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COMPETITION FOR ANCHOVY (*Engraulis capensis*) AND SARDINE (*Sardinops sagax*) BETWEEN THE CAPE GANNET (*Morus capensis*), CAPE FUR SEAL (*Arctocephalus pusillus pusillus*) AND THE PURSE-SEINE FISHERY ON THE WEST COAST OF SOUTH AFRICA

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Dedicated to:

My parents, Kumaran and Mahaluxmi Pillay and
my other parents Indres Naidoo and Gabi Blankenburg

" I would not put among the list of my friends, a person who put his/her foot upon a worm."

William Cowper

" Enthusiasm is no substitute for perseverance"

Dr. Michael Lan (2001)

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DECLARATION

I hereby declare that this thesis represents my own work. Although the staff at Marine and Coastal Management undertook all the data collection, I did all the data analysis and interpretation and participated in one collecting trip. The project was designed in collaboration with my supervisors, Dr. R. J. M. Crawford, Mr. H. W. Oosthuizen and Prof. J. G. Field. Other avenues of input were from Dr. J. H. M. David, Dr. B. Clark and Mr. B. M. Dyer. This work has not been submitted for a degree at any other institute and all the assistance that I received during the execution of this research is fully acknowledged.

Signed by candidate

Pavitray Pillay

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ABSTRACT:

Competition for pelagic fish resources was investigated by assessing the overlap in the food base of three land-based predators: Cape gannet (*Morus capensis*), Cape fur seal (*Arctocephalus pusillus pusillus*) and humans operating via a purse-seine fishery. Multivariate analysis the diet composition of gannets and seals and the catch composition of the pelagic fishery indicated that there were three "feeding regimes" during the 21-year study period: (1978-1998), an anchovy-dominated regime (1978-1983), an intermediate regime (1984-1990) and a sardine-abundant regime (1991-1998). It further showed that anchovy (*Engraulis capensis*) and sardine (*Sardinops sagax*) contributed substantially to the catches of all three top predators. Analysis of size-distributions of catches showed that the three predators generally caught the same sizes of anchovy and sardine, reflecting very little resource partitioning. The analysis demonstrated stronger competition between gannets and the purse-seiners than between gannets and seals, especially during seasons of poor recruitment. Furthermore, seasonal differences in the catches of the three predators are related to the recruitment, growth and migration of the prey species. The study confirmed previous observations that gannets prefer sardine to anchovy by showing gannet exploitation of sardine in the early 1990s, when anchovy was still abundant. The gannets, which are species-specific feeders, may be impacted by substantial removals of pelagic fish resources by a large seal population and a large fishery.

CHAPTER ONE
INTRODUCTION

1.1 THE BENGUELA UPWELLING SYSTEM:

The Benguela system is one of the world's four major eastern boundary current regions where biological production is enhanced by wind-driven upwelling. The Benguela upwelling system is unique among upwelling systems in that it is bounded on both equatorward and poleward sides by the warm water of the Agulhas and Angola currents (Shannon *et al.* 1992).

The physical aspects of the Benguela system have been described extensively in papers such as Parrish *et al.* (1983), Lluch-Belda *et al.* (1989), Mann (1992) and Shannon *et al.* (1992). Along the coast of South Africa, the most active upwelling centres are located off the Northern and Western Cape, at Hondeklip Bay, Cape Columbine and the Cape Peninsula (Fig. 1.1).

During upwelling, nutrient-rich water reaches the surface near the shore. The water temperature of these upwelled plumes is usually below 12°C and the warmer, surface water is displaced and transported away from the coast. Phytoplankton makes use of the nutrients brought to the surface by the upwelled water, resulting in dense phytoplankton blooms, followed by major zooplankton growth. This abundance of phytoplankton and zooplankton supports large populations of fish and other marine vertebrates and invertebrates resulting in dynamic, complex multispecies interactions. See Crawford (1987), Patterson *et al.* (1992), Richardson *et al.* (1997) and Mitchell-Innes *et al.* (1999) for papers on zooplankton consumption and utilisation. It has been calculated that the upwelling systems of the world account for more than 38% of the marine primary production (Longhurst *et al.* 1995) thereby sustaining more than 30% of the world's marine fish catches (F.O.A. 1996 and Jarre-Teichmann *et al.* 1998). As a consequence, the Benguela system has been exploited by several sectors of the fishing industry, e.g. the demersal trawl fisheries, the purse-seine fisheries and most recently demersal long-line fisheries.

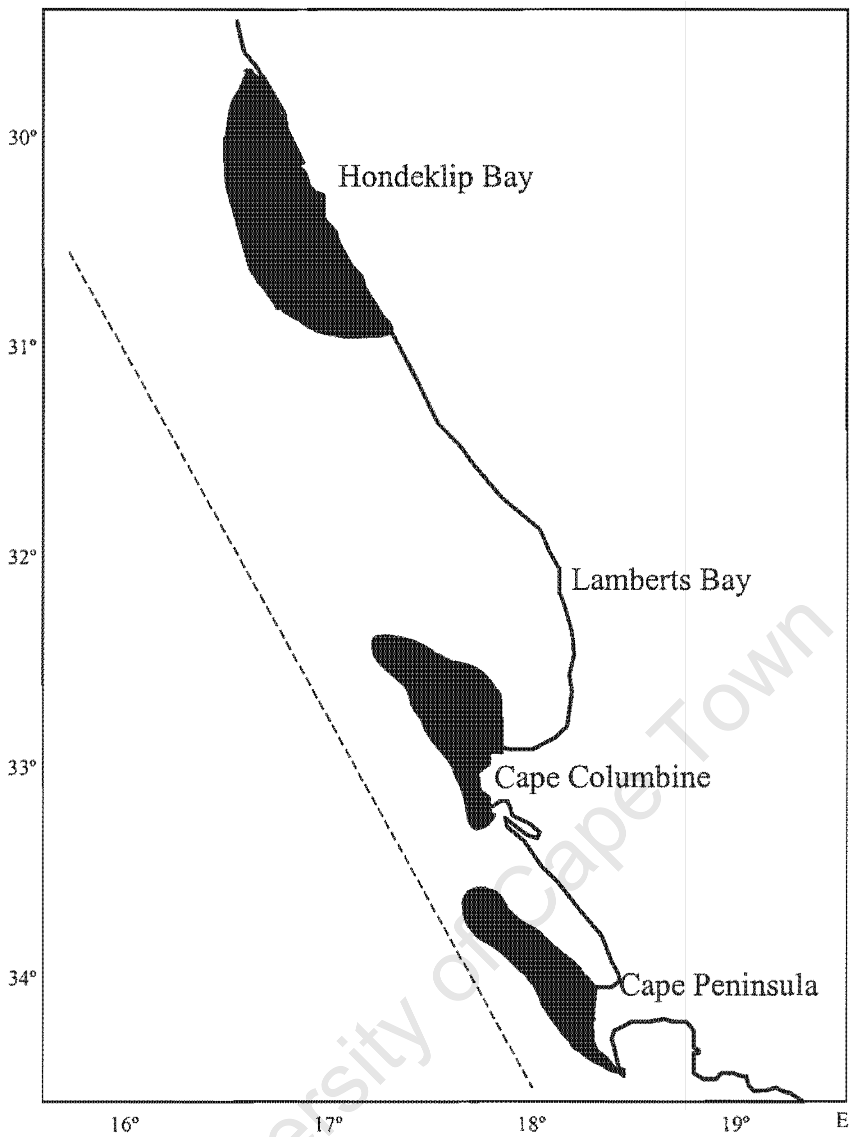

Fig. 1.1 The major upwelling sites off southwestern Africa (modified from Ware 1992).

1.2 MULTISPECIES INTERACTIONS:

The Benguela system supports a variety of pelagic shoaling fish species such as anchovy (*Engraulis capensis*), sardine (*Sardinops sagax*), redeye/roundherring (*Etrumeus whiteheadi*) and horse mackerel (*Trachurus capensis*), with anchovy and sardine being the most abundant. The large biomasses of epipelagic fish provide the forage food base for assemblages of marine avian and mammalian fauna. Therefore, within this system is the potential for extensive competition between top predators (humans being one of them) for a few plentiful but limited resources.

Within natural systems, predator-prey and predator-predator interactions are important in sustaining both viable predator and prey populations as well as energy flow (Begon *et al.* 1990). While such interactions do not occur in isolation from environmental and physical aspects, they are mostly self-sustaining with occasional peaks and troughs. However, when one top predator targets unusually high abundances of the prey items, this very often leads to either prey collapse, predator collapse or both. These collapses are normally sustained for some time and the recovery by both the prey and the predator is slow (Begon *et al.* 1990 and Crawford *et al.* 1992).

Modern fisheries research has therefore been moving towards a multispecies approach in an effort to guarantee sustainability and optimum utilisation of the resources, which cannot be achieved without taking into account the ecological and economic roles of seabirds, marine mammals and fisheries. Examples of previous studies of multispecies interactions in the Benguela system include Crawford & Shelton (1978), Cooper (1981), Furness & Cooper (1982), Berruti (1987), Berruti & Colclough (1987), Ryan & Moloney (1988), Cairns (1992) and Adams *et al.* (1992). Furthermore multispecies fishing is capable of making minor modifications to switch target species (Shelton 1992). Therefore fishery-avian and fishery-mammal interactions has became the focus of much research in the late 1980s because of the many effects the fauna exert on the different types of fisheries, and vice versa. For example, Crawford & Shelton (1978) showed that decreases in seabird populations were strongly related to declining fish stocks. While correlation does not mean causality, reduced food supplies appear to have had an "instantaneous negative" effect on the reproductive success of all seabirds dependent on sardine and anchovy stocks (Cooper 1981, Crawford & Shelton 1981, Burger & Cooper 1982 and Thomas 1988).

Ryan & Moloney (1988) found that commercial trawling activities led to expanded distributions of Cape gannets (*Morus capensis*) and Cape fur seals (*Arctocephalus pusillus pusillus*), resulting in an increase in co-occurrence of these species and subsequently an increase in competition for food even though trawled fish was an "artificial" food source. Berruti (1987), David (1987), Crawford *et al.* (1994) and Miller *et al.* (1996) maintain that intensive fishing operations such as by demersal trawlers and purse-seiners have provided a supply of easily accessible food for opportunistic seals and gannets with the result, these species often have overlapping diets (Jarre-Teichman *et al.* 1998 and Shannon & Jarre-Teichmann 1999) and are therefore altering the dynamics of the ecosystem.

The competitive multispecies relationships between the Cape gannet, the Cape fur seal and the purse-seine fishery (Crawford & Shelton 1978, Berruti 1987 and Berruti *et al.* 1993), provided the impetus for this study. The relationship between these three fisheries (considering predator consumption as a fishery and the commercial fishery as a predator) primarily involves competition for shared pelagic resources, particularly sardine and anchovy.

Sharing the same resource has meant that all three fisheries are subject to the same fluctuations in the recruitment and abundance of epipelagic fishes. Reduced fish abundance has meant reduced breeding success by predators, particularly gannets (Crawford *et al.* 1983). On the other hand, fish stocks are influenced by predators, as well as by many other environmental pressures. Very often these two factors have contributed to reduced fish abundance and poor recruitment. One such occasion was in 1983 –1984, when a Benguela El Niño led to extended periods of warm water on the Namibian continental shelf. These periods had an adverse effect on the anchovy resource off the Namibian coast (Shannon *et al.* 1992).

Besides competing for resources, there are also operational interactions between seals, gannets and the fishery (Wickens 1992). Operational interactions occur as a result of conflicts during fishing operations between natural predators of a resource and the fishery (Wickens 1992). Operational interaction is usually confined to seals, which are seen plaguing fishing boats and removing fish from the nets. Purse-seine fishermen have complained that seals disrupt fishing operations by causing fish shoals to sound and/or by damaging equipment (Wickens 1992, Miller *et al.* 1996).

Such direct interactions have consequences for all top predators within the system. For seals, scavenging from purse-seine fishing nets have led to injury and death, either by being shot by fishermen or tangled in nets and drowned. Conversely, the ready supply of food in purse-seine nets and other fisheries (e.g. trawling) has probably been a key factor in the recent growth of the South African seal population (Butterworth *et al.* 1995, David 1989 and Punt *et al.* 1995). This feeding behaviour has meant that not only do seals have a scavenged component to their diet, but they also consume sardine and anchovy of a similar size to these caught by the fishery, thereby allowing for an overlap in resource partitioning as well. This affects the food available to gannets, which may compete with both seals and the fishery for energy-rich resources.

While extensive studies have been done on top predators in the Benguela system related to their trophic position, a thorough investigation of the overlap in utilisation of different prey species and prey sizes has not been undertaken. Therefore, the main objective of this study is to examine the extent of prey overlap by three conspicuous top predators. Furthermore the implications of potential competition for food for the three land-based predators will be considered particularly focussing on sardine and anchovy.

1.3 THESIS OUTLINE:

Chapter two: - Diet Composition

The overlap in species composition of catches by Cape gannets, Cape fur seals and the purse-seine fishery on the west coast of South Africa is examined. The chapter tests the following hypothesis: there are no major differences in the prey composition of gannets, seals and the purse-seine fishery.

Chapter three: - Size Distribution

This chapter examines whether dietary overlap extends not only to the same prey species but also the same length classes of fish, focussing on anchovy and sardine. Interannual and seasonal trends in the sizes of anchovy and sardine removed by gannets, seals and the purse-seine fishery are documented.

Chapter four: - Conclusions

Finally, the conclusions of the thesis are discussed. With the degree of prey overlap established, its impact on predator numbers is examined. Suggestions are made regarding management of the purse-seine fishery, and the gannet and seal populations.

CHAPTER TWO

RELATIVE COMPOSITION OF THE DIETS OF GANNETS AND SEALS COMPARED WITH THE PURSE-SEINE FISHERY

2.1. INTRODUCTION:

Pelagic fish provide the forage food for many top predators within the Benguela system. However, little is known about the degree of prey overlap that exists between the various predators. To investigate resource sharing within the Benguela ecosystem, the overlap of prey between Cape gannets, Cape fur seals and the purse-seine fishery was examined.

Furthermore, this study provides an indication of whether the degree of overlap in prey utilization was influenced by the species contributing the major portion of the forage food base. Although the catches of the gannets, seals and the purse-seine fishery are not based solely on anchovy and sardine, over the study period, these two fish species were the most abundant resources and dominated the catches.

2.1.1 The Cape gannet

Location

The Cape gannet (*Morus capensis*) is one of the endemic seabird species that occur along the coast of southern Africa. It is a member of the family Sulidae, which is comprised of boobies and gannets. Cape gannets breed at six colonies off the Namibian and South African coasts: Mercury Island, Ichaboe Island, Possession Island, Bird Island (Lamberts Bay) and Malgas Island located in the Benguela upwelling system and Bird Island in Algoa Bay, inshore of the Agulhas Current (Fig. 2.1- Crawford *et al.* 1983 and Berruti *et al.*1993).

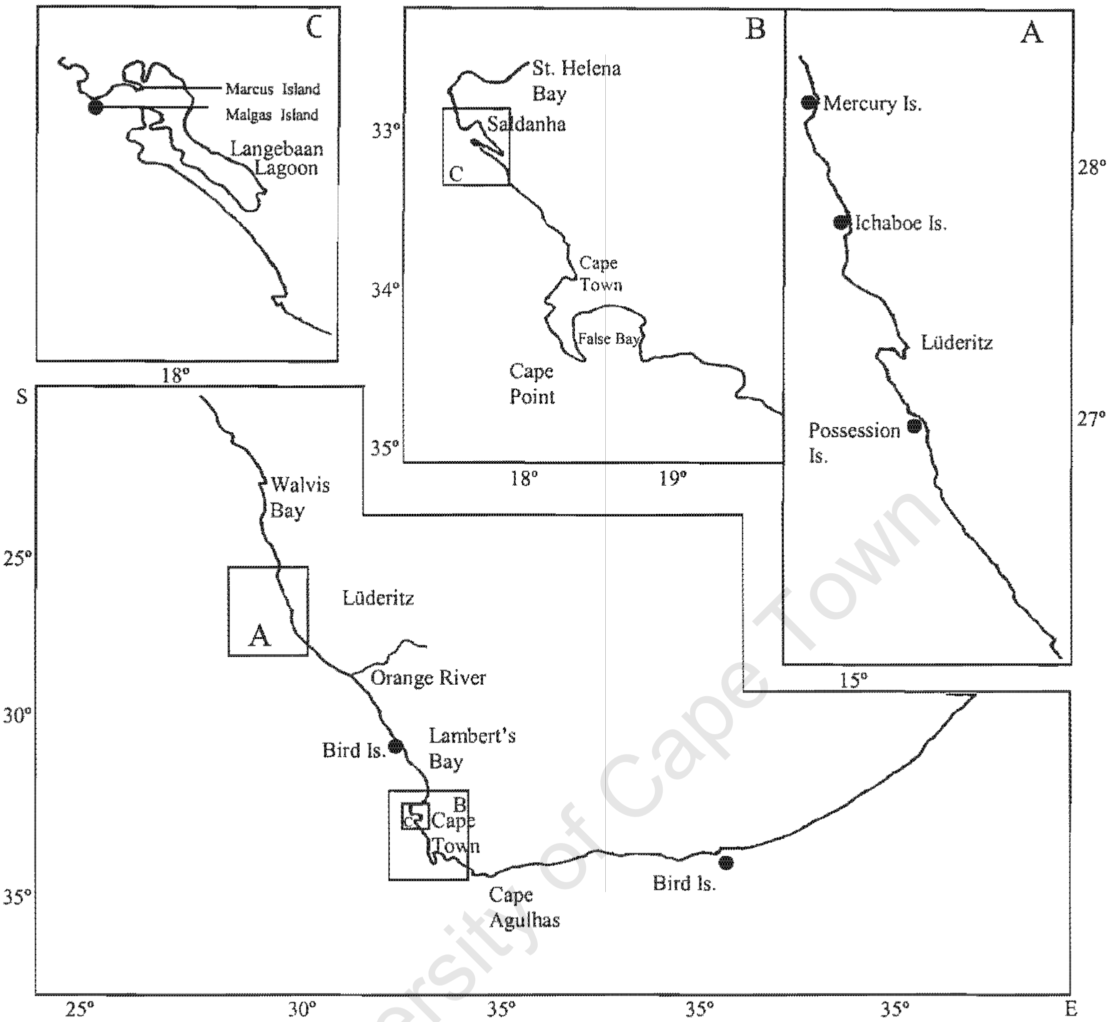

Fig. 2.1 Breeding colonies of the Cape gannet along the South African and Namibian coastlines. Diet data were collected from two of the breeding colonies, Malgas Island and Lamberts Bay. Other localities are also indicated.

