulk 1993), the behaviour of the Californian Current off Baja California from SST images (Gallaudet & Simpson 1994), and the behaviour of the coastal upwelling system off Mauritania also from SST images (Maus in prep.).

The advantage of PCA as a method of analysing sequential raster images lies in its ability to provide both spatial and temporal output for as many different features as are detected by the analysis. Insofar as the spatial patterning of SSTs in the northern Benguela can reflect the state of play between processes leading to enrichment, retention and concentration, as described by the Triad theory (Bakun 1993, see also section 1.6.2), it is hoped that this technique may help identify and track oceanographic

features thought to be important in influencing the recruitment success of the northern Benguela's pilchard and anchovy stocks.

4.2 MATERIAL AND METHODS

4.2.1 Data Preparation

The study window within which the analysis was performed is illustrated in figure 4.1. 235 weekly composites from July 1981 to August 1987 were retained for analysis, and 60 (20%) were discarded due to excess cloud cover. (It was not possible to include the entire time series due to ERDAS Imagine™ having an upper limit of 255 layers on which it can perform PCA). Composites were discarded if there was more than 30% cloud contamination within the entire study region, and/or more than 60% cloud contamination within any of the following latitudinal sub-divisions of this area: 16°-18° S, 18°-21° S, 21°-24° S, and 24°-26° S. Areas of cloud contamination in the 'chosen composites' were replaced by the distance weighted average of SSTs in the surrounding non cloud contaminated pixels.

All pixel values (i.e. SSTs) outside of the study window were set to zero and for the purposes of the analysis were ignored. For each composite the SST values within the study window were standardised according to the mean spatial SST and spatial standard deviation of the particular composite in question. Standardisation was judged to be an important step due to there being a wide range in levels of spatial SST variability amongst the weekly composites, and the fact that PCA works on the variance structure of the input data set. Spatial standardisation forces each time step to have a spatial variance of 1, and so gives each time step equal weight in PCA. (Both Eastman & Fulk (1993) and Fung & Le Drew (1987) conclude that standardised PCA is more effective than unstandardised PCA in the analysis of change in multi-temporal image datasets).

Lastly, the standardised composites were concatenated into a $t \times n$ matrix \mathbf{X} , where t = the number of time steps (i.e. 235) and n = the number of pixel sites within the study window (about 12 500).

4.2.2 Principal Components Analysis

The mathematics of the technique is presented in box 4.1. In applying PCA to a time series of images, each image should be thought of as a separate variable (or

dimension) and each pixel site as a separate sample. Output is both spatial and temporal. Principal component images are the spatial output, and as such, each successive component represents a spatial pattern of residual variance which is uncorrelated with previous components. The first component represents the spatial pattern which accounts for most of the variability in \mathbf{X} ; the second component represents the spatial pattern of as much as possible of the residual variability in \mathbf{X} which is uncorrelated with the first component; and so on for successive components.

Each principal component has an associated eigenvalue, which reveals the amount of variance the principal component accounts for. PCA produces as many principal components as there are time steps (i.e. input images), although in practice the first few components often account for most of the variance in the input dataset. In a standardised dataset, where each time step has a variance of 1 (i.e. the variance of each row in \mathbf{X}), the sum of all the the eigenvalues will equal the number of time steps.

'Loadings' are the temporal output from the analysis¹, with each principal component having its own set. As such, the loadings on a particular component indicate the similarity in spatial pattern between successive time steps and the component image. Loadings may be positive or negative, according to whether the time steps show similar or inverse spatial patterns to those described by the principal component.

4.2.3 Presentation and Interpretation of Results

There are no hard and fast rules as to how many principal components should be retained for interpretation. In theory every principal component may tell us something useful and is of potential interest. In practice, however, when there are reasonable levels of association (i.e similarity) between the different dimensions (i.e. time steps) most of the overall variance will be captured by the first few components.

In order to decide exactly how many components should be kept for interpretation two different rules of thumb are often used (Chatfield & Collins 1980). The first is to retain only those components with eigenvalues greater than or equal to one. The second involves looking at the pattern of eigenvalues and including only those components which occur above a natural breakpoint where the amount of additional variance explained by successive components becomes very much reduced (sometimes referred to as the 'scree test'). The latter rule is the one used in this analysis.

¹ Loadings are also sometimes referred to as 'component correlations', although they are not correlations in the strict statistical sense.

1) Calculation of the Covariance Matrix

$$\mathbf{R} = [1/(t-1)] \mathbf{X}\mathbf{X}^{-1}$$

where \mathbf{X} is the $t \times n$ matrix of concatenated images, t = the number of time steps, n = the number of pixel sites covered by the analysis, and \mathbf{R} is the $t \times t$ covariance matrix.

2) Calculation of Eigenvectors (Eigenmatrix) and Eigenvalues

$$\mathbf{E}\mathbf{R}\mathbf{E}^T = \mathbf{V}$$

where \mathbf{E} = the $t \times t$ eigenmatrix, \mathbf{V} = the $t \times t$ matrix of eigenvalues (in which all the non-diagonal elements = 0), and \mathbf{E}^T = the transpose of \mathbf{E} .

By convention the eigenvalues in \mathbf{V} are ordered according to size, with the largest coming first. The first eigenvalue represents the amount of variance accounted for by the first principal component, and so on for successive components. Likewise, the eigenvectors in the eigenmatrix are ordered according to the size of their associated eigenvalues. An important feature of the eigenvectors is that they are all orthogonal to each other. (In this way the variability accounted for by each component is uncorrelated to any of the other components, and each successive principal component accounts for the maximum proportion of residual variability in the input dataset not accounted for by previous components).

3) Calculation of the Principal Component Images

The principal component images are derived by linearly recombining the input matrix \mathbf{X} with the inverse of the eigenmatrix \mathbf{E} , as formalised below,

$$\mathbf{Y} = \mathbf{E}^{-1}\mathbf{X}$$

where \mathbf{E}^{-1} = the inverse of \mathbf{E} , and \mathbf{Y} = the $t \times n$ output matrix of principal component images, in which the pixel values of the i^{th} principal component are found along row i . The units in the output images (i.e. in \mathbf{Y}) are the same as the input units.

4) Derivation of Loadings

The loading values for each component are derived from the successive elements in their respective eigenvectors. For example, the first element in the eigenvector associated with the first principal component is the loading of the first image in the time-series on this component.

Box 4.1. The mathematics of principal components analysis for image time series analysis, some of the notation is similar to that in Gallaudet & Simpson (1994).

Component images were prepared for presentation by mapping a white-red palette onto positive values, and a white-blue palette onto negative values. The loadings for each component are presented as time-series plots. In order to resolve any underlying seasonal trends a 13-point smoothing routine was applied to each set of loadings. Spectral analysis was then performed on the smoothed loadings so as to confirm the presence or otherwise of any seasonal signals.

Each component was interpreted according to both its spatial and temporal output. Component images were evaluated in terms of the residual patterns of spatial SST variability they represented. In order to relate the components and their loadings back to SST patterns in the original (i.e. unstandardised composites), a total of 45 composites were inspected per principal component. This was done by observing the similarities amongst, and differences between, the following groups: composites which corresponded to the highest 15 loadings, those which corresponded to the lowest 15 loadings, and a selection of 15 composites which corresponded to zero loadings. Interpretation of the individual components was augmented by examining the smoothed curves and power spectra for evidence of seasonal & interannual, trends, and noting whether these trends corresponded with known (i.e. published) aspects of the system's behaviour.

4.3 RESULTS

The first three principal components (PCs) were retained for interpretation. Between them they account for roughly 87 % of the total variance in the standardised input dataset, as shown in table 4.1. The other components were discarded on the basis that individually they account for very little additional variance beyond that which has already been explained by the first three, as shown in table 4.1 and figure 4.2. The images of these first three components and their temporal loadings are illustrated in figures 4.3 and 4.4.

Principal Component I. PC I accounts for 79.25 % for the total variance. It represents the average spatial SST structure of the system, as deduced by the similarity between the patterns in figure 4.3a and the patterning of mean SSTs in figure 4.1, and by the lack of any substantial fluctuations in its temporal loadings, as illustrated in figure 4.4a. As such it conforms to previous observations on the nature of the first principal component. Namely, that when all the dimensions (i.e. time steps) are positively correlated then PC I is in effect an average, and that when the input is standardised the dimensions all have similar loadings on this component (Chatfield &

Collins 1980). (In view of these results it was considered unnecessary to perform spectral analysis on the loading values).

Principal Component II. PC II accounts for 5.21 % of the total variance. The spatial output (figure 4.3b) shows a pattern of very negative coastal values in the north grading into positive values as one moves south and away from the coast. The highest values are found offshore between 21° and 24° S, where there are two fairly distinct 'hotspots'; one between 21° and 22° S and the other between 23° and 24° S. In addition there is a third, albeit less well pronounced, offshore 'hot spot' at approximately 19° S. Except for the region north of 17° S, the general orientation of the gradients between areas with different standardised values is inshore-offshore.

The loadings in figure 4.4b are highly variable. Nonetheless the presence of some kind of a seasonal cycle is discernible from the smoothed plot, and is confirmed by the seasonal peak (i.e. at one cycle per year) in its power spectrum (figure 4.5a). In general the highest annual smoothed loadings appear to occur during summer, between November and January, whilst the lowest occur between late summer and early winter, February to May. These seasonal trends are particularly well developed between 1984 and 1987.

Interannual trends, however, are of greater relative importance as deduced by the two dominant spectral peaks occurring at frequencies of less than one cycle per year in figure 4.5a. Examination of the smoothed loadings shows that 1984 and 1986 have the lowest loadings, whilst 1986 and 1987 have the highest. The former corresponds to the strong southerly intrusions of warm Angolan water in the north during 1984 and 1986 (Boyd *et al.* 1987), and the latter to the northerly influx of Agulhas Current water in the south during the late winter/spring of 1986 (Shannon & Agenbag 1987; Shannon *et al.* 1990).

Principal Component III. PC III accounts for 2.36 % of total variance. In the component image for PC III both the northern and southern ends of the system have negative values, with positive values being found in between. The lowest values are found adjacent to the coast in the north, and between 17° and 19° S there exists a region with relatively strong gradients from negative to positive values. The highest values are found adjacent to the coast between 19° and 23° S. In addition there are two distinct 'hot spots' offshore of the 200m depth contour between 18° and 19° S and between 19°30' and 21° S.