Distribution

The Cape gannet feeds in the highly productive waters of the Benguela system on the west coast of southern Africa and over the Agulhas Bank. There are from 80 000 to 100 000 breeding pairs along the South African coast (Crawford *et al.* 1983). The number of birds at colonies is variable, especially during the non-breeding season (April to July, Crawford *et al.* 1983).

During the breeding season, parents share duties including incubating the egg and guarding the young chick (Berruti 1987). Periods of parental absenteeism from the nest are variable and are presumably related to the distribution and abundance of food. Cape gannets move considerable distances during feeding and migration. Adults can move up to 3300 km from their breeding locality (Crawford *et al.* 1983). During the non-breeding season (June-July), many move to tropical waters off west Africa (4°N:6°E) while others move to Kwa-Zulu Natal on the east coast of South Africa, following the annual "Natal sardine run" (Broekhuysen *et al.* 1961 and Crawford *et al.* 1983).

Feeding

Cape gannets are plunge divers and consume what is most abundant and readily accessible (Crawford *et al.* 1983 and Adams 1993). They are referred to as archetypal pelagic feeders and are influenced by fluctuations in the abundance of prey species (Ashmole 1971 and Crawford *et al.* 1983). Cape gannets feed during the day, leaving the nests at sunrise and normally returning in the evening. Although Cape gannets are active hunters, they are also opportunistic and scavenge fish and offal discarded from demersal trawlers (Crawford & Shelton 1981 and Burger & Cooper 1982).

The major constituents of the Cape gannet's diet are anchovy (*Engraulis capensis*), sardine (*Sardinops sagax*), saury (*Scomberesox saurus*), shallow-water hake (*Merluccius capensis*), deep-water hake (*Merluccius paradoxus*) and to a lesser extent, redeye/roundherring (*Etrumeus whiteheadi)*, chub mackerel (*Scomber japonicus*), snoek (*Thyrsites atun*), southern mullet (*Liza richardsoni*) and pelagic goby (*Sufflogobius bibarbatus,* Crawford *et al.* 1983 and Berruti 1987). Sardine and anchovy are important prey species for the Cape gannet, the latter more so because of their high-energy content (Batchelor & Ross 1984 and Adams & Klages 1999). Cape gannets are estimated to consume 18% of the 13 000 tons of sardine and anchovy eaten annually by seabirds along the southern African coast (Crawford *et al.* 1991). According to Jarre-Teichmann *et al.* (1998) for the period of 1980-1989, anchovy made up 36.5% of the total seabird diet while sardine only comprised of 8.4% of the total dietary composition. Therefore combined, these pelagic species made up more than 40% of the seabirds diet, making it a very important resource to seabirds such as the Cape gannet.

Cape gannets share their food resource with other top predators in the Benguela system, such as the African penguin (*Spheniscus demersus*), Cape cormorant (*Phalacrocorax capensis*), Cape fur seal and snoek. The importance of the pelagic resources to the Cape gannet and the other marine predators it shares this resource with, makes the Benguela system within which these predators persist a highly competitive ecosystem.

2.1.2 Cape fur seal

Location

The Cape fur seal is the only resident pinniped in southern Africa. Seals are non-migratory, coastal species that generally forage in shallow, shelf waters (Rand 1959, David 1987 and David 1989). The range of the population extends from the non-breeding colony of Cape Frio in Namibia (18°S, 12°E) to Black Rocks, on the east coast of South Africa (34°S, 26°E, Wickens *et al.* 1991, Wickens 1992 and Miller *et al.* 1996). The population is unevenly distributed, with 60% occurring in Namibian waters, 35% inhabiting the west coast and 5% the south coast of South Africa (Butterworth *et al.* 1995 and Wickens *et al.* 1991).

There are approximately 25 breeding, and 9 non-breeding, colonies off the southern African coast (Fig. 2.2). In the 1990s, the population was estimated to be close to 2 million seals, making the Cape fur seal one of the most numerous fur seals worldwide (Wickens *et al.* 1991, Wickens 1992 and Miller *et al.* 1996). Seals have colonized most South African islands and some mainland sites and have displaced many seabirds from breeding colonies (Shaughnessy 1984 and Crawford *et al.* 1989). The colonizing of mainland localities has been one of the explanations put forward for the exponential increase in the seal population, as there is more space available on which to breed, and less competition for space with seabirds.

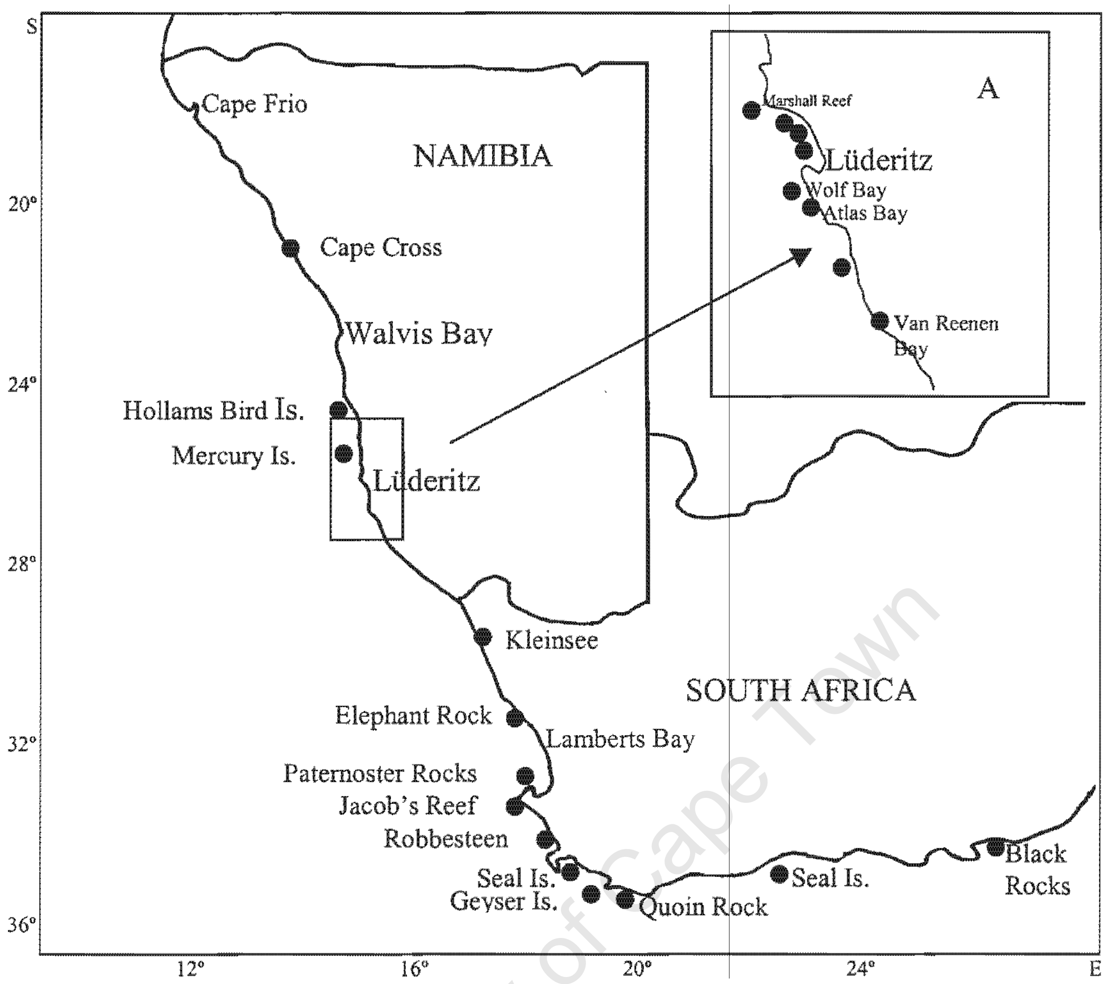

Fig. 2.2 Important breeding and non-breeding colonies of the Cape fur seal along the southern and western coasts of South Africa and Namibia.

Of the six mainland colonies on the west coast of southern Africa, five are within established, restricted diamond mining areas, while the sixth colony is a national reserve (Cape Cross National Reserve). Consequently, seals are no longer disturbed by humans or restricted for space in South Africa (David 1989), and natural land-based predators such as lions (*Panthera leo*), black-backed hyaenas (*Hyaena brunnea*) and jackals (*Canis mesomelas*) have been reduced by human removal. However hyaenas remain the main land-based predator of the Cape fur seal on mainland colonies.

Feeding

Like Cape gannets, Cape fur seals feed on inshore pelagic fish resources, but they also prey on cephalopods, midwater fish such as snoek, and both deep water and shallow water hake species. Cape fur seals are efficient hunters, but are also opportunistic and regularly scavenge from purse-seine and demersal boats and more recently from long-liners (David 1987, David 1989, Crawford *et al.* 1992, Wickens *et al.* 1992 and Punt *et al.* 1995). However, the total Cape fur seal consumption is estimated to be well over 500 000 tons of which more than 25% comprises of anchovy (25.2%) and sardine (2.8%, Jarre-Teichmann *et al.* 1998).

Cape fur seals experience gender-related fattening and fasting seasons. Male seals return to the colonies only during the mating season (October – March, Rand 1959, David 1989 and Wickens 1993). Prior to this mating season the male seals spend all their time fattening up, consuming as many fish and cephalopods as possible. Once the male seals are at the colonies, they will not leave for fear of losing their territories to other males. By remaining at the colony, they strengthen their chances of siring many pups. This means that for five weeks of the year, breeding male seals do not consume any fish at all. Female and juvenile seals feed throughout the year.

Breeding

For a female seal, a good food source is vital because, while she is lactating a young pup, she is already carrying the next season's pup. Seals display delayed implantation i.e. approximately two weeks after giving birth, female seals are ready to mate and will mate with the male within whose territory she stays at the colony. However, the development of the pup is delayed for up to three months. At this time, females cannot travel long distances because they need to return every few days to feed lactate their pups. Therefore they need adequate prey availability within a limited range (100-150 km) from the breeding colony. Thus sufficient food resources play a very important role in the survival of the Cape fur seal, for both males and females (Rand 1959, David 1987 and David 1989).

2.1.3 The Purse-seine Fishery of South Africa

A third major consumer of pelagic resources is the commercial pelagic (purse-seine) fishery that operates within the foraging areas of the Cape gannet and the Cape fur seal on the west coast. Cape gannets and Cape fur seals therefore may affect the fishery and be adversely influenced by the fishery.

The purse-seine fishery is a multispecies fishery focusing on several species of clupeoid fishes, of which anchovy and sardine are the most valuable. Anchovy and sardine are relatively short-lived, feed mostly on plankton over shallow continental shelf regions and are largely epipelagic, making them highly susceptible to overexploitation and stock collapses (Fowler 1998). As well as being an important food source for larger fish, seabirds and marine mammals, clupeoids are of major commercial and socio-economic value worldwide, making up 30% of the global yield of marine fish (Hunter & Alheit 1995). They are a major contributor to South Africa's protein resources (Fowler 1998).

Anchovy spawn between October and February on the Agulhas Bank (Crawford & Shelton 1978, Hutchings & Boyd 1992 and Richardson *et al.* 1997). Eggs and larvae are then transported northwards along the west coast towards an inshore nursery region north of St. Helena Bay. The young-of-the-year (0–group) anchovy later migrate southwards in autumn/spring to spawn on the Agulhas Bank in the following spring/summer. It is during this southward migration that the recruit-based fishery catches anchovy. Adult anchovy, which generally remain on the Agulhas Bank (Crawford 1998), are not available to the industry during the spawning season because the shoals break up into smaller, diffuse shoals and occur below the warm surface water on the spawning grounds (Hutchings & Boyd 1992 and Richardson *et al.* 1997). However, they may be caught after spawning as 1-year olds in summer (January-March).

Young-of-the-year anchovy and sardine occur in mixed shoals, display the same migration patterns, and are often caught together. Mixed shoals later separate into single-species shoals because of the different growth rates of anchovy and sardine.

Some shoals of both species migrate eastwards across the Agulhas Bank when fish are 1-2 years old (Hutchings & Boyd 1992 and Richardson *et al.* 1997).

Sardines have a less well-defined spawning season than anchovy and spawn both on the Agulhas Bank and the west coast, with peak spawning occurring between August and March (Crawford 1998, Crawford & Dyer 1995 and Barange *et al.* 1999). The fishery targets adult sardines from January–March, when they occur west of Cape Agulhas, and also removes juveniles on the west coast (Hutchings & Boyd 1992, Crawford 1981, Fowler 1998 and Barange *et al.* 1999).

Stock size fluctuations within clupeoid populations have often been attributed to overfishing. However, large changes in rates of deposition over centuries of fossil scales in sediments has revealed that major changes in clupeoid populations cannot always be ascribed to fishing (Lasker 1985). Several hypotheses have been suggested to try to explain the fluctuations, such as attributing large variations in year-class strength in clupeoid stocks to the impact of the environment (Wooster & Bailey 1989 and Hunter & Alheit 1995). The short lifespan of the fish means that recruitment variability has a pronounced impact on stock biomass.

Small populations can produce large year-classes, so that recruitment fluctuations often occur independently of changes in parent stocks (Wooster & Bailey 1989, Schwartzlose *et al.* 1999). This suggests that environmental influences on the early life stages are the main cause of recruitment variability and the concomitant fluctuations in population size (Lasker 1985, Wooster & Bailey 1989 and Fowler 1998). Fishing may intensify the fluctuations, shortening the duration of peaks of abundance and extending the durations of troughs (Schwartzlose *et al.* 1999).

The South African purse-seine fishery started in 1943 in the St Helena Bay area. By the end of 1958 it had expanded to include the area between Lamberts Bay and Cape Hangklip. By 1964, boats were operating as far north as Port Nolloth, and by 1974 as far east as Cape Infanta (Crawford 1987). Sardine catches peaked in 1962, at some 410 000 metric tons, but the stock collapsed during the mid 1960s and only 69 700 tons were landed in 1967. Until recently, annual sardine catches only exceeded

10 000 tons on three occasions (Armstrong *et al.* 1989) because of reduced biomass and conservative TACs (total allowable catches).

During the mid 1960s (1964-65), the mesh size for purse-seine nets in South African fishery was reduced from 32 mm to 12.7 mm, in order to catch anchovy, following the collapse of the sardine. Anchovy has sustained the fishery to the present. The sardine resource began a recovery in 1983, due to one or more stronger year classes occurring, with substantial catches again being reported in the latter half of the 1990s (Crawford 1998, Barange *et al.* 1999 and Schwartzlose *et al.* 1999). Most of the sardine catches are canned for human consumption, whereas anchovy are predominantly processed as fishmeal and oil. Sardine is therefore more valuable than anchovy. Clearly then anchovy and sardine are pivotal prey species for the Cape gannet, the Cape fur seal and the purse-seine fishery.

2.2. STUDY AREA:

Information on the diet of Cape gannets was obtained by staff of the Department of Environmental Affairs and Tourism: Marine and Coastal Management (MCM), at the breeding colonies on the west coast of South Africa, namely Lamberts Bay (32°05`S, 18°18`E) and Malgas Island (33°03`S, 17°55`E). Data on the diet of Cape fur seals were obtained from animals shot at sea between Cape Point and the Orange River, at the Namibian–South African border. Data on catches of the purse-seine fishery were taken from records of catches maintained by and samples of catches undertaken along the west coast of South Africa by MCM.

2.3. METHODS:

2.3.1 Gannet diet sampling

The data used in this study are part of an ongoing investigation into the diet of Cape gannets by MCM that commenced in December 1977 at Lamberts Bay, and in December 1978 at Malgas Island. Information subsequently was collected at both localities on a monthly basis. For this study only data from 1978 to 1998 were analysed. Both non-breeding and breeding birds were captured with a gannet crook immediately after returning from sea (a telltale sign being a distended stomach). The birds were inverted over a bucket and pressure was applied with the palm of the hand to the stomach region. This caused the bird minimal yet sufficient discomfort to regurgitate its stomach contents. (Berruti & Colclough 1987 and Berruti *et al.*1993). For every regurgitation, the number and mass or volume of prey items were established and the caudal lengths of whole prey items were measured. All otoliths were collected and identified to species level where possible.

Since most of the dietary contents were only partially digested, identification of prey species was straightforward. No distinction was made between the two species of hake, because these prey species were often only represented by fish offal, confirming that Cape gannets readily scavenge hake discarded by the demersal trawlers (Ryan & Moloney 1988). An average of 50 birds were sampled per month, resulting in more than 12 000 gannet regurgitations being collected per site from 1978-1998.

2.3.2 Cape fur seal diet sampling

Cape fur seals were sampled by MCM on 19 research cruises along the west coast of South Africa from 1982-1996. In order to restrict this analysis to seals removed only between Cape Point and the Orange River, the Geographical Information System (GIS) program Arcview was used to map the co-ordinates of the location of each seal that was shot. This procedure involved thematic mapping and labelling, as well as layouts of longitudes and latitudes of the positions of the seals. These points were then plotted on a map of the southern African coastline. The GPS readings attained needed to be converted to decimal degrees for the program to function and, since South Africa is west of the Greenwich Meridian and south of the equator, the following functions were utilized:

$$\text{Latitude }(x) = -((\text{Degrees}) + (\text{Minutes}/60) + (\text{Seconds}/3600))$$

$$\text{Longitude }(y) = (\text{Degrees}) + (\text{Minutes}/60) + (\text{Seconds}/3600)$$

Each seal was given a tag number, which the programme held as a record. Those seals, which were not within the required area, were disregarded and their tag numbers deleted (Appendix I).

Seals were shot at sea from a dinghy with a 12 bore shotgun, after which their stomachs were removed and frozen. Once in the laboratory, the stomachs were defrosted and the contents of the stomachs weighed. The contents were analysed and teleost fishes, cephalopods and other invertebrates identified to species level. Each species was weighed and caudal lengths were obtained, where possible (David 1987).

Fish otoliths were also present in large numbers this study, the otoliths were identified to species level, paired and then counted in order to estimate numbers of each prey species that was eaten.

2.3.3 Purse-seine fishery sampling

Records of catches of purse-seine fishery were maintained by Marine and Coastal Management. Biological data were obtained by MCM staff by removing samples of fish from boats before they offloaded, identifying the fish to species level, weighing and measuring the contribution of each species separately and recording the location of where they were fished.

2.3.4 Analysis of shifts in feeding regime

Species composition analysis – percentage mass

For this study, the proportional contributions by mass of species to the diet of Cape gannets and Cape fur seals were computed using a formula employed by Punt *et al.* (1995):

$$Fp = Xp' / \sum Xp$$

Where $\sum Xp$ = sum of the mass of all the prey species and Xp' is the mass of a particular species. The fraction (Fp) was then converted to percentage mass. The flaws encountered when applying such a formula include the assumption that digestion time is independent of species, length, ambient temperature, mass, etc. (Punt *et al.* 1995). While such a supposition is incorrect, it is reasonable to assume that typical differences in evacuation time vary less among teleost fish than among classes of prey, and that since the key species being studied are anchovy and sardine, the assumption holds (Punt *et al.* 1995). Percentage mass of digested prey items as well as extrapolated mass data from otolith data were not considered for both seals and gannets stomach analysis, as pilot analysis showed these data to be unreliable.

Percentage mass values were utilized in a multivariate analysis and to produce histograms. The histograms were drawn to illustrate the variation in the proportion contributed by each species over time. Within the gannet analysis, prey items that were rare in the diet, such as kob (*Argyrosomus hololepidotus*), mullet (*Liza richardsoni*), Cape silverside (*Atherina breviseps*) and jacopever (*Helicolenus dactylopterus*) were lumped as "other". The seal diet was more diverse than that of gannets, so minor contributors to the diet were categorized as: "other pelagic fish", "other demersal fish" and "other". "Other pelagic fish" consisted of southern mullet, saury and chub mackerel. Contributors to the "other demersal fish" and "other" categories are listed in Table. 2.1.

Multivariate analysis of species composition

Multivariate cluster analysis has commonly been used to assess the effects of pollutants or other impacts on communities, particularly benthic communities (Clarke & Warwick 1994). Ecological multivariate (cluster) analysis is based on abundances (or relation abundances) of many species/taxa in samples. The data matrix is used to compute a triangular matrix of similarities between all pairs of samples. The triangular similarity matrix in turn is depicted as a dendrogram and/or a graphical ordination (Clarke & Warwick 1994). Multivariate cluster methods allow for comparisons of samples at different times, and are therefore suited for a large data set such as this study of shifts in diet regimes of organisms over many years. Multivariate analysis does not require that the data be normally distributed or homoscedastic, thus allowing for samples with great variations in abundance and for missing data.

For seal and gannet diets, the masses of each prey species were summed on an annual basis, and then converted to a percentage, thereby weighting each year equally, allowing for comparative analysis. Transformation of the data using the root-root transformation permitted all species to contribute to the measure of similarity between samples, in an effort to investigate fully the shift in the diet regimes of seals and gannets over 21 years (1978-1998). It prevented domination of the analysis by abundant species.

Commercial purse-seine catches were used to ascertain whether all three predators would cluster in a similar pattern. This was achieved by calculating the percentage contribution of each species to the catch and using these values into a multivariate analysis. The hypothesis that no significant difference exists in the species composition of the catch of Cape fur seals, Cape gannets and the purse-seine fishery was then tested.

The data were displayed in the form of dendrograms and two-dimensional ordination plots, using the Bray-Curtis similarity indices to compare samples. The SIMPER analysis was used to isolate the species mainly responsible for the dissimilarities among groups (Field *et al.* 1982 and Clarke & Warwick 1994).

Table. 2.1:Prey items in Cape fur seals stomachs that did not make a major contribution to the diet.

Other demersal fish			**Other**		
Osteichthyes			**Crustacea**		
	West coast sole	*Austroglossus microlepis*		Amphipods	
	Cape gurnard	*Chelidonichthys capensis*		Isopods	
	Redspotted tonguefish	*Cynoglossus zanzibarensis*		Lobster	*Jasus lalandii*
	White seacatfish	*Galeichthys feliceps*		Decapoda	
	Kingklip	*Genypterus capensis*		Cape mantis shrimp	*Harpiosquilla harpax*
	Beaked sandfish	*Gonorhynhus gonorhynhus*	**Mollusca**		
	Jacopever	*Helicolnus dactylopterus*		Bivalves	
	Buttersnoek	*Lepidopus caudatus*	**Chondrichthyes**		
	Monk fish	*Lophius vomerinus*		St. Joseph shark	*Callorhincus capensis*
	West coast snake eel	*Mystriophis rosetellatus*			
	Cape hagfish	*Myxine capensis*	**Aves**		
	Cape hottentot	*Pachymetapon blochii*		Penguins	*Spheniscus demersus*
	Ladder dragnet	*Paracallionymus costatus*			
	Goby	*Sufflogobius barbatus*			
Other pelagic fish					
Osteichthyes					
	Chub mackerel	*Scomber japonicus*			
	Harder (mullet)	*Liza richardsoni*			
	Horse mackerel	*Trachurus trachurus*			
	Lantern fish	*Lampanyctodes hectoris*			
	Saury	*Scomberesox saurus*			
	Snoek	*Thyrsites atun*			

2.4 RESULTS:

2.4.1 Analysis of shifts in feeding regimes

Analyses of catch compositions

For all three consumers, there is a strong reliance on epipelagic fish resources, predominantly sardine and anchovy (Figs. 2.3-2.5). Both gannets and seals show clear shifts in the relative contributions of sardine and anchovy suggesting that both species are able to switch prey, as well as demonstrating the anchovy-sardine transition. During the late 1970s and from 1980-1988, anchovy was abundant in the diet with sardine increasing in importance from the late 1980s onwards (Figs. 2.3-2.4).

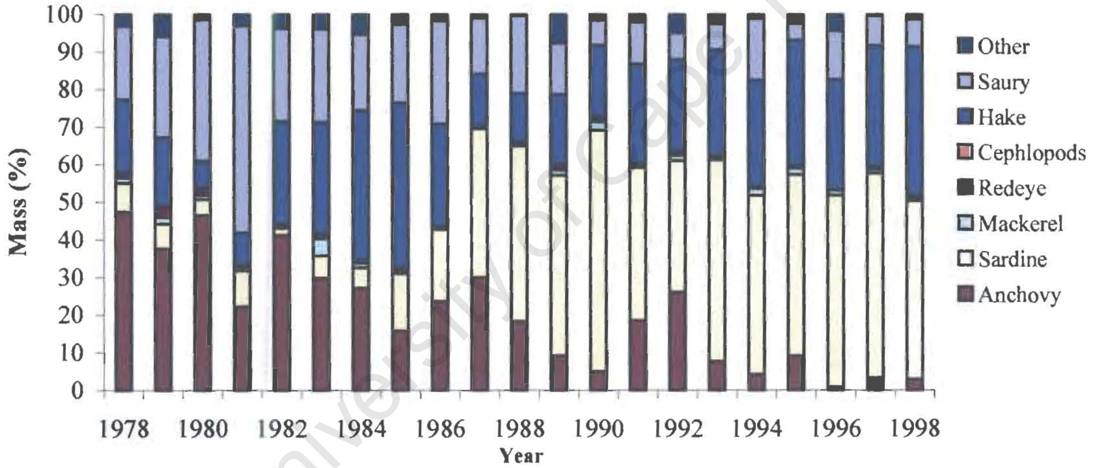

Fig. 2.3 Contribution of prey items to Cape gannet diet at Malgas Island and Lamberts Bay (1978-1998) (Data from MCM).

Other common prey items in the diet of gannets were saury and hake (saury occurs in surface waters and hake is scavenged). In the seal diet, fish species in the "other" category dominated, followed by "other pelagic" species (Table. 2.1, Fig. 2.4). Nonetheless, the anchovy-sardine switch can also be noted in the seal diet. Hake and cephalopods are also important dietary constituents.

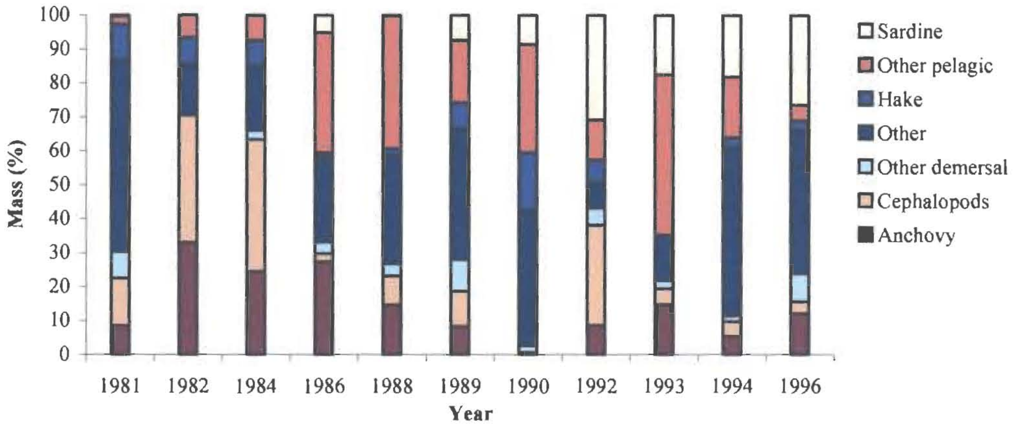

Fig. 2.4 Contribution of prey items to Cpae fur seal diet off the west coast of South Africa (1982-1996). (Data from MCM).

The catches landed by the purse-seine fishery between 1978 and 1995 consisted chiefly of anchovy, but from 1988 there was a progressive increase in sardine, mackerel and redeye catches (Fig. 2.5). The year 1992 does not follow the general trend as it has greater anchovy abundance. This trend is strongly influenced by management regulation: total allowable catches limited sardine catches in a successful endeavour to rebuild the resource. Anchovy were caught even when there was an increase in sardine abundance to fulfil the demand for fish meal and oil.

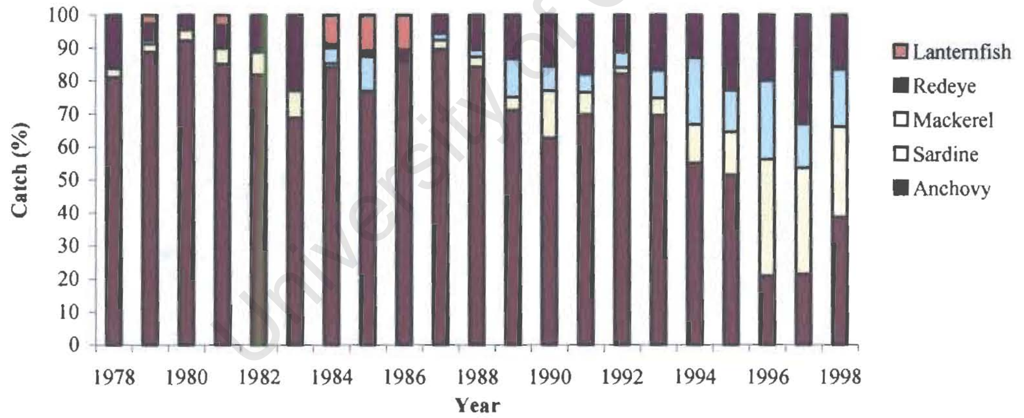

Fig. 2.5 Contribution of each species landed by the purse seine fishery (Data from MCM).

Multivariate analysis

Fishery analysis

Based on the Bray-Curtis similarity matrix (i.e. catch composition percentages in Appendix II), the annual fish catches separated into three groups at the arbitrary level of 84% similarity (Fig. 2.6). The groups comprised the "anchovy" group spanning the period 1978 – 1983, the "intermediate" group (1984-1986) and the "sardine" group (1987-1998, Fig. 2.6). These groups were further validated by the 2–dimensional ordination (MDS, Fig. 2.7) and the low stress level of 0.06.

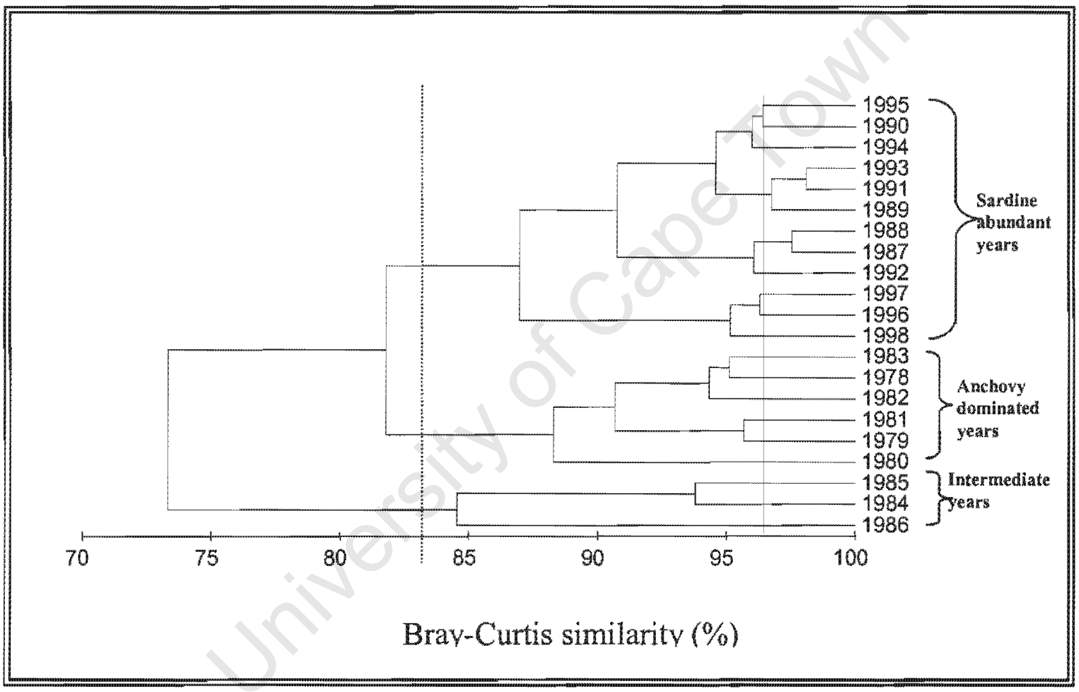

Fig. 2.6 Dendrogram showing similarities between years based on species composition of catches of the purse-seine fishery (1978-1998). Data were transformed using the fourth root transformation and grouped using group-average sorting. (Catch compositions from MCM).

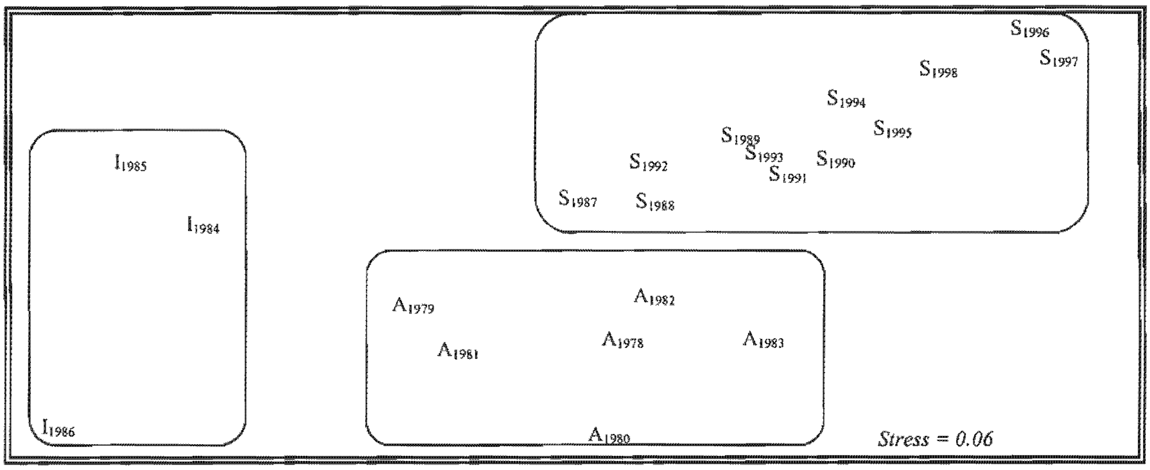

Fig. 2.7 MDS ordination showing similarities between years based on the catch composition landed by the purse-seine fishery from 1978 – 1998. The three distinct clusters are grouped as A = anchovy dominated years, I = intermediate years and S = sardine abundant years. Data were standardised, transformed using the fourth root transformation and grouped using multi-dimensional scaling. (Catch compositions from MCM).

The SIMPER program was used to establish the contribution of each prey species to the average dissimilarity between the defined groups, and to the average similarity within the groups. The similarity indices were very high and the results can be seen in Appendix II. The similarity results are not discussed here as they have little bearing on the objectives of this study.

The average dissimilarities calculated by the SIMPER program for the three feeding regimes were similar. The dissimilarity value between the anchovy and intermediate groups was 16.95%, followed by the dissimilarity between the anchovy and sardine groups (20.16%) and between the intermediate and sardine groups (19.32%). Although these dissimilarity values are low, and the intermediate years are not truly intermediate in the fishery data but rather isolated on their own in the MDS, the term intermediate has been retained to keep the discussion uniform.

In the dissimilarity table it is important to note that the average relative abundance of sardines differs little between the anchovy and intermediate years (Table 2.2a).

However, the same cannot be said for the differences in the average abundances of sardine and anchovy for the other two groups (Table. 2.2c)

Table 2.2: Breakdown of average dissimilarity between the anchovy, intermediate and sardine groups into contributions of top species, in order of decreasing contribution, for fishery data only. d*i* the average contribution of the *i*th species to dissimilarity between groups, and Cum d*i* (%), the cumulative percent contribution to the total dissimilarity.