Like for PC II, the loadings are highly variable. Nonetheless the smoothed plot in figure 4.4c and its power spectrum in figure 4.5b do indicate the existence of a

dominant seasonal signal. Indeed for all the years except 1986, figure 4.4c demonstrates that the highest annual loadings tend to occur sometime during the first six months of the year, whilst the lowest loadings tend to occur during late winter/spring (August to November).

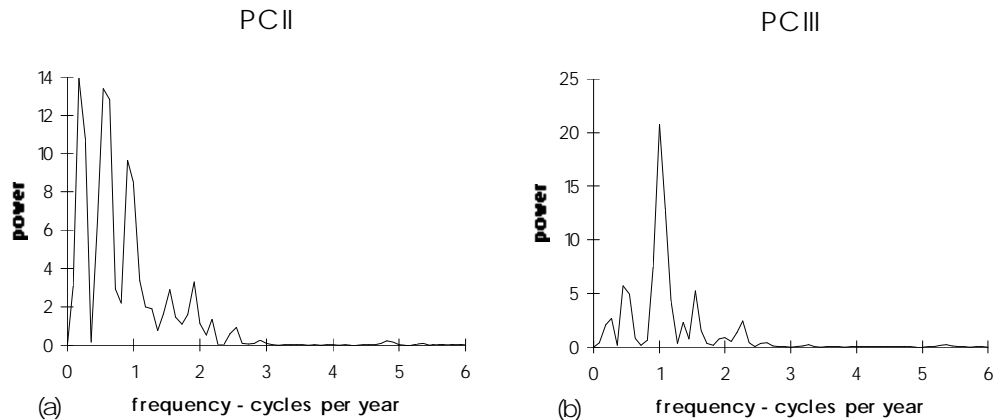


Figure 4.5. Power spectra of the smoothed loadings on PCs II (a) and III (b).

4.4 DISCUSSION

4.4.1 Interpretation of Results

Principal Component I. PC I represents the average spatial structure of the system in terms of its relative SST gradients; with the lowest relative SSTs being found in the Lüderitz region (24° - 28° S), and highest being found in the north where the northern Benguela upwelling system meets the warm tropical waters off Angola. Further interpretation was considered unnecessary due to the relatively uniform temporal loadings. However, it is worth noting that PC I from other principal component analyses of spatially standardised sets of images are similar to these results, insofar as they also represent mean spatial structure and have relatively constant loadings (e.g. Eastman & Fulk 1993, Maus 1997).

Principal Component II. PC II represents the balance in SST conditions between inshore coastal waters, especially in the north, and offshore waters, especially south of 21° S. From figure 4.3b we can predict that high loadings will occur when *relative to the south-west*, coastal SSTs in the north are cooler than usual, and likewise when *relative to coastal waters in the north*, offshore SSTs south of 21° S are warmer than

usual. The reverse being true for low loadings. Average (i.e. zero) loadings will thus result from the balance of SSTs between these different areas being roughly average. In addition, the orientation of the gradients in figure 4.3b might also lead us to expect high loadings when the dominant SST gradients are in the inshore-offshore direction, low loadings when the dominant gradients are in the longshore direction, and zero loadings when there is a mix of inshore-offshore and longshore gradients, as represented by the mean structure in PC I.

In practice figure 4.6 illustrates how high loadings do correspond to a dominant pattern of inshore-offshore SST gradients throughout the study region and upwelling in the north, whilst low loadings correspond to a dominant pattern of longshore SST gradients; with warm water in the north and cool water in the south. Composites corresponding to zero loadings (not shown) were mid way between either extreme.

In terms of the region's hydrology, relatively consistent inshore-offshore SST gradients within the study region indicate enhanced coastal upwelling activity in the north with respect to the Lüderitz upwelling region, and vice versa. Conversely, appreciable longshore gradients in SST indicate warming in the northern half of the system and the maintenance of at least some upwelling in the south. Potential causes of warming in the northern and central parts of the region include surface and sub-surface southward intrusions of Angolan water, shoreward intrusions of oceanic water, reduced upwelling combined with solar heating of the surface layers, or some combination thereof (e.g. Boyd & Agenbag 1985; Boyd *et al.* 1987). Further confirmation for these interpretations comes from the temporal characteristics of the loadings and the results from previous investigations into the physical dynamics of the region.

Charts of long term average SSTs by month and by degree latitude from shipping data (Boyd 1987, Boyd *et al.* 1987) verify that one would expect to find the lowest longshore gradients in SST, and hence the most regular inshore-offshore SST gradients, during early to mid-summer, which is consistent with the highest annual loadings tending to occur between November and January (figure 4.4b). As regards interannual trends, the unusually high loadings during late winter/spring in 1986 coincides with a strong influx of warmer water, originating from the Agulhas Current, into south-west African coastal waters. The effect of this warmer water on coastal hydrology was felt as far north as the Lüderitz region, where it suppressed the normally vigorous winter upwelling (Shannon & Agenbag 1987). (In terms of SST patterns, the presence of warmer water off Lüderitz would cause higher than usual loadings on PC

II, due to its effect in reducing longshore gradients and thus by association enhancing the consistency of inshore-offshore gradients throughout the region).

Seasonally, loadings tend to be lowest between late summer and early winter (figure 4.4b). This dovetails neatly with observations indicating that intrusions of warm saline Angolan water are most common, and that longshore gradients are strongest during late summer/autumn (e.g. Boyd *et al.* 1987; O'Toole 1980; Lutjeharms & Meeuwis 1987). More noticeable, however, are the interannual trends. The strong intrusions of Angolan water experienced during the Benguela Niño of 1984 and again in 1986 (Shannon *et al.* 1986; Boyd *et al.* 1987) are reflected in the very low loadings during the early part of these years. In contrast, late summer/autumn loadings during the cooler years of 1982, 1983 and 1985 were not so low.

Principal Component III. The residual pattern of SST variance high-lighted by this component (figure 4.3a) is of relatively warmer water in the middle of the study region (18° to 23° S) sandwiched by cooler water in the north and south. It would thus be expected that high loadings would occur when conditions in the central region are warmer than usual, mainly *with respect to* the north-east, but also with regards to the south; and the opposite for low loadings.

This interpretation is validated by figure 4.7. All the composites corresponding to high loadings clearly show higher SSTs in the central region relative to the north, and also to the south. Conversely composites with low loadings show the reverse; especially with regards to the existence of cooler water between 18° and 23° S relative to the waters north of 18° S.

In terms of the system's oceanography high loadings, and hence warmer SSTs between 18° and 23° S could be due to some combination of the following factors: reduced coastal upwelling, solar heating of the surface layers, and shoreward intrusions of oceanic water in association with a shoreward contraction of the offshore upwelling front. It is worth noting that although any warming in this central region must usually coincide with the maintenance of relatively vigorous upwelling activity north of 18° S for loadings to be high, this is not always the case. For example the third week in March 1984, as illustrated in figure 4.6g, had a high loading on PC III in spite of the marked absence of any relatively colder coastal water in the north. However, in this instance this is compensated for by the area to the south of 19° S corresponding very closely to the pattern in figure 3c, with relatively warm water lying inshore of cooler water between 21° and 25° S.

Unlike for PC II there is less in the literature with which we can compare temporal trends in the loadings. Nonetheless from temperature and salinity survey data between 1972 and 1974, O'Toole (1980) observed that seasonally the greatest onshore movement of oceanic water between 19° and 22° S occurred during summer which is consistent with annual loadings peaking between January and March during 1982, 1985 and 1987. This is not to say that there was no onshore movement of oceanic water during these months during the other years in the study, but if so it would have involved the suppression of the northern upwelling cells and so would not be reflected by high loadings on PC III.

Mesoscale Features. Although PC II and PC III primarily account for the macroscale dynamics of the region, distinct mesoscale features are drawn attention to by the 'hot spots' in figure 4.3a & c. It is possible that the offshore 'hot spots' in the vicinity of 19° S, 20° S, and between 21° and 24° S point to eddies being a common feature of these areas. Circumstantial evidence is provided by dynamic topography maps in the following publications which all indicate the presence of eddies at one or other of these locations: Stander (1964) as cited by Shannon (1985a), Boyd (1987), Salat *et al.*(1992).

4.4.2 Relevance to Recruitment Studies

PC II and PC III both highlight dynamic features of the northern Benguela which may have important roles in influencing the recruitment success of small pelagics in the region. In particular the loadings on these components directly reflect the presence or absence of conditions likely to promote egg and larval retention within the system. Strong negative loadings on PC II indicate the likelihood of longshore retention due to some combination of reduced upwelling activity in the north and southward intrusions of warm water, whilst high positive loadings on PC III indicate the likelihood of retention in the inshore-offshore direction due to some combination of reduced upwelling activity off central Namibia (relative to the north and south) and onshore intrusions of surface oceanic water.

The loadings on PC II could thus potentially act as an index of longshore retention and the loadings on PC III as an index of onshore retention. An important exception might occur, however, whenever there is a fairly uniform shoreward contraction of the offshore upwelling front due to reduced, but nonetheless similar, levels of upwelling activity along the entire coast. These conditions could also promote retention and would be reflected by positive loadings on PC II whenever inshore SSTs were greater than around 17° C, as illustrated in figures 4.6b and 4.6e. In order to account for

these exceptions, an additional measure of onshore retention could be constructed by weighting the positive loadings on PC II according to synoptic temperature conditions along the coast (see section 5.3.2).

The loadings on these two components may also indirectly reflect the presence/absence of thermal fronts and thermoclines, across which planktonic food for the larvae and juveniles may be concentrated. Off central and northern Namibia the presence of both these features is known to be related to the very same processes which enhance retention; namely reductions in upwelling activity and intrusions of warmer water masses (e.g. Boyd 1987).

With regards to enrichment the loadings on PC II and PC III reveal the relative difference in levels of enrichment between different parts of the system. Nevertheless, in no way are they suitable for deriving estimates of enrichment, according to gross levels of upwelling activity, due to the fact that the standardisation procedure in effect gives each input composite the same mean SST and exaggerates or diminishes the relative strength of the thermal gradients according to the range of SSTs found in the input composite.

Thus it would appear that the loadings on PC II and PC III provide reasonably direct measures of retention and indirect measures of concentration, but are of little use in reflecting levels of enrichment. Whether or not these loading values can in practice help with identifying predictable interactions between environmental conditions and the reproductive success of the region's pilchard and anchovy stocks will be investigated in the next chapter.

4.5 CONCLUSIONS

1. Standardised PCA is a suitable technique for quantifying the physical dynamics of the northern Benguela according to the evolution of its spatial structure through time; particularly as regards detecting differential levels of upwelling activity within the region and the intrusion of warmer water masses. The first three components accounted for 87 % of the total variance in the input data set, and were interpreted in terms of what is already known of the northern Benguela's oceanography.
2. PC I accounted for the mean thermal spatial structure of the region. PC II and PC III both identified and quantified aspects of the system's behaviour which may directly influence the retention or otherwise of clupeoid eggs and larvae, and which may indirectly result in the formation of strong thermal fronts and thermoclines

across which planktonic food may be concentrated for the first feeding larvae. The loadings on PC II measured the relative orientation of SST gradients from primarily inshore-offshore gradients to primarily longshore gradients, and as such clearly isolated thermal patterns associated with intrusions of warmer from both the north and the south. The loadings on PC III measured the difference in SSTs off central Namibia relative to the north and south, and as such clearly detected warming in the central region due reduced upwelling, solar warming and onshore intrusions of oceanic water.

3. The application of PCA to time series of satellite images promises in future to be a powerful technique of deriving environmental indices for use in studies of recruitment variability in eastern boundary upwelling regions.

CHAPTER 5

Environmental Influences on Clupeoid Reproduction in the Northern Benguela

5.1 INTRODUCTION

This chapter will examine how environmental conditions may be related to spawning activity, larval abundance, and recruitment success using the sea surface temperatures derived in chapter 3 and the principal component indices of spatial structure from chapter 4. The ultimate aim being the identification of sufficiently robust relationships between environmental conditions and recruitment to allow predictions of recruitment success for management purposes.

The variety of environmental processes which have been invoked to explain clupeoid recruitment variability were reviewed in section 1.6. The investigations in this chapter take place very much from the perspective of synthesis theories (see section 1.6.2). As such it is assumed that emergent features of the system's behaviour, such as sea surface temperatures and spatial structure, act as good proxies for a wide range of individual mechanistic processes (see section 1.6.1) which can influence recruitment. This assumption is justified on the grounds that many of factors thought to influence clupeoid recruitment in eastern boundary upwelling regions, such as upwelling activity, offshore transport, vertical stability of the water column, temperature, food production, turbulence, and warm water intrusions, not only often covary with each other but are also reflected by changes in SST and spatial structure.

With regards to spawning activity and larval abundance, previous studies give some idea of the kinds of relationships that we might expect to see. In both stocks we would generally expect to find increased spawning and larval densities with increasing sea surface temperatures and when conditions are suitable for the retention of eggs and larvae (e.g. O'Toole 1977; Parrish *et al.* 1983; Le Clus 1990; Le Clus 1991). Any such relationship with SST is unlikely to be indefinite, however, given that at the very high water temperatures found during Benguela Niño years spawning activity and larval abundance have been reduced due to impoverished feeding conditions (Boyd *et al.* 1985; Le Clus 1986).

In contrast, previous investigations have shed far less light on the combination of environmental conditions likely to lead to the eventual recruitment of strong versus weak year classes. The significant positive relationships between anchovy & pilchard year class strength and sea surface temperatures in the region found by Shannon *et al.* (1988) confirm that environmental conditions may play an important role in determining year class strength. Nonetheless these correlations hold true for selected groups of years only, and so provide no reliable basis for predicting recruitment success.

Assuming that there is indeed an underlying relationship between recruitment success and environmental conditions, there are three reasons why these linear correlations may break down during some years. The first is the presence of non-linearities in the relationship between environmental indices and recruitment success (e.g. Cury & Roy 1989), which may result in linear correlations holding true for selected groups of years only. The second is that the use of environmental indices which have been averaged over an entire region, and over the course of long time frames (such as a year) will inevitably mask shorter term and smaller scale events; events which in themselves may be important to eventual recruitment success. The third is related to the wide number of factors which can potentially influence recruitment success; for instance a correlation may break down if a factor which is not adequately reflected by the environmental index being used suddenly assumes a more dominant role in determining final year class strength.

The various investigations into environmental-recruitment relationships in this chapter have been designed to take these three problems into account. Firstly, whether or not there are any non-linearities between long term SSTs, from the COADS database, and recruitment is assessed using the same non-linear multiple regression technique employed by Cury & Roy (1989) for testing their *optimal environmental window* theory of clupeoid recruitment in upwelling regions. Secondly, an alternative measure of SST conditions has been devised which involves counting the number of weekly 0.5° latitude 'SST events' above certain cut-off temperatures from figure 3.13. In this way local and short term events which may influence recruitment are more likely to be fully integrated into the index and not be masked out. Finally, with regards to the problem of multi-causality, it is hoped that factors which are not adequately reflected by inshore SST fluctuations and which may nonetheless influence recruitment success may be identified by supplementing the high resolution CORSA SSTs, in figure 3.13, with information on the spatial structure of the system, from the loadings on the principal components in chapter 4.

The fact that the CORSA dataset only goes back as far as July 1981 will, however, act as an important constraint on any conclusions that can be drawn from using the SSTs and principal component loadings derived from this dataset, given that there is only six years overlap with the available estimates of recruitment success from VPA. This is not long enough to undertake a rigorous testing of theories, insofar as the overlap is less than the dominant 11 year period in inter-annual variability in the northern Benguela during the last 30 years (section 3.3.2 and figure 3.8c), and is much shorter than the multi-decadal climatically driven regime shifts thought to be responsible for instigating and maintaining dominance shifts between anchovy and pilchard populations (Lluch-Belda *et al.* 1989; Sharp & McLain 1993).

Nonetheless, the overlap is large enough to notice any obvious trends given the wide spread in recruitment success of both stocks (figure 5.1) and in environmental conditions (figure 3.13) between 1982 and 1987. Moreover the fact that intra-specific density-dependent regulation would have been minimal during the 1980s, due to the small size of the adult populations (see figures 2.6 and 2.9), means this is a period where the effects of density-independent recruitment regulation are likely to stand out especially clearly.

The chapter is split into three main sections followed by a conclusion; namely a section looking at relationships between the environment and egg & larval abundance, a section on the environment and recruitment success, and a discussion section.

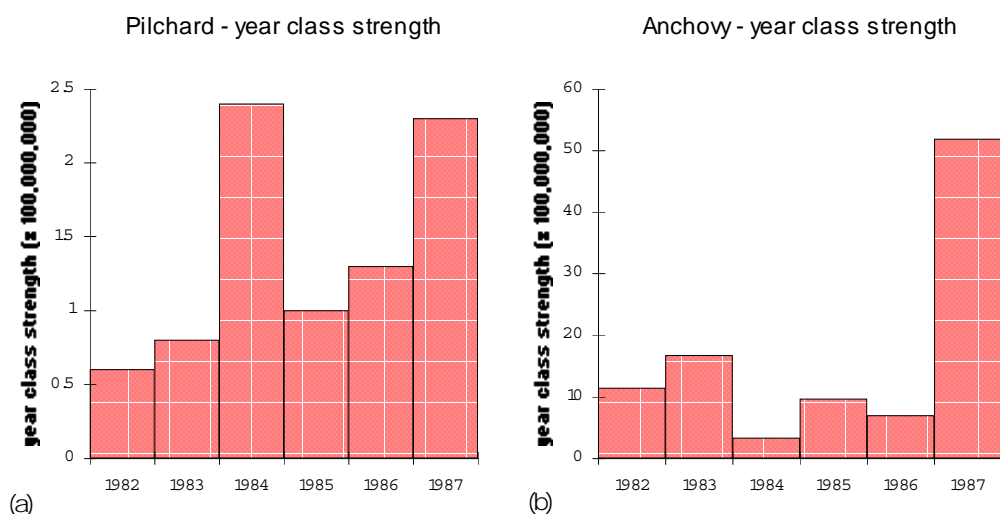


Figure 5.1. Year class strength for (a) pilchard and (b) anchovy from 1982 to 1987. The data was from Le Clus *et al.* (1988).

5.2 SPAWNING, LARVAL ABUNDANCE, AND THE ENVIRONMENT

Patterns in spawning activity and larval abundance are identified using data from combined egg and larval surveys conducted along the Namibian coast between 1981 and 1985. Relationships with environmental conditions during the course of the surveys are assessed using the coastal SST data from chapter 3 and the principal component indices of spatial structure from chapter 4.

5.2.1 Data Sources

Estimates of egg and larval abundance come from the South West African Pelagic Egg and Larval Surveys (SWAPELS). These surveys were conducted on a semi-regular basis during the main pilchard and anchovy spawning season (September to March) from 1971 to 1985. This study only uses data from the 19 SWAPELS surveys that were conducted after July 1981. The main detail of these surveys can be found in appendix III, and the sampling grid used is illustrated in figure 5.3s. The data itself was kindly made available to me by Frances Le Clus and John Hewitson from the Sea Fisheries Research Institute in Cape Town. No data was available for pilchard larvae. Hence, this study focuses on spawning activity in both species, and larval densities for anchovy only.

Sampling was conducted with 0.3 mm mesh Bongo nets, which were obliquely towed to a maximum depth of 50 m (Boyd *et al.* 1985). At each station the number of larvae sampled per size class were standardised to the number under 10 m² of ocean using flowmeter readings, mouth area of the bongo nets, and depth of the haul, using the method outlined in Smith & Richardson (1977) (as cited by Boyd *et al.* 1985). The number of eggs found per station were also standardised; this time to the number spawned under 10 m² every 24 hours. In addition to flowmeter readings, mouth area of the bongo nets, and depth of the haul, a correction factor was also used in the standardisation procedure to correct for the effect of temperature in influencing the time taken for the larvae to hatch from the eggs (see Le Clus 1983 for more details).

The sea surface temperatures used are the same as those from which the time and latitude-specific SST colour charts in chapter 3 were constructed (figure 3.13), and the loadings on PC II and PC III from chapter 4 are used as indices of the system's spatial structure (figure 4.3).

5.2.2 Method

Bar charts of the average number of samples collected per station per survey were constructed to illustrate differences in egg and larval abundance between surveys, and maps were produced to show the distribution of eggs and larvae sampled during each survey. In both the bar charts and maps 'total numbers of anchovy larvae' were used. Larvae were not broken down into their different size classes due to variable biases in the sampling of larvae of different lengths (Badenhorst & Boyd 1980, Hewitson 1987).

Eggs and larvae collected to the south of 24° S were omitted from the calculation of 'average number of samples per station per survey' due to the surveys during the 1984/85 spawning season only extending as far as 24° S. This is not a serious problem, however, given that very few eggs or larvae were ever found to the south of this latitude. The maps were created by applying a distance-weight interpolation routine to the standardised numbers of eggs and larvae found per station. The routine was performed using the *interpol* module in IDRISI™ according to a six-station search radius and a distance-weight exponent¹ of 2.