Species	Ave. Abundance (%)	Ave. Abundance (%)	d*i*	Cum. d*i* %
(a)				
Anchovy vs. Intermediate	Anchovy Group	Intermediate Group		
Lantern Fish	1.11	**4.36**	31.58	31.58
Mackerel	0.50	**5.53**	25.50	57.08
Sardine	**4.70**	3.61	21.92	79.00
Redeye	**10.70**	7.28	21.00	100.00
(b)				
Anchovy vs. Sardine	Anchovy Group	Sardine Group		
Mackerel	0.50	**13.23**	33.95	33.95
Lantern Fish	**1.11**	0.00	26.34	60.28
Sardine	4.70	**16.75**	16.15	76.43
Anchovy	**83.00**	51.04	12.10	88.53
Redeye	10.70	**18.98**	11.47	100.0
(c)				
Intermediate vs. Sardine	Intermediate Group	Sardine Group		
Sardine	3.61	**16.75**	28.61	28.61
Lantern Fish	**4.36**	0.00	24.52	53.13
Redeye	7.28	**18.98**	17.50	70.63
Mackerel	5.53	**13.23**	17.45	88.08
Anchovy	**79.21**	51.04	11.92	100.00

Gannet analysis

The gannet diet data (Appendix III) were also transformed using the root-root transformation. The Bray-Curtis similarity matrix separated the data into five groups at the arbitrary similarity value of 90% (Fig. 2.8).

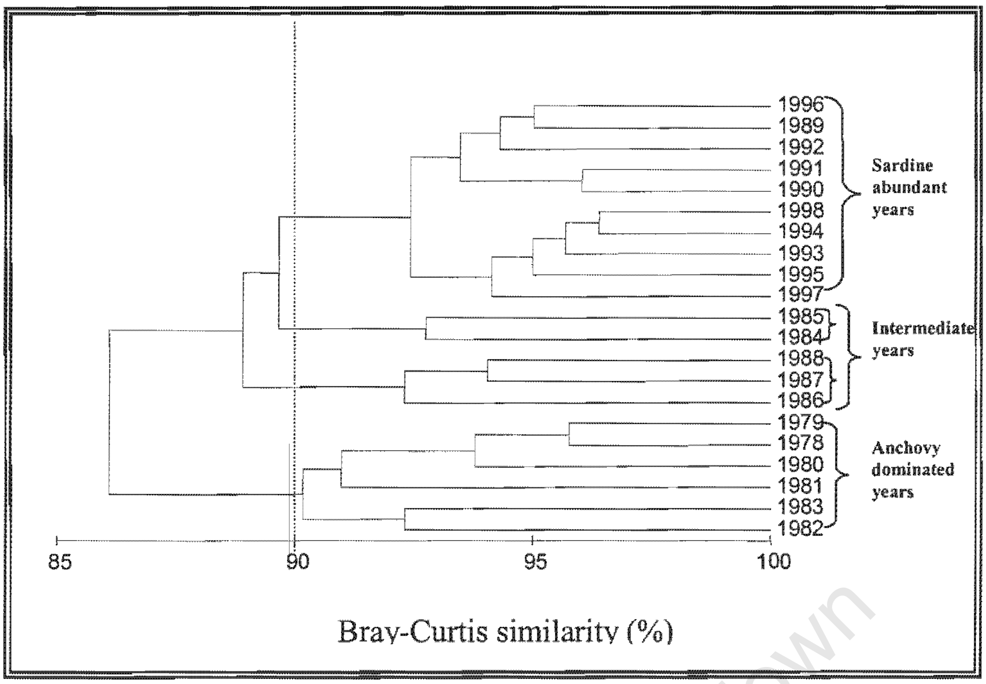

Fig. 2.8 Dendrogram showing similarities between years based on the species composition of the Cape gannet's diet (1978-1998). Data were transformed using the fourth root transformation and grouped using group-average sorting. (Data from MCM).

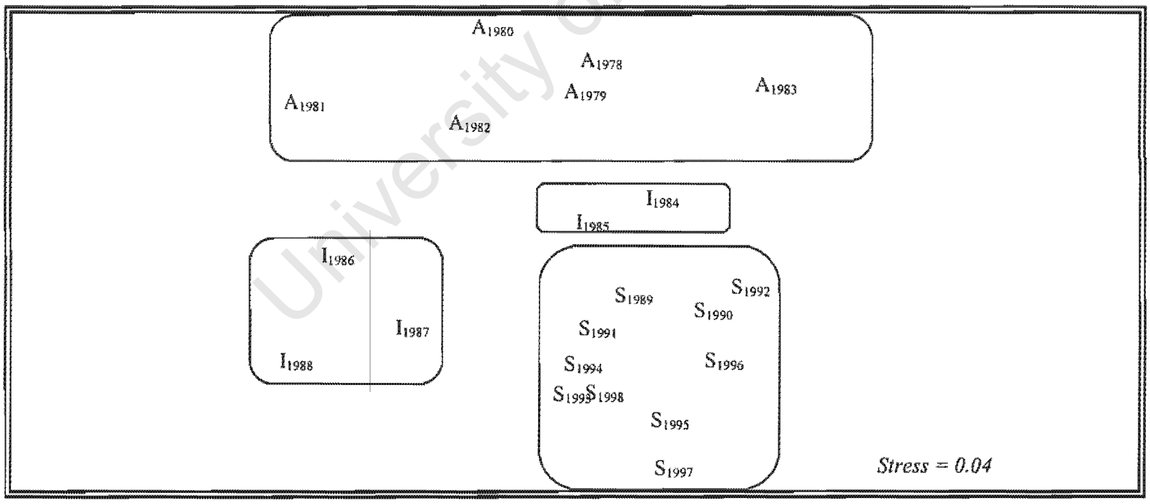

Fig. 2.9 MDS ordination showing similarities between years based on the diet composition of the Cape gannet from 1978 – 1998. The three distinct clusters are grouped as A = anchovy dominated years, I = Intermediate years and S = sardine Data were transformed using the fourth root transformation and grouped using MDS. (Data from MCM).

The five groups comprised years similar to those produced by the analysis of the fishery catch data. There was an "anchovy" group (1978–1983), an "intermediate" group (1984–1988) and a "sardine group" (1989–1998, Fig. 2.8). This grouping pattern was validated by the 2-dimensional ordination (MDS) with a low stress level of 0.04 (Fig. 2.9). It should be noted that the sardine-dominated group is a far closer pattern then the anchovy-dominated years (Fig. 2.9).

The discriminating species responsible for the 12.4% dissimilarity between the anchovy and intermediate groups included sardines, redeye and other prey items (as presented in Table 2.3a). Anchovy contributed minimally to the dissimilarity index of the anchovy versus intermediate years (Table 2.3a).

Comparatively, anchovy and saury abundance in the gannet diet has decreased considerably from the "anchovy" to the "sardine" years (Table 2.3b). While it would be expected that scavenged hake abundance would be high during the intermediate years because of sardine and anchovy being rare (Table 2.3a), it is in the "sardine" and "anchovy" dominated years that hake is still important in the gannet diet (Table 2.3b). Nonetheless sardine became more important in the diet in the "sardine" period. The average abundance of saury and anchovy declines substantially in the sardine-abundant regime when compared to the intermediate years (Table 2.3c).

Seal diet analysis

Once again the Bray-Curtis similarity matrix clustered the data (Appendix II) into three groups defined as anchovy dominated years (1982-1984), intermediate years (1986, 1988 & 1993) and sardine abundant years (1989, 1992, 1994 & 1996, Fig. 2.10). There were three years which did not conform to the pattern i.e. 1990 was categorised as an outlier, 1993 grouped with the intermediate years and 1981 grouped with the sardine abundant years which could be due to the sampling mainly offshore unlike the other sampling years (Fig. 2.10).

Table 2.3: Breakdown of average dissimilarity between the anchovy, intermediate and sardine groups into contributions of top species, in order of decreasing contribution, for gannet data only. d*i* is the average contribution of the *i*th species to dissimilarity between groups, and Cum d*i* (%), the cumulative percent contribution to the total dissimilarity.

Species	Ave. Abundance (%)	Ave. Abundance(%)	d*i*	Cum. d*i* %
(a)				
Anchovy vs. Intermediate	"Anchovy" Group	"Intermediate" Group		
Sardine	4.37	**27.13**	27.94	27.94
Redeye	**3.68**	0.18	13.41	41.35
Other	**5.04**	4.03	11.74	53.09
Hake	10.35	**16.13**	11.21	64.20
Mackerel	**3.16**	1.35	9.66	73.87
Cephalopods	0.36	**0.46**	9.64	83.50
Anchovy	**53.56**	34.99	9.23	92.73
(b)				
Anchovy vs. Sardine	"Anchovy" Group	"Sardine" Group		
Sardine	4.37	**48.07**	33.40	33.24
Anchovy	**53.56**	19.34	17.25	50.49
Saury	**24.08**	7.39	14.81	65.29
Redeye	**3.68**	1.49	9.43	74.73
Hake	10.35	**14.90**	7.16	81.88
Other	**5.04**	4.83	6.40	88.28
Mackerel	3.16	**3.75**	5.89	94.17
(c)				
Intermediate vs. Sardine	"Intermediate" Group	"Sardine" Group		
Saury	**16.75**	7.39	14.87	14.87
Sardine	27.13	**48.07**	14.64	29.51
Anchovy	**34.99**	19.34	14.26	43.77
Other	4.03	**4.83**	13.42	57.19
Mackerel	1.35	**3.75**	12.51	69.70
Cephalopods	0.46	**0.54**	11.60	81.30
Hake	**16.13**	14.90	9.85	91.14

Again, the ordination plot agreed well with the dendrogram with a low stress level of 0.04 (Fig. 2.11). Both the "anchovy" and the "intermediate" years grouped together very loosely, which could be a product of the small sample sizes for the seal data. However the general pattern of three periods is clear.

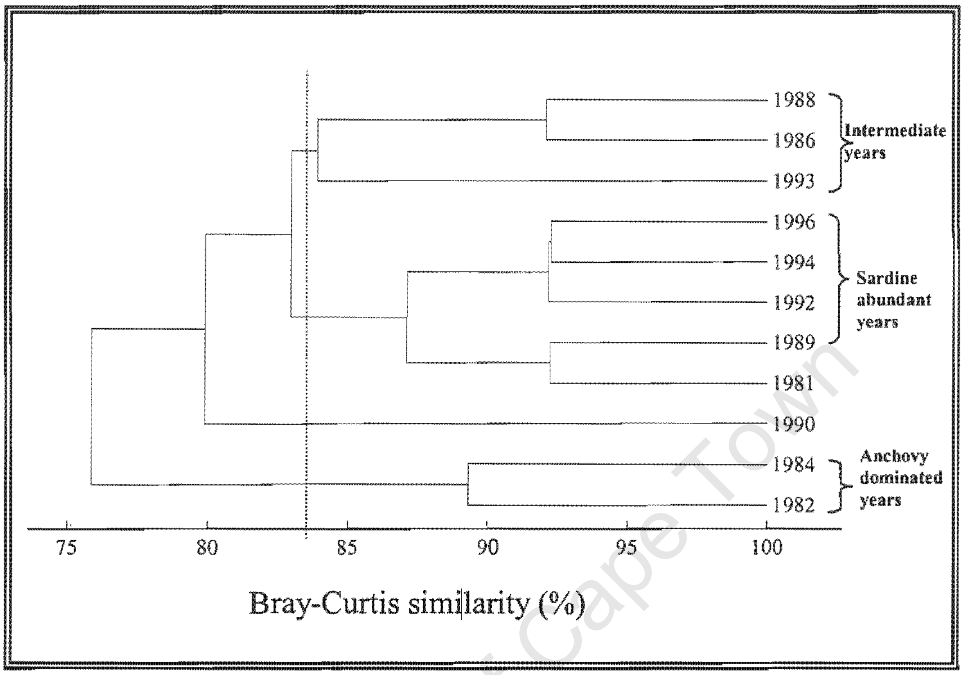

Fig. 2.10 Dendrogram showing similarities between years based on the species composition of the diet of Cape fur seals (1982-1996). Data were transformed using the fourth root transformation and grouped using group-average sorting. (Data from MCM).

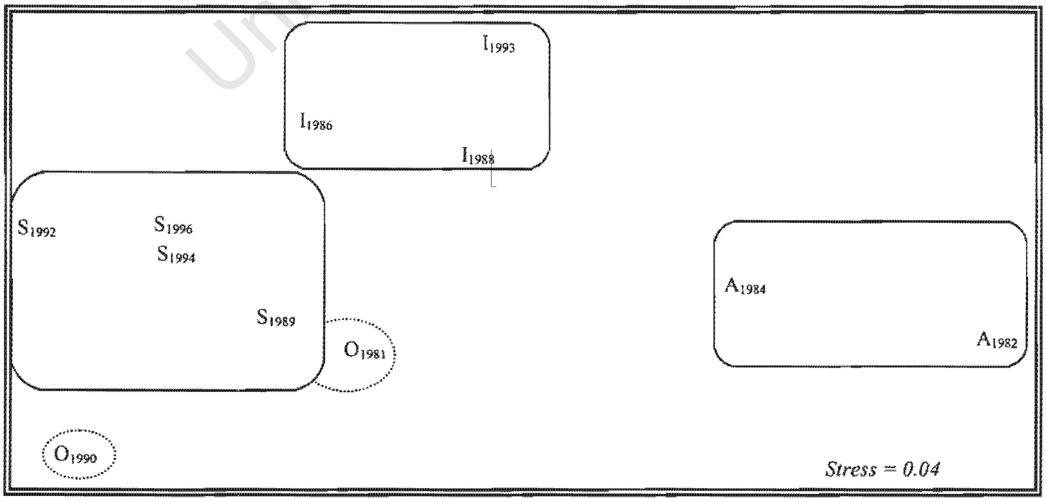

Fig. 2.11 MDS ordination showing similarities between years based on the diet composition of the Cape fur seal from 1982 – 1996. The three distinct clusters are grouped as A = anchovy dominated years, I = Intermediate years and S = sardine abundant years, with O = outlier.

For the anchovy and intermediate groups, the major contributors were other pelagic prey species such as snoek, mackerel and saury, while cephalopods were also a major contributor to the diet (Table 2.4a). Interestingly though, cephalopods have a higher average relative abundance in the anchovy group than in the intermediate group, this can be explained by the availability of "other pelagic" species such as saury, snoek and mackerel, during the intermediate group. For the seal and gannet cluster

Table 2.4: Breakdown of average dissimilarity between the anchovy, intermediate and sardine groups into contributions of top species, in order of decreasing contribution - seal data only. d*i* is the average contribution of the *i*th species to dissimilarity between groups, and Cum d*i* (%), the cumulative percent contribution to the total dissimilarity.

Species	Ave. Abundance (%)	Ave. Abundance (%)	d*i*	Cum. d*i* %
(a)				
Anchovy vs. Intermediate	"Anchovy" Group	"Intermediate" Group		
Pelagic other	3.45	**34.16**	32.56	32.56
Cephalopods	**30.15**	5.53	26.14	58.70
General Other	**32.18**	31.72	17.85	76.55
Anchovy	**21.99**	20.98	10.93	87.48
Hake	**8.66**	1.52	7.58	95.06
(b)				
Anchovy vs. Sardine	"Anchovy" Group	"Sardine" Group		
General other	32.18	**54.60**	26.49	26.49
Cephalopods	**30.15**	4.80	26.23	52.71
Sardine	0.12	**19.65**	20.21	72.92
Anchovy	**21.99**	8.38	14.71	87.63
Hake	**8.66**	3.90	4.93	92.56
(c.)				
Intermediate vs. Sardine	"Intermediate" Group	"Sardine" Group		
Pelagic other	**34.16**	3.40	32.71	32.71
General other	31.72	**54.60**	24.35	57.06
Sardine	1.83	**19.65**	18.97	76.03
Anchovy	**20.98**	8.38	13.44	89.47
Cephalopods	**5.53**	4.80	4.21	93.68

analysis, the intermediate years tended to group close to the sardine abundant years (Fig. 2.9 & 2.11), as a result of the slow increase in the sardine abundance (Table 2.3 & 2.4).

With regard to the anchovy versus sardine dissimilarity comparison, sardine was one of the key prey items differentiating these groups (Table 2.4b). However, while there is an increase in sardine abundance and a decrease in cephalopod abundance, anchovy is relatively prevalent during the sardine abundant years in the seal diet (Table 2.4b).

Finally, the multivariate analysis for the intermediate group versus sardine group showed that other pelagic fish (which consist of snoek, lantern fish and particularly mackerel and saury) contributed to this difference (Table 2.4c). It might be reasoned that as sardines were low in abundance during the intermediate years, cephalopods would contribute a greater proportion of the diet as shown to be the case in table 2.4b. Anchovy and "other" formed a large percentage of the seal diet.

2.5 DISCUSSION:

Competition among species may be assessed by making the assumption that the removal of pelagic prey by gannets, seals and the fishery is proportional to their prey's relative abundance (Berruti & Colclough 1987 and Crawford *et al.* 1992). If this assumption does not hold, the alternative is that the predators remove the prey of their choice. The aim of this study was to provide an indication of whether the degree of overlap in prey utilisation was influenced by the most abundant prey species of the food base, i.e. what is the extent of this prey overlap and does the competition vary in severity under different fishing scenarios?

The multivariate analysis of species composition distinguished three groups on the basis of prey taken by the three predators. During the period 1978-1983 anchovy dominated the catches, followed by an intermediate period (1984-1990) and finally a period of sardine abundance (1991-1998). These groupings clearly demonstrate that within the Benguela system, there are few abundant clupeoids such as anchovy and sardine, which govern the system at different times (Crawford & Shelton 1981, Burger & Cooper 1982, Berruti & Colclough 1987, Crawford *et al.* 1992 and Crawford, 1998). Following this argument, these prey populations are shared by gannets, seals and the fishery, which are in turn influenced by prey abundance (Crawford 1987 and Crawford *et al.* 1992).