Rough comparisons between environmental conditions and egg-larval abundance during each survey were enabled in two different ways. Firstly, weekly SST images were produced from the CORSA dataset for the 'week' which corresponded most closely to the dates of each survey (see appendix III). Given that the sampling duration of the surveys was usually anywhere between 9 and 11 days the most appropriate week was chosen according to the week in which most of the survey occurred and/or the week in which most of the eggs were found. If there was any doubt the earlier week was always used. Cloud cover prevented the use of the most appropriate week for one survey only (Nov/Dec 1981). Secondly, symbols representing the order of magnitude of standardised numbers of eggs and larvae collected per transect per survey were overlaid onto the colour charts of mean weekly inshore SSTs (figure 3.13).

Whether or not spawning activity and larval abundance were in fact related to environmental conditions was then investigated with greater quantitative rigour, again using two different approaches. The first involved finding the relative frequency with which different orders of magnitude of eggs and larvae corresponded to different inshore SSTs. The inshore SSTs for each transect were taken from figure 3.13 for the week which corresponded most closely to the dates of each survey. The relative

¹ 2 was the default exponent value used by *interpol*. For a smoother result one would need to use a lower exponent value, conversely for a coarser result one would use a higher exponent value.

frequency with which different SSTs matched different levels of egg and larval abundance were calculated for three 'abundance classes'; namely: none, 1 - 100, and greater than 100 eggs and larvae per transect.

The second approach involved comparing spawning activity and larval abundance with the spatial structure of the system according to the loadings on principal components (PCs) II and III in figure 4.3. Plots were made of the loadings on PC II vs. PC III for those weeks which overlapped most closely with dates of the SWAPELS surveys. (The most closely overlapping weeks corresponded to same weeks for which the weekly SST maps were produced, as described above). For spawning activity, the loadings during the 8 surveys with the highest densities of pilchard and anchovy eggs were then compared to the loadings during the other 11 surveys. For the larvae, five surveys stood out as having very much higher numbers of larvae, so loadings were examined for these five with regard to the rest.

5.2.3 Results

Patterns in spawning activity and larval abundance can be seen in the maps and charts presented in figures 5.2 to 5.5. Two general trends are evident. The first is that for these years spawning activity and larval abundance tended to be highest either during January, February or March. The only exception being the intense pilchard spawning which occurred off northern Namibia during September 1981 (figure 5.3a). The second general trend is that most of the eggs and larvae tended to be found between 18° S and 25° S. There are exceptions, however, as illustrated by figures 5.3a, 5.4c, and 5.4d which indicate that high levels of spawning may occur in Angolan waters to the north of 17°30' S where they would have been missed by the surveys.

The range of different environmental conditions which occurred during these surveys is illustrated in figure 5.6. Comparisons of the egg abundance maps with figure 5.6 suggests that in both the pilchard and anchovy stocks spawning activity is greatest when there is moderate warming along the Namibian coastline north of 24° S, as shown by the presence of SSTs between 19° and 22° C over the continental shelf. This general trend, albeit with some exceptions, is further indicated by figures 5.7 and 5.8. Similarly, figure 5.9 and a comparison of the maps in figures 5.5 with those in figure 5.6 also suggests that warmer conditions generally appear to favour the presence of high concentrations of anchovy larvae.

Solid evidence for these observations is provided by figure 5.10. Levels of pilchard and anchovy spawning both show similar relationships with inshore SSTs; namely

background levels of spawning (1 - 100 eggs per transect) which display no strong relationship with SSTs, and elevated levels of spawning (> 100 eggs per transect) which do, in the form a dome shaped relationship between SST and the relative frequency with transects have greater than 100 eggs. For both species elevated levels of spawning activity are the norm when SSTs are between 17° and 23° C. The small peak at 14°-15° C in the relative frequency of pilchard spawning (figure 5.10a) may be due the remnants of the older age classes (2+), which prior to the collapse of the stock are thought to have been largely responsible for the elevated levels of spawning activity in cooler water during spring (Crawford *et al.* 1987).

The pattern for anchovy larvae is broadly similar although the dome shaped relationship is absent for elevated levels of larval abundance. Instead the relative frequency with which transects have greater than 100 larvae continues to increase in a more or less straight line relationship from low to high SSTs. Nevertheless the confidence that can be placed in the relative frequencies for the two highest temperature classes (20°-23° C and > 23° C) in figures 5.10a, 5.10b and 5.10c is compromised by the small number of transects with SSTs in these two classes, as illustrated in figure 5.10d.

The relationship between the system's spatial structure and patterns in egg and larval abundance is illustrated in figure 5.11. Once again the pattern is fairly similar for pilchard and anchovy spawning. For both species the eight surveys with the highest levels of spawning activity are located in similar areas of the PC II vs PC III plots. Insofar as positive loadings on PC III reflect oceanographic conditions which promote retention and concentration in the inshore-offshore direction (see section 4.4), the groupings in figure 5.11a and 5.11b do indicate that peak spawning often occurs when conditions are most suitable for inshore-offshore retention and concentration.

In contrast the fairly even spread of positive and negative loadings on PC II during these eight surveys presents more of a problem for interpretation. Given that negative loadings are associated with conditions which may promote longshore retention and concentration, due to intrusions of warmer water from the north (see section 4.4), it is tempting to conclude that these conditions are less important than those associated with inshore-offshore intrusions of oceanic water in promoting spawning activity. This is supported in part by the relatively low levels of spawning activity during surveys 15 and 16, which were the survey with the lowest loadings on PC II. Nevertheless, it needs to be remembered that the loadings values give little idea as to levels of enrichment (see section 4.4), and both these surveys occurred during the 1984

Benguela Niño when the unusually high temperatures and low nutrient concentrations were held responsible for poor clupeoid spawning (Boyd *et al.* 1985; Le Clus 1986).

The picture for PC II is further obscured by the fact that positive loadings on PC II may under certain circumstances indicate conditions promoting retention and concentration in the inshore-offshore direction, as discussed in section 4.4.2. An example is provided by the January 1984 survey (survey 13), when reduced levels of upwelling activity throughout the region combined with a fairly uniform (inferred) onshore movement of oceanic water, as illustrated in figure 5.6m, could promote retention and concentration.

The main exception to the groupings in figures 5.11a and 5.11b is the high level of pilchard spawning during the September 1981 survey. The loading values and a glance at figure 5.6a confirm that conditions at the time would hardly have been conducive to 'retention' and 'concentration' within the region. Whilst this demonstrates that macroscale conditions which promote 'retention' are not necessarily a pre-requisite for strong pilchard spawning, there are two other considerations which need to be taken into account. The first is that most of the spawning activity was located in a small area at the very northern end of the system where local conditions might have had a more important role in promoting spawning activity than the general macroscale configuration of the system as measured by the PC II and PC III loadings. The second is these high levels of spawning may, as has already been mentioned, be due to the remnants of the older age classes (2+), which prior to the collapse of the stock are thought to have been largely responsible for elevated levels of spawning activity between late winter and early summer (Crawford *et al.* 1987).

With regards to the abundance of anchovy larvae figure 5.11c shows that 4 of the 5 surveys with the high larval numbers occurred when conditions were likely to have promoted onshore retention and concentration as indicated by the positive loadings on PC III. Survey 5 is the odd one out insofar as the negative loading on PC III indicates that conditions would not have been so conducive for the retention of larvae. This survey was unusual, though, in that it was dominated by a larger (6-10 mm) size class of larvae, as illustrated in figure 5.12. Assuming larval growth rates of 0.4-0.6 mm per day (Badenhorst & Boyd 1980) most of these larvae would have been in the 0-5 mm size class during the previous week when their numbers would have been even higher, and when oceanographic conditions were more geared to retention and concentration, as illustrated by the 'X' in figure 5.11c. Thus on closer inspection even the March 1982 survey is not at odds with the observation that anchovy larval abundance appears to be

greatest when oceanographic conditions are suitable for onshore retention and concentration.

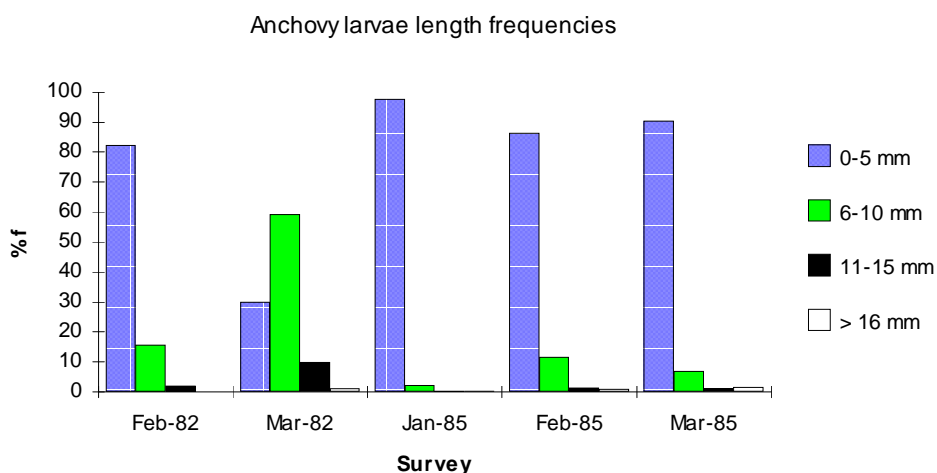


Figure 5.12. Relative length frequencies of anchovy larvae sampled during the five SWAPELS surveys between September 1981 and March 1985 with the highest larvae densities.

5.3 RECRUITMENT AND THE ENVIRONMENT

Potential relationships between environmental conditions and recruitment success were investigated by looking at both sea surface temperatures and the principal component indices of spatial structure over the course of an entire reproductive season. The investigations were divided between looking at long-term trends and trends during the 1980s, depending on whether the COADS or CORSA datasets were the source of environmental data.

5.3.1 Data Sources

Recruitment success up to and including 1987 was estimated according to the size of the age 0 year class from a virtual population analysis (VPA) conducted after the end of the 1987 fishing season, as reported in Le Clus *et al.* (1988). Problems with the estimation of current year biomasses' (and hence with current year estimates of year class strength) from VPA were reported in section 1.5, and evidence showing inaccuracies in current year estimates was presented in figure 2.11. Nonetheless, independent, albeit circumstantial, evidence for strong anchovy and pilchard year

classes during 1987 is provided by there being a high proportion of one year olds in the pilchard and anchovy landings during 1988 (see Hewitson *et al.* 1989).

Sea surface temperatures came from both the COADS and CORSA datasets. The same long term COADS SST anomalies presented in chapter 3 (figure 3.8a) are also used in this chapter, as are the mean monthly SSTs for the whole area illustrated in figure 3.3b from which the anomalies were calculated. SSTs from the CORSA dataset are the same as presented in figure 3.13. Lastly, the loadings on PC II and PC III in chapter 4 (figure 4.4) are used to represent the system's spatial dynamics.

5.3.2 Method

LONG-TERM TRENDS

Long term general trends between recruitment and environmental conditions were investigated using the COADS dataset. The same non-linear multiple regression technique used by Cury and Roy (1989) to test for 'optimal environmental windows' was employed here to uncover the nature of any underlying relationships between recruitment success, adult stock size and environmental conditions, as represented by the long term SSTs. The technique aims to find optimal transformations of the input data so as to maximise the R^2 value of the multiple regression. In this case with two independent variables, adult stock and sea surface temperature, the multiple regression is of the following form,

$$T_r = T_a + T_s$$

where T_r = the optimal transformation of annual recruitment success in terms of the number of year 0 fish $\times 10^9$, T_a = the optimal transformation of average annual adult stock size in terms of the number of adults $\times 10^9$, and T_s = the optimal transformation of average annual sea surface temperature.

The functional nature of the relationship between the two independent variables and recruitment success can be deduced by plotting the transformed values of the variables against their original values. Calculation of the optimal transformations and multiple regression statistics was performed using the ACE (Alternating Conditional Expectation) iterative algorithm. For more details of this algorithm the reader is referred to Cury and Roy (1989).

The analysis was run twice for both anchovy and pilchard using the data presented in table 5.1; each time using mean SST values from the COADS dataset, for the area in

figure 3.3b, which had been averaged over a different time span. The first time-span was from September of the previous year to August of the current year. The second time-span was designed to coincide with the summer/autumn period of peak spawning and larval/juvenile development, and was from November of the previous year to May of the current year. In all cases the optimal transformation of annual recruitment success was constrained to be linear so as to highlight any non-linearities in the influence of the independent variables.

Lastly, in order to estimate the amount of recruitment variance accounted for by adult biomass on its own and SST on its own, the analysis was run separately with each of these parameters as the sole independent variable. Once again the optimal transformation of annual recruitment success was constrained to be linear.

Year	Year class strength		Adult stock		SST	SST
	pilchard	anchovy	pilchard	anchovy	sep - aug	nov - may
1961	42.20		40.40		17.07	18.37
1962	53.80		48.24		16.43	17.58
1963	64.20		53.21		18.35	19.45
1964	40.00		63.15		17.10	18.19
1965	22.80		74.67		16.69	18.20
1966	16.80		66.76		16.64	17.81
1967	11.50		51.42		16.67	17.80
1968	10.00		38.08		17.11	18.53
1969	8.30		25.86		16.58	17.95
1970	9.10		15.02		16.58	17.97
1971	12.40		9.10		16.66	17.79
1972	19.60	43.50	8.20	15.90	16.97	18.15
1973	13.60	50.10	9.60	18.10	17.05	18.10
1974	10.30	39.60	14.60	13.30	17.69	18.95
1975	4.10	45.10	14.30	9.80	17.13	18.39
1976	1.40	33.50	10.80	12.70	16.74	17.88
1977	1.40	30.90	5.50	15.30	16.78	18.08
1978	0.40	52.60	1.90	14.80	16.56	17.52
1979	0.30	34.20	0.70	8.90	16.79	18.06
1980	1.50	39.20	0.30	3.70	17.06	18.20
1981	2.50	38.40	0.10	6.20	17.23	18.52
1982	0.60	11.40	0.70	6.30	16.62	17.59
1983	0.80	16.70	1.20	3.90	16.51	17.31
1984	2.40	3.30	0.70	2.40	18.07	19.40
1985	1.00	9.60	0.50	2.60	17.12	18.24
1986	1.30	6.90	1.10	2.30	17.42	18.75
1987	2.30	51.80	0.80	3.50	17.06	18.10

Table 5.1. Year class strength and adult stock size (numbers $\times 10^9$) of the northern Benguela's pilchard and anchovy stocks, as estimated from VPA (Le Clus *et al.* 1988), and average SSTs for two different time frames from the COADS dataset for the area illustrated in figure 3.3b.

TRENDS DURING THE 1980S

Environmental-recruitment relationships during the 1980s were investigated using the sea surface temperature and spatial structure indices derived from the CORSA dataset. Two approaches were used. The first involved determining the number of environmental 'events' during the main summer/autumn reproductive period which would be likely to promote successful recruitment. This was done by counting the number of weekly 0.5° latitudinal blocks in figure 3.13 between 17° S and 24° S which were over a certain temperature from November to May. Five cut-off temperatures were used: 17°, 18°, 19°, 20°, and 21° C. The strength of any relationship between recruitment success and the number of 'reproductively important environmental events' was assessed by fitting linear regression curves.

Secondly, a model of the relationship between recruitment success and environmental conditions was constructed for both species. It incorporates information on the spatial dynamics of the system, from the loadings on PC II and PC III, with SST data from figure 3.13. Its purpose was to enable the identification of domains in the relationship between SST and the system's spatial dynamics over the course of a reproductive season which would lead to differing levels of recruitment success.

The model was constructed by plotting an integrated inshore-offshore retention index for the months from November through to May against the total number of coastal 0.5° latitude blocks between 17° S and 24° S with mean weekly SSTs greater than 19° C during the same period. Calculation of the inshore-offshore retention index is covered in some detail below. 19° C was decided upon as a suitable cut-off SST given that the R^2 values from the regressions of recruitment success against number of SST events (see figures 5.18 & 5.19) was high for both species at this temperature. The final step was to identify domains in the relationship between the two variables associated with high, intermediate, and low levels of recruitment success.

The inshore-offshore retention index was calculated from the sum of positive loadings on PC III and the temperature weighted sum of positive loadings on PC II. Positive loadings on PC II were included in the retention index if the inshore temperatures from figure 3.13 were over 17° C (see below for the weighting procedure) so as to include conditions when there was a fairly uniform contraction of the offshore upwelling front and onshore flow of surface water throughout the region (see section 4.4.2 for more details). Calculation of a longshore retention index was not considered necessary as strong longshore intrusions of warm water from the north would invariably be associated with a high number of coastal SST events above 19° C.

It should be added that the inshore-offshore retention index may also indirectly act as a concentration index given that onshore movements of surface water will be associated with the onshore movement of the offshore upwelling front and the formation of thermoclines (Boyd 1987).

Mathematically the weighting and summation procedure for calculating the annual inshore-offshore retention index can be expressed as follows,

$$r_t = \sum_{i=1}^{i=28} (a_i + |a_i|)/2 \cdot (p_i / 14) + \sum_{i=1}^{i=28} (b_i + |b_i|)/2$$

where r_t = the annual inshore-offshore retention index for year t , i = the week (28 weeks between the beginning of November and the end of May), a_i = the loading on PC II during week i , $|a_i|$ = the absolute size of the loading on PC II during week i , p_i = the number of coastal 0.5° latitude blocks between 17° S and 24° S with SSTs greater than 17° C during week i (fourteen 0.5° blocks in total), and b_i = the loading on PC III during week i .

The terms $(a_i + |a_i|)/2$ and $(b_i + |b_i|)/2$ ensure that only positive PC II and PC III values are included for weighting and summation. If there were gaps in the loadings due to cloud cover, the mean of the values either side of the gap were used. In terms of spawning activity, 17° C was a suitable temperature for weighting the positive loadings on PC II, given that peak anchovy and pilchard spawning tends to occur from this temperature onwards (see figure 5.10).

5.3.3 Results

LONG TERM TRENDS

Long term smoothed SST anomalies and relative recruitment success for both species is shown in figure 5.13. The overall rise in pilchard relative recruitment since 1961, and especially after 1978, can be ascribed to the dramatic reduction in adult biomass (figure 2.6) and the associated reduction in intra-specific density-dependent recruitment regulation this would have entailed. Thus when assessing whether or not there is any relation between the SST anomalies and relative recruitment it is the fluctuations in relative recruitment that are of importance and not the magnitude.

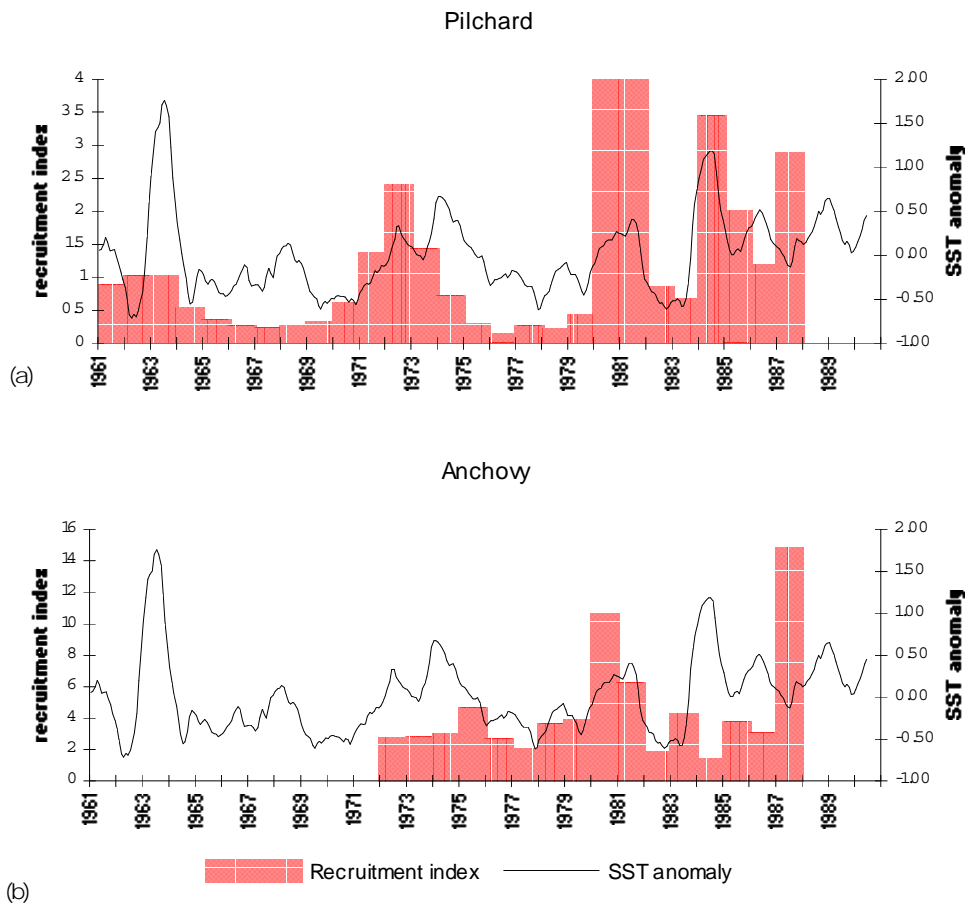


Figure 5.13. Comparison of the relative recruitment success of (a) pilchard, and (b) anchovy in the northern Benguela with smoothed SST anomalies for the region. The SST anomalies are the same as presented in figure 3.8a, and the relative recruitment values are the same as in figures 2.5 and 2.8.