Whereas top predators may exploit the most abundant pelagic resource, such as anchovy (1978-1984), it does not mean that only anchovy were targeted. Gannets and seals did exploit sardines (occurring in mixed shoals) and other prey items. However, the presence of these prey items was overpowered by the abundance of anchovy (Berruti 1987), indicating that the removal of the dominating resource is maximal and the diet reflects the dominant prey in the ecosystem.

The gannets were the first predators to show significant exploitation of the increasing sardine resource. Since 1983, following powerful year classes of sardine that is thought to have been responsible for the increase in sardine abundance (Armstrong *et al.* 1987, Crawford 1998 and Barange *et al.* 1999), sardine abundance slowly increase in the gannet diet. Furthermore, gannets seem to be removing sardine while anchovy still persist at reasonably high abundances, as can be seen from the purse-seine catches, bearing in mind that the purse-seine fisheries are restricted by demand, economic markets and more importantly quotas. Nonetheless the presence of sardine in the gannet diet when anchovy was still abundant also reinforces the ideas of Batchelor & Ross (1984) and Adams & Klages (1999) that sardines are the preferred prey of gannets. Furthermore, the reduction of fishing pressure on a species such as sardine might increase its abundance within the gannet diet and possibly make the prey more accessible to gannets (Berruti & Colclough 1987). Therefore, if the fishery exploits the sardine stocks unsustainably or prematurely, i.e. before the stocks have reached a high enough abundance, this would have an adverse effect on gannet populations.

Gannets tend to be mainly restricted to pelagic prey, much like the purse-seine fishery. Seals have a far more varied diet, removing cephalopods, hake and non-commercial pelagic and demersal prey species. This supports David's (1990) postulation that whereas seals do consume approximately the same amount of fish as the fishery, most of the seal diet consists of species that are not commercially valuable. Nevertheless, the seal diet shows the anchovy-sardine switch with sardine making a significant appearance in 1992 (Fig. 2.4). The seal and gannet diets differ because seals are able to feed throughout the water column, whereas gannets are restricted to the upper layers (Adams & Klages 1999). Although seal diets show no major reliance on anchovy and sardine, this may reflect the opportunistic feeding habits of seal. Intensive scavenging from purse-seine nets, demersal trawlers and snoek long-lines has shown seals to be highly adaptive and opportunistic feeders (David 1987, David 1989, Miller *et al.* 1996 and Wickens 1992). Therefore, their diet may show what is most easily attainable.

Nevertheless, one cannot rule out the importance of pelagic resources in the seal diet, particularly for females and juvenile seals (David 1987, 1989 and Wickens 1992). Females and many juvenile males often forage inshore where most of the recruits of sardine and anchovy shoal, and utilise this resource to ensure self-nourishment, particularly in the case of lactating females. Male seals remove sardine and anchovy during the fattening up period before spending five weeks at the colonies protecting their harems of females (Rand 1959, David 1987 and 1990). While this study did not make any distinction between male, female or juvenile seal stomach contents due to sample size limitations, from the cited literature, age and sex of Cape fur seals play an important role is diet composition.

Likewise gannets depend on sardine and anchovy during their breeding season (Crawford 1989). Young chicks are fed on regurgitated fish, so that the parents need to catch sufficient food to sustain both the chick and themselves. The switch from anchovy to sardine by gannets, even when anchovy abundances were high, may indicate as Batchelor & Ross (1984) and Adams & Klages (1999) have shown that chicks fed on sardine have a higher fledgling success than chicks fed on anchovy or hake. Clearly therefore, prey availability is a key factor not just prey abundance.

Additionally, Berruti & Colclough (1987) have shown that sardine in gannet diet and fishery catches appear to be positively linearly correlated. However, this may not be true during years of high sardine abundance, as the fishery would exert a heavy fishing mortality on sardine to capitalise on the resource, but to the detriment of other land-based predators. Such a comparison is not evident in this study, as substantial resumption of sardine catches has not yet occurred in the purse-seine industry due to regulation preventing this.

While the birds alone remove a minimal amount of pelagic resources (18% of 13000 tons removed by all seabirds, Crawford *et al.* 1991), if the fisheries and to a lesser extent the seals remove large numbers of the prey, not forgetting other predators of pelagic fish such as hake, snoek and squid, the gannets may be badly affected. Particularly when Butterworth *et al.* (1995)'s base case scenario is considered. It predicts that in 20 years from 1995 (if no seals are removed), seals alone will consume 2.8 million tons of food per year of which 90% will be teleost fish. Such a scenario plus the resumption of sardine targeted fishing will adversely affect the gannets and eventually the seals and the fishery. Therefore to fully investigate the degree of competition between gannets, seals and the purse-seine fishery, assessment of whether the three predators are removing the same size classes needs to be examined. This is addressed in Chapter 3.

CHAPTER THREE

SIZE DISTRIBUTION OF PELAGIC FISH IN THE DIETS OF GANNETS, SEALS AND FISH CATCHES

3.1 INTRODUCTION:

In chapter two, it was shown that there is considerable overlap in the species composition of diets of Cape gannets and Cape fur seals and the catches by South African purse-seine fishery. This suggests that these three consumers may compete for forage fish resources and makes it of interest to know to what extent partitioning of the resources occurs. To investigate this aspect, the size distributions of catches of anchovy and sardine by gannets, seals and the fishery were compared.

Both these clupeoid fishes (i.e. anchovy and sardine) are seasonal spawners (Richardson *et al.* 1997). Anchovy spawn between October and February (Shelton 1986, Richardson *et al.* 1997 and Barange *et al.* 1999). Sardines have a protracted spawning season, peaking between August and March. Sardine and especially anchovy are relatively short-lived, feed mostly on plankton in shallow coastal regions and are largely epipelagic (Shelton 1986, Richardson *et al.* 1997 and Fowler 1998). The larvae and juveniles of both species are transported north along the west coast of South Africa towards the Orange River. The area north of St. Helena Bay is regarded as the nursery ground for young sardine and anchovy (Shelton 1986, Richardson *et al.* 1997 and Fowler 1998). The following autumn/winter (April-August) the juveniles swim southwards where they later may spawn on the Agulhas Bank.

Different sizes of these fish species are available to predators and the fishery at different times of the year. Hence, the season when catches are taken influences their size composition. To account for this, size compositions of catches by the three consumers were compared for each month of the year where there was sufficient information to permit such a comparison.

3.2 METHODS:

3.2.1 Cape gannet and fisheries sampling

The lengths of anchovy and sardine caught by gannets and the fishery were sampled as described in Chapter 2 by the staff at Marine and Coastal Management.

3.2.2 Cape fur seal sampling

The staff of Marine and Coastal Management also collected the seal data. However, only whole fish found in stomachs were recorded. This study entailed sorting and then pairing anchovy and sardine otoliths. Pairing required finding a right and a left otolith, which once completed, allowed the number of fish ingested to be established. There are several problems when working with otoliths removed from the stomachs of animals. Digestion of the otoliths has the effect of reducing some of the prominent features and eroding the margins (Smale *et al.* 1995). Consequently, the lengths and weights of fish calculated from measuring such otoliths will tend to underestimate the original size of the prey (Smale *et al.* 1995).

To overcome these problems, part of this study necessitated sorting otoliths into non-digested, partially digested and well-digested groups. All broken otoliths were discarded immediately. The rest of the samples were viewed under a dissecting microscope in an effort to group them into the above categories. Criteria were then established to separate out usable and non-usable otoliths. These criteria were based on the premise that only the otolith length would be measured.

The criteria used were:

I. Has the otolith retained its basic shape? Anchovy otoliths are oblong to fusiform, whereas sardine otoliths are ovate.
II. Is the sulcus visible or partially visible? The sulcus is a longitudinal groove or depression on the dorsal surface of the otolith (Fig. 3.1).

III. Is the excisural notch still present? This is very closely linked to the presence or absence of a rostrum (Fig. 3.1). Both sardine and anchovy otoliths have a well-defined rostrum. If either the excisural notch or the rostrum had completely been eroded, the otoliths were discarded.

Once the otoliths were deemed suitable based on these criteria, they were measured using a 10-mm graticule eyepiece, to one decimal place.

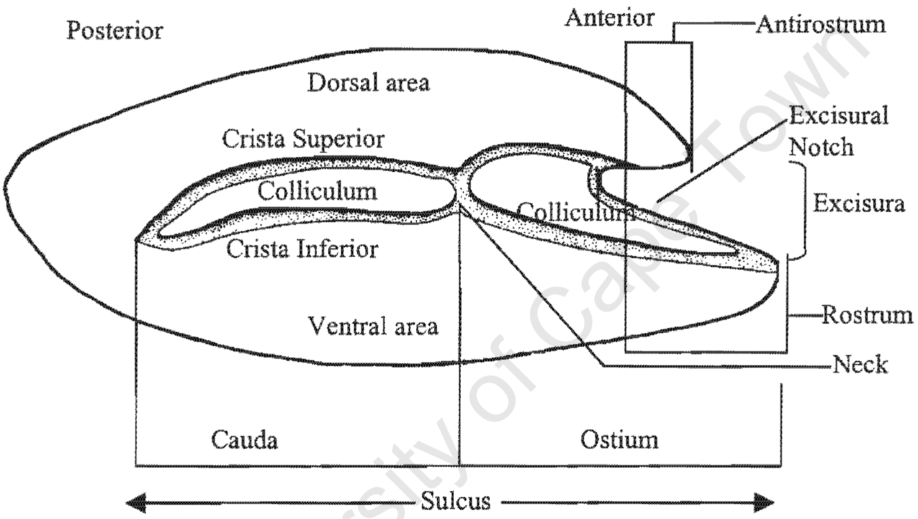

Fig. 3.1 A diagram of a heteromorph otolith illustrating features which were used to assess whether otoliths found in the seal diet could be used to estimate fish length (modified from Smale et al. 1995)

For the sardine, a relationship between otolith length and fish length was generated by regression using known fish and otolith lengths from work currently being undertaken at Marine and Coastal Management (Dr. Michael Kerstan). The equation obtained was:

$$\textit{Sardine length (mm)} = -0.526 + 5.221 * \textit{Otolith length (mm)}$$

For the anchovy, a regression calculated by Prosch (1986) was used:

$$\textit{Anchovy length (mm)} = 0.6534 + 3.1506 * \textit{Otolith length (mm)}$$

3.2.3 Data Analysis

Size distribution analysis

The size distributions of anchovy and sardine removed by gannets, seals and the fishery were assessed for the three periods (anchovy dominated period 1978-1983; an intermediate period 1984-1990, and a sardine abundant period 1991-1998), established in Chapter 2 using the STATISTICA and PRISM software packages.

PRISM version 4.0 was used to produce histograms of frequency of occurrence of different length classes of sardine and anchovy in the catches of the three predators. This allows for visual comparison of length classes removed by each predator. The data were not normal or homoscedastic, having differences in the variances. Therefore, non-parametric tests were employed using STATISTICA to test the null hypothesis that there are no significant differences in the size classes of anchovy and sardine removed by gannets, seals and the fishery. The most appropriate test is the Kolmogorov-Smirnov test (KS test), which allows for examination of the overlap in utilization of particular length classes of prey items by predators. The test is sensitive to differences in the general shapes of the distributions in the samples (e.g. dispersion, skewness, spread, etc.).

The KS test is a comparison whereby the lengths of anchovy and sardine removed by each of the three consumers are compared in pairs. Therefore, six comparisons were performed (three for each prey species) for each of the three periods established in Chapter 2. However, it is well known that applying a pairwise comparison to test multisample hypotheses is problematic (Zar 1996 and Peres-Neto 1999). The main concern is that the number of "inflated" significance values cannot be controlled (Peres-Neto 1999). Therefore, relying on such a test could increase the probability of committing the classic Type I error, i.e. the rejection of the null hypothesis when it is actually true. Peres-Neto (1999) shows that this problem can be overcome by using sequential Bonferroni corrections. This approach was taken in this study when significant values were found in the KS pairwise comparison test.

Graphic Analysis

The program Surfer32 was used to generate 3–dimensional diagrams having frequency as the dependent variable, length and year/time as the independent variables. Kriging was found to be the most appropriate interpolating method because it attempts to express trends in the data by connecting high points (or low points) along a ridge (or trough), rather than isolating the points by a "bulls–eye" type contour. Such data manipulation illustrates the contribution of year-cohorts of fish to the diets of predators and the fishery for the duration of their occurrences in the catches.

The technique permits inferences to be made about predator-prey interactions over time. Additionally relative abundance and growth in size of recruiting cohorts and older age groups can be inferred. This information is useful in fisheries management because of the great variation in early mortality of most fish species.

Only data from gannets and the fishery were used to infer any trends because of the lack of consecutive years of seal dietary data. The analysis requires a substantial amount of data and more importantly data from consecutive months or years, to establish coherent, interpretable trend lines. Data from the two gannet islands were analyzed separately because of the different feeding grounds of the birds at the two islands (Crawford *et al.* 1994). This may result in their feeding on anchovy and sardine of different ages and sizes. Cape gannet data are from 1978-1998 and the fishery data from 1978-1996.

Seasonal Analysis

PRISM was used to generate histograms of the sizes of anchovy and sardine caught monthly by gannets and the fishery. The same procedure could not be done for seals because information was collected less frequently. The gannet and fishery data for each month were pooled for different years to give seasonal means and standard deviations.

3.3 RESULTS:

3.3.1. Anchovy Length Frequency Analysis

Figure 3.2 shows the size distributions of anchovy removed by the gannets, seals and the fishery during the three periods. For all three periods, the data for gannets and the fishery display a typical Gaussian bell-shaped distribution, with the mode being approximately 100 mm. Both sets of consumers removed similar size classes of anchovy, mainly fish caudal lengths of 70 – 120 mm (Fig. 3.2). However, the curves differ in that the gannet data produce a far more spread out or flat curve, while the fishery data show a very narrow curve indicating the fishery to be more selective or this could be indicative of the fishes behaviour (Fig. 3.2). These curves suggest that gannets feed on a far wider size range of anchovy, while the fishery catches a far more restricted size (Fig. 3.2).

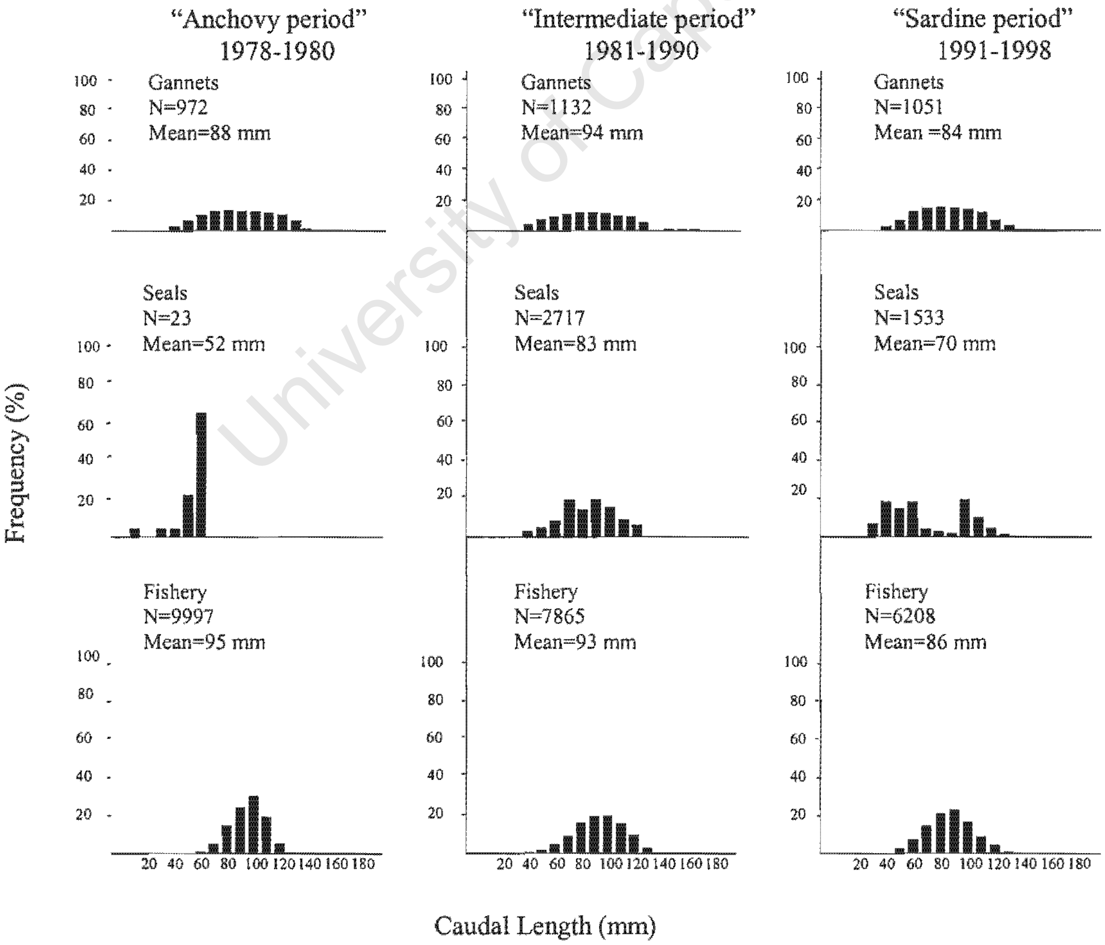

Fig. 3.2 Size distributions of anchovy caught by gannets, seals and the fishery during the three periods. Seal data extends only from 1982 - 1996

Few data were available for the seals for 1978-1983 (anchovy dominated period). Although the data for this period show a large proportion (n=23) of 70 mm anchovy being removed (Fig. 3.2), this may be an artifact of the small sample size or the gut contents of other sardine and anchovy predators (such as snoek), which seal readily consume. From 1984-1990 size classes eaten by seals were similar to those caught by the fishery. From 1991-1998, there were two modes in sizes of anchovy eaten by the seals (Fig. 3.2). One mode shows smaller size classes than are caught by the fishery.

The mean size of anchovy caught by the fishery decreased from 95 mm in 1978-1983 to 86 mm in 1991-1998 (Fig. 3.2). For both gannets and seals, there was a decrease in mean sizes of catches between intermediate and sardine years.