For pilchard it appears that there is a positive relationship between the SST anomalies and recruitment from figure 5.13a, although the years 1965-1975 indicate that any such trend is not clear cut. The presence or absence of any relationship with SST anomalies for anchovy recruitment is less obvious (figure 5.13b), although it does appear that in general relative recruitment success is greatest at intermediate temperatures. For instance, the three strongest year classes all occurred during years when the SST anomalies were close to zero (1980, 1981 and 1987).

These observations are supported by the results from the non-linear multiple regressions. Plots of the relationship between the original values and the transformed values for each of the variables are presented in figures 5.14 to 5.17. The results are much the same irrespective of the time frame over which the sea surface temperature

values have been averaged. The R^2 values of these multiple regressions are presented in table 5.2, and indicate that the optimal transformations of adult biomass and sea surface temperatures, between them, explain between 67 % and 82 % of recruitment variance in the pilchard and anchovy stocks.

Time Span for Averaging SSTs	Anchovy recruitment	Pilchard recruitment
Annual (Sep-Aug)	0.76	0.82
Summer/Autumn (Nov - May)	0.67	0.75

Table 5.2. The R^2 values from the optimal multiple regression transformations of recruitment success versus adult stock and mean SST, as shown in figures 5.14 to 5.17.

The R^2 values from running the analysis with only one dependent variable are presented in table 5.3. Interannual differences in environmental conditions typically account for somewhere between 14 and 30 % of overall recruitment variability. These results also indicate that over the time period of the analysis the relative importance of environmental conditions in determining recruitment success is greater for anchovy than pilchard, and vice versa for the importance of adult stock size. It should be noted, however, that there is a far greater range in the size of the adult stock for pilchard (between 1961 and 1987) than for the anchovy (between 1972 and 1987), thus making it likely that pilchard recruitment would on average have been subject to a greater degree of density-dependent regulation (see figures 2.4 and 2.7).

Independent Variable	Anchovy recruitment	Pilchard recruitment
Adult Stock (no.s $\times 10^9$)	0.54	0.65
Mean SST (Sep-Aug)	0.30	0.24
Mean SST (Nov-May)	0.29	0.14

Table 5.3. The R^2 values from the optimal regression transformations of recruitment success versus a single independent variable.

For pilchard the transformations of adult stock (figures 5.14b and 5.15b) indicate a Ricker type density-dependent stock-recruitment relationship, with increases in adult stock at very large stock sizes actually having an inhibitory effect on recruitment success. The influence of environmental conditions, in terms of SST, is not so clear,

but the transformation plots (figures 5.14c & 5.15c) generally show that as sea surface temperatures rise so too does recruitment success. This trend is more evident in figure 5.14c when SSTs have been averaged over the reproductive season only.

The anchovy adult stock transformations in figures 5.16 and 5.17 indicate a similar density-dependent relationship between stock size and recruitment success as pilchard. This time, however, the shape of the transformation is more like a Beverton-Holt stock-recruitment curve than a Ricker curve. The relationship between the original and transformed SST values is, however, very different to pilchard with the dome shaped plots in figures 5.16c and 5.17c showing the presence of an optimal environmental window for anchovy recruitment. Depending on whether the mean annual SST is averaged across the whole year or only from November to May, figures 5.16c and 5.17c demonstrate that recruitment success is maximised at average SSTs of 17° C and 18.25° C, respectively, and drops off the further SSTs deviate from this point, irrespective of whether towards warmer or cooler conditions.

TRENDS DURING THE 1980S

The relationship between the number of coastal SST events above a minimum cut-off value and recruitment success for both species is presented in figures 5.18 and 5.19. In all cases 1987 was identified as an outlier, and was omitted from the regression curve fits. This omission is justified on the grounds that strong recruitment during 1987 may have been at least partially fuelled by the northward advection of clupeoid eggs and larvae from the southern Benguela during the anomalous intrusion of Agulhas Current water into the northern Benguela during the latter part of 1986 (Shannon & Agenbag 1987; Hewitson 1987; Le Clus *et al.* 1988).

Outliers apart, pilchard and anchovy both had highly significant relationships between recruitment strength and the number of coastal SST events above certain temperatures from 1982 to 1986. For pilchard the relationship is positive and is strongest for cut-off SSTs of 19°, 20° and 21° C, whilst for anchovy the relationship is negative and strongest for cut-off SSTs of 17°, 18° and 19° C. Five years is clearly not long enough to draw any definite conclusions from. Nevertheless, the strength of these relationships not only tells us something of the likely relationship between environmental conditions and recruitment success during these years, but also indicates the advantage of counting SST events rather than averaging SSTs over large area and time frames.

The combined spatial structure and SST models of pilchard and anchovy recruitment are presented in figure 5.20. For both species various domains have been outlined in

which one might expect to find good, intermediate, and poor recruitment success, based on the levels of recruitment success following on from each of the six plotted reproductive seasons (see figure 5.1). The models clearly need to be tested further with more years worth of data. Nonetheless an important feature that they both share is that by including the system's spatial dynamics the 'outlier' reproductive season of 1986/87 can also be taken into account irrespective of whether recruitment during this year originated from within or outside of the northern Benguela.

5.4 DISCUSSION

The results presented in this chapter confirm some previously observed trends with regards to clupeoid spawning activity and larval abundance in the northern Benguela, whilst also providing some new insights into the relationship between environmental conditions over the course of a reproductive season and recruitment success.

5.4.1 Spawning and Larval Abundance

The results in figures 5.10 & 5.11 further confirm that peak spawning in both species, and peak anchovy larval abundance, occur during periods of reduced upwelling, increased water column stability and intrusions of warmer water masses (especially from offshore); insofar as elevated coastal SSTs and the loadings on PC II and PC III act as suitable proxies for these process. Moreover, the dome shaped relationship in figures 5.10a & 5.10b and the low levels of spawning activity during February and March 1984 (see figures 5.11a & 5.11b) are further confirmation that strong longshore intrusions of very warm water from Angola can lead to reductions in spawning activity (Boyd *et al.* 1985; Le Clus 1986).

The 'bet-hedging' (Stearns 1977) spawning strategy used by these two stocks is also illustrated by figure 5.10. Peak spawning only occurs when the synoptic environmental conditions are geared to promoting enhanced survival of the early life history stages. However, given the high variability of the system there is no guarantee that the optimal conditions into which the eggs may have been released will persist for very long. As insurance against this both stocks appear to maintain a more or less constant level of background spawning irrespective of surface temperature conditions.

Nonetheless a certain amount of caution should be exercised when drawing conclusions from these results, given that they only cover four years and nineteen surveys. For instance, as has already been mentioned in section 5.2.3, pilchard in

earlier years were known to spawn relatively heavily between late winter and early summer (September to November) (Crawford *et al.* 1988), when macroscale conditions would generally be less favourable for retention and concentration than from mid summer to autumn.

5.4.2 Recruitment and Sea Surface Temperature

By and large the relationships between sea surface temperatures and recruitment success found in this chapter confirm previously observed trends for pilchard in the northern Benguela but not for anchovy.

That pilchard recruitment success generally has a positive relationship with SSTs, as illustrated by figures 5.15c and 5.18, is in agreement with Shannon *et al.'s* (1988) findings. Assuming that the VPA estimates of year class strength are reasonably accurate, the wide spread of temperature conditions between 1961 and 1987, including two strong Benguela Niño warm events (1963 and 1984), mean that the results in figure 5.15 can be treated with confidence.

The lack of any domed optimal environmental window relationship between SSTs and pilchard recruitment suggests that even during Benguela Niño years there are always sufficient levels of enrichment in the northern Benguela to promote the successful feeding and survival of the early life-history stages. The omnipresence of the Luderitz upwelling cell may provide a reason for this, given that even during the Benguela Niño event in 1984 some upwelling activity was maintained, as illustrated by the monthly SST maps in the appendix (appendix I). Consequently, there is good reason to believe that pilchard recruitment in the northern Benguela is not so much enrichment limited, but rather is limited by levels of retention and concentration.

Anchovy in contrast appear to have a less clear cut relationship with SST. Figure 5.19 shows a negative relationship between the number of SST events above various temperatures and recruitment success, whilst figures 5.16 and 5.17 indicate the existence of an optimal environmental window with recruitment success being maximised at intermediate SSTs. Either way, one can conclude that the influence of environmental conditions on anchovy recruitment is different to pilchard, insofar as the relationship between recruitment success and SST is definitely not positive. Moreover, these findings are in some agreement in indicating that anchovy recruitment in the region, unlike pilchard, could be limited by levels of enrichment, insofar as warmer conditions indicate less upwelling activity.

These results, however, directly contradict Shannon *et al.*'s (1988) finding of a positive relationship between SST and anchovy recruitment from 1972 to 1983. However, all can be accounted for by the optimal environmental window model. The years from 1972 to 1983 were generally very much cooler than the following four years (e.g. see figure 5.13). Hence they tend to lie on the left hand side of the domed transformation plots in figures 5.16c and 5.17c where there is indeed a local positive relationship between SST and recruitment success.

The optimal environmental window model cannot, however, explain the difference between the dome shaped optimal transformation results and the negative relationship between recruitment and the number of coastal SST events above various temperatures (figure 5.19). The years from 1981 to 1987 covered a wide range of temperature conditions and so do not lie on one side or the other of the domed relationships in figures 5.16c and 5.17c. Nonetheless there are two possibilities as to why the results in figure 5.19 do not even show a semblance of a domed relationship. The first is that six years is simply not long enough to resolve any underlying trends.