The KS test showed significant differences at the 99% confidence level in size distributions of anchovy caught for all three comparisons for all three periods considered (Table. 3.1). The Bonferroni inequality correction also rejected the null hypothesis in sizes of anchovy caught at α=0.01. Although the differences in the size frequency distributions are significant, there is clearly a large overlap in sizes of anchovy caught by these three consumers. This is probably due to the KS test being extremely sensitive and detecting any small differences in the size distributions.

Table 3.1: Pairwise comparison results using both the Kolmogorov-Smirnov statistical test ($p< 0.01$) and corrected for using the sequential Bonferroni correction ($p< 0.01$) for anchovy sizes removed by the fishery, gannets and seals for the three established periods

Size Distribution Comparisons	Kolmogorov-Smirnov p value (before correction)	Accept/Reject	Bonferroni's correction $p_i <= alpha/(1+k-i)$ (after correction)	Accept/Reject
a)"Anchovy period"				
Fishery vs. Gannets	p<0.001	Reject	p<0.003	Reject
Fishery vs. Seals	p<0.001	Reject	p<0.005	Reject
Gannets vs. Seals	p<0.001	Reject	p<0.001	Reject
b)"Intermediate period"				
Fishery vs. Gannets	p<0.001	Reject	p<0.003	Reject
Fishery vs. Seals	p<0.001	Reject	p<0.005	Reject
Gannets vs. Seals	p<0.001	Reject	p<0.001	Reject
c)"Sardine period"				
Fishery vs. Gannets	p<0.001	Reject	p<0.003	Reject
Fishery vs. Seals	p<0.001	Reject	p<0.005	Reject
Gannets vs. Seals	p<0.001	Reject	p<0.001	Reject

3.3.2. Sardine Length Frequency Analysis

For sardine, there were bimodal distributions in the sizes caught by gannets, seals and the fishery (Fig. 3.3). For gannets and seals, this pattern is related to the migrations of adult sardine during spawning on the one hand and juvenile movement on the other.

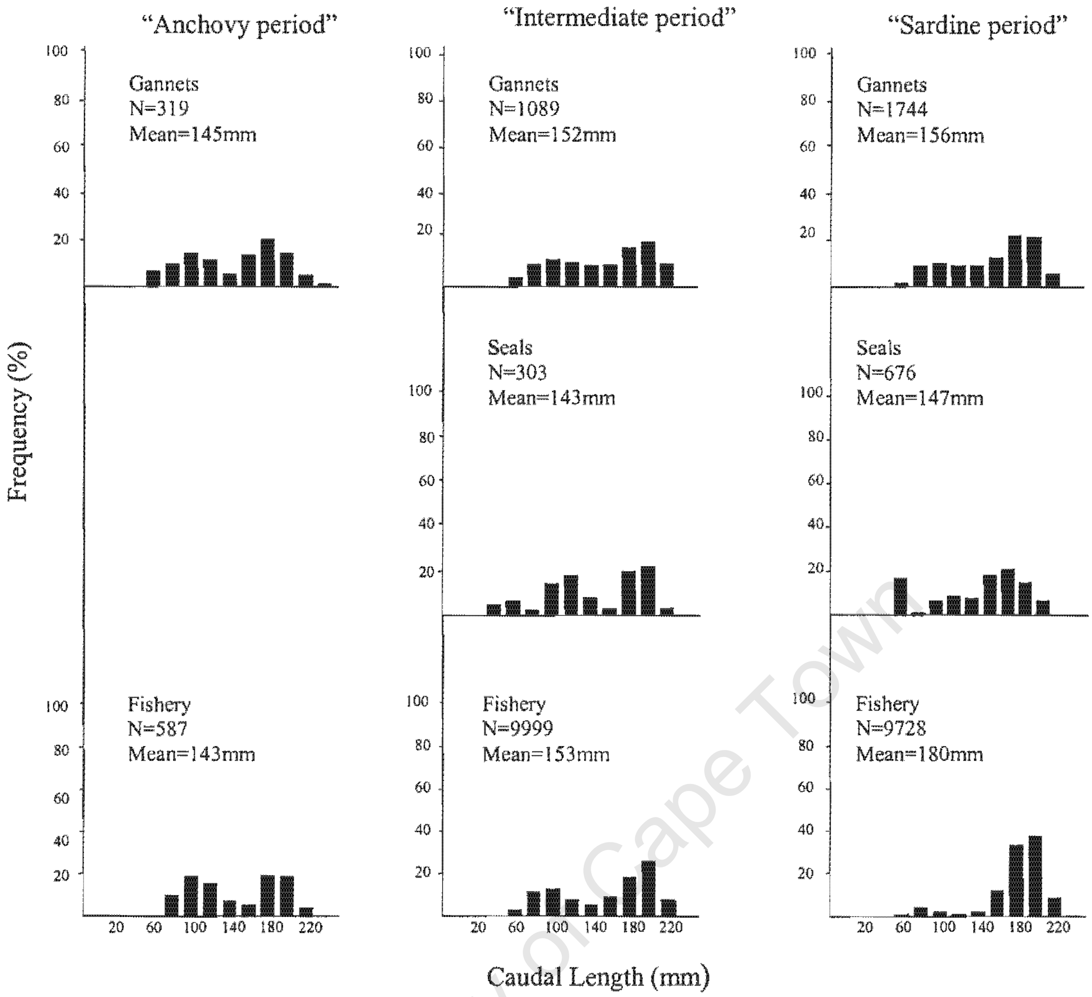

Fig. 3.3 Size distributions of sardine caught by gannets, seals and the fishery during the three periods. There are no data available for seals from 1978 - 1983

Again, for all three consumers there is overlap in sardine size distributions and the mean prey lengths are similar (Fig. 3.3). For all three consumers, the mean lengths of sardine taken increased through the three periods examined (Fig. 3.3). The KS test comparisons for the intermediate period (1984 –1990) and sardine-abundant period (1991-1998) rejected the null hypotheses of no differences in sizes of fish caught by the three consumers ($p<0.01$, Table. 3.2). However, there was no significant difference between gannets and the fishery for the anchovy period (1978- 1983, $p<0.01$). The Bonferroni inequality correction was in agreement with the KS comparison tests and accepted the null hypothesis of no differences in sizes removed by gannets and the fishery in the anchovy period (1978-1983), but the null hypothesis for the intermediate period (1984-1990) and the sardine-abundant period (1991-1998) comparisons was rejected at $\alpha=0.01$ (Table. 3.2).

Table 3.2: Pairwise comparison results using both the Kolmogorov-Smirnov statistical test ($p< 0.01$) and corrected for using the Bonferrroni correction ($p< 0.01$) for sardine sizes Removed by the fishery, gannets and seals for the three established periods

Size Distribution Comparisons	Kolmogorov-Smirnov p value (before correction)	Accept/Reject	Bonferroni's correction pi <= alpha/(1+k-i) (after correction)	Accept/Reject
a)"Anchovy period"				
Fishery vs. Gannets	$p<0.100$	Accept	$p<0.100$	Accept
b)"Intermediate period"				
Fishery vs. Gannets	$p<0.001$	Reject	$p<0.003$	Reject
Fishery vs. Seals	$p<0.001$	Reject	$p<0.005$	Reject
Gannets vs. Seals	$p<0.005$	Reject	$p<0.01$	Reject
c)"Sardine period"				
Fishery vs. Gannets	$p<0.001$	Reject	$p<0.003$	Reject
Fishery vs. Seals	$p<0.001$	Reject	$p<0.005$	Reject
Gannets vs. Seals	$p<0.001$	Reject	$p<0.001$	Reject

3.3.3. Seasonality

Anchovy

There were clear seasonal changes in the caudal length of anchovy ingested by the Cape gannets (Fig. 3.4). Fish in the size class 100-110 mm were found predominantly in the gannet diet from December to February. Modal lengths were at their smallest (80-90 mm) from May to September and increased again in November (Fig. 3.4). Trends in sizes of anchovy caught by the fishery were similar (Fig. 3.4). Larger anchovy were caught from December to April, and then smaller anchovy (recruits of the year) predominated until October. In November, the lengths were intermediate.

Sardine

Figure 3.5 shows the length classes of sardine ingested by Cape gannets. From May to October, there was a bimodal distribution with catches of sardines measuring between 80 –100 mm and 180 – 200 mm. This bimodal distribution is a reflection of the bimodal spawning periods of the sardine species (May-November and January, Crawford 1981). From November to March, gannets ate mainly large sardines (180 – 200 mm, Fig. 3.5).

The purse-seine fishery also exploited two size categories of sardine: juveniles of 80 – 100 mm and older fish (180 – 200mm, Fig. 3.5). From December to April, larger fish predominated. The bimodal distribution represents the bycatch removed from mixed anchovy and sardine shoals (smaller fish) and the directed sardine fishery (larger fish, Fig. 3.5).

The bumper recruitment year of 1983 can be traced in both the fishery and the gannet catches particularly in the diets of the Malgas Island gannets. Furthermore, the good recruitment years of the late 1990s are also visible in the gannet diet, especially the gannets at Lamberts Bay. These birds removed much larger sardines with a maximum caudal length of 200 mm.

3.3.4. Graphic Analysis

Anchovy

The fishery consistently removed anchovy of caudal length 60-120 mm (Fig. 3.6c). Smaller or larger anchovy were not exploited throughout the study period. Cape gannets at both Lamberts Bay and Malgas Island exploit anchovy of similar sizes (Fig. 3.6a & b).

During years of poor recruitment (1989-1990 & 1994) according to recruitment surveys (Barange *et al.* 1999), gannets at both colonies were exploiting very small anchovies of between 40-50 mm. This trend is evident in the fishery catches as well (Fig. 3.6a, b & c). Good recruitment years are also reflected in the gannet diets, i.e. 1985-1988. Before acoustic surveys, which commenced in 1984, the gannet diet shows years of good recruitment in 1979-1981, particularly conspicuous at Malgas Island (Fig. 3.6b). This is not as pronounced in the fishery catches (Fig. 3.6c).

Sardine

The two size classes removed by the fishery are clearly displayed in figure 3.7c. The Cape gannets exploit a wide size range of sardine but are clearly geographically restricted. The Lamberts Bay gannets predominantly exploit the smaller sardines (40-100 mm) while the Malgas Island gannets, which forage further south, remove larger sardines (100-200 mm). However, owing to separate foraging grounds (Berruti 1987) and prey migration patterns, the Lamberts Bay gannets remove many smaller sardines than do the Malgas Island gannets (Fig. 3.6a).

3.4. DISCUSSION:

Competitive resource sharing plays a significant role in the trophic functioning of the Benguela ecosystem (Berruti 1987, Crawford & Dyer 1995 and Cury *et al.* 2000). Accordingly there is extensive overlap in prey utilisation (Berruti 1987, Berruti & Colclough 1987 and Crawford 1987). The results of this study show substantial overlap in resource utilisation between the fishery and seals for size ranges of anchovy and sardine also eaten by gannets (modal classes for anchovy 90-100 mm and for sardine 80-100 mm and 180-220 mm).

Furthermore, this study shows that all three consumers remove both juvenile and adult anchovy and sardine. Berruti (1987), Berruti *et al.* (1993) and Barange *et al.* (1999) obtained similar results. The three consumers also forage upon shoals of adult fish

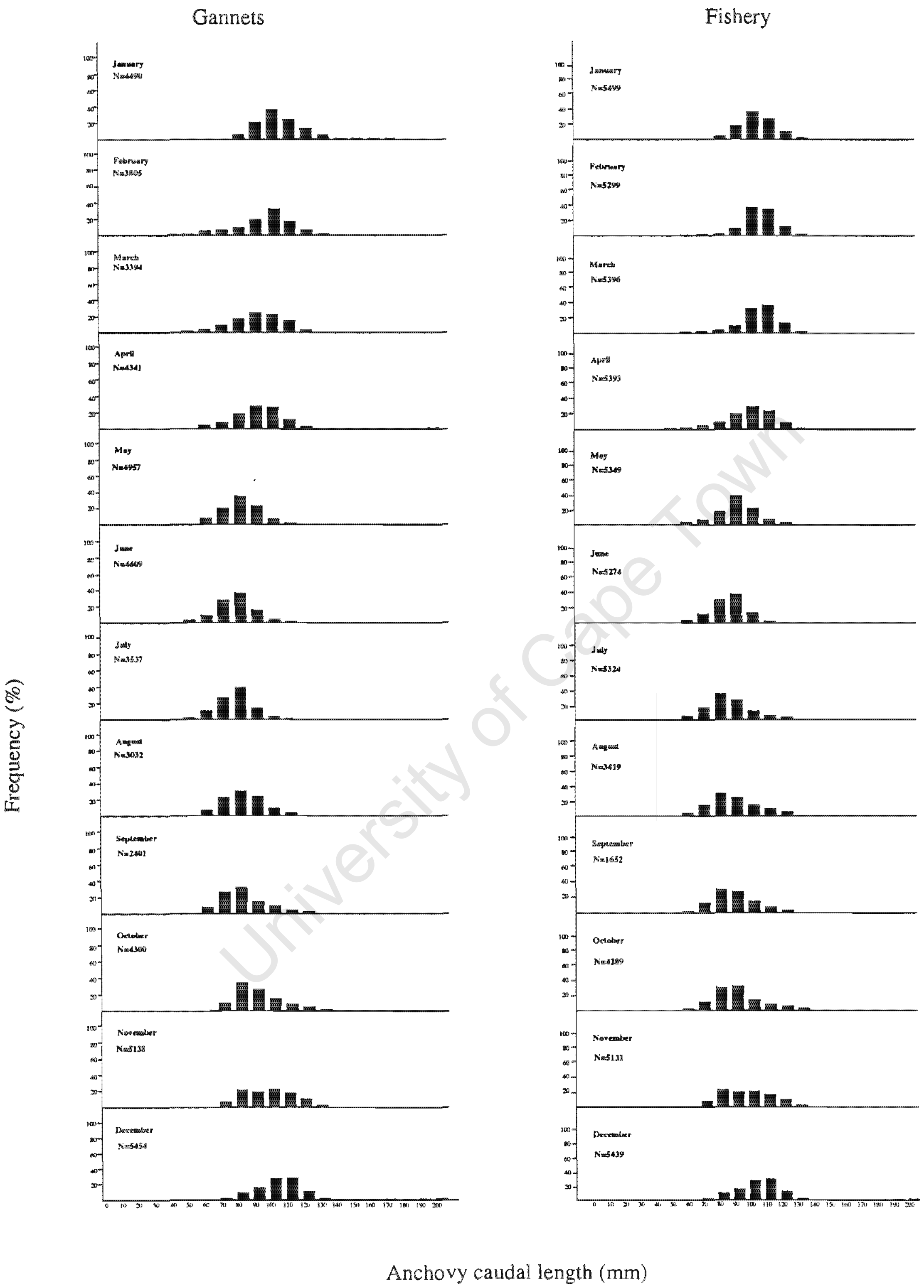

Fig. 3.4 Size distribution of anchovy caught by gannets and the fishery in different months. Data pooled from 1978-1998 for the gannets and from 1978-1996 for the fishery.

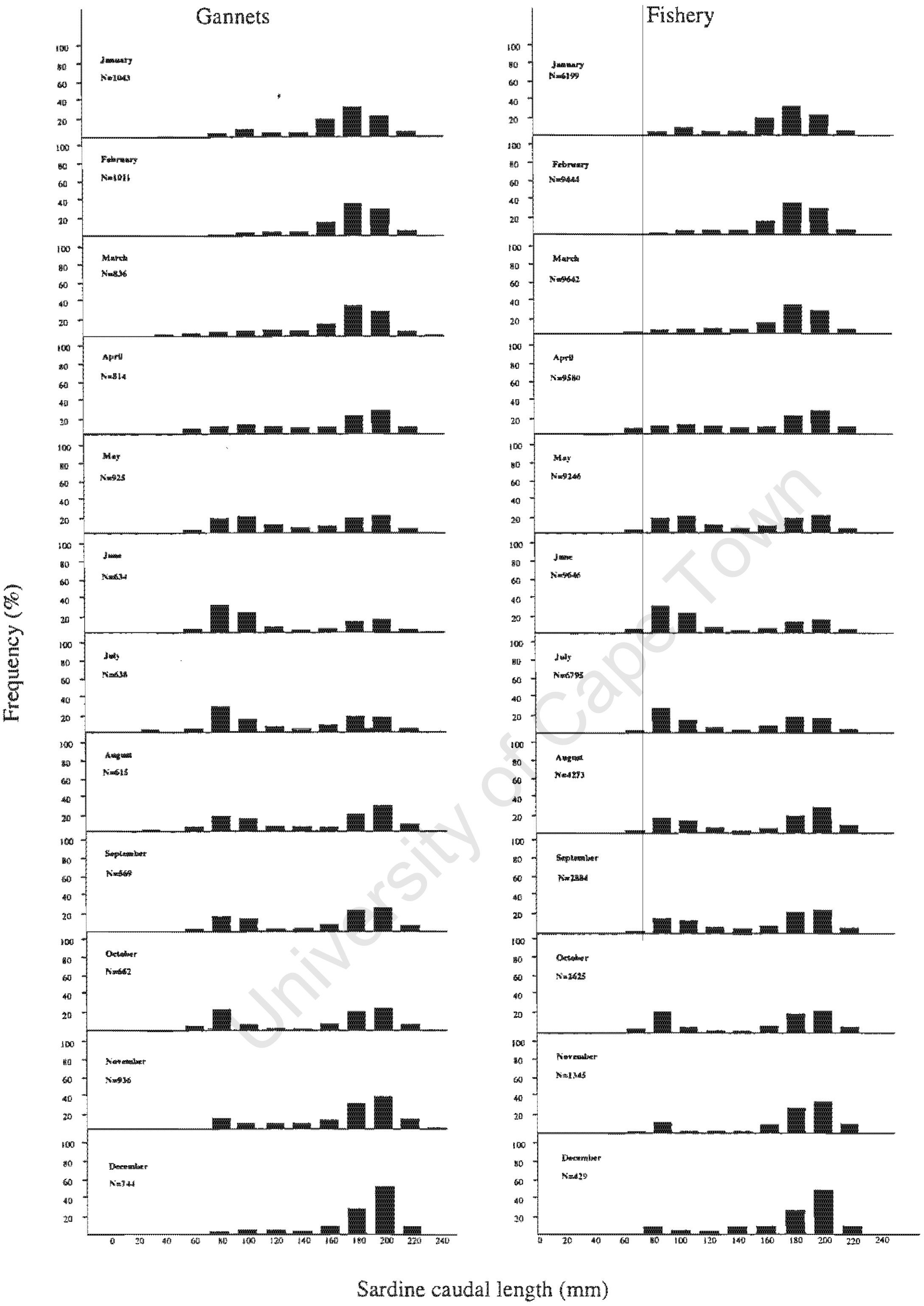

Fig. 3.5 Size distribution of sardine caught by gannets and the fishery in different months. Data pooled from 1978-1998 for the gannets and from 1978-1996 for the fishery.