The second possibility concerns the apparent disparity between the 1986/87 spawning season having intermediate temperatures from the COADS dataset and having low temperatures from the coastal CORSA data (see figure 3.13). If this spawning season had an intermediate number of SST events above the cut-off temperatures then some kind of an optimal environmental window might be resolvable from the plots in figure 5.19.

The reason for this disparity between the two datasets is that the area from which the COADS mean monthly SSTs were extracted stretches further offshore than the 50 km outer boundary of the 0.5° latitude coastal areas used to construct figure 3.13 (see figures 3.3b and 3.3c). A comparison of the mean monthly SST maps from November to May for 1986/87 with 1981/82 and 1982/83 (appendix I) shows that although the 1986/87 reproductive season had similar mean monthly inshore SST values to these other two cool years, sea temperatures further offshore were often higher. Hence given that the COADS SST values were extracted from an area which extended further offshore, it follows that they would be higher too. Why it was that offshore temperatures during the 1986/87 spawning season were higher than during the either the 1981/82 or 1982/83 seasons is a separate question, but is likely to be linked with the anomalous intrusions of Agulhas water into the Benguela system during the later part of 1986 (Shannon & Agenbag 1987).

In spite of these discrepancies between the COADS and CORSA SST indices, however, anchovy and pilchard recruitment success clearly have very different relationships with temperature conditions in the northern Benguela. Moreover, it means that these stocks conform to the general pattern that has been observed both in the eastern Pacific and the eastern North Atlantic; namely that pilchard/sardine stocks flourish under warm conditions, and that anchovy populations flourish during cooler conditions (Sharp & McLain 1993, Cushing 1996).

Why it is that anchovy generally appear to thrive under cool conditions, whereas pilchard do better during warmer periods, may in turn be linked to differences in the larval feeding preferences of both species, in terms of prey type and prey size. In upwelling systems it has been well established that different levels of upwelling activity are associated with differences in abundance, species composition and size distribution of phytoplankton and zooplankton (e.g. Hutchings *et al.* 1995; see also section 2.2.5 and section 2.2.6). During cool upwelling conditions productivity levels are high, phytoplankton production is dominated by large diatoms, and zooplankton production is dominated by macro & mega-zooplankton. During warm stable conditions productivity is much lower, the phytoplankton become dominated by micro & dino-flagellates, and smaller zooplankton are favoured.

Sadly there is no information on clupeoid larvae feeding habits in either the northern or southern Benguela (van der Lingen pers. comm.). Nonetheless the results from two studies conducted elsewhere, one in the Californian system on *Engraulis mordax* and *Sardinops sagax* larvae (Arthur 1976) and one in the Peruvian system on *E. ringens* and *S. sagax* (Muck *et al.* 1989), give us some idea of what we might expect to find. In both systems the first- & early-feeding larvae (< 7 mm) of anchovy/anchoveta and sardine show evidence of some niche differentiation, insofar as the anchovy/anchoveta larvae have a mainly phytoplanktophagous or mixed diet whereas the sardine larvae are mainly zooplanktophagous.

As regards the preferred prey size of the early feeding larvae, Arthur's (1986) results (as reproduced by Blaxter & Hunter 1982) show similar size preferences for anchovy and pilchard; whereas Muck *et al.*'s (1989) indicate that the early feeding anchoveta larvae prefer smaller prey than equivalent sized sardine larvae. Nonetheless, both studies are in agreement in showing that at lengths greater than about 9 mm the anchovy/anchoveta larvae start to prefer very much larger prey to the sardine larvae.

If these trends hold true for anchovy and pilchard larvae in the northern Benguela, then based on the assumption that adults will tend to spawn in areas and times which

maximise the feeding success of their early-feeding larvae, they are in tune with two observations. The first is that anchovy prefer to spawn further inshore than pilchard (see section 2.3.4). If anchovy larvae in the region are mainly phytoplanktophagous and pilchard larvae mainly zooplanktophagous these inshore-offshore spawning preferences would make sense, given that the belts of maximum phytoplankton concentration tend to occur inshore of the areas of maximum zooplankton concentration off central and northern Namibia (see section 2.2.6).

The second observation is that although similar oceanographic conditions appear to promote peak spawning in both stocks (see figures 5.10 and 5.11) eventual recruitment success is favoured by different conditions. The elevated inshore SSTs (17° - 23° C) associated with peak anchovy and pilchard spawning seem to promote recruitment success in pilchard only, as illustrated by figure 5.17. In contrast, figure 5.18 demonstrates how successful anchovy recruitment appears to require the relative absence of the same inshore SSTs which promote peak spawning.

A dramatic increase in the preferred prey size of anchovy larvae, relative to pilchard larvae, after reaching lengths of about 9 mm might just explain this paradox. If the early feeding anchovy larvae have similar preferred prey sizes to the pilchard larvae then it makes sense that peak anchovy spawning occurs during similar conditions to peak pilchard spawning. After growing to 9 mm, however, the feeding success and survival of anchovy larvae would then be maximised by cooler upwelling conditions when larger prey would be more prevalent. Moreover, if this were true then it would be consistent with the increasingly held view, as reported in Cushing (1996), that if there is a critical larval period influencing eventual recruitment success it occurs at larger larval sizes rather than at the first feeding stages proposed by Hjort (1914).

5.4.3 Towards Recruitment Prediction: Incorporating Spatial Structure

Figures 5.18 and 5.19 illustrate one of the classic problems with the prediction of recruitment success. Although there may be good relationships between recruitment success and environmental indices for most of the years in a time series, these relationships do not always hold. In these two instances although the number of SST events above a certain temperature usually appear to act as a good proxy of conditions which determine recruitment success, this was certainly not the case during 1987. However, by taking the spatial structure of the system into consideration and identifying patterns which are likely to lead to the successful retention of eggs and larvae, and concentration of suitable food across thermal fronts and thermoclines, the

models in figures 5.20 illustrate how years with unusual conditions such as 1987 may be taken into account.

Whether or not the high levels of recruitment during 1987 resulted from the northward advection of eggs and larvae into the northern Benguela during the 1986/87 reproductive season, as proposed by Shannon & Agenbag (1987), has never been resolved. Some support is offered by the finding of unusually large larvae off Lüderitz during the January and February egg-larval cruises during 1987 (Hewitson 1987). Nonetheless, back calculation of anchovy birthdates from the 1987 fishing season, using growth curves, indicated that most of the 1987 bumper anchovy recruitment was from eggs which had been spawned much earlier than usual, from August to October, and that the larvae found off Lüderitz were in fact too small to have been spawned that early in the season (Le Clus *et al.* 1988). Furthermore, in order for there to have been recruitment from the southern Benguela stocks there would need to have been spawning strongly from August to October, and usually they only start spawning in November. Sadly no egg and larval surveys were conducted in the southern Benguela during August, September or October 1996, so the crucial evidence is lacking.

Nevertheless the results in figure 5.20 show that one need not look for causes outside the system to account for the high levels of recruitment success in both species during this year. Indeed according to the Triad theory, conditions during 1987 would have been excellent for recruitment success given that not only were oceanographic conditions excellent for the onshore retention of eggs and larvae, but also that levels of enrichment were high as indicated by the low coastal SSTs. Moreover, the combination of good levels of enrichment combined with the onshore movement of oceanic water would most likely have resulted in good levels of food concentration across thermal fronts and thermoclines.

1987 is clearly a year in which our usual assumptions as to the relationship between inshore SSTs and the behaviour of the system are inappropriate given that levels of upwelling activity and inshore-offshore retention were both high. Without the information on the system's spatial structure it would not have been possible to identify this, insofar as we would normally assume that low inshore SSTs meant high levels of upwelling activity, high levels of offshore transport, and thus low levels of inshore-offshore retention.

Lastly, figure 5.20 illustrates how the incorporation of information on the spatial dynamics of the system may in the future provide a robust basis for making predictions of year to year recruitment success for management purposes. Although the models must at this stage be considered tentative, given that they only cover six years, and

moreover six years in which the complicating effects of density-dependent recruitment regulation were likely to be particularly low, they are encouraging and serve as a useful prototype for the kind of studies which should be conducted in the future with more years worth of recruitment data.

5.5 SUMMARY AND CONCLUSIONS

1. Trends in the relationship between spawning activity and larval abundance are similar to those found in previous studies, and act as further confirmation that peak spawning in both species and peak anchovy larval abundance often occur during periods with reduced upwelling activity, increased water column stability, and intrusions of warmer water masses. In addition, conditions associated with the onshore movement of oceanic water appear more conducive to promoting high levels of spawning than those associated with strong longshore intrusions of warm water from the north.
2. The results from the investigations into recruitment success versus SST conditions justify taking potential non-linearities in their relationship into account, and also of using indices based on the number of SST events above a certain cut-off point rather than large space- and time-frame mean SSTs. Pilchard recruitment was found to have a generally positive relationship with SST, whilst anchovy recruitment had either negative or dome shaped optimal environmental window relationships with SST conditions, depending on the areas from which the SSTs were taken and whether average SSTs or the number of SST events above a certain cut-off temperature were used. On balance warmer conditions appeared to favour successful pilchard recruitment, whilst cooler conditions favoured anchovy recruitment.
3. Years which deviated from the general relationships between SST conditions and recruitment success could be accounted for when the spatial structure of the system was also taken into consideration. Different domains in the relationship between SST conditions and spatial structure over the course the main reproductive season (defined as being from November to May) were found to correspond closely to different levels of anchovy and pilchard recruitment success for the years from 1982 to 1987. Should these findings hold true when tested with more years worth of data, then the incorporation of information on spatial structure with SSTs might in the future provide a sound basis for making sufficiently good year to year predictions of recruitment success for management purposes.

CHAPTER 6

Summary and Conclusions

The purpose of this research as laid out at the beginning of chapter 1 was to investigate the oceanographic dynamics of the northern Benguela upwelling system primarily using a time series of weekly sea surface temperature (SST) images, and to relate observed environmental trends to existing information on the population dynamics and reproductive ecology of the region's anchovy and pilchard stocks. The ultimate goal being to identify any sufficiently reliable relationships between environmental conditions and recruitment success to be of use for management purposes. Rather than simply duplicating the conclusion and summary sections found at the end of each of the previous chapters, this brief chapter will highlight the general successes and limitations of this research as a whole, and will make suggestions for future research.

6.1 ENVIRONMENTAL DYNAMICS OF THE NORTHERN BENGUELA

The results from the analysis and manipulation of the mean weekly SST images in chapters 3 and 4 do not tell us anything new about the fundamental behaviour of the northern Benguela, nor do they reveal the existence of any hitherto undiscovered oceanographic features. Instead the value of these results lies with their confirmation of previously noted features and trends, and with the fact they provide the most detailed representation of the surface oceanographic behaviour of the region ever produced. Furthermore, they confirm that the behaviour of the system can be successfully quantified according to the evolution of its spatial structure through time using principal components analysis.