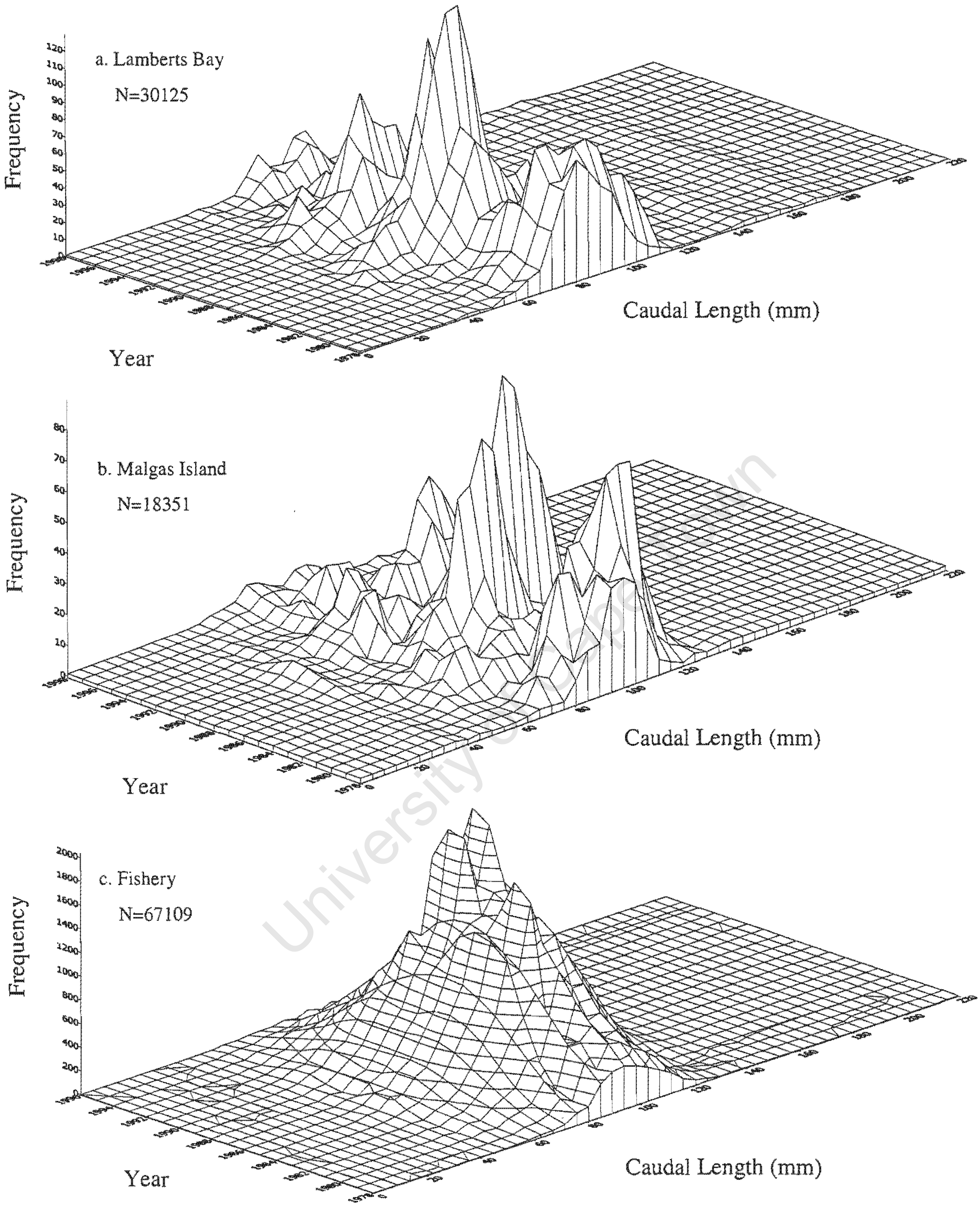

Fig. 3.6 Number by length of anchovy removed by a) Cape gannets at Lamberts Bay, b) Cape gannets at Malgas Island and c) purse-seine fishery. (Data from MCM).

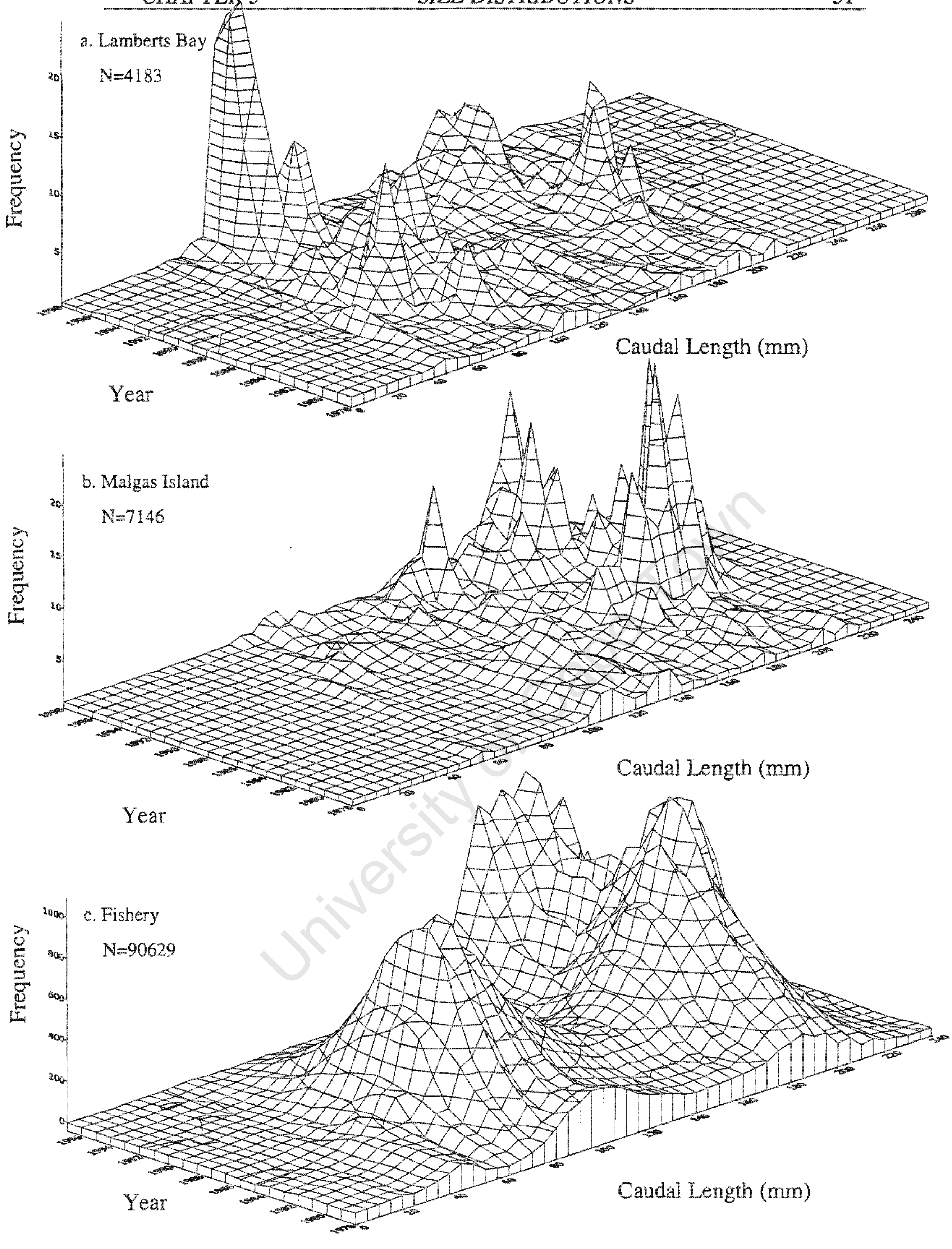

Fig. 3.7 Number by length of sardines removed by a) Cape gannets at Lamberts Bay, b) Cape gannets at Malgas Island and c) purse-seine fishery. (Data from MCM).

found on the Agulhas Bank, where both anchovy and sardine spawn (Barange *et al.* 1999). Sardines are also removed west of Cape Point, as is evident from the gannets removing larger sardines at Malgas Island than at Lamberts Bay (Berruti 1987, Crawford *et al.*1992, Berruti *et al.* 1993 and Crawford & Dyer 1995). Crawford *et al.* (1991) suggested that seasonal patterns in availability of prey species might be expected to influence the diets of predators, this is confirmed by the present study. The gannet diet and the fishery catches reflect seasonal availability of size classes of anchovy and sardine off western South Africa (i.e. west of Cape Agulhas). The seasonal changes in diets of the gannets are due to the migration and movement patterns of the two clupeoids.

The gannet diet reflects a bimodal pattern of spawning by sardine, with peaks in September-October and December-February (Crawford 1981). Small sardines appear in the diet in March and again in October. Although Cape gannets may prefer certain prey items (Batchelor & Ross 1984, Berruti & Colclough 1987, Adams & Klages 1999 and Bunce & Norman 2000), they are largely opportunistic on prey of suitable sizes that can be caught by plunge diving within the ranges and depths to which they can forage (Berruti 1987, Crawford *et al.* 1987 and Adams 1993). If prey biomasses are extremely low, gannets will resort to removing very small fish to subsist. In 1989 and 1990, when the sardine and anchovy were scarce (Barange *et al.* 1999 and Schwartzlose *et al.* 1999), gannets at Malgas Island were forced to remove anchovy of sizes 40-50 mm in length, competing with seals and the fishery at the same time (Fig. 3.6). This highlights even stronger competition for resources within years of poor recruitment of sardine and anchovy.

The fishery targets recruiting anchovy (<1 year) and sardine on their route back to the spawning grounds from the nursery grounds north of St. Helena Bay (Barange *et al.* 1999). Sardines one year and older are targeted in January-March for canning (de Oliveira *et al.* 1998 and Barange *et al.* 1999). As a result of intensive scavenging, seals follow the fishery trends very closely (Butterworth *et al.* 1995, David 1987 and Wickens 1992). Therefore, large takes of anchovy and sardine of size-classes removed by the fishery and seals, have the potential to impact food availability for the birds. This would not be the case if the gannets ate smaller sizes than their competitors and more importantly if there was no recruitment overfishing, i.e. fishing that reduces recruitment strength. Interestingly, seals consumed similar sized anchovy as the purse-seine fishery after commercial harvesting of seals had declined in 1983 and the seal population had begun to increase from 1990 onwards (David 1989, Wickens *et al.* 1991 & Wickens *et al.* 1992).

Food limitation is probably more significant for the birds, which are more dependent on pelagic resources than seals, which also feed in the midwater and scavenge discarded fish more readily. Food limitation may be expected to have a negative impact on the breeding success of the Cape gannet. This was the case after the pelagic stock collapse in Namibia in the 1970's (Crawford 1987*)*.

With many marine predators that breed on land, foraging ranges are restricted during breeding. The gannets at Malgas Island and Lamberts Bay have different feeding grounds (Berruti 1987), resulting in their different diets. Lamberts Bay gannets remove recruits from St. Helena Bay and northwards. Malgas Island gannets forage from Cape Columbine to Cape Point and Cape Agulhas (Berruti *et al.* 1993, Cooper 1981 and Crawford *et al.* 1983). Malgas Island birds ate larger fish (particularly sardine), especially after 1994 when sardine recolonised the west coast (Crawford *et al.* 1995, Crawford 1998 and Barange *et al.* 1999).

There were strong sardine recruitments in 1993, 1995 and 1999, subsequently a substantial portion of the sardine stock was concentrated in the St. Helena Bay region (Barange *et al.* 1999). Hence, if sardine abundance increases and their distribution continues to expand north, sardines will become more readily available to gannets at both colonies. It has also been shown that when sardine biomasses decrease substantially, sardines respond by contracting their distribution (Crawford 1981). During winter months, gannets at both Lamberts Bay and Malgas Island rely on anchovy recruits of the year as they migrate down the west coast. This is especially true of those at Lamberts Bay. This shows that gannets switch prey between sardine and anchovy when necessary for survival. Feeding grounds of both colonies overlap with fishing grounds of the purse-seine fishery (Berruti 1987). Thus, not only do the prey species overlap, but so do the predator distributions and foraging areas. Coupled with similar prey size removal, where there is little to no resource partitioning of anchovy and sardine, there may be substantial competition for these resources.

CHAPTER FOUR
CONCLUSIONS

4.1. CONCLUSIONS:

Marine mammals and birds are conspicuous predators that are present in waters used by many of the marine fisheries where predators are regarded as pests (Yodzis 2001). Much of the controversy regarding multispecies resource sharing surrounds the idea, particularly held by fishers, that mammals and birds remove fish that would otherwise be available to the fishery. This study investigated the extent of overlap in utilization of resources by the Cape gannet, the Cape fur seal and the purse-seine fishery, as a basis for considering the impact on predator species.

4.1.1. Competition and abundance

Diet composition analysis showed that there is extensive overlap in resource use between the Cape gannet, the Cape fur seal and the purse-seine fishery. All three consumers take substantial catches from two commercially important clupeoid species namely anchovy and sardine. Three different feeding temporal regimes were identified from diet and catch analysis; one dominated by anchovy, one when sardine were expanding and one when sardine were abundant (Chapter 2, Table. 4.1). In each of these feeding regimes, the fish intake by Cape gannets and Cape fur seals and the fishery catches reflected the abundance of prey species at the time, but this "model" is slightly modified by a selection preference for sardines by the Cape gannets and the purse-seine fisheries (further compounded by fishery quotas). Nonetheless, the "model" is typical of a "wasp-waist" ecosystem where the pelagic species are of paramount importance in marine food webs (Cury *et al.* 2000).

4.1.2. Resource partitioning and seasonality

Furthermore, gannets, seals and the fishery remove similar sizes of sardine and anchovy at the same times of the year (Chapter 3, Table. 4.2). The different prey size classes are available at different times because of the seasonal recruitment, growth and migration of sardine and anchovy. The Kolmogorov-Smirnov statistical analyses rejected the null hypothesis, i.e. there is no significant difference between the size classes of anchovy and sardine removed by the gannets, seals and the purse-seine fishery. However this could be due to the sensitivity of the test rather than the data. The size distributions show that all three consumers removed prey of similar mean sizes and mean lengths (Chapter 3, Table. 4.2). Gannets prefer sardine to anchovy (Chapter 2 & 3), but switch easily between the two prey items depending on their abundance and availability in the system.

Table 4.1: Summary of feeding regimes grouped out by the Multivariate Analysis (Dendrograms & MSD plots) in Chapter 2. Group names are based on the most abundant species present in the diets and catches.

Top predator	Grouped Years	Group Names
Cape gannet	1978-1983	Anchovy
	1984-1988	Intermediate
	1989-1998	Sardine
Cape fur seal	1982 &1984	Anchovy
	1988,86 & 1993	Intermediate
	1981,89 & 1992-1996	Sardine
	1990	Outlier
Purse-seine fishery	1978-1983	Anchovy
	1984-1986	Intermediate
	1987-1998	Sardine

4.1.3. Availability

The availability of prey sizes to the different consumers is dependent on the predators' capabilities and restrictions. For example, gannets have a limited depth of foraging and those at Malgas Island and Lamberts Bay have discrete fishing grounds. Malgas Island gannets forage from Cape Columbine southward, while those at Lamberts Bay forage from Cape Columbine northward (Berruti *et al.* 1993). Given the requirements of Cape gannets to feed chicks regurgitated fish and at the same time retain adult fitness, they are vulnerable to fluctuations in prey availability (Crawford & Shelton 1981, Crawford *et al.* 1983 and Crawford 1987).

Table 4.2: Summary of mean and modal size distributions of anchovy and sardine caught by gannets and seals and the purse-seine fishery from information in Chapter 3
* - Shows the bimodal distributions in the diets and catches

Years	Top predator species	Prey species	
		Mean size	Modal Size
		Anchovy	**Anchovy**
Anchovy group	**Cape gannet**	88mm	80mm
(1978-1980)	**Cape fur seal**	52mm	70mm
	Purse-seine fishery	95mm	100mm
Intermediate group	**Cape gannet**	94mm	90mm
(1981-1990)	**Cape fur seal**	83mm	80mm & 100mm*
	Purse-seine fishery	93mm	90mm
Sardine group	**Cape gannet**	84mm	90mm
(1991-1998)	**Cape fur seal**	70mm	70mm & 100mm*
	Purse-seine fishery	86mm	90mm
		Sardine	**Sardine**
Anchovy group	**Cape gannet**	145mm	100mm & 180mm*
(1978-1980)	**Cape fur seal**	---	---
	Purse-seine fishery	143mm	100mm & 180mm*
Intermediate group	**Cape gannet**	152mm	100mm & 200mm*
(1981-1990)	**Cape fur seal**	143mm	120mm & 200mm*
	Purse-seine fishery	153mm	100mm & 200mm*
Sardine group	**Cape gannet**	156mm	90mm & 180mm*
(1991-1998)	**Cape fur seal**	147mm	60mm & 180mm*
	Purse-seine fishery	180mm	60mm & 180mm*

Seals are less likely to be affected by the fluctuations in abundance of anchovy and sardine than gannets because they can forage throughout the water column and have a smaller degree of dependence on clupeoids in their diet. Therefore, seals are better buffered if there are large changes in the abundance of these prey species than are gannets (Chapter 2 & 3, Crawford 1987, David 1987, and David 1989). The fairly large seal population, sustained in part by discards from fisheries, removes approximately the same amount of fish as the fishery, but major portions of their diet are not commercially important (David 1987 and Crawford et al. 1992) or available to gannets. On the other hand, seals do target pelagic resources (Chapter 2, David 1987 and David 1989), which may intensify the competition between the three predators.

Culling or harvesting of Cape fur seals as a form of management is not suggested because, as has been recommended by many authors (Wickens *et al.* 1992, Wickens 1992 and Balmeli & Wickens 1994), culling or harvesting seals would not necessarily result in extra fish for the fisheries or, in this case, for gannets either. Early estimates suggested that predatory fish (such as snoek) and squid probably consume at least as much pelagic fish as do seals, birds and the fisheries combined (Wickens *et al.* 1992 and Butterworth *et al.* 1995). The trophic flow models of Jarre-Teichmann *et al.* (1998) confirm this. Seals also readily utilize snoek. Therefore, removal of seals may in fact increase the snoek predation on clupeoids (Wickens *et al.* 1992). Having drawn these conclusions with regards to the seal diet, the study also recognises that the seal data were not uniform and constant. However stomach contents were a clear indication of what was being consumed over the study period.

Currently, total allowable catches (TACs), closed seasons, mesh size limitations and market value (among other factors) control the purse-seine fishery and therefore, the fishery does not target prey proportionally to the prey's abundance. However, fishing has intensified the natural fluctuations of anchovy and sardine stocks by shortening the durations of the peaks and lengthening the durations of the troughs (Schwartzlose *et al.* 1999). Furthermore from trophic flow modelling, Jarre-Teichmann *et al.* (1998) has shown that fishery catches are generally a larger cause of fish mortality than mammals, seabirds and other predatory fish. Thus this results in less food for the predators and may also be a major factor in reducing populations of the predators. In order to fully assess the degree to which the fisheries fully affect the Cape gannet and Cape fur seal populations, a study needs to be done that shows the correlation between stock size (from surveys) of sardines and anchovy and consumption by top predators as well as catches by fisheries.

Gannets, seals and the purse-seine fishery exist in a highly dynamic ecosystem. This study alludes to the fact that in order to sustain and manage a system such as the Benguela upwelling system, several factors must be considered. These factors include: competition for the same resources (with resource partitioning), similar geographical ranges, unpredictable and relatively short-lived prey species, and highly variable environmental and physical pressures. Only once the afore mentioned factors can be fully understood and predictive models generated, will multi-species management of the Benguela upwelling system be successful, thereby allowing all three major predators (i.e. gannets, seals and the fishery) to persist and sustain within the system.

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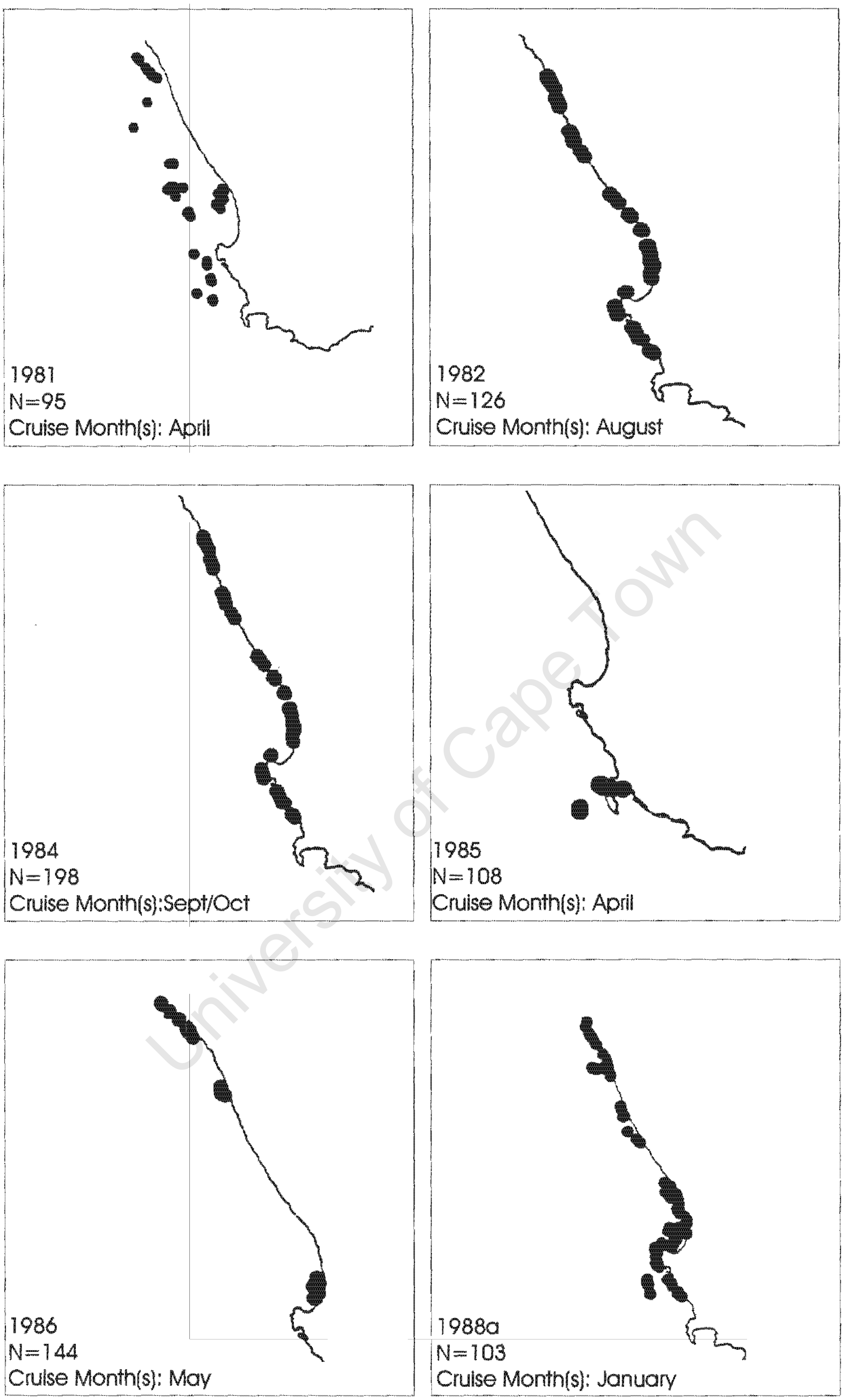
APPENDICES



1981
N=95
Cruise Month(s): April

1982
N=126
Cruise Month(s): August

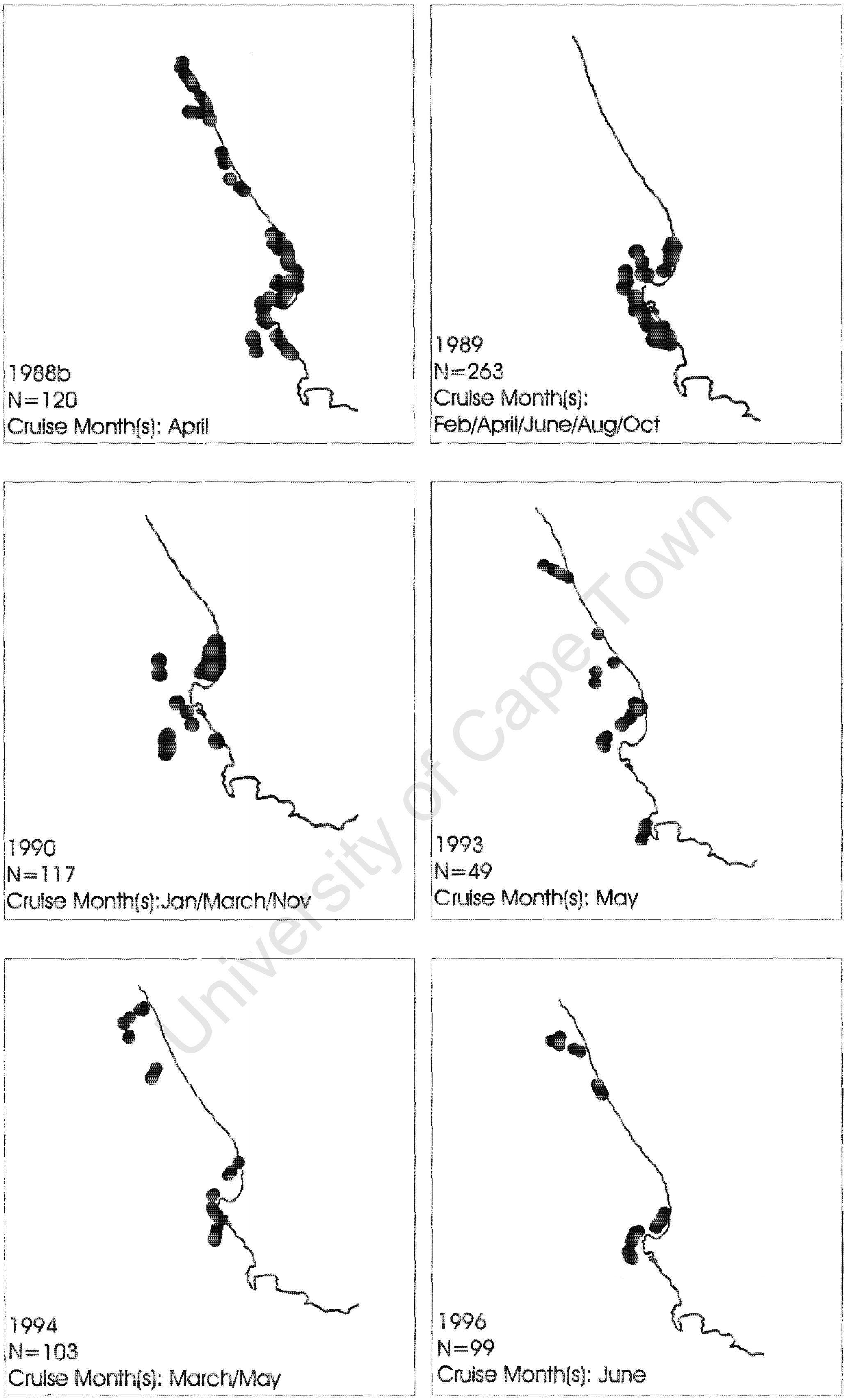
1984
N=198
Cruise Month(s):Sept/Oct

1985
N=108
Cruise Month(s): April

1986
N=144
Cruise Month(s): May

1988a
N=103
Cruise Month(s): January

Fig. 1 Seal data plotted along the west coast of South Africa to establish samples that could be utilized. The study area was restricted to seals removed between Cape Point and the Orange River. Each dot represents a seal that was killed.



1988b
N=120
Cruise Month(s): April

1989
N=263
Cruise Month(s):
Feb/April/June/Aug/Oct

1990
N=117
Cruise Month(s):Jan/March/Nov

1993
N=49
Cruise Month(s): May

1994
N=103
Cruise Month(s): March/May

1996
N=99
Cruise Month(s): June

Fig. 2 Seal data plotted along the west coast of South Africa to establish samples that could be utilized. The study area was restricted to seals removed between Cape Point and the Orange River. Each dot represents a seal that was killed.

SIMILARITY TABLES

Breakdown of average similarity within the anchovy, transitional and sardine groups into contributions of top species, in order of decreasing contribution, for the fisheries only. Š*i* the average contribution of the *i*th species to similarity within a group and Cum Š*i* (%), the cumulative percent contribution to the total similarity.

Species	Ave. Abundance (%)	Š*i*	Cum. Š*i* %
(a)			
Anchovy Group			
Anchovy	83.00	41.84	41.84
Redeye	10.00	22.08	63.92
Sardine	4.70	18.68	82.60
Lanternfish	1.11	9.23	91.83
(b)			
Transitional Group			
Anchovy	79.21	46.65	46.65
Redeye	7.28	20.66	67.31
Horse mackerel	5.53	17.58	84.89
Sardine	3.61	11.12	96.01
(c)			
Sardine Group			
Anchovy	51.04	31.58	31.58
Redeye	18.98	25.50	57.08
Horse mackerel	13.23	21.92	79.00
Sardine	16.75	21.00	100.00

SIMILARITY TABLES

Breakdown of average similarity within the anchovy, transitional and sardine groups into contributions of top species, in order of decreasing contribution, for the gannets only. Š*i* the average contribution of the *i*th species to similarity within a group and Cum Š*i* (%), the cumulative percent contribution to the total similarity.

Species	Ave. Abundance (%)	Š*i*	Cum. Š*i* %
(a)			
Anchovy Group			
Anchovy	53.56	22.89	22.89
Saury	24.08	17.31	40.20
Hake	10.35	13.64	53.84
Other	5.04	12.02	65.86
Sardine	4.37	10.35	76.22
Horse mackerel	3.16	9.94	86.15
Redeye	3.68	8.81	94.97
(b)			
Transitional Group			
Anchovy	34.99	20.49	20.49
Sardine	27.13	18.43	38.91
Saury	16.75	17.24	56.15
Hake	16.13	15.46	71.62
Other	4.03	9.21	80.83
Horse mackerel	1.35	8.08	88.91
Redeye	0.81	7.11	96.02
(c)			
Sardine Group			
Sardine	48.07	21.07	21.07
Anchovy	19.34	15.89	36.96
Hake	14.90	15.77	52.73
Saury	7.39	12.38	65.12
Other	4.83	10.53	75.65
Horse mackerel	3.75	10.39	86.03
Redeye	1.49	8.19	94.22

SIMILARITY TABLES

Breakdown of average similarity within the anchovy, transitional and sardine groups into contributions of top species, in order of decreasing contribution, for the seals only. $\check{S}i$ the average contribution of the *i*th species to similarity within a group and Cum $\check{S}i$ (%), the cumulative percent contribution to the total similarity.

Species	Ave. Abundance (%)	$\check{S}i$	Cum. $\check{S}i$ %
(a)			
Anchovy Group			
Cephalopods	30.15	33.68	33.68
General other	32.18	29.79	63.47
Anchovy	21.99	21.31	84.78
Hake	8.66	11.78	96.56
(b)			
Transitional Group			
General other	31.72	38.20	38.20
Pelagic other	34.16	35.50	73.71
Anchovy	20.98	17.69	91.40
(c)			
Sardine Group			
General other	54.60	62.49	62.49
Sardine	19.65	17.64	80.13
Anchovy	8.38	8.35	88.48
Demersal other	5.23	3.48	91.96

APPENDIX III Data used in the Multivariate Analysis of species composition of gannet diets, seal diets (% mass) and fishery catches (% catch)

Gannets

Species	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
Anchovy	47.39	37.63	46.50	22.21	41.19	29.80	27.18	15.84	23.62	29.99	18.31	9.17	5.00	18.58	26.05	7.60	4.21	9.10	0.84	3.25	2.88
Sardine	7.62	6.55	4.22	9.58	1.85	5.98	5.41	15.14	19.13	39.56	46.60	47.88	64.13	40.53	34.89	53.59	47.54	48.15	50.87	54.32	47.38
Mackerel	1.40	1.70	1.11	0.91	0.29	4.53	1.16	0.51	0.09	0.63	0.38	1.40	2.27	0.69	1.38	0.69	1.79	1.74	1.30	0.99	0.59
Redeye	1.33	2.74	1.71	0.41	0.56	0.27	0.59	0.90	0.55	0.10	0.78	1.35	0.93	0.31	1.12	0.19	0.33	0.62	0.08	0.69	0.93
Cephlopods	0.09	0.30	0.23	0.04	0.18	0.90	0.21	0.20	0.00	0.02	0.02	0.05	0.31	0.05	0.11	0.04	0.19	0.02	0.03	0.03	0.00
Hake	19.40	18.28	7.17	8.67	27.40	29.80	39.90	43.94	27.44	13.82	12.91	18.86	19.21	26.67	24.46	28.51	28.47	33.58	29.57	32.41	39.67
Saury	19.61	26.97	37.62	55.16	24.83	24.80	20.32	20.83	27.56	14.88	20.67	13.64	6.68	11.13	7.10	6.97	16.43	4.36	13.00	8.04	7.28
Other	3.15	5.85	1.44	3.02	3.69	3.92	5.23	2.63	1.62	0.99	0.31	7.65	1.47	2.04	4.89	2.40	1.04	2.42	4.31	0.26	1.26

Fishery

Year	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
Anchovy	81.14	88.77	92.23	85.11	81.94	68.83	84.19	76.81	85.94	89.59	84.28	71.03	62.62	69.72	82.08	69.45	54.97	51.38	20.85	21.33	38.54
Sardine	2.59	2.40	3.31	4 85	6.85	8.18	1.09	0.12	0.00	2.74	2.97	4.04	14.35	6.83	1 97	5.29	11.73	13.15	35.27	32.22	27.55
Mackerel	0.28	1.17	0.00	0.34	0.87	0.32	4.77	10.51	0.07	2.13	2.25	11.59	7.42	5.44	4.67	8.38	20.25	12.53	23.93	13.23	17.36
Redeye	15.71	5.02	4.40	6.53	10.17	22.34	1.03	1.55	3.38	5.54	10.50	13.34	15.60	18.01	11.28	16.88	13.05	22.94	19.95	33.22	16.56
Lanternfish	0.28	2.64	0.05	3.16	0.17	0.33	8.92	11.00	10.61	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Seals

Species	1981	1982	1984	1986	1988	1989	1990	1992	1993	1994	1996
Anchovy	8.50	33.00	24.48	27.40	14.56	8.27	0.23	8.58	14.76	5.30	12.13
Cephalopods	14.03	37.50	38.92	2.39	8.66	10.43	0.28	29.54	4.67	4.39	3.51
Other demersal	7.81	0.00	2.63	3.39	3.58	9.30	2.00	5.07	2.41	1.75	8.28
Other	56.46	15.10	19.08	25.13	32.00	38.66	40.00	7.58	13.29	49.58	42.20
Hake	10.58	7.89	7.52	1.12	1.92	7.55	17.00	6.58	0.03	3.05	2.90
Other pelagic	2.26	6.61	7.37	35.52	39.09	18.56	32.00	11.84	47.36	17.86	4.57
Sardine	0.36	0.00	0.01	5.03	0.18	7.23	8.50	30.81	17.48	18.07	26.42