It should be remembered, however, that with satellite imagery we are dealing purely with surface patterns. Although the strong thermal gradients associated with coastal upwelling make it fairly easy to interpret these surface patterns, the lack of direct current measurements in the region are a handicap when it comes to inferring surface water flows associated with some mesoscale and macroscale patterns. When the thermal gradients involved are very large this is unlikely to be a problem. For instance,

strong longshore gradients in SST are clearly indicative of the southward flow of warm tropical water from the north. The problems start, however, with weaker thermal gradients.

For instance, thermal patterns associated with the seasonal warming off central Namibia during summer and autumn may be due to some combination of reduced upwelling activity, onshore intrusions of oceanic water, surface and sub-surface longshore intrusions of tropical water, and solar heating. Without surface current measurements it is not possible to fully determine, for instance, the extent to which these patterns reflect onshore movements of oceanic water rather than other factors such as solar heating or the upwelling of warmer water. The establishment of routine shipboard monitoring of surface currents using acoustic doppler equipment would provide a solution to this problem, and would allow the system's spatial structure as revealed by thermal imagery to be directly matched with surface flow measurements.

6.2 CLUPEOIDS AND THE ENVIRONMENT

The findings in chapter 5 clearly show that environmental conditions are likely to play a major role in influencing reproductive activity and eventual recruitment success of the pilchard and anchovy stocks in the northern Benguela. Given that this chapter will still be fresh in the readers mind these findings will not be spelt out again in any great detail here. However, the certainty with which we can state that the prevalence of certain environmental conditions leads to particular trends in spawning activity, larval survival and recruitment success is limited by the relatively small overlap between the available fisheries data and the satellite data; four years in the case of the egg-larval surveys, and six years with regards to the estimates of recruitment success from VPA.

The most important finding to emerge from this research is the existence of separate domains in the relationship between sea surface temperatures and the system's spatial structure which correspond to differing levels of pilchard and anchovy recruitment between 1982 and 1987. Other investigations into the effect of the environment on clupeoid recruitment in the region, both in this thesis and elsewhere, merely indicate the presence of general relationships between sea surface temperature conditions and recruitment success. The advantage of incorporating information on the system's spatial structure was that it enabled exceptions to the general relationships between SST and recruitment to be accounted for in terms of the three processes circumscribed by the Triad theory (*enrichment, retention, and concentration*).

Lastly, on a more philosophical note, one of the underlying assumptions behind the work contained in this thesis is that reasonably consistent relationships do exist between environmental conditions and recruitment success. Consequently, much of the debate has been geared towards the nature of these relationships and the best ways of quantifying environmental processes in order to uncover them, rather than whether any relationships exist in the first place. Given that we are unable to keep track of the unique sequence of environmental conditions each developing larvae is exposed to, we inevitably have to investigate environment-recruitment linkages at scales which are far removed from the immediate cause and effect levels of larval mortality. When choosing environmental indices for fisheries research it is crucial that we are aware of what bio-physical processes they are likely to be measuring, and to tailor their spatio-temporal resolution as appropriate. In this regard the Triad theory provides a convenient base to work from, insofar as it provides three broad and conceptually satisfying classes of process that can be referred back to when evaluating how to best measure a system for the purposes of investigating recruitment variability.

6.3 FUTURE RESEARCH AND IMPLICATIONS FOR MANAGEMENT

Understanding recruitment well enough to enable reliable predictions of year class strength remains one of the great challenges of fisheries science. For clupeoids in the northern Benguela the results presented in figure 5.20 are very encouraging, but the fact that they only cover six years is in itself sufficient reason for caution. It is important that the techniques used and developed in this thesis be extended to cover a greater number of years, so as to establish whether these relationships are genuine or not, and if so, whether they are sufficiently sound to be used as a basis for making year to year forecasts of recruitment success.

With regard to the techniques themselves, there is plenty of scope for refining the way in which the three processes circumscribed by the Triad theory are measured. For instance, seasonal variations in solar heating mean that inshore SSTs on their own are probably not the best measures of enrichment and retention, according to levels of upwelling activity and offshore transport, as was discussed in section 3.4.1. Although the results in chapter 4 show that retention can be successfully quantified using standardised principal components analysis, enrichment still remains a problem.

There are two avenues which may be worth following in attempting to improve the way in which enrichment is measured. The first is to experiment further with Fourier transforms for removing the regular seasonal component in SST fluctuations due to

solar heating (see section 3.4). The second is to use estimates of chlorophyll concentration from ocean colour images. Although this would provide the most direct measure of enrichment, it is subject to the constraint that at present there are no ocean colour scanners in operation. The SeaWiFS (Sea-viewing Wide Field-of-view Sensor) satellite has still not been launched and the last readings taken by the Coastal Zone Colour Scanner (CZCS) were in 1986 (Hooker *et al.* 1993). Nonetheless, the European Commission's Joint Research Centre has recently compiled a time series of mean monthly ocean colour images for coastal waters around Africa from CZCS data (Nykjaer¹ pers. comm.), which means the opportunity does now exist for using remotely sensed estimates of chlorophyll concentration for retrospective recruitment studies in the region.

Speculating in detail on how environmentally-based forecasts of pilchard and anchovy recruitment success in the northern Benguela could be incorporated into the management of these stocks is somewhat premature at the moment. Should sufficiently reliable forecasts prove possible, however, a good start would be to either replace or incorporate some of the parameters used in virtual population analysis (VPA) with recruitment forecasts based on environmental conditions. For instance, estimates of recruitment success based on average stock-recruitment relationships could be modified according to whether environmental conditions were likely to have promoted average, below average or above average levels of recruitment. These recruitment estimates could then be used with VPA in two ways. Firstly, to replace estimates of current year class strength based on dubious relationships between fishing mortality and fishing effort; and secondly, for forecasting recruitment success when making biomass projections (see section 1.5).

Establishing whether or not the relationships illustrated in figure 5.20 hold true over a longer period of time is, however, the very first priority. If they do, it will represent an important step in our understanding of how environmental factors can regulate the reproductive success of clupeoids in the northern Benguela. Not only would this open the door for similar environmental-fisheries studies in other eastern boundary upwelling systems, but it would also enable progress to be made in our quest to develop truly sustainable industrial fisheries. Fisheries in which management was based not only on the effects of fishing and density-dependent pressures, but also on a wider appreciation of how the environment can affect stocks.

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APPENDIX I

Maps of mean monthly sea surface temperatures from the COSRSA dataset are shown on the following ten pages for the period from July 1981 to December 1990.

APPENDIX II

Research cruises from which temperature at depth measurements were used to calculate the vertical stratification indices in chapter 3. Included are the latitudinal boundaries within which temperature at depth measurements were taken during each cruise, and the mean weekly SST satellite images which correspond to the dates when the temperature readings were taken in the three areas in figure 3.19a. (The code 810902 refers to the weekly SST image for week 2 September 1981, likewise 810903 refers to the image for week 3 September 1981, and so on).

Cruise	Dates	Ships	Latitudinal extent	Area 1	Area 2	Area 3
Sep 81	11/9 - 24/9	Benguela	17°30' - 26° S	810902	810903	810903
Nov 81	12/11 - 15/11	Sardinops	21° - 24° S	-	-	810903
Nov/Dec 81	26/11 - 14/12	Sardinops	17°30' - 26° S	811201	811201	811201
Jan 82	10/1 - 20/1	Sardinops	17°30' - 20°30' S	820102	820103	-
Feb 82	9/2 - 25/2	Sardinops	17°30' - 25°30' S	820203	820203	820203
Mar 82	15/3 - 1/4	Sardinops	17°30' - 24°30' S	820303	820304	820304
Sep 82	11/9 - 22/9	Benguela	17°30' - 27° S	820902	820903	820903
Nov 82	9/11 - 21/11	Benguela	17°30' - 26° S	821102	821102	821103
Jan 83	10/1 - 20/1	Benguela	17°30' - 26° S	830102	830102	830103
Feb 83	7/2 - 18/2	Benguela	17°30' - 26° S	830202	830202	830202
Mar 83	14/3 - 24/3	Benguela	17°30' - 24° S	830303	830303	830303
Sep 83	16/9 - 25/9	Benguela	21° - s24° S	-	-	830904
Nov 83	11/11 - 20/11	Benguela	21° - 24° S	-	-	831103
Jan 84	9/1 - 20/1	Benguela	21° - 24° S	-	-	840102
Feb 84	7/2 - 20/2	Benguela	21° - 24° S	-	-	840203
Mar 84	11/3 - 22/3	Benguela	21° - 24° S	-	-	840303
Nov 84	15/11 - 24/11	Benguela	18° - 24° S	841104	841103	841103
Jan 85	12/1 - 28/1	Benguela	18° - 24° S	850104	850103	850103
Feb 85	11/2 - 20/2	Benguela	19° - 24° S	850203	850202	850202
Mar 85	15/3 - 27/3	Benguela	18° - 24° S	850303	850303	850303

APPENDIX III

Dates of the egg and larval SWAPELS surveys used in Chapter 5 (section 5.2), and details of the mean weekly SST images (i.e. time steps) which overlap most closely with each survey. Criteria of how the overlapping SST images were chosen are outlined in section 5.2.2. All of the surveys were conducted from the *RV Benguela*. (The code 810903 refers to the weekly SST image for week 3 September 1981, likewise 811202 refers to the image for week 2 December 1981, and so on).

Cruise	Dates	Overlapping SST Image/Time Step
September 1981	11/09 - 24/09	810903
November/December 1981	01/12 - 12/12	811202
January 1982	10/01 - 20/01	820102
February 1982	13/02 - 23/02	820203
March 1982	20/03 - 29/03	820304
September 1982	11/09 - 22/09	820903
November 1982	09/11 - 21/11	821102
January 1983	10/01 - 20/01	830102
February 1983	07/02 - 18/02	830202
March 1983	14/03 - 24/03	830303
September 1983	16/09 - 25/09	830903
November 1983	11/11 - 20/11	831102
January 1984	09/01 - 20/01	840102
February 1984	07/02 - 20/02	840202
March 1984	11/03 - 22/03	840302
November 1984	15/11 - 24/11	841103
January 1985	12/01 - 28/01	850103
February 1985	11/02 - 20/02	850202
March 1985	15/03 - 27/03	850303

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